

Drawings of Scandinavian Plants 33–36

Rubus L. Subgen. Rubus

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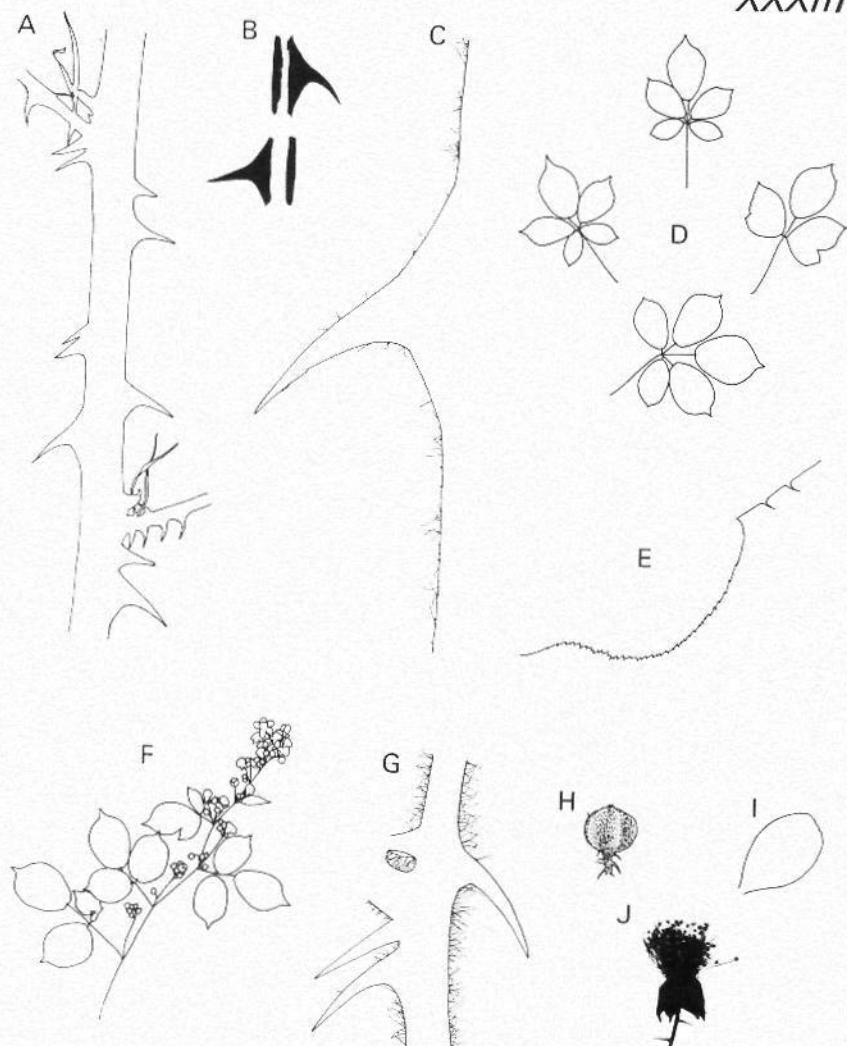
Rubus lindebergii PH. J. MÜLLER 1859

Stem arching, hairy; *prickles* 7–9 mm long, straight or falcate, base 5–9 mm long, rather strong but relatively narrow; *leaves* (3) 5-foliolate, sparsely hairy above, softly pubescent, green–grey tomentose beneath; *terminal leaflet* obovate; *inflorescence* narrow, long, leafy below, prickles numerous, strong, hooked, glands absent; *flowers* about 2.5 cm across; *sepals* tomentose, light grey, prickles usually absent; *petals* white, obovate; *filaments* about 5 mm long.

Normally, the stem is 3–5 m long, strong, with a creeping tip, five flat sides, and green or brownish red in colour; the prickles are rather numerous and have a red base; the leaf surfaces are flat, dark greyish green above; the serration of the leaflets is even and fine; the terminal leaflet, except the short tip, is twice as long as the petiolule; the sepals are deflexed. *R. lindebergii* often grows in stony meadowlands or along streamlets in forests. The species occur along the south-eastern coast of Norway (Lillesand to Kragerö); in Sweden, it is rare in Halland, Blekinge, and southernmost Småland, but rather common on the ridges of Skåne; in Denmark the species is common on Fyen and sporadically distributed on Sjælland, Lolland, and eastern Sønderjylland.

Rubus armeniacus FOCKE 1874

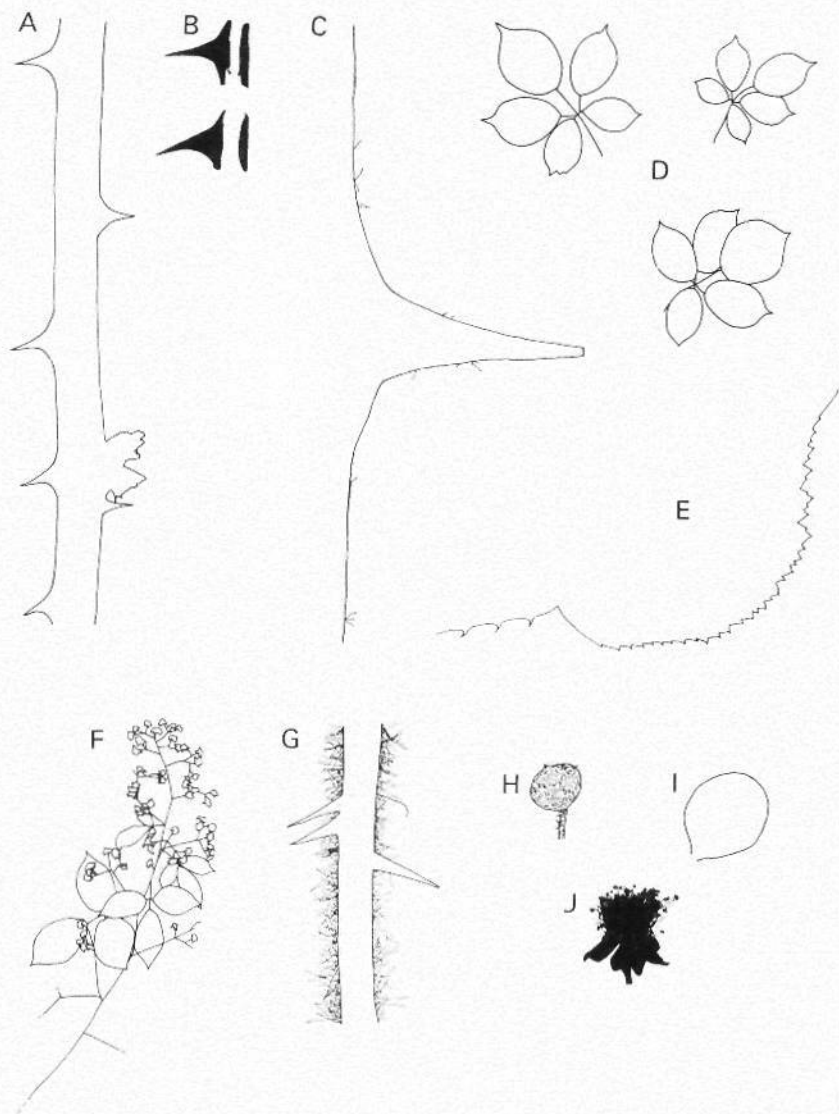
Stem arching, hairy; prickles about 10 mm long, patent or slightly bent, base 8–12 mm long, strong; *leaves* 5-foliolate, glabrescent above, white-felted beneath; *terminal leaflet* broadly obovate—orbicular; *inflorescence* large, lax, pyramidal, leafy below, prickles straight, small in the branches, glands absent; *flowers* about 3 cm across; *sepals* grey tomentose, prickles absent; *petals* pink or white, broadly obovate; *filaments* about 6 mm long.



PL. XXXIII. *Rubus lindebergii* PH. J. MÜLLER. — Remark: E refers to a 5-foliolate leaf.

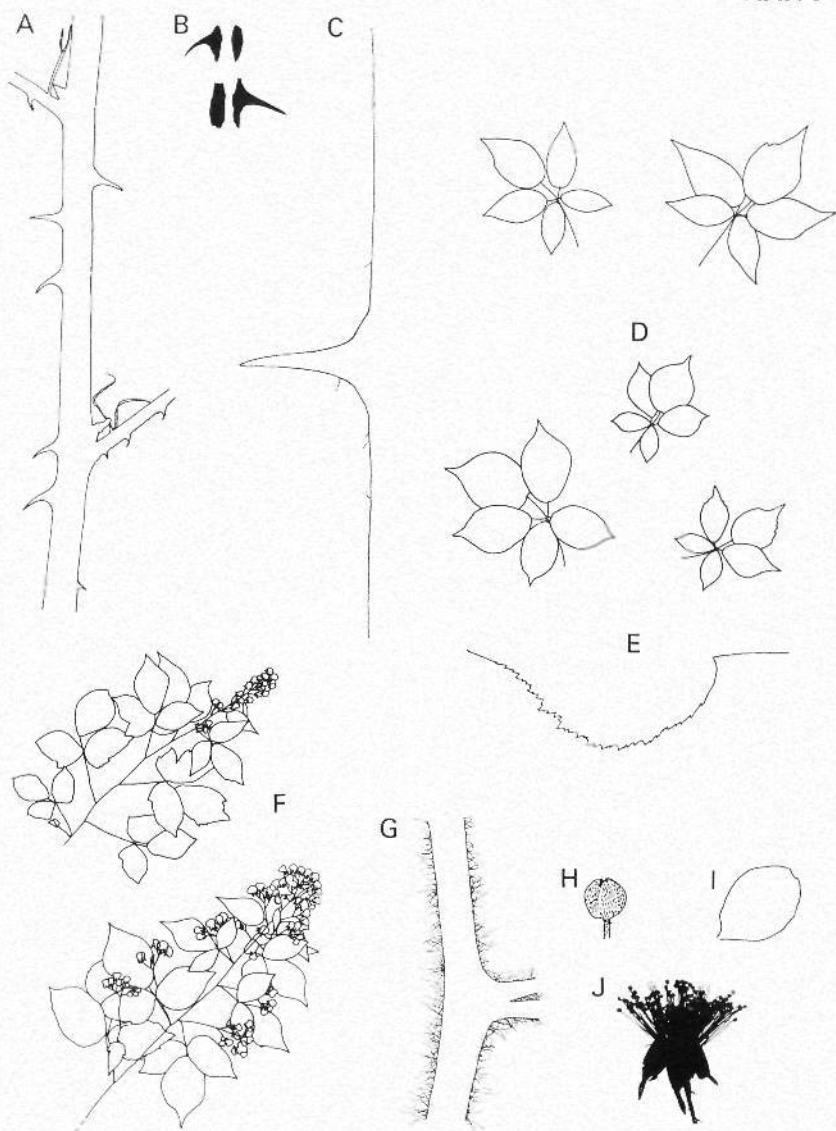
GENERAL LEGEND FOR THE PLATES

First-year growth (primocane): A. Stem with prickles. 1: 1. — B. Prickles, drawn from the side and from above. 1: 1. — C. Stem with prickles, glands, and hairs. 4: 1. — D. Leaves (without serration and petiole diameter shown). 1: 8. — E. Margin of a terminal leaflet with a petiole. 1: 2. — *Second-year growth (floricane)*: F. Inflorescences (without prickles, serration of the leaves,

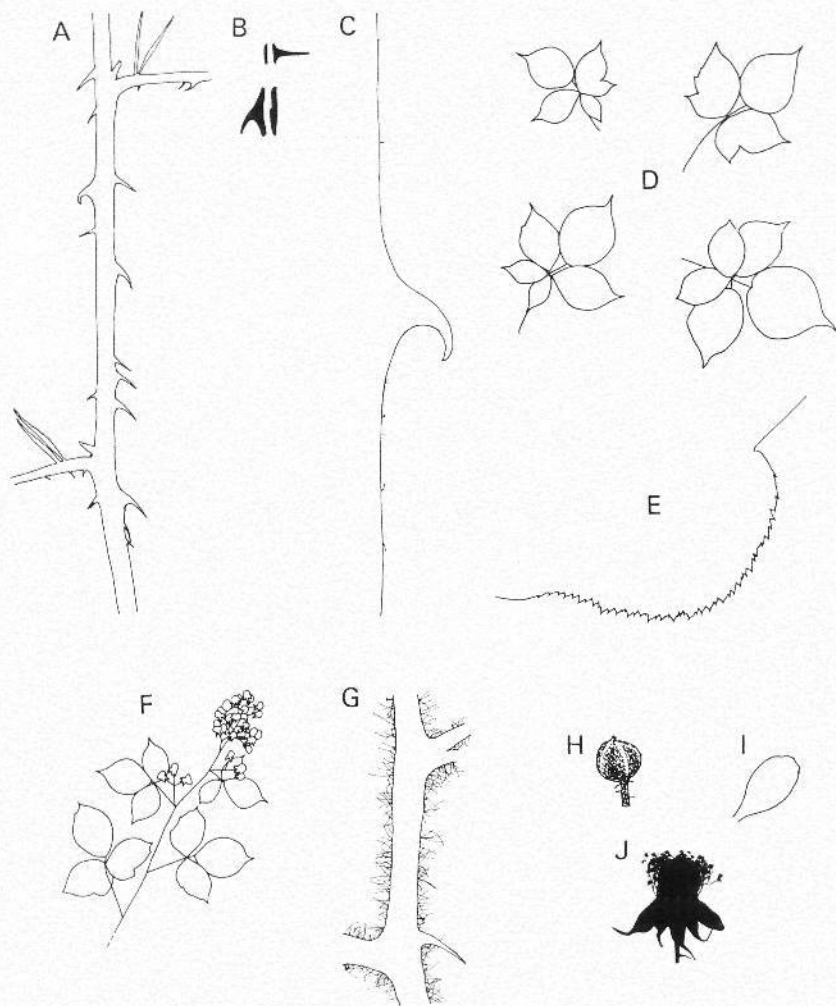


Pl. XXXIV. *Rubus armeniacus* FOCKE. — Remark: F refers to a specimen collected in December 1969.

and axis diameters shown). 1: 8. — G. Rachis with prickles, glands, and hairs. 4: 1. — H. Floral bud with prickles. 1: 1. — I. Petal (without hairs). 1: 1. — J. Flower (without petals, glands, and hairs). 1: 1.



Pl. XXXV. *Rubus thysanthus* FOCKE. — Remark: The two upper leaves in D refers to extreme varieties.



Pl. XXXVI. *Rubus vesterdicensis* C. E. GUSTAFSSON. — Remark: E refers to a 5-foliolate leaf.

Normally, the stem is robust, green, sparsely hairy; the prickles are rather numerous, and have a relatively narrow base; the leaves are large; the serration of the leaflets is coarse; the sepals are deflexed; the fruits, ripening late, are large and flavorful. *R. armeniacus* is cul-

tivated for the blackberries; and where the climate is mild, the species may occur even as an escape outside gardens.

Rubus thyrsanthus FOCKE 1877

Stem erect—arching, glabrous or with a few hairs; *prickles* 4—7 mm long, recurved, base 3—6 mm long, rather strong; *leaves* 5-foliolate, glabrescent above, softly pubescent, grey—white tomentose beneath; *terminal leaflet* ovate; *inflorescence* long, narrow, dense, leafless, or large, pyramidal, leafy, prickles few, small, bent, glands absent; *flowers* 2—2.5 cm across; *sepals* grey tomentose, reflexed, prickles absent; *petals* pink, broadly obovate; *filaments* about 5 mm long.

Normally, the stem is 0.5—2 m long, recurved, sulcate, purple; the leaves are shiny olive-green above; the serration of the leaflets is coarse and uneven; the terminal leaflet, except the tip, is three times as long as the petiole; the flowers have a scent of apples; the fruits are small, semisterile. *R. thyrsanthus* prefers stony ground in pasturelands and forests. The species also occurs on sea-shores. In Norway, the species occurs both along the south-eastern and south-western coasts; in Sweden, it occurs along the east coast from the middle of Uppland to Skåne, but is rare along the west coast; in Denmark, the species is known from different parts of the country.

R. thyrsanthus belongs to a group of blackberries that are related to *R. candicans* WEIHE. The leaflets of the former species display a great variety of shapes. When they are narrowly elliptic and long-acuminate, this taxon may be confused with the latter species.

Rubus vestervicensis C. E. GUSTAFSSON 1938

Stem arching—creeping, hairs and glands few; *prickles* 4—6 mm long, straight or bent, base 3—7 mm long, bristles, sometimes glandular, few or none; *leaves* (3) 5-foliolate, glabrescent above, greyish green—grey tomentose beneath; *terminal leaflet* orbiculate or broadly ovate—obovate, long-acuminate; *inflorescence* with a dense, relatively short and broad, leafless apex and a few axillary branches below, prickles few, small, straight, glands present; *flowers* about 2.5 cm across; *sepals* greyish green, tomentose, with a white-felted border, acuminate; *petals* white—pink, narrowly obovate—spathulate; *filaments* 5—6 mm long.

Normally, the stem is angled; the prickles are rather numerous; the leaves are provided with rather rigid hairs beneath; the leaflets have relatively short petiolules, the basal ones are sessile; the stipules are about 1.5 cm long, red, attached to the petiole 4—7 mm from the axil; the sepals are deflexed. *R. vestervicensis* is known since 1915 from an island (S. Malmö) outside Västervik on the east coast of Sweden. GUSTAFSSON (1938) has discussed the possibility that this blackberry is a hybrid between *R. bellardi* WEIHE & NEES and *R. thyrsanthus* FOCKE.

In the next paper, I shall deal with *R. vestitus* W. & N., *R. radula* WEIHE, *R. taeniaram* LINDEB., and *R. fuscus* W. & N.

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Ecological Studies in a Scanian Woodland and Meadow Area, Southern Sweden

II. Plant Biomass, Primary Production and Turnover of Organic Matter

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CONTENTS

Abstract	9	Additional computations	24
Introduction	9	Application to stand	25
Description of locality	10	Results	25
Investigated ecosystems	10	Plant biomass and production of	
Structure of the woodland	12	woody plants in the woodland ..	25
Structure of the meadows	17	Regressions	25
Terminology	18	Mean dimensional relations of	
Investigation model	19	sample trees and shrubs	29
Methods of estimation plant biomass		Above-ground plant biomass	
and production	20	and production	33
Introductory	20	Below-ground plant biomass	
Field work procedure	21	and production	35
Stand analysis	21	Litter fall	37
Treatment of sample trees and		Plant biomass and production of	
shrubs	21	non-woody plants in the wood-	
Sampling of the field layer and		land	39
additional fractions	22	Total plant biomass and produc-	
Laboratory procedure	23	tion of the woodland	40
Computations	23	Plant biomass of the meadows	41
Above-ground biomass	23	Distribution of organic matter in	
Volume of logs. Mass of		the woodland and in the tall herb	
logs 23. Mass of branches		meadow	43
24.		Turnover of organic matter	44
Above-ground production. Log		Conclusions	47
wood production. Log bark		Acknowledgements	49
production. Branch wood pro-		Literature cited	49
duction. Production of cur-			
rent twigs with leaves	24		

ABSTRACT

ANDERSSON, F.: Ecological Studies in a Scanian Woodland and Meadow Area, Southern Sweden. II. Plant Biomass, Primary Production and Turnover of Organic Matter. — Bot. Notiser 123: 8—51. Lund.

As a part of an IBP project "The productivity of the South Swedish deciduous woodland ecosystems and their secondary successional stages" a comparison between the distribution of organic matter in a mixed deciduous woodland dominated by *Quercus robur*, *Tilia cordata*, *Corylus avellana* and *Anemone nemorosa* and a tall herb meadow with *Filipendula ulmaria* within the Nemoral zone in the Southernmost part of Sweden has been made.

Estimations of the plant biomass and production in the woodland was made by a dimension analysis applying allometric equations. A total plant biomass of 240 t/ha was found with 201 t/ha and 39 t/ha as above- and below-ground figures respectively. The corresponding figures of the net primary production are 15.6, 13.3 and 2.3 t/ha. A production of 0.77 t/ha is included for the above-ground production of the field layer. The litter fall, fractions less than 50 cm long, during a three year period amounted to 5.28 t/ha with considerable variation between years. Including coarser litter fractions an yearly input to the ground of 6.5 t/ha was found. After estimation of the remaining litter before the leaf fall, 6.1 t/ha, the yearly turnover of the litter layer is calculated to 52 %. As the humus fraction amounts to 218 t/ha, the total content of organic matter in the woodland ecosystem thus is 463 t/ha with an almost equal distribution between above- and below-ground portions.

In the meadow the distribution of above- and below-ground portions of the organic matter is 1/49, calculated from the following figures: above-ground biomass 4.7 t/ha, below-ground biomass 13.2 t/ha, surface litter 2.4 t/ha and humus 304 t/ha making the total organic matter of the meadow ecosystem 324 t/ha. The yearly above-ground production is estimated to be 7.2 t/ha and taking this as the yearly litter input to the ground and taking the remaining litter into account a turnover of the litter layer of 75 % is calculated. This suggests a more intensive turnover in the meadow than in the woodland.

INTRODUCTION

The present investigations have been extended from a study of the differentiation of vegetation in relation to the soil-water factor within an area of mixed deciduous woodland and moist meadows in the vicinity of Lund (F. ANDERSSON 1970). It was found that different soil-water regimes create obvious morphological features in the soil profile with a distinct differentiation of humus types. These are a result of the different water regimes in the ecosystems regulating the turnover of organic matter. With this fact in mind the investigations were directed

towards a study of the yearly formation and breakdown of organic matter or in other words a study of the primary productivity of the ecosystems.

This general approach coincides with that of the International Biological Programme (IBP) and the present investigations form part of an IBP project entitled "Productivity of the South Swedish deciduous forest ecosystems and their secondary successional stages" (F. ANDERSSON 1968).

In this paper the results of the estimates and determinations of plant biomass and partially primary production of a mixed deciduous woodland and meadow ecosystems are given. Further, an approximation to a functional analysis of the woodland and a meadow ecosystem is made by considering the turnover of organic matter.

DESCRIPTION OF LOCALITY

Linnebjerg is situated 7 km ENE of Lund in the southernmost province of Sweden ($55^{\circ}44'N$, $13^{\circ}18'E$) within a Silurian slate area. The soil, a moraine of heavy clay, is shallow and has a depth of 1–2 m. The hydrotopographical conditions, a moderately sloping terrain and impervious properties of the shallow soil, render a superficial groundwater, the effect of which is easily seen in the soil profiles. They all show hydromorphic features with a brown forest soil in the higher situated woodland and mullgley-anmoorgley soils in the meadows, which are situated in smaller depressions within the area. A detailed account of environmental as well as vegetational structures is given in F. ANDERSSON 1970.

INVESTIGATED ECOSYSTEMS

The study area of Linnebjerg (Fig. 1) embraces an area of 23 ha of which 22 ha is wooded and one ha is occupied by more or less open moist meadows. In the northern part of the Wood a representative area — the Special Area — with dominating mixed deciduous forest type of *Quercus robur* and *Corylus avellana* and moist meadows has been selected as a measurement area comprising sample areas (Fig. 2).

As a criterion for the identification of ecosystems the vegetation has been chosen. According to the map in Fig. 2 seven ecosystems have been identified. The investigations have mainly been restricted to four

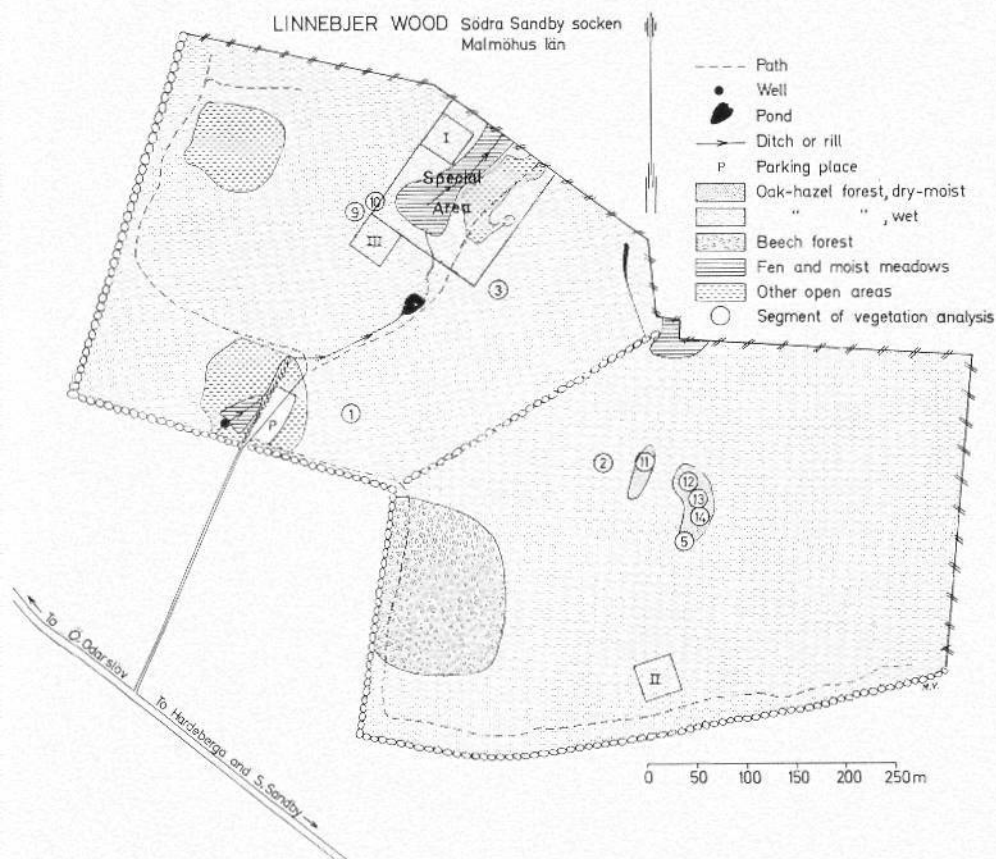


Fig. 1. Schematic map of the Linnebjerg Wood. The squares marked I, II and III show the situation of the analysed woodland stands. The scale is approximate.

of these, one woodland ecosystem and three moist meadow ecosystems, viz.:

- A. *Quercus robur* - *Oxalis acetosella* ecosystem — mixed deciduous woodland,
- E. *Filipendula ulmaria* ecosystem — tall herb meadow,
- F. *Carex flacca* ecosystem — grass-sedge meadow,
- G. *Carex caespitosa* ecosystem — tall sedge meadow.

The most intensive investigations have been carried out within ecosystems A and E.



Fig. 2. Map of the Special Area showing ecosystems and sample areas. — Key: A. *Quercus robur*-*Oxalis acetosella* ecosystem; B. *Quercus robur*-*Geum rivale* ecosystem; C. *Quercus robur*-*Athyrium filix-femina* ecosystem; D. Clearing phase of ecosystem A and B; E. *Filipendula ulmaria* ecosystem; F. *Carex flacca* ecosystem and G. *Carex caespitosa* ecosystem. In the sample area of ecosystem A ■ and ● shows the situation of litter traps and rain gauges respectively.

Structure of the Woodland

From the physiognomic point of view four distinct layers can be identified in the woodland ecosystem (F. ANDERSSON 1970 p. 46):



Fig. 3. Photo of the sample area I of the woodland ecosystem (A) showing litter traps and rain gauges. — Photo: Author May 1969.

- Overstory layer or tree layer, > 15 m
- Understory layer or upper shrub layer, 2—15 m
- Shrub layer or lower shrub layer, < 2 m
- Ground layer or field and bottom layer

The overstory layer is composed of oak (*Quercus robur*) with lime-tree (*Tilia cordata*) as a codominant species. The understory layer is formed of lime-tree and *Sorbus aucuparia*. An extremely well developed shrub layer of hazel (*Corylus avellana*) is present (Fig. 3). A lower shrub layer of the species mentioned and in addition *Crataegus mono-*

Table 1. Structural survey of tree and shrubs layers of the woodland ecosystem (A).

	<i>Quercus robur</i>	<i>Tilia cordata</i>	<i>Sorbus aucuparia</i>	<i>Corylus avellana</i>	Other species	Totals
Stems (no./ha)	102	184	46	4,393	-	-
Mean height (m) (range)	23.0 (13-29)	11.3 (3-27)	9.5 (3-14)	- (2-13)	-	-
Mean diameter (cm) (range)	50.4 (32.5-72.5)	15.2 (2.5-42.5)	9.5 (2.5-15.0)	- (2.5-15.0)	-	-
Basal area (m ² /ha)	21.88	4.31	0.32	4.64	0.23	31.38
" " in 0/0	70	14	1	14	1	100
Conic stem surface (m ² /ha)	0.196	0.065	0.005	0.121	0.003	0.390
" " in 0/0	50	17	1	31	1	100
Parabolic stem volume (m ³ /ha)	259.6	36.0	1.7	23.6	1.9	322.8
" " in 0/0	80	11	1	7	1	100
Age (mean age of sample trees) (range)	149 (125-190)	46 (35-60)	38 (12-57)	- (0-19)	-	-

For calculation of basal area, conic stem surface and parabolic stem volume see p. 24.

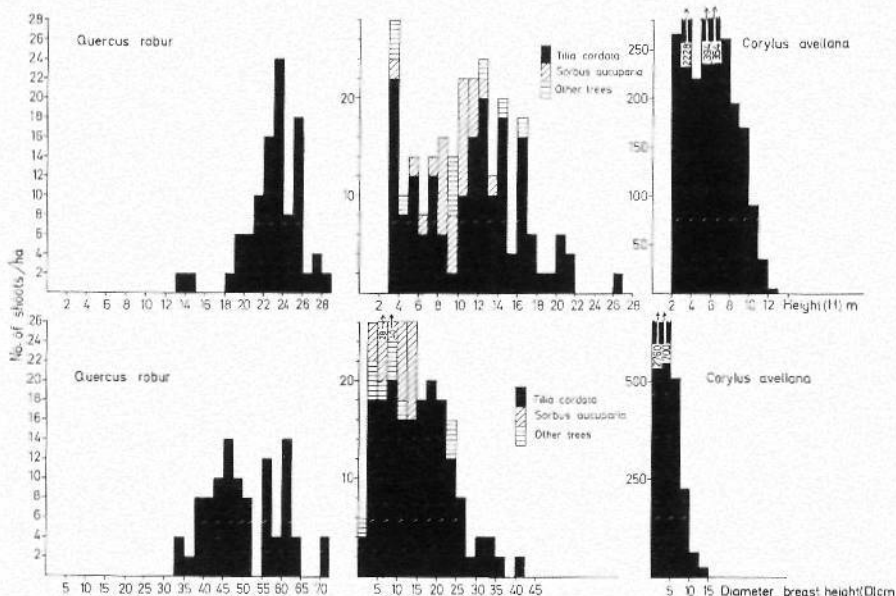


Fig. 4. Diameter- and height-class distribution of trees and shrubs in the woodland ecosystem (A).

gyna, *C. oxyacantha* and *Viburnum opulus* occurs. The ground vegetation shows seasonal aspects with dominance of *Anemone nemorosa*, *Convallaria majalis* and *Oxalis acetosella* during spring, early summer and late summer respectively. In particular the two former aspects are well developed with a complete cover of the ground. Bryophytes are scattered.

The numerical description of the tree stands (Fig. 4 and Table 1) as well as the distribution of the main tree and shrub species on classes of height and diameter (Fig. 4) show the structure of overstorey and understorey tree- and shrublayers. In this type of woodland a wide range of diameters as well as heights is encountered.

The age structure of the stand has not been fully investigated and therefore only information from the annual-ring analysis of the sample trees is available. The oak ranges from 125 to 190 years, limetree 35—60 years, *Sorbus aucuparia* 12—57 years and hazel up to 50 years. An uneven-aged woodland is thus present.

The understorey species, especially the hazel and the limetree, have an average age of 40 years. This corresponds to the time period since the last coppicing of the woodland (F. ANDERSSON 1970 p. 36).

Table 2. Survey table of the vegetation of the meadow ecosystems (E—G).

Ecosystem	Filipendula ulmaria	Carex flacca	Carex caespitosa
Filipendula ulmaria	●	○	○
Geum rivale	○	+	○
Geranium palustre	○	.	.
Ranunculus auricomus	+	.	.
Brachythecium rutabulum coll.	○	.	○
Lysimachia vulgaris	○	○	+
Caltha palustris	○	○	○
Myosotis palustris	○	○	○
Ranunculus repens	○	○	+
Angelica sylvestris	+	○	○
Crepis paludosa	+	○	○
Valeriana dioica	+	○	○
Equisetum arvense	○	●	○
Caliergonella cuspidata	+	●	○
Mnium affine coll.	+	○	○
Cirsium palustre	+	○	+
Juncus conglomeratus	.	○	.
Lychnis flos-cuculi	.	○	.
Carex flacca	.	○	.
Carex Hartmanii	.	○	.
Carex panicea	.	○	.
Molinia caerulea	.	●	.
Juncus articulatus	.	●	.
Eriophorum angustifolium	.	○	.
Eleocharis uniglumis	.	+	.
Dactylorhiza majalis	.	+	.
Briza media	.	+	.
Carex caespitosa	.	.	●
Lophocolea bidentata	.	.	○

Frequency : + 25-50% ○ 50-75% ○ 75-100%
 ● dominating ○ not dominating

The overstory layer of oak has a height of 23 m (13—29 m). The diameter at breast height (*D*) ranging from 32.5 to 72.5 cm. A few individuals of limetree reach the top layer. A complete cover of the ground is given by the foliage of the over- and understory components. The understory with hazel forms a second canopy beneath that of the overstory. The conspicuous layer of hazel has 500 stools/ha with 8—30 individual shoots per stool reaching a maximum height of 13 m.

The stand density (HUSCH 1963 p. 203) has been described in Table 1 in terms of stems/ha, basal area in m²/ha and parabolic volume in m³/ha. The conic stem surface is also given. For the structure of the ground vegetation see F. ANDERSSON 1970 p. 47.



Fig. 5. Photo of the tall herb meadow ecosystem (E) with dominating *Filipendula ulmaria*. — Photo: L. Páhlsson July 1965.

Structure of the Meadows

Three meadow ecosystems have been dealt with and the main species composition is surveyed in Table 2. Two of the ecosystems are tall grown, viz. the *Filipendula ulmaria* meadow (Fig. 5) and the *Carex caespitosa* meadow. The latter has a tussocky growth, while the former has an even distribution of species in spite of the tussocky appearance of *Filipendula ulmaria*. Finally, the *Carex flacca* meadow is a fen-like ecosystem characterized by lower plants compared with those of the previous ecosystems. It has a firm lawn of dense penetrating roots in

the upper part of the soil. Moreover, a more or less consistent layer of bryophytes exists. For a detailed description see F. ANDERSSON 1970 p. 61—73.

TERMINOLOGY

The terminology adopted in this work is mainly derived from WESTLAKE (1963 p. 387—388), NEWBOULD (1967 p. 6—7) and MILNER et al. (1968 p. 4—5).

Primary production refers to the process of formation of plant matter by photosynthesis. If considered for a specific period of time it corresponds to the gross primary production. Through respiration a certain amount is lost and the amount present then corresponds to net primary production or simply primary production. In an ecological sense the net primary production is interpreted as the formation of plant tissues and reserve substances of plant biomass which is incorporated and translocated in an ecosystem. In fact, when regarded for a specific period of time the net primary production value corresponds to a rate and is termed the production rate or the productivity. Plant biomass (phytomass) or, in this paper if nothing else stated, the biomass corresponds to the weight of living plant matter at a given moment in an ecosystem. The biomass includes, in woody species, even heartwood and bark. Branches without buds are regarded as dead and as long as they are fixed to the living plant this fraction is termed "attached dead". The total plant biomass includes above-ground and below-ground plant biomass.

Dead or living plant material which is rejected from the plants forms the litter. The litter fall designates in this study the finer fractions of the litter as it is measured in litter traps (50×50 cm) but it includes also coarser fractions (> 50 cm) as branches and wood. The surface litter is the litter present at any occasion on the soil surface. In the soil formation of litter occurs by the dying off from roots and other below-ground organs. This litter is termed root litter.

The plant biomass and litter fractions are expressed as dry weight or dry matter, including the minor fraction of inorganic constituents. The weights of plant biomass are referred to 85°C. A correction factor of one % can be applied for obtaining weights at 105°C. The organic

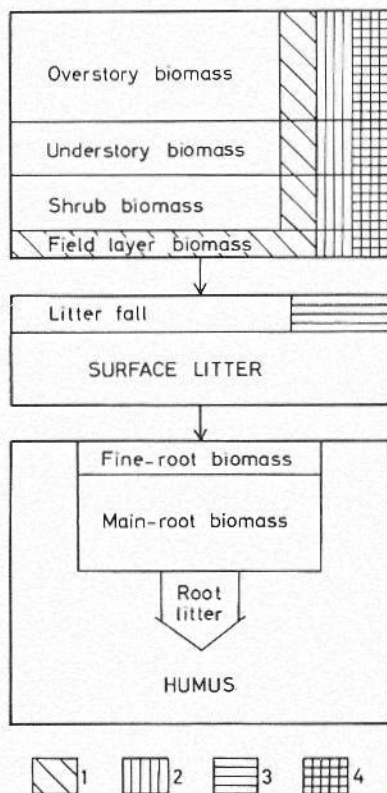


Fig. 6. Investigation model for the study of plant biomass, net primary production and turnover of organic matter in a mixed deciduous woodland. For the estimations the following fractions are used: 1. Apparent growth, increment — B_{2N} . 2. Plant losses by consumers — G . 3. Plant losses by death and shedding — L . 4. Attached dead material, not included in the plant biomass.

matter of the soil, the humus, refers to 105°C and corresponds to corrected values of loss on ignition (see p. 43). Usually the weights are given as metric ton/ha (t/ha), which equals 10^3 kg/ha.

INVESTIGATION MODEL

The estimation of biomass and primary production forms part of the determination of the distribution of organic matter in the ecosystems, which is necessary for the analysis of ecosystem functioning. As organic matter occurs not only as above-ground and below-ground plant biomass but also in dead organic fractions as litter and humus a model designed for this type of investigations necessarily will include additional determinations of the latter fractions.

A model (Fig. 6) was designed with respect to the structure of the

investigated woodland described and the fractioning indispensable for obtaining information on the yearly production of organic matter. As a guiding line in this work the method 2, according to NEWBOULD (1967) is applicable, i.e. estimation of biomass once at the end of the growing season including stem and branch analysis of sample trees with a separation of plant matter into older and current year parts. The latter taken together give the apparent production (B_{2N}). The net primary production (P_N) is estimated when consumed parts (G) and losses by death and shedding (L) — rejects — are added. Thus $P_N = B_{2N} + L + G$. For the field layer production, the formula $P_N = \Delta B + L + G$ ought to be followed. ΔB stands for the change in biomass during the period t_1 — t_2 (MILNER et al. 1968 p. 5). Usually ΔB is calculated as a sum of changes in plant biomass between consecutive periods. With this design the model is applicable to both woodland and such open ecosystems as meadows.

The model comprises four main boxes or compartments. The relations or connections between these as to transferred and transformed amount of organic matter reveal the functioning or the metabolism of the ecosystem. In this form the model reflects the main pathways of the organic matter and at the same time parts of the energy flow. The biogeochemical cycle is possible to attach to this model.

METHODS OF ESTIMATION PLANT BIOMASS AND PRODUCTION

Introductory

The present research requires methods (NEWBOULD 1967, MILNER et al. 1968), which give not only estimates of biomass and productivity but also further information as physiognomy, surface of respiration and photosynthesis, biomass- and production relations between species as parameters in the study of dominance-diversity relations and competition of plants, and in addition a basis for the study of mineral and energy turnover. Because of a complex diameter and age structure of the woodland the applied methods must include all diameters and heights present. The most adequate system of analysis of a woodland ecosystem is found in the dimension analysis as worked out by WHITTAKER (1961, 1962, 1963, 1966), WHITTAKER et al. (1963) and WHITTAKER & WOODWELL (1968, 1969 a). The latter authors (1969 b) give a general survey of the methods for the measurements of net

primary production of forest and especially the dimension analysis. References are also given to KIRA & SHIDEI (1967). Information on general forest mensuration is taken from HUSCH (1963). The ground vegetation has mainly been studied according to the seasonal maximum-minimum approach (NEWBOULD 1967 p. 29—30). Cf. also MILNER et al. (1968 p. 22—24) and ŁOMNICKI et al. (1968 p. 147—149).

Four basic steps can be recognized in the estimation procedure:

1. Stand analysis — non-destructive measurements.
2. Destructive measurements or dimension analysis of sample trees and shrubs including above and below ground parts in order to obtain allometric regressions of the type $y=ax^b$ (KIRA & SHIDEI 1967 p. 71) between non-destructive parameters as diameter at breast height (D) and height (H) and destructive parameters as total weight of biomass derived from individual regressions of the sum of various fractions as current leaves and twigs, branch wood and bark, stem wood and bark.
3. Calculation of stand biomass and production by applying the data from the stand analysis to the regressions found according to 2.
4. Additional observation throughout the year as collection of litter fall to obtain a value of the parameter L in the production equation of the investigation model.

In the following these steps will be described in an integrated way under the headings field-work procedure, laboratory procedure and computations.

Field-Work Procedure

STAND ANALYSIS

Three sample areas of 40×40 m (situation given in Fig. 1) were analysed giving a total area of 0.48 ha. Diameter at breast height (D) and height (H) are the parameters recorded. The caliper is graduated in mm. Height is measured in m with a tree height meter type Suunto PM — 5/1120 P to the nearest half meter.

TREATMENT OF SAMPLE TREES AND SHRUBS

Sample trees and shrubs are chosen according to the size-class distribution of the stand table. Cf. discussion p. 26. Usually, 10 trees and 15 shrubs of the dominant and codominant species are analysed.

Sample trees and shrubs are felled and the length is recorded from base to tip. As the limit between above-ground (shoot) and below-ground (root) parts, the lower 'epiphyte-limit' is chosen (where epiphytes cease to grow). Heights and diameters for the stumps are recorded. Branches are taken off one by one and the distance above the 'epiphyte-limit', basal diameter and age (discs are sampled from every branch) are recorded. Sample branches from upper, middle and lower portions of the crown are sampled (at least five branches for each tree and level mentioned). The sample branches are treated as above and, in addition, the number of current twigs with leaves, the number of fruits, the fresh weight of living sample branches, current twigs with leaves and dead material, attached dead, is recorded. Subsamples of living and dead woody material of the branches with different diameters are taken for drying to constant weight at 85°C.

Twig samples are taken for determination of twig properties. These samples are taken in upper, middle and lower portions of the crown. If the material cannot be treated immediately after arrival at the laboratory, it is stored, wrapped in polythene bags in a deep freeze.

After the branches are removed the stem is sectioned into logs 250 cm long (always more than eight logs per tree). Diameters are cross-calipered over bark at the base, middle and top. Diameter at breast height (D) is measured in the same way as log diameter. 10 cm discs are taken from the lower end of each log. The bark is peeled off and diameters are measured again in the same directions and in the same places as over bark measurements. If possible, fresh weight is determined for each intact log. Fresh weights are also determined on bark and wood of the discs.

Woody species less than 2 m long make a minor fraction and are therefore treated in an approximative way.

Roots of trees and shrubs are dug out and collected down to 0.5 cm diameter giving the main-root biomass (NEWBOULD 1967 p. 237). Finer roots or roots having a diameter less than 0.5 cm including tree and shrub roots and the below-ground organs of the field layer are sampled from pits 50×50×60 cm giving the fine-root biomass. Ten pits were taken in a transect at a regular distance of two metres.

SAMPLING OF THE FIELD LAYER AND ADDITIONAL FRACTIONS

The above-ground biomass of the field layer is sampled on occasions corresponding to the maximum development of the seasonal aspects. In the woodland production figures are obtained as the sum of the maximum figures of investigated species. 16 squares of 0.5×0.5 m are taken at random on each sampling occasion. In the meadow the above-ground biomass of the field layer is only determined once in squares of 0.5×0.5 m randomly distributed. Various numbers of squares have been used.

The below-ground biomass in the meadow is collected on 50×30 cm pin-boards of plywood with steel needles 8 cm long, placed 5 cm apart (FERGEDAL 1967, SCHURMAN & GOEDEWAAGEN 1965).

The litter fall in the woodland is collected in 16 litter traps ($50 \times 50 \times 30$ cm; sides made of wooden board and with a nylon net bottom; placed 20 cm above the ground surface) arranged in a systematic way (cf. Fig. 2). Coarser litter fraction as twigs and logs longer than 0.5 m is collected yearly in a square 20×20 m.

Random samples of surface litter are taken twice a year, before and after the shedding of the leaves in 16 quadrates 50×50 cm.

Laboratory Procedure

Subsamples of branches, discs and bark or other fractions are dried at ca. 37°C . Final dry weight at 85°C is determined on further subsamples. Before the drying of discs they are subject to annual-ring analysis for growth on four radii over five or ten year periods, and total age determinations. The annual-ring analysis is made under a stereomicroscope with slide callipers fitted with a vernier. Measurements are made to the nearest 0.2 mm. Twig samples are treated for determination of total dry weight, number of leaves per twig, weight of blades, petioles and the rest of the current twig. Leaf area and damaged leaf area are measured with a planimeter.

Sampled roots are washed and dried at the same temperatures as above. For the final weight no allowance is made for the mineral soil particles attached the root material.

Computations

ABOVE-GROUND BIOMASS

Volume of logs. By means of the end diameters (D_1 and D_2) over and under bark and the length of the logs the log volumes are calculated as follows: $V = D_m \cdot \pi \cdot l/4$, where V = volume in cm^3 , D_m = mean diameter in cm according to the formula $D_m = \sqrt{D_1^2 + D_2^2}/2$ and l = length of log in cm. The following log fractions are calculated:

Log volume (L_V) — wood volume (W_V) = bark volume (B_V).

Mass of logs. When fresh weights of logs and discs are available the dry weights of log, wood and bark are obtained in the following way:

1. Calculate the quotient fresh weight/dry weight (f) of the discs.
2. Calculate log dry weight (L_G) as $L_G = \text{log fresh weight}/f$.
3. Calculate wood dry weight (W_G) as $W_G = \text{log dry weight } (L_G) \times \text{wood volume } (W_V) / \text{log volume } (L_V)$.
4. Calculate bark dry weight (B_G) as $B_G = \text{log dry weight } (L_G) \times \text{bark volume } (B_V) / \text{log volume } (L_V)$ or $B_G = L_G - W_G$.

Corrections of the bark and stem weights are necessary due to differences in their densities. Moreover, the furrows of the bark are included in the determination of the bark volume, which affects the value of the density. The

necessary corrections are made according to WHITTAKER & WOODWELL (1968 p. 3).

When total fresh weights of logs are not determined the weights are obtained by multiplying the calculated log volume by the wood and bark densities. All volumes and weights for logs are summed to calculate the whole stem value.

Mass of branches. From regressions giving the relation between the basal diameter and the dry branch weight of the sample branches the mass of all branches is obtained. The allometric equation of the type $y = ax^b$ corresponding to $\log y = A + b \log x$ is used. End diameters of all branches of the sample trees are measured and for the calculated regressions estimates of corresponding branch mass are obtained. These are summed to make up weights of all living branch wood and bark, current twigs with leaves and fruits of a sample tree or shrub.

ABOVE-GROUND PRODUCTION

Log wood production is calculated using the results of the annual-ring analysis according to the formula assuming linear growth: $\Delta W_V = W_V - W_V^t/n$, where W_V is the volume at the time of leaf fall and W_V^t the volume n years earlier. Obtained volumes are transformed to weights by multiplication with the wood density.

Log bark production is calculated from the regressions log diameter/bark thickness and log age/bark thickness (WHITTAKER 1961). Results calculated as volumes are transformed to weights using the bark density.

Branch wood production is calculated from branch weight, branch age and b — the growth exponent from the allometric regression of branch diameter/branch weight. Thus the branch growth (Δy) is calculated: $\Delta y = b y/x$, where y = branch weight, b = growth exponent and x = branch age.

Production of branch bark is ignored.

Production of current twigs with leaves is obtained from the regression branch diameter/weight of current twigs and leaves also including fruits.

ADDITIONAL COMPUTATIONS

Below-ground plant biomass. If possible the main-root biomass of trees and shrubs are correlated with non-destructive parameters and the regressions are given in the same allometric equation as for above-ground biomass. The fine-root biomass of the woodland and the meadows are calculated directly on an area basis.

Estimative ratios. In order to give a comprehensive description of the stand (Table 1) from a forestry point of view the following units have been used (cf. WHITTAKER & WOODWELL 1968 p. 13):

Basal area = the cross-sectional area at breast height (1.3 m) of trees and shrubs and calculated as $\pi \cdot r^2$, where r = radius at breast height on bark;

Conic stem surface = $\pi \cdot r \cdot h$, where h = height of tree or shrub;

Parabolic volume of tree or shrub = $0.5 \cdot \pi \cdot r^2 \cdot h$;

Estimated volume increment ($EVI = 0.5 \pi h(r^2 - c^2)$), where $c = r - i$; i is the annual wood radial thickness increment at breast height.

These estimative ratios are also used for a comparison with similar values obtained through dimension analysis (Table 4) and these latter values are then termed true values.

Application to Stand

The treated calculations give values of volume, biomass and weights of various tree and shrub fractions. These are summed to give values for the whole tree or shrub. New regressions are then calculated for diameter (D) and height (H) expressed as D^2H and whole shoot and main-root data. The non-destructive parameters from the stand analysis are then applied to these new regressions giving the stand biomass and production. According to the investigation model data on biomass and production of the field layer as well as the litter fall must also be added to those of trees and shrubs to give the total stand biomass and production.

The calculation of total plant biomass and production have been done in a computer. A programme was written to give not only these figures but on the same time the total error involved at the estimation procedure (see p. 27).

RESULTS

Plant Biomass and Production of Woody Plants in the Woodland

REGRESSIONS

Allometric equations are widely accepted and are a necessary requisite especially when dealing with biomass and production estimations of mixed and uneven-aged forests composed of several species and a wide range of diameters and heights. As pointed out by KIRA & SHIDEI (1967 p. 71) not only different species — even different lifeforms according to WHITTAKER & WOODWELL (1968 p. 23) — but also species from different localities may be treated together in one and the same regression. The allometric equation $y = ax^b$ or $\log y = A + b \log x$ thus offers a tool for a structural description of the stand by using various properties of the equation as intercept (A)-value, correlation and regression coefficient, and, more important gives the possibility of obtai-

ning biomass and production figures for the whole stand as well as for the individual tree or fractions of the tree such as stem wood, stem bark, branches, current twigs and leaves.

The regressions are influenced by several factors (WHITTAKER & WOODWELL 1969 b) two of which will be treated in the following, viz. the selection of sample trees and the choice of the independent variable.

According to that mentioned in the methodological part earlier the selection of the sample trees must follow the stand table approach (BASKERVILLE 1965). In the present investigations the sample trees were chosen in such a way that the range of diameters was evenly covered. However, oaks with the widest diameters were avoided. Furthermore, representative trees were looked for and those showing extreme forms and deviating growth were avoided. The reason for omitting the larger trees in the analysis is purely mathematical.

The slope of the regression line will be greatly influenced by these values giving an overestimation of biomass and production values when a common regression is applied for all the species.

The main aim has been to obtain total biomass and production figures. Therefore the testing of independent variables in the allometric equation valid to the whole tree for individual species or all species combined has been restricted to variables including diameter and/or height. In Table 3 a comparison of correlation coefficients (r) and mean square deviations (MS) between the variables diameter (D) and the squared diameter times height (D^2H) is given. Generally speaking the D^2H expression simulates a volume and this gives a closer relationship to the weight figures than does the diameter. This has earlier been emphasized by inter alia KIRA & SHIDEI (1967 p. 71) and in accordance with them I therefore use the D^2H -basis since an improvement in both biomass and production estimations is obtained. High coefficients of correlation are always obtained when using allometric equations (BUNCE 1968 p. 763). In the present study this is also demonstrated. However, the correlation coefficient of the production regressions are lower.

Table 4 compiles regressions of various fractions of the tree, whole shoot data for individual species as well as species combined. Some of these are also given in Figs. 7 and 8. For comparisons with similar investigations in the future this way of presentation is adequate. Up to now it has been used by several investigators (WHITTAKER & WOODWELL 1968 p. 15—20). The independent variable, however, varies. By giving the A (intercept)- and the b (regression coefficient) values it

Table 3. Comparison of correlation coefficients and mean square deviations (MS) for \log_{10} dry weight of trees and shrubs with $\log_{10} D$ (diameter) and $\log_{10} D^2H$ (squared diameter times height).

	n	D^2H		D	
		r	MS	r	MS
Biomass					
All species	35	0.998***	0.0072	0.970***	0.1320
<i>Quercus robur</i>	11	0.938***	0.0014	0.828***	0.0036
<i>Tilia - Sorbus</i>	6	0.995***	0.0068	0.998***	0.0021
<i>Corylus avellana</i>	18	0.998***	0.0101	0.885***	0.2653
Production					
All species	35	0.990***	0.0224	0.941***	0.1532
<i>Quercus robur</i>	11	0.847***	0.0027	0.811***	0.0033
<i>Tilia + Sorbus</i>	6	0.904***	0.0567	0.942***	0.0354
<i>Corylus avellana</i>	18	0.989***	0.0128	0.839***	0.2769

n = number of samples; r = correlation coefficient; MS = mean square deviation from regression. Significance level of r : ***, $P = 0.001$.

is possible to construct the regression line. Further r (correlation coefficient) and E (relative error of estimates of a logarithmic regression) are given.

WHITTAKER & WOODWELL (1968 p. 15) use E as a measure of the relative accuracy of the estimation. In analogy with a linear regression the estimate of the relative error (e) or the spread of the points from a regression line for a logarithmic regression is calculated as the standard error of estimate (SE) divided by the mean value of the dependent variable (\bar{y}), i.e. $e = \frac{SE}{\bar{y}}$ where $SE = \sqrt{\frac{d^2}{n-1}}$. In the latter equation d = the difference between the actual value and that from the regression estimated y value for a given x value and n = the number of x and y values. An e value of 0.059 for a linear regression corresponds in a logarithmic regression to an E value, which is obtained by taking its antilog, thus giving $E = 1.15$. The expected error will then range from 1.15 y to $y/1.15$.

This way of estimation the error gives a relative description of the accuracy without connections to the confidence limits of the regression line. The E value fulfil thus only a descriptive purpose.

In order to give an adequate calculation of the total error of the estimation the deviation (probability = 0.05) from the regression line of each individual tree and shrub in the stands have been calculated (cf. HUSCH 1963 p. 401—402). The deviations have been summed and the lower and upper deviations from the regression line in percentage of the totals of plant biomass and production were calculated (Table 6).

Table 4. Regressions of shoot dimensions for trees and shrubs in the mixed deciduous woodland ecosystem (A).

	<i>Quercus robur</i>	<i>Tilia cordata + Sorbus aucuparia</i>	<i>Corylus avellana</i>	All species
A. Whole shoot regressions $\log_{10} D^2H$ (cm ² m) (x) on				
Biomass				
<i>Log</i> , above-ground total dry weight (kg) (y)				
<i>A</i>	-0.5000	-1.2382	-1.4813	-1.4301
<i>b</i>	0.7659	0.9039	1.0017	0.9699
<i>r</i>	0.938	0.995	0.994	0.998
<i>E</i>	1.028	1.106	1.063	1.146
<i>Log</i> , stem dry weight (kg)				
<i>A</i>	-0.6702	-0.6931	-1.4441	-
<i>b</i>	0.7720	0.6297	0.9378	-
<i>r</i>	0.900	0.827	0.995	-
<i>E</i>	1.038	1.764	1.065	-
<i>Log</i> , stem wood dry weight (kg)				
<i>A</i>	-0.8376	-	-1.6335	-
<i>b</i>	0.7985	-	0.9675	-
<i>r</i>	0.905	-	0.988	-
<i>E</i>	1.039	-	1.894	-
<i>Log</i> , stem bark dry weight (kg)				
<i>A</i>	-0.6037	-	-1.8164	-
<i>b</i>	0.5398	-	0.8114	-
<i>r</i>	0.834	-	0.908	-
<i>E</i>	1.056	-	4.453	-
<i>Log</i> , branch wood and bark dry weight (kg)				
<i>A</i>	-1.3575	-2.3522	-2.7737	-
<i>b</i>	0.8240	1.0426	1.2425	-
<i>r</i>	0.809	0.977	0.974	-
<i>E</i>	1.074	1.498	5.452	-
Production				
<i>Log</i> , above-ground total production, dry weight (kg/year)				
<i>A</i>	-1.2611	-1.0585	-1.7905	-1.6184
<i>b</i>	0.6341	0.5871	0.8169	0.7251
<i>r</i>	0.847	0.904	0.989	0.990
<i>E</i>	1.072	1.781	2.461	1.950
<i>Log</i> , stem wood production (kg/year)				
<i>A</i>	-1.0285	-2.1850	-1.8230	-
<i>b</i>	0.4627	0.7336	0.6241	-
<i>r</i>	0.446	0.904	0.985	-
<i>E</i>	1.275	3.026	1.398	-
<i>Log</i> , stem bark production (kg/year)				
<i>A</i>	-3.8484	-	-	-
<i>b</i>	0.8195	-	-	-
<i>r</i>	0.929	-	-	-
<i>E</i>	1.410	-	-	-

Table 4. Continued.

	<i>Quercus robur</i>	<i>Tilia cordata + Sorbus aucuparia</i>	<i>Corylus avellana</i>	All species
<i>Log</i> , branch wood and bark production (kg/year)				
<i>A</i>	1.8407	-2.4362	-2.6341	-
<i>b</i>	0.7251	0.8404	0.8992	-
<i>r</i>	0.821	0.983	0.980	-
<i>E</i>	1.104	1.111	13.812	-
<i>Log</i> , current twig and leaf production (kg/year)				
<i>A</i>	-1.8109	-0.7005	-2.3218	-
<i>b</i>	0.6837	0.3631	0.8668	-
<i>r</i>	0.826	0.694	0.981	-
<i>E</i>	1.107	4.192	7.510	-
B. Branch regressions \log_{10} cm (<i>x</i>) on				
<i>Log</i> , branch wood and bark dry weight (g) (<i>y</i>)				
<i>A</i>	-1.5315	-1.5319	-1.5744	-
<i>b</i>	2.6557	2.7886	2.9714	-
<i>r</i>	0.973	0.934	0.968	-
<i>E</i>	2.684	3.042	4.834	-
<i>Log</i> , current twig and leaves dry weight (kg)				
<i>A</i>	-1.7844	-2.3568	-1.6446	-
<i>b</i>	1.9028	2.4738	2.0946	-
<i>r</i>	0.962	0.842	0.911	-
<i>E</i>	10.790	22.072	9.647	-

All regressions are in the form $\log_{10} y = A + b \log_{10} x$. *b* = regression coefficient, *r* = correlation coefficient and *E* = antilog of the standard error of estimate.

MEAN DIMENSIONAL RELATIONS OF SAMPLE TREES AND SHRUBS

From the dimension analysis of the sample trees and shrubs some important and descriptive characteristics of the woodland are given (Table 5 a and b), which give a further description of the woodland structure. Some relationships (Table 5 a:E) reveal even functional aspects of the woodland ecosystems.

Compared with Table 1 the mean diameters and heights deviate, to some extent, from those given in Table 5 a:A. This is a result of the way in which the sample trees were selected as discussed in the previous section.

The proportions of stem-wood biomass decreases and the stem-bark biomass increases with decrease in size of the plant (Table 5 a:C) — from tree to shrub forms — and this is also valid within species. With diminishing plant size a corresponding proportional increase in branch

Table 5 a. Mean dimensional relations of sample trees and shrubs of the mixed deciduous woodland ecosystem (A). Weight figures at 85°C.

	<i>Quercus robur</i>	<i>Sorb. auc. + Tilia cord.</i>	<i>Corylus avellana</i>
A. Mean shoot relations			
Number of shoots investigated	11	6	18
Diameter at breast height (cm)	43.5	14.1	4.7
Height (m)	19.7	12.0	6.8
Age (years)	149	42	21
Biomass (dry kg)	987.8	105.7	14.2
Net production (dry kg/yr)	42.6	11.2	2.0
Bark thickness (mm)	16.4	5.0	2.6
Wood radial increment (mm/yr)	1.59	2.90	1.20
B. Volume (cm³)			
Parabolic volume estimate	1,235,000	151,600	12,600
True stem volume	1,490,000	175,900	18,800
Wood volume	1,259,000	146,500	16,000
Estimated volume increment (EVI)	19,500	5,300	770
True volume increment	24,200	6,800	930
C. Shoot dry weight distribution, % in:			
Stem wood	64.6	59.2	53.4
Stem bark	7.3	11.7	11.4
Branch wood and bark	25.7	25.4	28.2
Current twigs and leaves	2.4	3.7	6.0
Fruits	—	—	1.0
D. Root/shoot relations			
Number of stumps investigated	3	3	3
Mean root system dry weight (kg)	165.3	28.3	19.4
Mean root/stem ratio	0.17	0.19	0.26
Ratio in large tree	0.16	0.17	0.20
Ratio in small tree	0.20	0.21	0.41
Mean biomass % in:			
Stem	62.2	85.5	79.3
Branches	22.2		
Root crown and roots	15.6	14.5	20.7
E. Above-ground net production distribution, %			
Stem wood	28.5	30.5	26.0
Stem bark	1.9		
Branch wood and bark	21.2	35.0	28.3
Current twigs and leaves	48.4	34.5	45.7
F. Interrelations			
Biomass accumulation ratio	23.2	9.4	7.2
(biomass/production)			
Basal area increment/basal area (%/a) ..	1.6	10.4	21.1
Shoot net production/leaf dry weight ..	3.08	5.48	2.12
Shoot net production/leaf area (g/m ²) ..	113	164	158
Leaf area (m ²)	378.2	72.6	1.6
Leaf area index for all species		5.4	

Table 5 b. Twig and leaf data from sample trees and shrubs of the mixed deciduous woodland ecosystem (A).

	<i>Quercus robur</i>	<i>Tilia cordata</i>	<i>Sorbus aucuparia</i>	<i>Corylus avellana</i>
Current twigs with leaves				
Dry weight, twig with leaves (g)	9.132	5.728	9.795	6.436
% in twig	31.1	18.3	17.6	13.2
% in petiole	2.0	6.7	17.6	2.7
% in blade	66.9	75.0	65.8	84.1
Insect damage (% of blade)	7.8	5.9	<1.0	14.6
Number of leaves/twig	7.7	4.4	2.7	4.8
Leaf blade area per leaf (cm ²)	22.53	20.45	96.04	47.99
Blade dry weight/area (mg/cm ²)	3.57	4.95	3.00	7.37

For *Sorbus aucuparia*: 2.7 composite leaves per twig with 14.0 leaflets per leaf. Weight correction for consumption is not entered.

wood and bark as well as an increase in current twigs and leaves was found. This is in accordance with earlier facts reported by inter alia OVINGTON (1962 and 1965) and WHITTAKER & WOODWELL (1968).

Confirmation of the general condition of decreasing shoot/root ratio with increasing tree size is also apparent in the table. However, the ratio of *Corylus avellana* does not follow this rule. A discussion of this deviation follows on p. 35.

The percentage distribution of the above-ground production (Table 5 a:E) shows that *Quercus robur* has half the production in current twigs and leaves, a third as stem wood and bark production and a fifth in branch wood and bark production. The suppressed *Tilia cordata* and *Sorbus aucuparia* have an equal distribution with a third for each fraction mentioned. The dominating shrub *Corylus avellana* had higher production of branch wood and bark compared with *Quercus robur* and similar figures for the production of current twigs and leaves. It is striking to find that the small biomass fraction of leaves and twigs, 2.5–6 %, from the production point of view corresponds to percentage figures of 35–50, when all species are considered. Equally striking is that the stem wood and bark percentages of 65–72 only correspond to production of ca. 30 %.

In Table 5 b some data on twig and leaf relations are given, which makes recalculations of the figures given possible. Also amongst the data the amount of insect damage to leaves is given. If this is regarded as consumed parts of leaves it corresponds to a consumption of 0.4 t/ha/year.

Table 6. Above-ground biomass and production of trees and shrubs in the three sample areas of the mixed deciduous woodland ecosystem (A). Figures given as metric ton/ha dry weight at 85°C. Consumed and rejected material is not included.

Species	Above-ground biomass						Above-ground production					
	Sample area no. and area in ha			Totals/0.48 ha	Totals/ha		Sample area no. and area in ha			Totals/0.48 ha	Totals/ha	
	I	II	III	ton	ton	% error	I	II	III	ton	ton	% error
	0.16	0.16	0.16				0.16	0.16	0.16			
<i>Quercus robur</i>	27.0	30.2	17.4	71.6	155.3 ± 6.6/6.3		1.06	1.25	0.69	3.00	6.25 ± 9.7/9.0	
<i>Tilia cordata</i>	1.0	3.0	8.3	12.3								
<i>Sorbus aucuparia</i>	0.5	0.1	0.1	0.7	28.5 ± 4.3/4.1		0.19	0.27	0.54	1.00	2.08 ± 7.5/7.0	
<i>Prunus apium</i>	0.3	-	-	0.3								
<i>Ulmus glabra</i>	0.3	-	-	0.3								
<i>Populus tremula</i>	-	-	0.1	0.1	17.4 ± 3.5/3.4		0.45	0.64	0.36	1.45	3.02 ± 6.5/6.5	
<i>Corylus avellana</i>	3.0	3.4	2.0	8.4	201.2 ± 6.3/6.0		1.70	2.16	1.59	5.45	11.35 ± 8.6/8.0	
Totals above-ground	32.1	36.7	27.9	96.7								

Error given as lower/upper 95 % confidence limits as percentages of the total figures of dry weight.

ABOVE-GROUND BIOMASS REGRESSIONS

$$\log y = b \log x + A$$

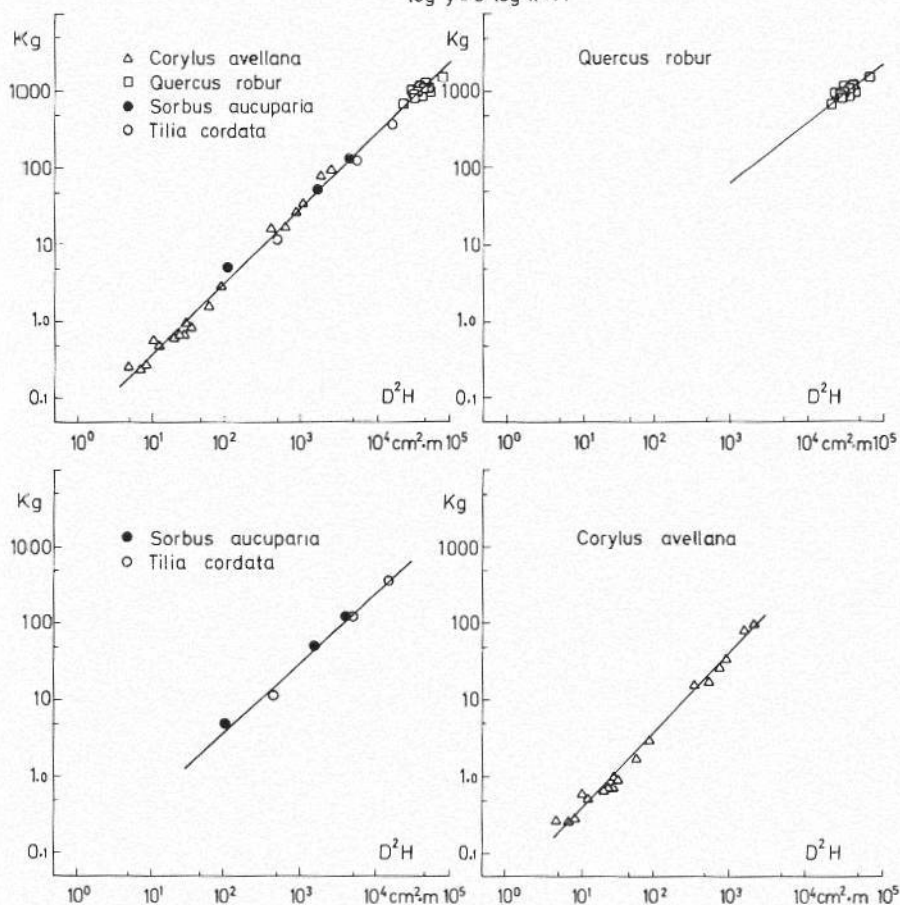


Fig. 7. Regressions of above-ground biomass of trees and shrubs.

ABOVE-GROUND PLANT BIOMASS AND PRODUCTION

By means of the non-destructive parameters diameter at breast height (D) and height (H) obtained at the stand analysis and the described regressions derived from the destructive measurements the total above-ground or shoot biomass (Fig. 7) and production (Fig. 8) of the stands have been calculated. The calculations of both biomass and production were done from the combined regressions for all species but oak. For oak the combined regression gave a considerable over-estimation — an effect caused by the great oaks in the regression pre-

ABOVE-GROUND PRODUCTION REGRESSIONS

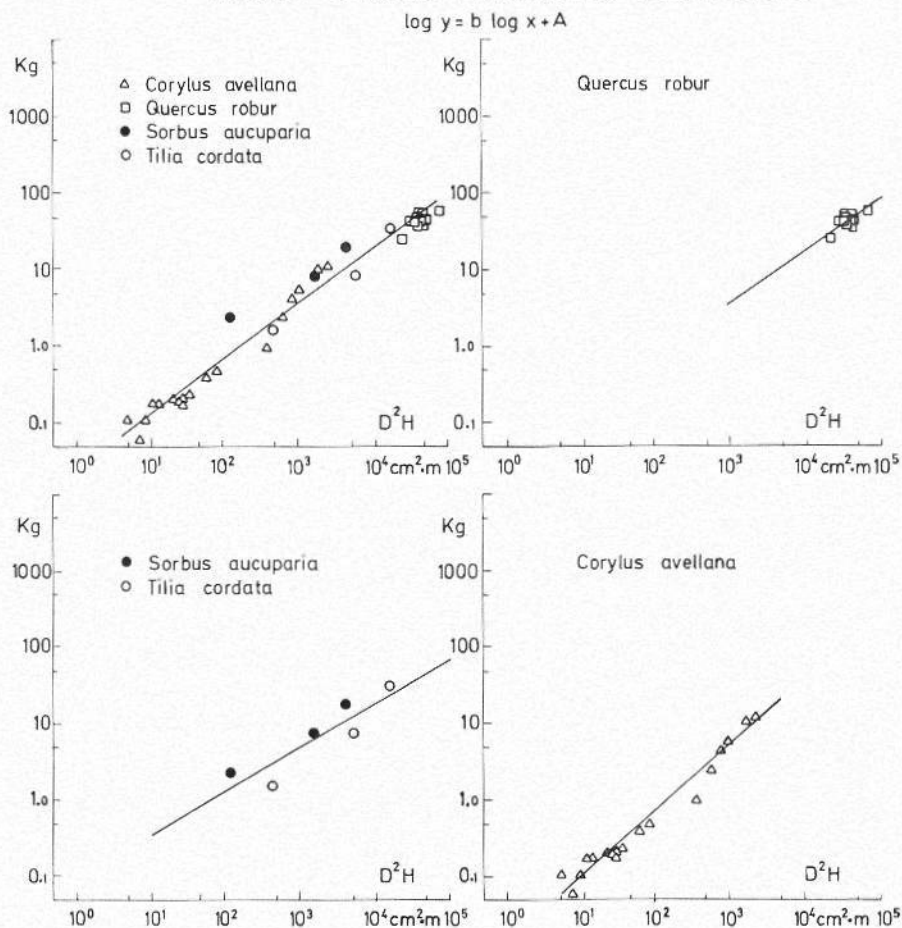


Fig. 8. Regressions of above-ground net production of trees and shrubs.

viously discussed albite precautions were taken in the selection of sample trees (p. 26). The overestimation of the oak shoot biomass and production amounted to 34 % and 76 % respectively. To avoid this shortcoming the use of the individual oak regressions proved to give a satisfactory result in spite of less accurate regression characteristics. The above-ground biomass of trees and shrubs amounts to approximately 20 t/ha (± 6.2 %) and the production to 11.4 (± 8.3 %) (Table 6). The latter figure does not imply any correction for rejected and consumed materials.

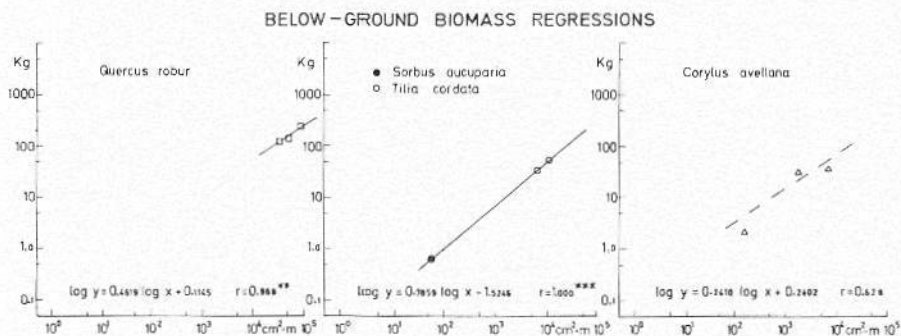


Fig. 9. Regressions of below-ground biomass of trees and shrubs. For *Corylus avellana* an approximate regression line was used at the estimation. Independent variable given as squared diameter times height (D^2H).

BELOW-GROUND PLANT BIOMASS AND PRODUCTION

Information on the main-root biomass has been obtained from a limited material of investigated root systems, viz. three oaks, two *Tilia cordata*, one small *Sorbus aucuparia* and three stools of hazel (Fig. 9). Trees and shrubs with representative diameters covering the actual diameter range of the individual species were selected. The biomass of the samples was expressed in the allometric equation on a D^2H basis as the independent variable.

Encouraging results have been obtained with the very few samples examined concerning *Quercus robur* and *Tilia cordata* together with *Sorbus aucuparia*, while *Corylus avellana* shows a deviating regression. The latter situation is easily explained by the fact that the below-ground parts of the stools are older than the above-ground parts. This may also be the case with the other frequently coppiced species, *Tilia cordata*, but those were avoided as sample trees. For obtaining stand biomass of roots for hazel an approximate regression line was drawn. Furthermore, the total sum of above-ground parts of each stool was used as the independent variable. The combined regression of *Tilia* and *Sorbus* has been used for other occurring species.

A calculation of the standard deviation (probability=0.05) of the regression gave for oak, *Tilia* and *Sorbus* an error less than $\pm 20\%$ for the mean tree. These figures are higher than those of the error of the above-ground estimations. Regarding that the below-ground biomass accounts for ca. 14% of the total biomass the estimated figures are acceptable.

Table 7. Main-root biomass of the tree and shrub layers in the mixed deciduous woodland ecosystem (A). Figures given in metric ton/ha dry weight at 85°C.

Species	Sample area no. and area in ha			Totals/ 0.18 ha	Totals/ ha
	I 0.16	II 0.16	III 0.16		
<i>Quercus robur</i>	3.6	4.5	2.4	10.5	21.9
<i>Filix cordata</i>	0.2	0.6	1.2	1.9	4.0
<i>Sorbus aucuparia</i>	0.1	(0.01)	(0.03)	0.2	0.4
<i>Prunus avium</i>	0.1	—	—	0.1	0.2
<i>Ulmus glabra</i>	0.1	—	—	0.1	0.2
<i>Populus tremula</i>	—	—	(0.02)	(0.02)	—
<i>Corylus avellana</i>	1.1	1.2	0.8	3.1	6.5
Total main-root biomass	5.2	6.3	4.4	15.9	33.2

An average main-root biomass of 33.2 t/ha was found (Table 7). To this figure the fine-root biomass (Table 8) is added to give the total below-ground biomass of trees and shrubs. This part has been estimated to 3.4 t/ha, thus giving a total amount of 36.6 t/ha.

The distribution of the fine-root biomass is mainly confined to the upper 25 cm of the soil. To describe the structure of the fine-root biomass an approximative percentage calculation on weight and length has been done based on the results from four of the examined pits. The following was found:

Root fraction in mm	2—5	1—2	< 1
Weight %	50	27	23
Length %	6	14	80
Length in m/m ²	3,700	8,700	48,000

For further information on root systems see LYR & HOFFMAN (1967) and the literature cited there.

Due to its complexity any real studies of root production have not been carried out. As to the problems involved in such a study see NEWBOULD 1967 and 1968 and the literature cited there. It is of general interest to give a figure of the total stand production and in this situation, however vague the estimation may be, the assumption of equal production rates of above- and below-ground fractions has been accepted. From the above-ground biomass and production (p. 34) and the below-ground biomass of tree and shrub roots an estimated figure of

Table 8. Fine root biomass of the mixed deciduous woodland ecosystem (A). Sampling time: June 1969. Tree and shrub roots less than 0.5 cm in diameter are included. Figures given as arithmetic means of ten pits 50×50×60 cm in metric ton/ha dry weight at 85°C. Within parentheses the 95 % confidence limits as percentages of the mean.

Tree and shrub layer	Root fraction and weight t/ha			Totals/ha
Diameter in mm	2-5	1-2	<1	
Weight in ton/ha	1.68	0.94	0.78	3.40 (±6.7 %)

2.1 t/ha is reached of which the fine-root fraction of trees and shrubs gives, 0.2 t/ha.

LITTER FALL

An important parameter in studies of forest ecosystems is the litter fall. Firstly it is essential for the estimation of production. Furthermore it offers an index from which the dynamic stage of the ecosystem can be interpreted (OLSON 1963).

In Table 9 the results of the measurements during three years in periods from April to March are given. The litter traps were emptied four times during the year, viz. before and after the bursting of leaves and before and after the main leaf fall. The following fractioning was applied: leaves of oak, hazel and other species; bud scales, flowers and fruits; miscellaneous materials and finally bark fragments, twigs and branches less than 50 cm long. Coarser fractions of the litter, especially branches longer than 50 cm and wood were collected annually on a 20×20 m area. Objections to the scarce emptying of the traps may be lodged as an instant and considerable leaching of the litter is known to occur (WITKAMP & OLSON 1963).

An expected variation between years was found. In order to explain this further detailed and prolonged observations of the litter fall in connection with environmental parameters are necessary. The obtained values of leaf litter and total litter are in the same range as those for similar ecosystems given by BRAY & GORHAM (1964), CARLISLE et al. (1966), DUVIGNEAUD et al. (1969) and KIRA & SHIDEI (1967). A comparison with some of these recent investigations is given next.

Table 9. The litter fall in the mixed deciduous woodland ecosystem (A), during 1966—69. Figures given as arithmetic means out of 16 litter traps and in kg/ha dry weight 85°C. Within parentheses the 95 % confidence limits as percentages of the mean.

Period	Twig Bark	Tree and shrub leaves				Bud scales, flowers, fruits	Miscel- laneous materials	Totals	
		Total kg	Percentage distribution on					Excl. twigs	Incl. twigs
			oak	hazel	other species				
1966 April—June	245	53	62	—	38	310	8	371	616
July—September	238	212	61	8	31	204	174	590	828
October—November	87	1,491	60	23	17	110	49	1,650	1,737
1967 December—March	465	1,048	84	12	4	—	38	1,086	1,551
April—June	310	170	58	—	42	295	61	529	839
July—September	95	269	59	9	32	42	27	338	433
October—November	382	2,305	75	19	6	68	193	2,566	2,948
1968 December—March	19	303	28	—	72	—	231	534	553
April 1966—March 1967	1,035 (±31.9%)	2,840 (±6.7%)	66	19	15	624 (±13.1%)	269 (±9.8%)	3,697 (±5.5%)	4,732 (±9.6%)
April 1967—March 1968	806 (±40.4%)	3,047 (±5.4%)	67	17	16	405 (±33.2%)	515 (±12.1%)	3,967 (±5.7%)	4,773 (±10.3%)
April 1968—March 1969	1,370	2,880	—	—	—	488	606	4,974	6,344
Mean values	1,070	3,256	—	—	—	506	463	4,213	5,283

	Linnebjerg 1967/68	Virelles I 1967/68	Grizedale 1964
Totals in kg/ha and yr . .	5,201	5,217	3,858
% distribution on:			
Leaves	59	60	55
Bud scales, flowers, fruits	8	10	10
Miscellaneous	10	3	5
Twigs and small branches	16	14	11
Big branches	7	13	19

The figures of Linnebjerg include the fraction of longer branches and wood with 428 kg/ha.

Notes on localities:

Virelles, Belgium: *Quercus robur*, *Carpinus betulus*, *Acer campestre*, *Corylus avellana*, *Hedera helix* and *Mercurialis perennis*. Age 75—135 years height 21 m. DUVIGNEAUD et al. 1969 b.

Grizedale, England: *Quercus petraea*, *Fraxinus excelsior*, *Corylus avellana*, *Deschampsia flexuosa*. Age 40—120 years. CARLISLE et al. 1966.

Plant Biomass and Production of Non-Woody Plants in the Woodland

Table 10 gives the biomass of the field layer, an additional fraction to the total stand biomass and production. The sum of the maximum above-ground biomasses of the individual species, which may be regarded as a minimum estimate of the above-ground production, give a production value of 0.77 t/ha. The maximum above-ground biomass

Table 10. Plant biomass of the field layer in the mixed deciduous woodland ecosystem. Figures given as arithmetic means and in metric ton/ha dry weight at 85°C. Within parentheses 95 % confidence limits as percentages of the mean.

	<i>Anemone nemorosa</i>	<i>Convallaria majalis</i>	<i>Oxalis acetosella</i>	Other species	Totals/ha
Above-ground biomass					
May 1966	0.48	0.01	0.02	0.03	0.53 (± 22.4 %)
June 1966	0.02	0.04	0.03	0.07	0.17
September 1966	—	(0.004)	0.18	0.02	0.21
Maximum biomass . .	0.48 (± 26.9 %)	0.04	0.18	0.07	0.77 (± 17.0 %)
Below-ground biomass					
Weight kg/ha	2.32 (± 17.7 %)	0.29			2.61 (± 14.7 %)

Above-ground biomass derived from 16 squares of $1/4$ m² and below-ground biomass from 10 pits 50×50×60 cm.

occurs in the vernal aspect with 0.53 t/ha. The figures of the below-ground biomass refers to an early summer determination and amounts to 2.6 t/ha. When the corresponding above-ground figures are added a total biomass of 2.8 t/ha is reached. An estimation of the below-ground production according to the assumption discussed on p. 37 gives a value of 0.2 t/ha.

A detailed study of the biomass and production of the woodland field layer has been carried out during 1969 (F. ANDERSSON & BRUCE in prep.).

TOTAL PLANT BIOMASS AND PRODUCTION OF THE WOODLAND ECOSYSTEM

Summing up the various fractions of plant biomass and production presented the total stand biomass and production of the mixed deciduous woodland is obtained (Table 11). A total stand plant biomass of 240 t/ha with 201 and 39 t/ha above- and below-ground respectively is present. The corresponding production figures found are 15.6, 13.3 and 2.3 t/ha.

The comparison below is restricted to some recent investigations carried out within the same biogeographical region as Linnebjerg and in which similar methods of investigations have been applied, viz. Virelles-Blaimont in Belgium (AMBROES 1969, DUVIGNEAUD 1969, DUVIGNEAUD et al. 1969 a and b) and Meathop Wood in England (BUNCE 1969, SATCHELL 1969).

	Biomass in t/ha			Production in t/ha			Basal area of trees m ² /ha
	Total	Above-ground	Below-ground	Total	Above-ground	Below-ground	
Linnebjerg	240	201	39	15.6	13.3	2.3	31.38
Virelles ¹	156	121	35	14.4	12.2	2.2	21.21
Meathop Wood ²	140	118	22	12.7	10.8	1.9	—

Both Virelles and Meathop Wood are growing on Carboniferous rocks and on shallow soils. Linnebjerg on the other hand is also growing on shallow soil, but which in general has a more ample supply of soil water during the year. Brown forest-soil conditions with mull prevail

¹ Description of locality see p. 39 and DUVIGNEAUD & AMBROES 1969, DUVIGNEAUD et al. 1969 b.

² A mixed deciduous forest with *Quercus robur* and *Q. petraea*, *Fraxinus excelsior*, *Betula spp.*, *Acer pseudoplatanus*, *Corylus avellana*, *Euonymus europaeus*, *Rhamnus cathartica*, *Rubus fruticosus*, *Mercurialis perennis* and *Anemone nemorosa*. See further BUNCE 1969.

Table 11. Plant biomass at the end of the growing season and net primary production of the mixed deciduous woodland ecosystem (A). Figures given as metric ton/ha dry weight at 85°C.

	Biomass		Production	
Shoot				
Overstory trees	155	-	6.3	-
<i>Quercus robur</i>	-	151.8	-	6.25
Understory trees	29	-	2.1	-
<i>Tilia cordata</i>	-	25.5	-	-
<i>Sorbus aucuparia</i>	-	1.6	-	-
<i>Prunus avium</i>	-	0.6	-	-
<i>Ulmus glabra</i>	-	0.6	-	-
<i>Populus tremula</i>	-	0.2	-	-
Shrubs	17	-	3.0	-
<i>Corylus avellana</i>	-	17.1	-	3.02
Field layer	-	0.2	0.8	0.77
Plant losses by death and shedding (L) ..	-	-	0.7	-
Plant losses by consumers (G)	-	-	0.4	-
Total above-ground	201	-	13.3	-
Root				
Fraction >0.5 cm ϕ — Main-root biomass	33	-	1.9	-
<i>Quercus robur</i>	-	21.9	-	-
Understory trees	-	4.8	-	-
<i>Corylus avellana</i>	-	6.5	-	-
Fraction <0.5 cm ϕ — Fine-root biomass	6	-	0.4	-
Trees and shrubs	-	3.4	-	0.2
Field layer	-	2.6	-	0.2
Total below-ground	39	-	2.3	-
Total	240	-	15.6	-

on all three localities. The stocking of trees in Linnebjerg is similar to the other sites, but the trees have wider diameters and tend to be taller. Further the understory trees and especially the shrub layer of hazel are denser and with a vigorous growth. At the present stage it is too early to go into a detailed comparison, but the figures so far show accordance in a decreasing order from Linnebjerg to Virelles and Meathop Wood of the distribution of plant biomass and production, totals as well as above- and below-ground portions. Further comparisons will be carried out when climatic and final information is available. For a regional comparison with previous works see OVERTON (1962) and RODIN & BASILEVIČ (1965, 1967, 1968).

Plant Biomass of the Meadows

A restricted study of the plant biomass of the meadows has been carried out and the figures obtained are mostly tentative. As informa-

Table 12. Plant biomass of the moist meadow ecosystems (E—G). Figures given as arithmetic mean in metric ton/ha dry weight at 85°C. Within parentheses the 95 % confidence limits as percentages of the mean.

	<i>Filipendula ulmaria</i> ecosystem	<i>Carex flacca</i> ecosystem	<i>Carex caespitosa</i> ecosystem
Above-ground biomass			
No. of 1/4 m ² squares	52	23	19
<i>Filipendula ulmaria</i>	3.24	1.37	0.68
Other herbs	1.26	0.21	0.90
Gramineous plants	0.20	1.73	2.59
Totals	4.70 (± 1.5 %)	3.31 (± 1.4 %)	4.17 (± 1.4 %)
Bryophytes	0.04	1.24	0.40
No. of 1/4 m ² squares	3	3	3
Range	0.04–0.04	1.24–1.24	0.39–0.42
Below-ground biomass			
No. of samples	3	—	—
Biomass	13.2	—	—
Range	8.0–20.7		

Sampling time of the above-ground biomass: July 1966; below-ground biomass June 1969; sampling depth 0–50 cm.

tion on plant biomass of various ecosystems are of interest all figures are given, even if incomplete and not all statistically significant (Table 12).

If the uncertain figures of the ground layer are taken into account the maximum above-ground biomass is fairly similar in all the ecosystems, with the highest figures found in the *Filipendula ulmaria* meadow. In order to show the vegetational structure of the meadow ecosystems the above-ground biomass distribution on the main life-forms is given.

Information on the below-ground biomass is so far only available for the tall herb meadow with *Filipendula ulmaria*. A tentative figure of 13.2 t/ha was found in June 1969 (Table 12).

The production has not been studied neither is it possible to derive it from these determinations of biomass. From a methodological study (F. ANDERSSON & ALDÉN in prep.) of production and breakdown of organic matter during the growth period 1969 in the *Filipendula* meadow according to a modified method of WIEGART & EVANS (1964) an estimated yearly production of 7.2 t/ha was obtained, which exceeds the maximum biomass by approximately 35 %.

Table 13. Amounts of surface litter at the end of the growth period in the mixed deciduous woodland ecosystem (A). Figures given as metric ton/ha dry matter at 85°C. Within parentheses 95 % confidence limits as percentages of the mean. n=number of sample squares.

Time	n	Litter excl. branches	Branches	Totals
September 1967	13	4.03 (± 15.6 %)	1.38 (± 19.2 %)	5.41 (± 14.8 %)
September 1968	16	3.99 (± 22.3 %)	2.43 (± 24.0 %)	6.42 (± 23.0 %)
September 1969	11	5.20	1.21	6.41
Arithmetic mean	-	4.41	1.67	6.08

Distribution of Organic Matter in the Woodland and in the Tall

Herb Meadow

In order to make as complete an assessment as possible of the organic matter of the ecosystems some additional fractions must be treated, viz. the surface litter and the humus.

Surface litter was collected in September before the leaf fall in both the ecosystems. In the woodland (Table 13) the total surface litter, excluding branches and woody material longer than 50 cm, amounts to 6.1 t/ha of which 4.4 t/ha is non-branch litter. An important, but not studied, fraction of the surface litter is the above mentioned branches and woody material longer than 50 cm. The yearly input of this fraction to the ecosystems has been estimated as 0.4 t/ha. The supply however, is greater.

The surface litter of the *Filipendula* meadow estimated in 1968 and 1969 was 2.1 t/ha (± 19.5 %) and 2.6 t/ha (± 25.0 %) for 15 sample plots of 0.25 m². Figures within parentheses give the 95 % confidence limits of the mean. A mean of 2.4 t/ha will be used in the following calculations.

The humus fraction has been calculated from the determinations of loss on ignition after correction for losses of volatile substances according to HOWARD (1966). The correction factors are obtained by calculating the regression % loss on ignition on % organic carbon. As to determination and values of loss on ignition and carbon see F. ANDERSSON (1970). The point where the regression line cuts the y-axis, is the point where the contents of carbon equals 0 and is the correction factor i.e. the intercept of the regression equation. For the woodland and the meadow the following correction factors were obtained: 0—20 cm 3.3 and 3.3 respectively; 20—50 cm 3.8 and 4.1. In the upper 50 cm

Table 14. Distribution of organic matter in the mixed deciduous woodland and the tall herb meadow. Figures given as metric ton/ha dry weight. % error=95 % confidence limits as percentages of the mean.

	Woodland			Meadow		
	Weight t/ha	% of totals	% error	Weight t/ha	% of totals	% error
Above-ground matter						
Assimilating parts						
Field layer	0.8	1	±17	4.7	1	± 2
Trees and shrubs	4.1			-	-	-
Non-assimilating parts	197	42	± 6	-	-	-
Attached dead	?	?	?	?	-	-
Surface litter						
Material <50 cm	6.1	2	±19	2.1	1	±22
Material >50 cm	?	?	?	-	-	-
Below-ground matter						
Total plant biomass	39	8	<±20	13	4	-
Humus (0-50 cm)	218	47	± 6	304	94	± 9
Totals	463	100	± 6	324	100	± 9

of the soil 218 t/ha and 304 t/ha for the woodland and the meadow was found of which the A₁ horizon, the mull horizon, contained 102 and 204 t/ha respectively.

Another fraction for a complete description of the biomass distribution of the woodland is that of the above-ground biomass attached dead material. Insufficient data are available at present to give a reasonable estimate of that fraction.

In Table 14 the various fractions of the organic matter of the two investigated ecosystems are summed and the percentage distribution of fractions is given. Further, the error of estimations is surveyed. The striking difference in the distribution of the organic matter between a woodland and a grassland is demonstrated with an equal distribution of the organic matter between above- and below-ground portions (cf. MALMER 1969) and in the meadow as much as 98 % is found as below-ground matter. The figures of assimilating parts corresponds to maximum figures.

Turnover of Organic Matter

In the following a tentative description of the functioning of the woodland and the meadow ecosystems in terms of turnover of organic

matter is given. For this purpose the investigation model (Fig. 6) must be put into mathematical terms to describe the interrelation between its components. Deciduous forests have from the turnover of organic matter point of view been subject to special interest and therefore models are available. OLSON (1963) has expressed the previous used equations (JENNY et al. 1949, GREENLAND & NYE 1959) in an appropriate mathematical model valid for forests with continuous and discrete litter fall. The latter has been used in the present study (see also KIRA & SHIDEI 1967 p. 84).

The turnover of organic matter is associated with processes on and in the soil and therefore the amount of organic matter in the soil profile including the litter, is essential. The amount of organic matter accumulated in the soil, X , at a given time, t , is described with the relation

$$\frac{dX}{dt} = L - kX$$

where L is the amount of organic matter supplied to the soil and k is a factor for the decomposition rate. Assuming that incomes and losses are identical, a steady state condition is reached. The relation can be written as $L = kX$ or $k = \frac{L}{X}$. By means of k the dynamics of the litter (A_0) layer can be characterized, but it can also be applied to the total organic matter of the soil. Even if this model is not designed for meadow conditions the same factors can be used for a general description of the turnover of that ecosystem. L corresponds then to the yearly production above-ground, which all becomes litter during the year.

From the specific exponential equation (OLSON op. cit. p. 325—326) other characteristic parameters can be derived, viz. the turnover time or the reciprocal of the decomposition rate, $\frac{1}{k}$, which gives the time required for decomposition of the organic matter equal to the organic matter in the soil (JENKINSON 1966); the half time, the time required for decomposition of half the organic matter present in the soil. The exponential equation gives $0.5 = e^{-kt}$ or $-1 \ln(0.5)/k = 0.6931/k$; the 95 % time, the time required for obtaining 95 % decomposition of the organic matter in the soil. This corresponds to $3/k$.

Table 15 gives the fractions necessary for the calculation of the turnover parameters and the following characteristics were obtained:

	Woodland		Meadow	
	Litter layer	Total humus	Litter layer	Total humus
Decomposition rate, k	0.516	0.039	0.750	(0.045)
Half time, $0.6931/k$	1.34	17.77	0.924	(15.40)
Turnover time, $1/k$	1.93	25.64	1.33	(22.22)
95 % time, $3/k$	5.81	76.92	4.00	(66.66)

52 % of the surface litter is decomposed during the year in the woodland and the corresponding meadow figure is 75 %. In weight organic matter this gives 6.5 and 7.2 t/ha respectively. Assuming the root litter fraction of the woodland — estimated as discussed on p. 34 — and the root litter of the meadow equal the above-ground production and also are assumed to be fully decomposed during the year, it was found that the turnover of the total organic matter in the soil of the woodland was 3.9 % and about half a percentage higher in the meadow. With regard to the amount of humus present in the woodland and in the meadow, 218 t/ha and 304 t/ha respectively, these percentages correspond to a yearly turnover of 9 t/ha in the woodland and approximately 50 % more in the meadow. It must be stressed that the assumption of root-litter production is highly hypothetical, especially in the meadow, and so the estimates of the turnover of organic matter

Table 15. Yearly input to and total storage of organic matter in the soil.
Figures given as metric ton/ha dry matter.

	Woodland	Meadow
Input		
Surface litter		
Leaves, bud scales, miscellaneous, twigs	5.3	—
Tree and shrub branches	0.4	—
Field layer	0.8	7.2
	6.5	—
Root litter estimated	2.2	(7.2)
	8.7	(14.4)
Storage		
Surface litter		
Litter of the year	6.5	7.2
Older litter, finer fractions	4.4	2.4
Older litter, coarser fractions	1.7	—
	12.6	9.6
Root litter	2.2	(7.2)
	14.8	(16.8)
Humus 0–50 cm	218	304
Total storage	233	321

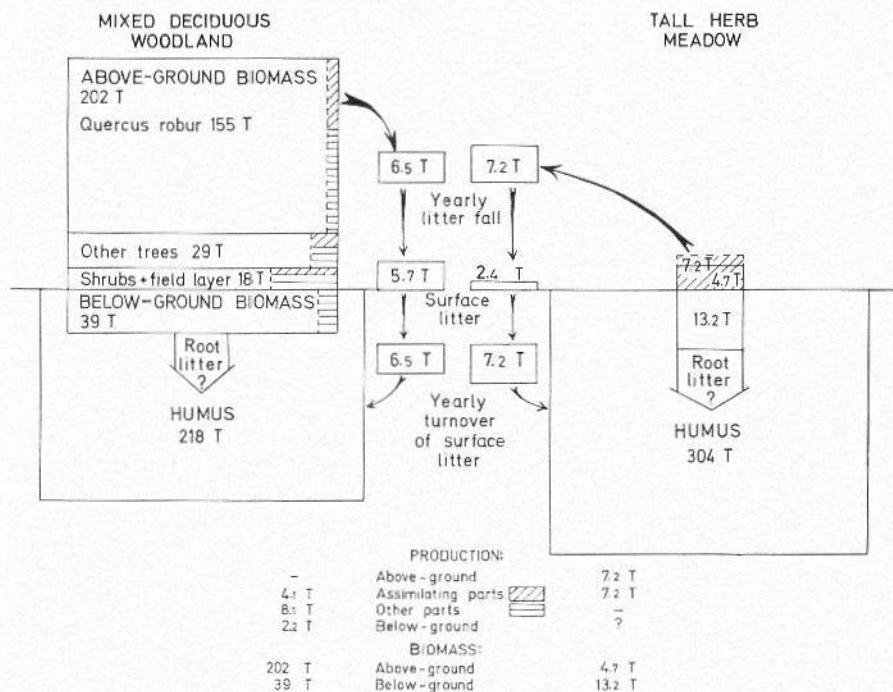


Fig. 10. Schematic diagram showing the distribution and yearly turnover of organic matter in a mixed deciduous woodland and a tall herb meadow ecosystem. Figures given as metric ton (T)/ha.

regarding the total soil. However, these values are brought forward as an incitement to further work in obtaining a more detailed assessment of the organic matter. As a steady state is supposed to exist the inputs to the ecosystems equal the outputs.

CONCLUSIONS

In Fig. 10 the main results of these investigations on plant biomass, primary production and turnover of organic matter are summarized and the principal differences between a woodland and a meadow ecosystem are shown.

From the methodological point of view the estimation of plant biomass and production of the woodland according to allometric equations has proved to be an excellent tool. However, the nature of the

allometric regression must be carefully examined in order to avoid overestimations and misinterpretations. An adequate stand table approach is essential for escaping an overestimation. In literature it has often been stated that a combined regression with material from different localities and of different species gives better regression characteristics. This is obviously true due to the fact that a greater number of variates is obtained by combining material from different localities and of different species. However, existing differences of species or sites may in this way be concealed in the combined regression and therefore the individual regression probably will reveal these differences if a sufficient number of variates are included. The advantages of the combined regression in mixed forests must still be remembered, mainly the reduction of sample trees per species.

The results of the dimension analysis have, up to now, only been used for a structural description of the woodland. A detailed examination of area, volume and mass are, however, essential for the functional characterization of the woodland in terms of production in relation to such processes as photosynthesis and respiration. The biomass/production relation is one important expression in evaluating the dynamical stage of the ecosystem — conditions which will not be discussed with references to the limited material presented here.

Investigations of meadows as well as other open ecosystems need proper methods for determination of production and other fractions essential to the calculations of the turnover of organic matter. In the present investigation for example the use of the maximum biomass as a measure of the above-ground production is inadequate and should give an underestimation of 35 %. In addition, from the methodological point of view the estimation of below-ground production in meadows as well as in woodlands is an unsolved problem.

The applied methods have given estimates which prove to be satisfactory. Thus the total organic matter, excluding the small part of consumers, has been determined with an error of ± 6 % and ± 9 % for the woodland and the meadow respectively. However, some minor fractions must be determined with higher accuracy.

A comparison between the woodland and the meadow shows that a greater amount of organic matter is present in the woodland than in the meadow, 463 and 324 t/ha respectively. The above- and below-ground distribution is almost 1/1 and 1/49. The above-ground production is higher in the woodland than in the meadow, but the portion returned to the soil, the litter, is higher in the meadow as wood and

bark increment occur in the woodland. Possibly the attached dead of the woody species can give an additional amount of litter which equates the yearly litter fall with that of the meadow. Accepting some of these uncertain estimations higher rates of turnover of organic matter are found for the meadow. It is not possible to give a definite answer from the present results as some of the litter fractions must be studied further.

These latter speculative conclusions show the need for detailed and prolonged research, especially when dealing with forests, if satisfactory answers of the turnover of organic matter as well as energy and nutrient cycling shall be obtained. The main benefit of the present investigations up to now is the application of methods which give a detailed information of plant biomass and net primary production of a woodland.

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Studies in the Aegean Flora XV

Chromosome Numbers in Labiatae

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ABSTRACT

BOTHMER, R. VON: Studies in the Aegean Flora XV. Chromosome Numbers in Labiatae. — Bot. Notiser 123: 52—60. Lund.

The chromosome numbers of 14 species of *Labiatae* from the Aegean have been determined. For eight species the chromosome numbers have not been reported previously.

MATERIAL AND METHODS

The seed material used in the investigation was collected by Drs. RUNEMARK (R.), SNOGERUP (S), Lund, and NORDENSTAM (N), Stockholm, during excursions in the Aegean 1957—62.

For chromosome studies, material was cultivated in the greenhouses of the Botanical Garden, Lund. The plants were pretreated by cooling at 2—4°C over night, fixed in the Svalöf modification of Navashin-Karpeschenko, cut in microtome (sections 14 µ), and stained with crystal violet. The chromosome drawings were made by means of a camera lucida.

Amaracus tournefortii (S. & S.) BENTH. $2n=30$ (Fig. 1 C)

Material: A m o r g o s: the monastery of Panagia Chozoviotissa S exp. cliffs 200—450 m s.m. (R&S 12321).

The chromosome size is 1—1.5 µ. The median, primary constriction is very distinct in all pairs.

No chromosome number is reported earlier for the genus *Amaracus*. The genus has been included in *Origanum* L. by DAVIS (1949), a genus also having the basic number $n=15$ (cf. p. 54).

A. tournefortii is distributed on the eastern Kikladhes and eastern Crete (cf. Map 7 in RUNEMARK & al. 1960).

Calamintha exigua (S. & S.) HAL. $2n=36$ (Fig. 1 N)

Material: S a m o s: SW part of mt. Kerki 400—800 m s.m. (R&S 19589); mt. Kerki, the peak, 1000—1400 m s.m. (R&N 16944).

The chromosomes are rod-shaped or elliptic with a length of 1–2 μ . A faint median constriction has been observed in some pairs.

C. exigua is a tetraploid species ($x=9$), and the chromosome number has not been hitherto reported. Previously only diploid species ($2n=18$) are known in the *Acinos*-group of the genus *Calamintha*.

C. exigua is distributed in the eastern Mediterranean. Var. *integrifolia* BOISS., which is known from Crete and Cyprus, is low and has an entire leaf margin; otherwise the species is rather homogeneous.

Coridothymus capitatus (L.) RCHB. $2n=30$ (Fig. 1 F)

Material: I k a r i a: 0–1 km E Ag. Kirikos, phrygana (R&S coll. 11.7 1958). K e r o s: the islet of Antikeros, phrygana (R&S 12361).

The chromosome number is not previously known. The chromosomes are rodshaped or elliptic with a length of 1–1.5 μ and with a vague centromere. The chromosome numbers $2n=31$ and $2n=32$ have been observed in occasional metaphase plates.

The genus *Coridothymus* is monotypic but closely related to *Thymus*. The single species *C. capitatus* is omni-mediterranean and morphologically homogeneous throughout this area.

Lavandula stoechas L. $2n=30$

Material: N a x o s: valley 2 km E of Ag. Stefano, phrygana, 200–300 m s.m. (R&S 10161).

The chromosome number $2n=30$ is earlier reported by GARCIA (1942). *L. stoechas* has an omni-mediterranean distribution and is rather invariable.

Majorana onites (L.) BENTH. $2n=30$ (Fig. 1 A)

Material: P a r o s: 2–3 km N the peak of mt. Prof. Elias, 450–500 m s.m. (R&S 12694). K e r o s: E exp. limestone cliffs on the S part of the island, 100–250 m s.m. (R&S 10829). C r e t e: Dia. "Middle Bay", limestone cliffs (R&N 16468).

The chromosomes are rounded or rod-shaped with a length of 1–1.5 μ . The chromosome number is not earlier reported.

M. onites occurs in the eastern Mediterranean and is slightly variable.

Marrubium vulgare L. $2n=34$ (Fig. 1 L)

Material: Naxos: the bay N of Mountsounis, at a rill (R&S 10499).

The chromosomes are elliptic with a length of 1—2 μ . No constrictions have been observed. The chromosome number $2n=34$ was previously reported by RUTLAND (1941), TARNAVSCHI (1948), EPLING (1948), and LARSEN (1960). WULFF (1939) gave the number $2n=36$.

M. vulgare shows great morphological variation within its distribution range (Europe and the Mediterranean area). The investigated material belongs to var. *lanatum* BENTH.

Mentha pulegium L. $2n=20$ (Fig. 1 B)

Material: Ikaria: the sandy beach at Pharos (R&S 12489). Euboea: N of Akr. Merouthi, at a rill, 0—80 m s.m. (R&S 11873).

The chromosomes are rod-shaped with a faint median or submedian constriction, and have a length of 1—2 μ .

M. pulegium forms a polyploid series with the basic number $x=5$ throughout its entire European distribution range. MORTON (1956) gave the numbers $2n=10, 20, 30$ and 40 of plants from Central and Southern Europe. RUTTLE (1931) found the numbers $2n=20$ and 40 in material from Central Europe. The tetraploid number ($2n=20$) was also reported by POLYA (1950) and TARNAVSCHI (1948). Besides these counts, $2n=46$ was reported by NAGAO (1941).

Origanum heracleoticum L. $2n=30$ (Fig. 1 G)

Material: Naxos: the chapel N of Oros Zevs, 600 m s.m. (R&S 12790).

The chromosomes are rounded or rod-shaped with a length of ca. 1—1.5 μ . The chromosome number for the species is not earlier reported, but in the genus *Origanum* $2n=30$ is known.

O. heracleoticum is distributed in the eastern Mediterranean, and shows great morphological variation. HAYEK (1931) and RECHINGER (1943) distinguish two varieties differing in the shape of the inflorescence, and the shape and colour of petals and bracts. The investigated material belongs to var. *creticum* (L.) HAL.

Prasium majus L. $2n=34$ (Fig. 1 E)

Material: Sifnos: Ormos Kondros, 0—20 m s.m. (R&S 8348). Antimilos: 1 km S Akr. Zigraso, phrygana, 50—150 m s.m. (R&S 8737). Crete: Sitia, between Achladia and Paraspori, ca. 200 m s.m. (R&S 18543).

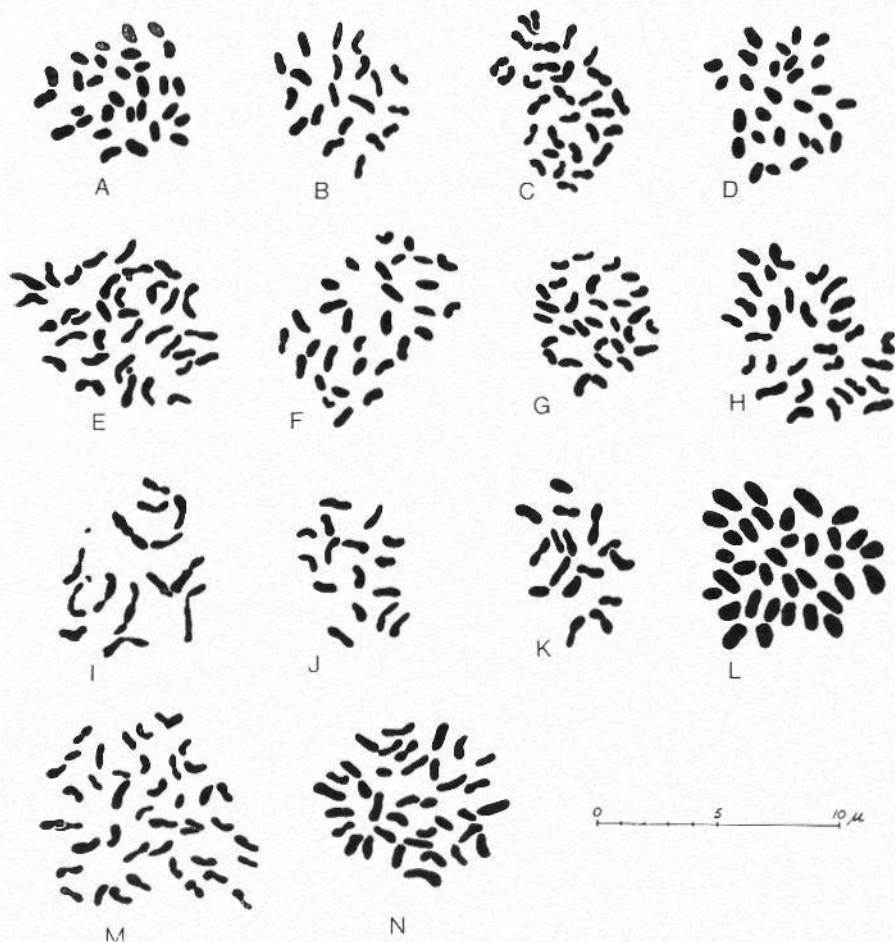


Fig. 1. Chromosomes in *Labiatae*. — A. *Majorana onites* (L.) BENTH. — B. *Mentha pulegium* L. — C. *Amaracus tournefortii* (SIBTH.) BENTH. — D. *Prunella vulgaris* L. — E. *Prasium majus* L. — F. *Coridothymus capitatus* (L.) RCHB. — G. *Origanum heracleoticum* L. — H. *Satureja thymbra* L. — I. *Salvia pomifera* L. ssp. *calycina* (SM.) HAYEK. — J, K. *Salvia viridis* L. — L. *Marrubium vulgare* L. — M. *Salvia verbenacea* L. ssp. *multifida* (SM.) BRIQ. — N. *Calamintha exigua* (S.&S.) HAL.

The chromosome number is not earlier reported for this monotypic genus. The chromosomes are 1—2 μ long with a median or submedian centromere. One pair of satellites situated on a medium sized chromosome pair has been observed.

P. majus has an omni-mediterranean distribution and is very variable in pubescence and leaf shape.

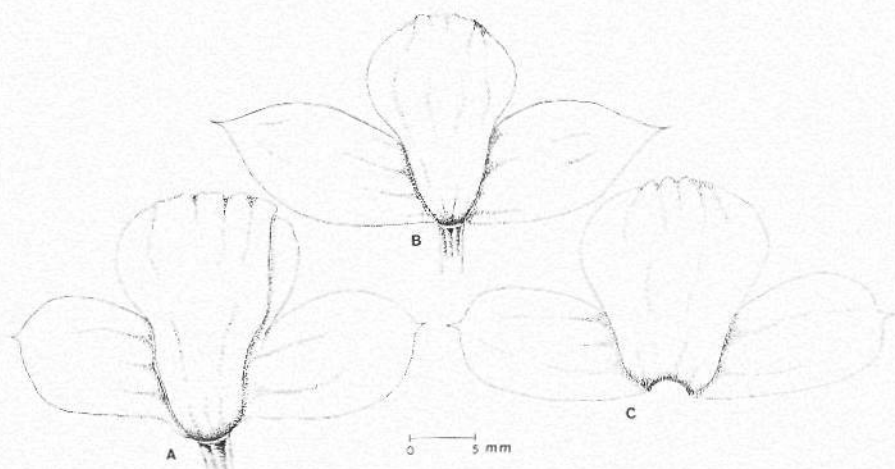


Fig. 2. Calyx shape in *Salvia pomifera* L. — A, B. ssp. *pomifera*, Crete [WALL 79 (S), REVERCHON 135 (LD)]. — C. ssp. *calycina* (SM.) HAYEK, Peloponnesos [RECHINGER 20021 (S, LD)].

Prunella vulgaris L. $2n=28$ (Fig. 1 D)

Material: Euboea: 3 km WSW of Akr. Kafirevs, at a rill (R&S 11732).

The chromosomes are rounded and ca. 1μ long. No constrictions or satellites have been observed.

Different chromosome numbers have been reported for *P. vulgaris*. $2n=32$ was reported by HRUBY (1932), BOCHER (1940), MATICK (1950), and HARA (1954). BOCHER (1949), however, contradicted his own and HRUBY's earlier reports and gave the number $2n=28$, which was also confirmed by LEVITSKY (1940), LÖVE (1954), and LÖVE & LÖVE (1956).

Salvia pomifera L. ssp. *calycina* (SM.) HAYEK $2n=14$ (Fig. 1 I)

Material: Attika: Porto Rafti, 1.5–2.0 km W of Ag. Nikolaos, 100–150 m s.m. (S 20333).

The karyotype shows chromosomes with median or submedian centromeres. Secondary constrictions have been observed on some chromosomes. One pair of satellites is frequently observed on a ca. 2μ long chromosome pair. One chromosome pair is distinctly larger than the others, and has a length of ca. 3μ .

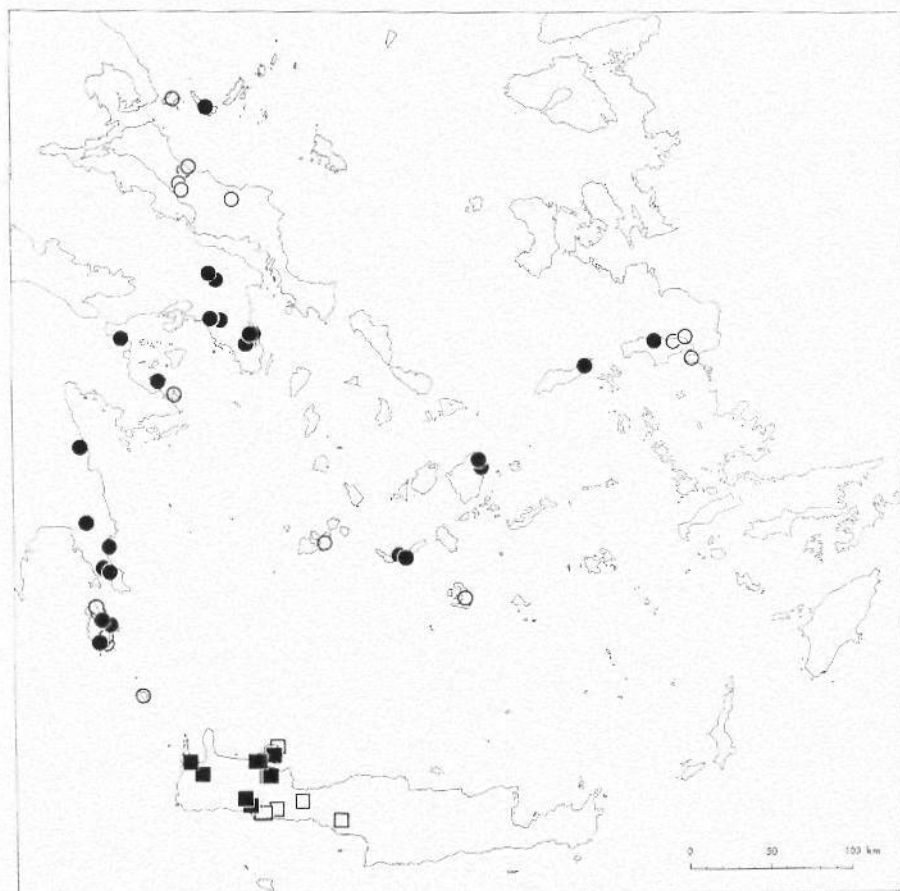


Fig. 3. Distribution range for *Salvia pomifera* L.: ■ ssp. *pomifera* (□ literature reports); ● ssp. *calycina* (SM.) HAYEK (○ literature reports).

The chromosome number is not earlier reported for *S. pomifera* but within the genus *Salvia* the basic number $x=7$ is known.

HAYEK (1929) reduced *S. calycina* SM. to a subspecies under *S. pomifera* L., differing from ssp. *pomifera* in leaf shape and pubescence of calyx (cf. GREUTER & RECHINGER 1967). The calyx shape, believed to be of diagnostic importance (RECHINGER 1943), is in fact much variable especially on Crete (Fig. 2). The distribution of the two subspecies is shown in Fig. 3. Most of the specimens on the island of Kythera and one on adjacent Peloponnesos must be classified as intermediate forms (cf. GREUTER & RECHINGER 1967).

Salvia verbenacea L. ssp. **multifida** (SM.) BRIQ. (=ssp. *clandestina* (L.) BATT.) $2n=42$ (Fig. 1 M)

Material: Crete: 1 km S of Ag. Nikolaos 0–20 m s.m. (R&S 17488). Folegandros: Pelagia, 30 m s.m. (R&N 14653). Ikaria: Ormos Yero, 0–10 m s.m. (R&S 6468).

The chromosome number $2n=42$ was reported by REESE (1957). For *S. verbenacea* the numbers $2n=54$ (BENOIST 1937), $2n=c. 58$ (BJÖRKQVIST & al. 1969), $2n=59$ (GADELLA & al. 1966), and $2n=64$ (YAKOVLEVA 1933) are also known.

S. verbenacea is omni-mediterranean. It is a very polymorphic species which has been subdivided into several subspecies (cf. QUEZEL & SANTA 1963, and GREUTER & RECHINGER 1967). Ssp. *verbenacea* and ssp. *multifida* (SM.) BRIQ. are represented in the Aegean.

Salvia viridis L. (= *S. horminum* L.) $2n=16$ (Fig. 1 J and K)

Material: "horminum type" (with coloured upper bracts):

Sirina: the central part of the island, phrygana, 50–350 m s.m. (R&N 14487); the valley S of the village, 20–200 m s.m. (R&S 7407). Iraklia: 1–2 km W of the village Chora, phrygana, 100–270 m s.m. (R&N 13323).

"viridis type" (with green upper bracts):

Crete: Sitia, between Achladia and Paraspori, ca. 200 m s.m. (R&S 18557); Sitia, Dionysades, Yanisada (R&S 18596); 1 km S of Ag. Nikolaos, 0–20 m s.m. (R&S 17479). Iraklia: Ormos Pegadi, limestone, 5 m s.m. (R&S 5317). Saria: 1 km N of Armyro Ormos, deserted field, 100–150 m s.m. (R&S 7737).

The chromosome number $2n=16$ has been reported by SCHEEL (1931), YAKOVLEVA (1933), HRUBY (1934), LINNERT (1955), and LIMA-DE-FARIA & SARVELLA (1958).

The chromosomes are rod-shaped in both form series, 1–2 μ long, and have a median or submedian centromere.

The taxonomic evaluation of "horminum" and "viridis" types has been much discussed. RECHINGER (1943) and HOLMBOE (1914) treat *S. horminum* and *S. viridis* as separate species. HOLMBOE, however, considers *S. horminum* as a probable variety of *S. viridis* on account of the much frequent intermediate types. QUEZEL & SANTA (1963) and GREUTER & RECHINGER (1967) treat the group as a single species, which is in accordance with the opinion of the present author.

The distinguishing character, blue coloured and enlarged upper

bracts in "horminum type", is extremely variable and all intermediate types exist. In the cultivated material much variation has been observed even in the progeny of a single individual.

Satureja thymbra L. $2n=30$ (Fig. 1 H)

Material: A n a f i: the central part of the island, phrygana, 200—400 m s.m. (R&N 14983).

The chromosomes are rod-shaped with a median or submedian constriction, and a length of ca. 1.5μ .

The chromosome number is not earlier reported for *S. thymbra*, but VAARAMA (1947) gives the same number ($2n=30$) for the closely related species *S. montana*.

S. thymbra occurs in the eastern Mediterranean and is morphologically constant in the Aegean.

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The Post-Glacial Immigration of *Picea abies* into Fennoscandia

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ABSTRACT

MOE, D.: The Post-Glacial Immigration of *Picea abies* into Fennoscandia. — Bot. Notiser 123: 61–66, Lund.

This work shows that the continuous immigration of *Picea abies* in Norway and Sweden was not synchronous around 500 BC. This result is based upon a distribution map made by aid of chronological datings.

In some pollen diagrams from Southern Norway, there appears to be a lapse of time between the decline of *Quercetum mixtum* (QM)-pollen and the steep rise of *Picea* about 500 BC (NYDAL 1960, LARSEN 1954, 1955 and HAFSTEN 1956 p. 97, pl. 7, 8, 15). Normally in this region the great expansion in *Picea*-percentages has been used as an indicator for the transition between the Subboreal and the Subatlantic periods (HAFSTEN 1956 p. 103). The argument for this has been that after the change of climate, around 500 BC, the spruce was able to compete successfully with the deciduous trees. The spruce-tail back into the Subboreal and Atlantic periods is interpreted either as long distance transport or as pollen from small groups of trees in front of the continuous distribution, depending on the height of the percentages (e.g. HAFSTEN 1956 p. 97, FLORIN 1944 p. 567). In some few Norwegian pollen diagrams from Beiarn and Skjerstad, Nordland county, in a sprucless area, I found up to 3 % *Picea* (of Σ AP). My opinion is that all this pollen is transported from North Swedish localities more than 100 km away (MOE unpubl.). It is therefore possible that *Picea* pollen up to 5 % could be long transported from a distance of more than 50 km (FÆGRI & IVERSEN 1964). FÆGRI (1950) has made pollenanalyses of the small West-Norwegian spruce localities, which were situated outside continuous distribution. The size of the stands varied from 100 m in diameter (for instance at Botnavatnet) to a forest area of 4×10 km (Skutletjern). In the first area the spruce reached a few per cent, in the last one up to 12 %. If we used my definition

Source, locality and age of material used for the map, (C^{14} age, T1/2 5568):

1. FROMM, E. 1938: Prästmon	ca.	1000 BC
2. LUNDQUIST, G. 1957: Adakgruven (LUNDQUIST, G. 1956). <i>Picea</i> after	1045 ± 75	BC
3. MOE, D. unpubl.: Kosmoli continuous long transport	790 ± 90	BC
4. PERSSON, C. 1966: Klockamyren	after 330 ± 75	BC
— 1967 a: Klockamyren	before 1375 ± 65	AD
5. — 1967 b: Sjetnemyren	ca. 1460 ± 65	AD
6. — 1967 a: Grövelsjömyren 10 % group	ca. 415 ± 70	AD
7. — 1966: Lövåsmynen	before 1875	AD
8. — 1966: Svendsjömassan	before 1875	AD
9. — 1966: Sundbornsmossan	ca. 825 ± 70	BC
10. — 1966: Mellstabromossan	ca. RY III	
— 1966: Mellstabromossan	after 905 ± 80	BC
— 1966: Mellstabromossan	before 75 ± 70	AD
11. LUNDQUIST, J. 1957: Gräsmark	ca. 480 ± 70	BC
12. — 1967: Blomma	ca. 210 ± 65	BC
13. PERSSON, C. 1966 a: Klaxsjömassan	after RY III	
14. NYDAL, R. 1960: Holtantjern	ca. 150 ± 130	BC
— 1960: Holtantjern	ca. 450 ± 150	BC
15. FRIES, M. 1951: Nordvästra Götaland	ca. 300	AD
16. DIGERELDT, G. unpubl.: Trommen (Växjö) 10 %	ca. 820 ± 100	AD
17. VORREN, B. unpubl.: Kirkmyra	ca. 1030 ± 80	AD
18. FRIES, M. 1962: Ösbysjön 10 %	before 935 ± 70	AD
— 1962: Ösbysjön 10 %	after 220 ± 80	BC
19. LUNDQUIST, J. 1957: Brätenmossen	ca. 480 ± 70	BC
20. — 1957: Åstorp mossen	before 730 ± 65	AD
21. — 1969: Hallviksmyren	ca. 665 ± 100	BC
22. — 1969: Hällåfloarna	ca. 500 ± 100	BC
23. — 1969: Stockbergsmyren	490 ± 75	BC
24. — 1969: Docksmynen	460 ± 75	BC
25. — 1969: Tranflon	just after 620 ± 100	BC
26. — 1969: Vattenfloen 10 %	35 ± 70	BC
27. — 1969: Blåhammarsmyren 10 %	675 ± 100	BC
28. — 1969: Lidsjömyren	ca. 445 ± 75	BC
29. — 1969: Trångomyren 10 %	180 ± 80	AD
30. — 1969: Tönningsfloarna 10 %	85 ± 70	AD
31. BERGLUND, B. E. 1966: Storemosse DP I, BP I	after 1570 ± 70	AD

in the first case, it does not necessarily indicate that the spruce exists in the area today. It is therefore difficult with a small amount of *Picea* pollen to determine what is long-transported and what is locally produced. Values between 5 % and about 10 % seem to denote either the presence of considerable numbers of the tree in the area (FÆGRI 1950, Skutletjern), or probably spruce in adjacent areas, 10 to 50 km away (listed as the 10 % group). I wish to define a limit where I am

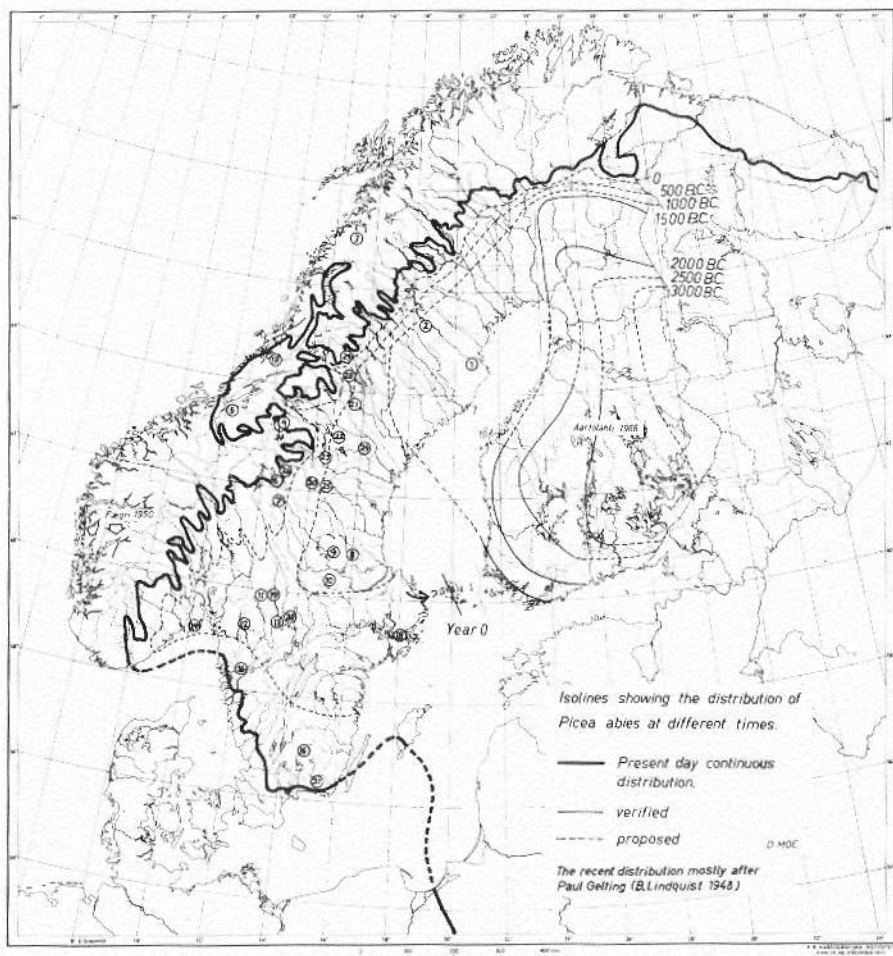


Fig. 1. Present and past distribution of *Picea abies* in Fennoscandia. Open rings with numbers indicate dated material, (see list).

wholly certain that the spruce in the area is part of a greater regional distribution (more than 15 %), and I have used this value as an indicator of *continuous* distribution. In front of this *Picea*-covered area, one has to calculate with small groups of trees. It is therefore extremely difficult to make maps of the post-glacial distribution at different times based on pollen alone. Macrofossils like roots and stems etc. have to be used, and care must be taken with fossils as cones and branches, because of the possibility of transport by man (BERGGREN 1956).

Sometimes we find a passing rise of *Picea*, up to 13—24 %, in some Swedish and Norwegian pollen diagrams in the subboreal period (FLO-RIN 1944, Elgsjømossan, HAFSTEN 1956, Balsrudmyr). The authors explain the material as locally produced pollen, and certainly this could be a possibility. However, I do not like to use this material before it have been dated by C^{14} or some other reliable method, since these two profiles are taken from basins which are filling in, and the *Picea*-maxima are placed near the stratigraphical border between limnic and telmatic material. The possibility for quagmires and redeposition are therefore present (TROELS-SMITH 1956). On account of all these problems I have based my map (Fig. 1.) of the *continuous* distribution at different times on chronologically dated levels.

First AARIO (1965) then AAROLAHTI (1966) made a map of the fossil distribution for Finland based on radiocarbon datings, and I have attempted to continue this work in Sweden and Norway. The number of dating is small, but the map provides us with interesting information. Mostly I have used C^{14} datings. For locality 1 varve-chronology is used, for locs. 7 and 8 ash-horizons which are historically dated, for locs. 10 and 13 RY III horizons, and for loc. 15 a good archaeological dating.

From 1500 BC to 500 BC *Picea* expanded fairly quickly from the northern part of Sweden and southwards, on an average about 9 km per 10 years. The forest of North-Sweden, before the occupation of the spruce, consisted mostly of *Pinus* and *Betula* (FRIES 1965). This vegetation is a more light-open type than the QM-forest in the south. Therefore the spruce could advance with great facility at this stage. A smaller, but useful spruce-colonization between 500 BC and 1 AD has been favoured by the decline of the QM-forest, and it is logical that it replaced it. The spruce produce much more pollen than QM-trees (POHL 1937) and therefore the spruce-percentages in the diagrams were necessarily higher than those of QM prior to decline.

After *Picea* had occupied, in the course of a couple of hundred years, most of the places after the QM-deforestation, the condition for further expansion was more difficult than previously, not only by reason of the denser vegetation but also of the meeting with the mountain-range and cultivation by man.

The spruce in West-Norway is young, varying in age from a few hundred years ago up to 1000 years (FÆGRI 1950). In Trøndelag, in the middle of Norway, the age is surprisingly young, and I think we will find the spruce still younger further north in this part of the

country. It is reasonable to presume that the spruce will have greatest expansion in this area, not least on account of the north-south direction of the vallies.

ACKNOWLEDGEMENTS

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Studies on Mire Vegetation in the Torneträsk Area, Northern Sweden

IV. Some Habitat Conditions of the Poor Mires

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CONTENTS

Abstract	68
Introduction	68
Sites investigated	70
Methods	70
Results	
Water	
Water level	76
Vegetational gradients in relation to water level	77
pH and electrical conductivity	78
Peat	
Relationship between some constituents analysed	
Extractable and total amounts	80
Correlation coefficients between some constituents	81
Vegetational gradients in relation to chemistry of peat	
Regional gradients	82
Local gradients	91
Elements in precipitation and in peat	93
Stratigraphy of some sites	
Introduction	95
Description of the profiles	96
Results and conclusions	100
The gradient ombrotrophy—minerotrophy in the investigation area	105
Acknowledgements	107
Literature cited	108

ABSTRACT

SONESSON, M.: Studies on Mire Vegetation in the Torneträsk Area, Northern Sweden. IV. Some Habitat Conditions of the Poor Mires. — *Bot. Notiser* 123: 67–111, Lund.

Results of investigation of some ecologic gradients of poor mires (bogs and poor fens) in a mountain area of North Scandinavia are presented. A close relationship between situation of the subsoil water table and plant communities along the gradient hummock—mud-bottom is demonstrated. In the upper levels of sites containing permafrost usually no free water occur on the frost table during the growth period. High positive correlations were apparent between total contents of Al, Cu, Fe, SiO₂, Ca and ash in hummock peat. These showed no or negative correlations with Na, Zn, Mn and Mg. Decreasing values for Mg, Zn and K, as well as for pH, with distance from the sea were obtained. A tendency of a similar relationship with distance was also noted for Ca and Na. Increasing values were evident for ash, Al and possibly also for Cu. Ca/Mg quotients are usually higher than 1.0 in hummock peat except in the westernmost sites. The amounts of Ca, Mn, Cu, Al, ash and SiO₂ as well as pH are correlated with the vegetational gradient poor—rich. Zn contents are higher in peat of higher rather than lower level in the sites. There is a fairly close relationship between the concentration of Mg and Ca in hummock peat and in precipitation. The K and Na contents in peat are better related to the total annual amounts in precipitation. The chemical stratigraphy of three bog-like sites was discussed. No evidence of a recently increased supply of air-borne matter was seen. The increase in content of most elements analysed in the superficial peat is probably due to retention by living organisms and capillary movements. Some of the contents at the permafrost table are partly due to previous flooding but it is also suggested to be an effect of changed concentration of elements in freezing water and an addition of colloids. When deducing whether the conditions in the sites with an ombrotrophic position are functionally ombrotrophic or minerotrophic to the plant cover neither the floristic composition of the present-day community nor that of the underlying peats would give conclusive evidence.

INTRODUCTION

In two earlier papers (SONESSON 1967, 1970) the variation of the poor mire vegetation (bog and poor fen vegetation) in the Torneträsk area, Northern Sweden, was discussed. Often the gradients are difficult to separate and seem to be interdependent. In a separate paper (SONESSON 1969) it was shown, that some of the variation is allied to differing winter conditions, but it was also shown that some variation along the gradient chionophobic—chionophilous was better

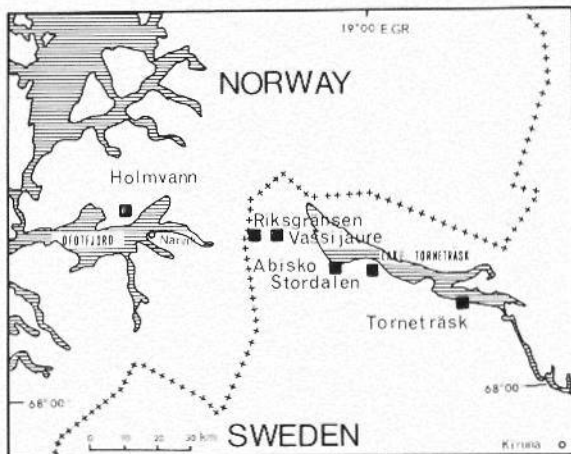


Fig. 1. Map showing the situation of the sampling sites (= solid quadrats) mentioned in the text.

related to the situation of the water table in the sites than to the winter conditions *per se*. The variation along the gradient poor—rich was even more obvious but seemed to be related to a variation along the gradient hummock—mud-bottom as well. Any differentiation along this gradient into bog communities and poor fen communities (ombrotrophic and minerotrophic communities, according to DU RIETZ 1954) using criteria in the plant cover only, was not possible to make. Nor would any conclusive evidence from the hydrotopography of the sites be found in all cases. Considering the extensive material of macro- and microfossil analyses of peat from many sites over the whole area (SONESSON in prep.) the possibility of temporary minerotrophic conditions even for the present-day bog vegetation was suggested (SONESSON 1970 pp. 29—30). However, a differentiation into ombrotrophic and minerotrophic peat using macrofossils implies a nutrient status of such peat corresponding to that which prevailed for the peat-forming community, which remains to be proved.

In order to elucidate these problems investigations of the situation of the water table as well as the chemical conditions in peat were carried out during 1962, 1963 and 1969 over Boreal mires representative with respect to vegetation from Holmvann near the Atlantic Ocean to Torneträsk ca. 100 km further east (Fig. 1). The result of these investigations is presented and discussed in this paper as well as the investigations of three selected peat profiles from Vassijaure, Abisko and Torneträsk. This is to show some of the variation in chemical stratigraphy found in the poor sites. Further stratigraphical

material, however, will be presented in future papers on the vegetational dynamics of the area.

A full description of the investigation area, the mires and the mire vegetation is given in SONESSON 1967 and 1970. The reader is referred to these earlier papers, where the terminology, nomenclature and basic environmental data are also given. The winter conditions of the mires are discussed in SONESSON 1969.

SITES INVESTIGATED

Boreal mires which are representative with respect to the vegetation were selected along a west—east transect about 100 km long. Mires selected were in the vicinity of Holmvann (about 150 m above sea level), Riksgränsen (470—500 m), Vassijaure (460—480 m), Abisko (360—380 m), Stordalen (340—380 m) and Torneträsk (340—360 m). See Fig. 1. A few samples (in the *Sphagnum lindbergii* variant) were also collected in Alpine mires in Vassivagge and on Mt. Luovare (see map in SONESSON 1970).

The snow depths in cm at Riksgränsen and Kiruna (about 50 km SE of Torneträsk) during late winter—early spring were :—

	1962		1963	
	April 15	25	April 15	25
Riksgränsen ..	100 (107)	82 (99)	145 (107)	144 (99)
Kiruna	95 (74)	43 (61)	60 (74)	52 (61)

The normal depths according to ÅGER (1964) are shown within parenthesis. For further data of the current precipitation and temperature during the sampling periods, see SONESSON 1969 Table 1. The winds are mainly westerly in the Torneträsk area (HOLDAR 1960 p. 231).

The values of elementary constituents in precipitation shown in Table 4 are means calculated from data for the period 1955—62. These are, to some extent, unrevised data distributed by the International Meteorological Institute in Stockholm. Recordings at Riksgränsen ceased in 1962.

METHODS

Water Level

The water level was measured approximately every four days from July 5th to September 9th 1962. The sites were visited and measurements carried out in a standardized order. Sporadic measurements were also carried out during May and during the period July 18th to August 29th 1963. For refer-

ence poles were struck down into the mires and marked at the level of the surface of the bottom-layer. Levelling before and after the measurements showed that the position of the poles during the period of 1962 had not changed, whereas in some cases great deviations were found having occurred during the winter 1962—63. For this reason some of the results from 1963 are not accounted for in Fig. 3. If open water was not available (only so in mud-bottoms) a water table was obtained by digging small pits ca. 75 cm deep (or to the frost table). Precipitation was measured with aid of rain gauges ("Perfekt", Bröderna Berglund Gävle) placed at a height of one metre in an open place in a neighbouring wood, one at each mire. No plot was situated more than 500 m from the gauge. To prevent evaporation oil was added to the container. Primary data from three of the mires, two western without frost during summer and one eastern with permafrost, are shown in Fig. 2 A—C. In all, 62 plots were observed and measured. Certain of them were omitted due to lack of water during the whole period of observation in 1962. All these were situated in eastern hummock-sites. The frost table was only slightly lowered and contained no or too little water to afford measurements.

pH and Electrical Conductivity of Water

pH of water and peat as well as electrical conductivity measurements were carried out during 1960—63 on fresh samples collected from the middle of the squares for vegetational analysis as well as in the pits for measurements of the water level. Most water samples were collected from the hollows dug to obtain peat for the pH determination (time of sedimentation ca. one hour or more). In the mud-bottoms containing water in undisturbed condition samples were taken before peat sampling was made. This means that these pH and κ_{rel} data are referable to the same plots and occasion and that the sampling covers a very wide range of time, geographical situation and climatical conditions.

The conductivity measurements were made using a bright platinum electrode (c approx. = 0.3) in a standardized order within twelve hours. κ_{rel} designates the conductivity after reduction of the conductivity due to the hydrogen ions (SjöRS 1952, MALMER 1960).

Peat

Sampling was carried out during the summers of 1963 and 1969 over different sites each year and within areas approximately 10,000—40,000 m².

The 1963 samples were taken between ca. 3 and 15 cm below the peat surface, the 1969 samples between 10 and 15 cm below the bryophyte/lichen surface. The samples were stored in plastic bags in a cold store (ca. +4°C) and were analysed within three months. The peat profiles were collected using a Nääs-Odentun core sampler (diameter 25 mm, see NÄÄS & ODENTUN 1958),

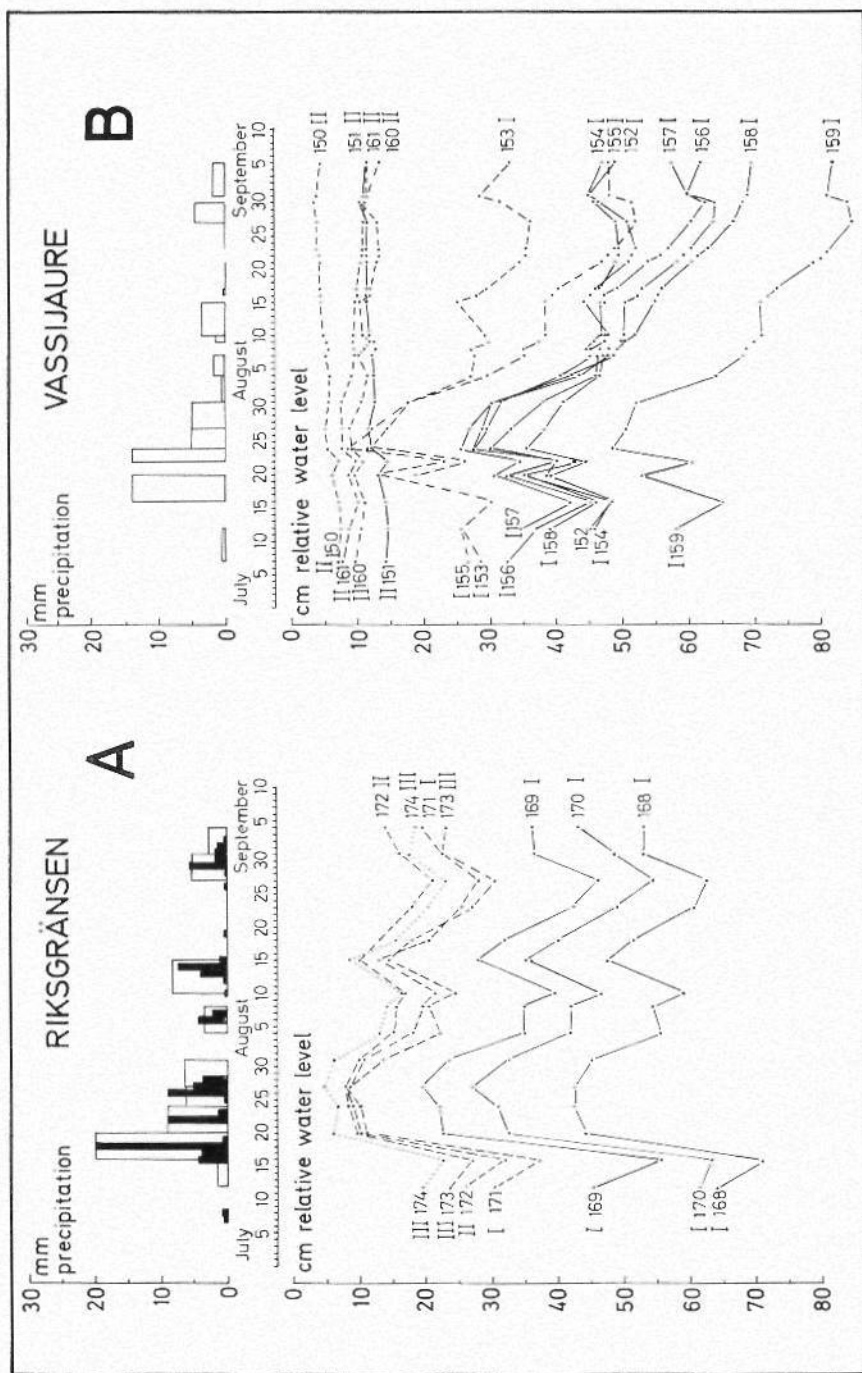


Fig. 2 A—B.

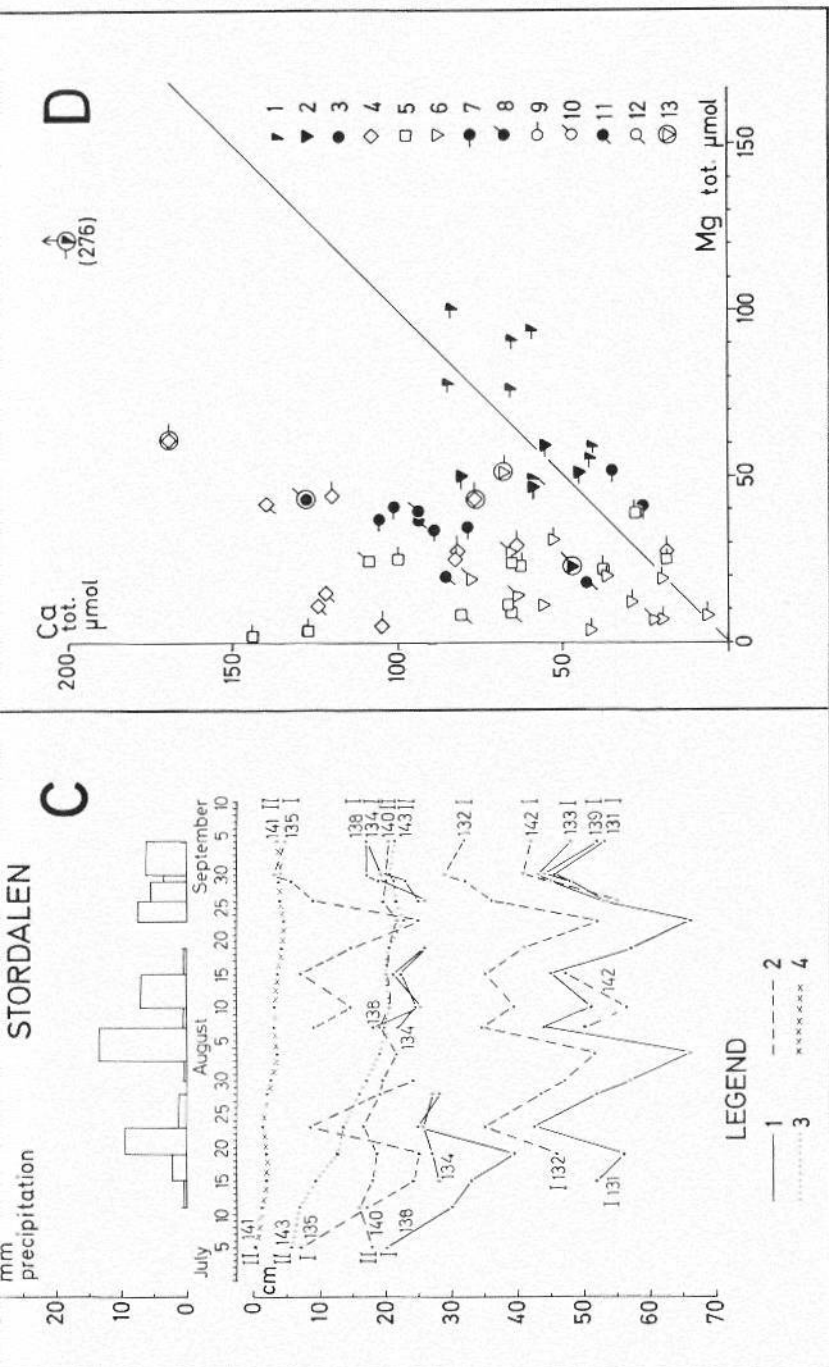


Fig. 2 A-C: Position of the water table in three mires during 1962. Open columns show the amount of precipitation close to the mire, solid columns precipitation at the meteorological station at Riksgränsen. The different sites are indicated by Roman numerals. Legend: 1. *Empetrum hermaphroditum*-*Vaccinium microcarpum* association, 2. *Carex rotundata*-*Drepanocladus schutzei* association, 3. *Sphagnum riparium* association, 4. *Drepanocladus procerus* association. — D: Total calcium and magnesium contents as $\mu\text{mol/g}$ dry matter in surface peat from hummock sites. Legend: 1. Holmvann, 2. Riksgränsen, 3. Vassijaure, 4. Abisko, 5. Stordalen, 6. Torneträsk, 7, 9. Communities of the upper levels, 8, 10. Communities of the lower levels, 11, 12. Poor lawn communities, 13. Fen plants present.

the superficial samples, however, with a Holmen auger (cutting edge area 100 cm², see HOLMEN 1964 pp. 137—138).

Peat samples for pH measurements only were collected during 1960—63 at the same occasions as the vegetational analysis and water sampling (see p. 71). pH was always measured electrometrically directly into fresh peat with a glass electrode.

The analyses were mainly carried out according to the methods described by MALMER and SJÖRS 1955 and MALMER 1962 a.

The extractable cations (=Ext., including the dissolved fraction, cf. TYLER 1968 p. 94) were extracted with 1 M neutral NH₂Ac and 1 M HAc (25 g fresh peat to 150 ml extractant). The samples were shaken for at least two hours (the 1963 samples for two hours, left overnight and filtered, see MALMER 1962 a; the 1969 samples for twelve hours before filtering). However, one hour proved to be sufficient according to a preceding equilibrium extraction series tested for calcium (see, however, BOATMAN & ROBERTS 1963 p. 189). The total contents (=Tot.) of metals and silica were obtained after digestion with HNO₃ and HClO₄. The residue insoluble in HCl is regarded as SiO₂. The exchange capacity for metal and hydrogen ions (=C.E.C.) was determined using BROWN'S method (BROWN 1943, cf. MALMER & SJÖRS 1955). The major ions were analysed separately. In the 1963 solutions determination were made for Na and K (flame photometer), Mg, Ca (EDTA titration), Mn, Fe, P (colorimetrically) and S (gravimetrically). Total N was determined with a micro-Kjeldahl procedure. See MALMER 1962 a pp. 184—189. In the 1969 solutions Na and K were analysed with a flame photometer and all other metals by means of an atomic absorption spectrophotometer, Ca after addition of LaCl₃.

To obtain the deviations due to analytic errors and inhomogenities of the samples some duplicates were run. The average deviations from the means (within 95 % confidence interval) of the duplicates calculated according to HALD (1948) are shown in Table 1.

The peat samples from the vertical profiles were usually too small, frozen or of a water content higher or lower than normal to permit determination of the degree of humification according to VON POST'S method (see POST & GRANLUND 1926 and KAILA 1956 p. 19). Therefore a colorimetric determination of extracts with 0.5 % NaOH on the dried peat (105°C) was made as an index of humification (EEL-colorimeter, filter no. 626). This means that the degree of humification is supposed to be related to the contents of NaOH soluble organic matter in the peat. For further details and discussions on this subject see ÖVERBECK 1947, KAILA 1956, OLAUSSON 1957, BAHNSON 1968. All samples were pretreated and analysed in the same way. Duplicates were run. Four samples determined with VON POST'S method were frequently run as a reference. The range of values obtained for these samples is shown in Figs. 6—8 as well as their degree of humification according to VON POST'S scale (H 1—H 10). A selective decomposition of plant remains seems to be probable, since there was often a weak correlation between high decomposition as determined with these methods and the degree of corrosion of bryophytes found in the peat (further in SONESSON in prep.).

Table 1. Average deviations from the means of duplicates (at the 5% level) according to HALD 1918. Total contents as $\mu\text{mol/g}$ dry matter. Number of duplicates shown within parenthesis. See text.

Element:	Class, standard deviation, frequency:			
Mg	<20.0	20.0—<50.0	50.0—105.0	
	± 0.35	± 1.78	± 4.0	
	(20)	(21)	(18)	
K	<5.0	5.0—<10.0	10.0—68.0	
	± 0.28	± 0.21	± 2.6	
	(25)	(16)	(19)	
Ca	20.0—<50.0	50.0—<100.0	100.0—530.0	
	± 1.87	± 1.21	± 5.8	
	(13)	(25)	(22)	
Mn	<0.20	0.20—<0.50	0.50—4.00	
	± 0.024	± 0.037	± 0.08	
	(14)	(24)	(12)	
Zn	0.020—<0.200	0.200—<0.500	0.500—1.160	
	± 0.037	± 0.030	± 0.18	
	(9)	(24)	(16)	
Fe	<20.0	20.0—<50.0	50.0—<100.0	100.0—256.0
	± 0.82	± 5.63	± 6.70	± 26.2
	(19)	(15)	(19)	(7)

The cores for the micro- and macrofossil analyses (details on methods in SONESSON 1968 and in prep.) from Abisko and Stordalen were collected during 1963 and those for the chemical analyses during 1969. The cores were taken as half metre lengths which were divided into ten equal pieces for the chemical analyses. Smaller samples were used for the fossil analyses. In each site all this sampling was carried out within the same area (ca. 0.25 m²). The possible differences in stratigraphy between these cores were tested for the macrofossil content. No differences were found. All data from Vassijaure refer to the same samples and sampling occasion (1963). This profile was dug and the peat was "peeled off" as broad sheets usually not exceeding 1 cm in thickness.

The level of reference mentioned here concerning the peat profiles discussed is always the surface of the living bryophyte and or lichen layer.

In each sample used for pollen analysis 600 tree pollens or slightly more were counted, except in some surface samples where a smaller number was counted due to the sparse pollen content. In the pollen spectra shown here (Figs. 6—8) a selection of the pollens (here meaning pollen grains as well as spores) is made.

The chemical values of the uppermost sample of each profile refer to one species of the living plant cover, viz. *Pleurozium schreberi* in Vassijaure and *Dicranum elongatum* in Abisko and in Stordalen. Most of these samples apparently consisted of living material.

RESULTS

Water

Water Level

The water level is greatly dependent on precipitation and the amount of snow during late winter—early spring (Fig. 2 A—C, cf. Sjörs 1948 pp. 38—42, 87). The differences found between the two periods of measurements are obviously due to a relatively higher precipitation especially during July 1963 (Kiruna) but also to a greater amount of snow in the western part this year (Riksgränsen). The highest water tables were recorded during May 1963 and the lowest during early summer and autumn 1962. During the observation period in May 1963 only the eastern sites had almost completely emerged from the snow, while the western sites were, to a large extent, covered with snow (SONESSON 1969 p. 488). The weather was, however, unusually warm during the period and a rapid melting of snow occurred. Practically no free water was seen, however, on the western hummock-sites after digging up the snow cover, which indicates a rapid run-off (SONESSON *loc. cit.*, cf. SONESSON 1970 Fig. 6). There are reasons to believe that the maximum water level and the maximum water level on unfrozen mire (MALMER 1962 a p. 156) approximately coincide in the western sites but are usually dissimilar in the eastern ones. This is mainly due to absence or only a slight occurrence of frost in the western sites and presence, although a variation in the situation of the frost table in the eastern sites during spring and summer (cf. SONESSON 1969 p. 488, 1970 p. 53).

The depths to the water table within the interquartile range (Fig. 3) are no doubt close to the compensation level (MALMER *loc. cit.*) but some of the total range shown here probably belongs to this level as well, since the measurements were made during relatively short periods.

The effect of rain and drought was approximately the same in the western and in the eastern sites. In the hummock-sites a considerable increase of the water table is seen as a result of the heavy rains at the end of July and in the beginning of August 1962, while the response was smaller in the plots of the carpet-sites or in plots close to such sites (cf. MALMER 1962 a p. 166).

Plots belonging to (vegetationally and morphologically) different sites have dissimilar responses to precipitation in the eastern mires as well as in Vassijaure, but not in the westernmost mire at Riksgränsen.

This mire is a typical example of the western mires with a relatively even topography where even the peat of the carpets is distinctly firmer than that usually prevalent in eastern carpets. The vegetation also deviates, containing mire margin species to some extent in the western ones (SONESSON 1970 p. 54 cf. MALMER 1962 a p. 219). The eastern carpets are usually quaking having mire margin species located more distinctly to their margins. The small carpet-structure of the Vassijaure mire is in this respect of an eastern type. The peat is relatively deep and the structure seems to receive an even influx of water through a small brook apparent in some places (SONESSON 1970 p. 94). Probably like many of the eastern carpets it may, in this way, be less directly dependent on precipitation than many of the western carpets. Thus in eastern mires as well as in western mires with a deep peat layer, there seems to be more diverse conditions as to hydrology than in western mires generally.

Vegetational Gradients in Relation to Water Level

On the whole there is an obvious relationship between the gradient hummock—mud-bottom and the situation of the water table (see Fig. 3). It should be emphasized that the reference level was the position of the moss layer at the beginning of the measuring period of 1962 which means that much of the range of the eastern carpet and all the mud-bottom values is apparent only.

In the plots of the hummock communities the medians and extremes are lower and the ranges wider than those of other vegetation observed. The hummock communities are usually situated more than 25 cm above the water table and seem to be situated above the maximum water level as well (cf. MALMER 1962 a p. 156). The lowest water levels are measured in the western sites. The low values from eastern sites are undoubtedly unnatural created by the digging, since depths to the frost table exceeding 50 cm are seldom measured (cf. SONESSON 1970 pp. 31—32). Some of the plots dug in stands of eastern hummock communities are not accounted for in Fig. 3 because no or only small amounts of water were present during the whole period of measurement. This indicates that much of the eastern hummock communities (probably all of the upper levels, cf. SONESSON 1970 p. 39) has slight or only occasionally free water on the frost table during the growth period. Since the surface peat usually is slightly decomposed

the run-off from peat underlying such vegetation is probably very rapid in spring and early summer but slower when the thaw has reached more decomposed layers.

The *lawn communities* are usually situated more than 10 cm above the water table but below the maximum water level, at least in the eastern plots. The covering of water after the snow thaw may then last for more than one month (SONESSON 1969 pp. 488—490).

The *carpet communities* are usually situated more than 5 cm above the water table. Many eastern carpets are probably situated above the maximum water level as well because of the quaking peat. The range of values shown are in these cases apparent only. However, this is not the case for the values from Riksgränsen. The ranges in this mire are similar to those of lawns. The vegetation of these western carpets is also deviating due to the occurrence of mire margin species (see above p. 77).

The *bottom layer of the mud-bottom communities* is floating on the water table. It is also often partly submerged (see SONESSON 1966 p. 396).

The gradient low—high water table is, to some extent, paralleled by the gradient poor—rich as well. Fen plants are rarer in the stands with a low water table (cf. MALMER 1962 a pp. 78, 168—183).

pH and Electrical Conductivity

The relationship between pH and κ_{red} shown to be typical to North Fennoscandian mire waters by SJÖRS (1952, see also PERSSON 1962) is also evident in the present material. Thus any correlation between pH less than ca. 6.0 and κ_{red} is not obvious ($n=230$). pH values higher than 6.0 are, however, usually allied to higher values of κ_{red} . Negative conductivity values were often obtained after reduction for the hydrogen ions, especially in humus coloured water. Obviously many of the ions are retained as complexes with colloidal matter in the water (MALMER 1963).

pH in water is generally higher than in peat from the same plots. The average differences were approximately 0.5 units ($n=170$). Such a relationship is shown earlier both for the Torneträsk area (PERSSON 1962 pp. 77—78) and for South Sweden (MALMER 1962 a p. 203).

There was no general relationship apparent between pH in water and the level of the water table during the observation periods. However, in spring a high water table is obviously related to a high pH.

Later during the growth period occasional very high water levels, probably much above the compensation level, are related to great pH deviations either positive or negative (cf. MALMER 1962 b pp. 23—24). MALMER (*op. cit.* pp. 22—28) found a distinct relationship between reduced conductivity and the water level on one hand and conductivity and pH on the other. However, a similar relationship may not be expected in the present material when considering conductivity values lower than ca. 50 $\mu\text{S}/\text{cm}$ and pH lower than ca. 6.0 (cf. above).

Some chemical data for intermediate mire water in the investigation area are shown in SONESSON 1966.

Peat

Relationship Between some Constituents Analysed

EXTRACTABLE AND TOTAL AMOUNTS. There is no conclusive evidence of differences between extractable amounts derived in 1963 and 1969 in spite of the somewhat different sampling and analysis. Similar results were obtained with NH_4Ac and HAc , except of K (often higher amounts with HAc).

In Fig. 4 the extractable amounts of Na, K, Ca and Mg are plotted against the total amounts in the same samples.

According to this material extractable amounts are, on average, roughly 20—40% lower than the totals. The high total amounts of K and Mg in relation to low extractable contents are most likely due to addition from the mineral soil (secondary ash) since these values refer to intermediate fen peat with a high content of Al, SiO_2 and ash ($> 200 \mu\text{mol}$, $> 380 \text{ mg}$ and $> 17 \%$ per g dry matter respectively). A contribution of potassium and magnesium to the minerotrophic sites seems possible due to various feldspars, micas etc. common in most mineral soils. There is probably often dolomite in the soils as well, at least in those rich in calcium, since the bedrock of the investigation area contains this mineral in many places (KULLING 1965, cf. MÅRTENSSON 1956 and PERSSON 1962).

The wide range apparent for the Na values is obviously to a large extent due to a lower accuracy in the Na determinations. As suggested above some of the range of the K and Mg values is due to the deviating properties of the peats analysed.

The relationship between extracted and total amounts of metal cat-

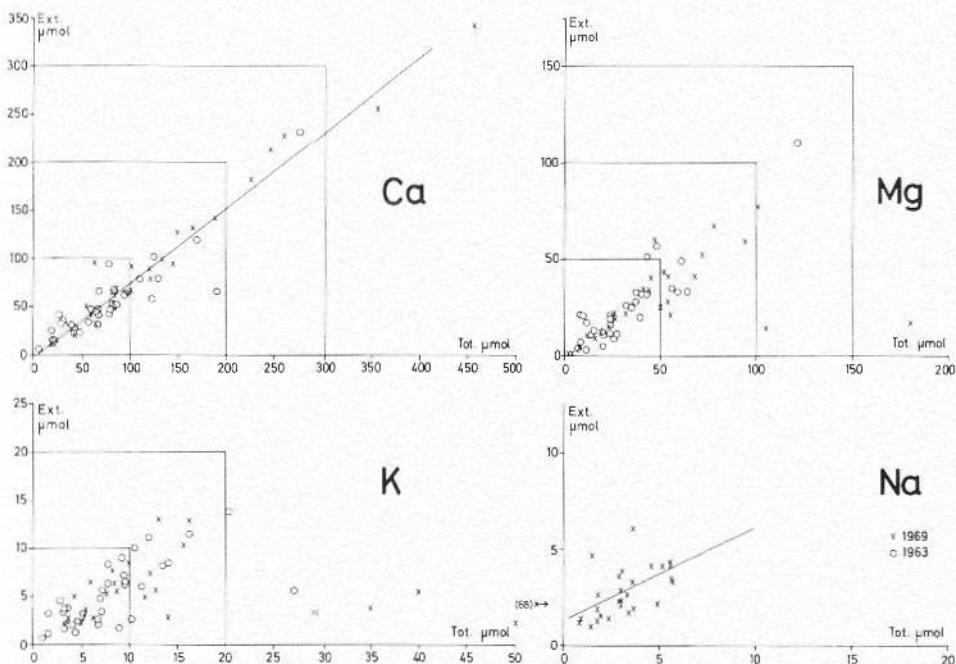


Fig. 4. Relationship between NH_4Ac extractable and total amounts of some elements in different kinds of surface peat as $\mu\text{mol/g}$ dry matter.

ions in peat is earlier investigated and discussed by GORE and ALLEN (1956) and by BOATMAN and ROBERTS (1963). GORE et al. showed the often great differences obtained due to different kinds of peat and BOATMAN et al. the differences due to the extractants used and to the time of extraction. Considering the differences between extracted and total contents of K found by them these range approximately between 0 and 40 % which is similar to the range for the material presented here when excluding the highest totals.

CORRELATION COEFFICIENTS BETWEEN SOME CONSTITUENTS. In Table 2 is shown the correlation coefficients between the contents of some constituents in peat from the higher levels of the hummock-sites (SONESSON 1970 p. 39). These are parts of the mires which are most likely to be nourished by air-borne nutrients only, viz. being ombrotrophic (DU RIETZ 1954). In all, forty samples were collected during the summers of 1963 and 1969, from different sites each year at the following localities: — Holmvann (9 samples, vegetation=no. 1 in Table 3), Riksgränsen (4 samples from one site in

1969, vegetation=nos. 2 and 3), Vassijaure (6 samples, vegetation=nos. 2 and 3), Abisko (8 samples, vegetation=nos. 5 and 6), Stordalen (6 samples, vegetation=nos. 5 and 6), Torneträsk (7 samples, vegetation=nos. 5 and 6).

Al, Cu, Fe, SiO₂, Ca and ash show high positive correlations. However, the coefficient between silica and calcium is not quite significant at the 5 % level ($0.1 > p > 0.05$). These constituents including K and Mg as well as small amounts of Mn are common in mineral soil (secondary ash).

As shown in the next section (pp. 104—107) the ash content of the peat profiles presented there is not higher at the surface than in the lower strata, which if it were, would indicate a recently increased contribution of secondary ash as reported for South Sweden (see e.g. MATTSON et al. 1955 p. 363). Neither is there any considerable increase evident in the content of Al. However, macroelements important in living organisms such as Ca, Mg and K usually increase towards the surface. Na, Mn and Zn increase too. This is also evident in a palsa profile from Torneträsk (SONESSON unpublished). In all surface peat samples studied after ashing mineral particles were present, but whether they were more abundant than in the lower strata was not investigated.

The low or lack of correlation between Al, Cu, Fe and SiO₂ on one hand and the other elements on the other may be due to a smaller contribution from secondary ash of the latter than that retained near the surface by living organisms (e.g. K) or continuously supplied by air-borne drift (e.g. Na). However, similar results would be obtained if a major part of these constituents were unevenly distributed over the investigation area and or in the peat profiles within the standardized sampling level. The westerly distributed Mg and Zn accordingly show no or slightly negative correlations with the ash as well as with some of the ash constituents separately which have a tendency to increase eastwards (see p. 84). There are also indications that the sampling within peat layers with a relative "depletion" of some elements could have occurred more frequently in eastern than in western sites (see pp. 71, 100—105).

Vegetational Gradients in Relation to Chemistry of Peat

REGIONAL GRADIENTS. Of the two regional vegetational gradients distinguished (SONESSON 1967 p. 272) the gradient west—east

Table 2. Correlation coefficients between contents of some constituents in surface peat of the upper hummock-levels. Total contents of SiO₂ and ash as mg others as $\mu\text{mol}/10 \text{ cm}^3$ fresh peat, n=40.

	Cu	Fe	Zn	SiO ₂	Mn	Ash	Na	K	Mg	Ca
Al	0.810***	0.677***	-0.103	0.806***	0.090	0.780***	-0.140	0.176	-0.236	0.420**
Cu	—	0.767***	0.013	0.620***	0.088	0.640***	-0.196	0.095	-0.270	0.606***
Fe	—	—	-0.107	0.623***	0.183	0.687***	0.090	0.256	0.014	0.605***
Zn	—	—	—	0.044	-0.081	0.061	-0.046	0.281	0.312*	0.119
SiO ₂	—	—	—	—	0.097	0.869***	-0.123	0.276	-0.081	0.263
Mn	—	—	—	—	—	0.306*	-0.009	0.133	0.115	0.059
Ash	—	—	—	—	—	—	-0.015	0.347*	0.010	0.436**
Na	—	—	—	—	—	—	—	0.293	0.340*	0.026
K	—	—	—	—	—	—	—	—	0.623***	0.235
Mg	—	—	—	—	—	—	—	—	—	0.097

* = 0.05 > p > 0.01; ** = 0.01 > p > 0.001; *** = p < 0.001.

is studied with respect to the chemical conditions of the peat. The data plotted against distance from the sea (Fig. 5) refer to those samples of the upper hummock levels mentioned before (pp. 81—82). These data are accordingly arranged along a west—east transect as well (see Fig. 1). It should be noticed that the distance is measured to the Ofotfjord at Narvik, not to the open sea proper. The sites on the Norwegian side are situated ca. 150 m above sea-level and those on the Swedish side ca. 350—500 m above sea-level.

The contents are calculated both on natural fresh volume basis and on dry weight basis. There is great intralocal variation evident which complicates the interpretation of the results in Fig. 5. The following conclusions and discussions should therefore be regarded as tentative only, awaiting further investigations. These should primarily take into consideration the variation within the separate sites, both horizontally and vertically.

The correlation between the content of elements and distance from the sea is evidently greatly dependant on the calculation basis used. Negative correlations were received for Mg both on dry matter and on volume, for Zn and K on dry matter basis only. According to the present material magnesium decreases by about 3 μmol per 10 cm^3 or 6 μmol per g and 10 km distance. These values differ significantly from zero ($p < 0.001$). Zn decreases by ca. 0.04 μmol ($0.01 > p > 0.001$) and K by ca. 0.6 μmol ($p < 0.001$) per g and 10 km distance. pH decreases by ca. 0.1 unit and 10 km ($0.01 > p > 0.001$), which means more acid conditions in the eastern than in the western hummock-sites. On dry matter there is a tendency towards decreasing contents for Ca ($0.1 > p > 0.05$) and for Na ($0.1 > p > 0.05$) as well.

Positive correlations were received for ash (fresh volume: $0.05 > p > 0.02$) and for Al (fresh volume: $0.02 > p > 0.001$; dry weight: $0.01 > p > 0.001$). When excluding the two highest values on fresh volume a regression coefficient of 0.27 was received for Al ($0.01 > p > 0.001$) corresponding to 2.5 μmol per 10 cm^3 and 10 km distance from the sea. There is a tendency towards increasing contents for Cu on volume basis ($0.1 > p > 0.05$) but not on dry weight basis. No correlation is seen for Mn, Fe or apparent density (=volume weight of fresh peat).

The variation in content of K, Na, Zn and Ca seems to be positively correlated with the variation in organic matter of the peat while Cu and Al are negatively correlated. Although weak, there is a tendency towards higher cation exchange capacity in western than in eastern

hummock peat (see Table 3). The relationship between cation exchange capacity of peat and degree of humification seems to be slight (PUUSTJÄRVI 1956), whereas different kinds of plant remains often mean different exchange properties (PUUSTJÄRVI 1955). No difference in degree of humification is apparent in the present material. However, the humification determination method used is far from being perfect. Different kinds of living plants may have different sorbing qualities as well (cf. BELL 1959). Considering the present material the contents of e.g. Ca and Mg in *Pleurozium schreberi* were 41 and 26 $\mu\text{mol/g}$ dry weight respectively (one sample) whereas in *Dicranum elongatum* 48—86 and 32—68 μmol respectively (three samples, see Figs. 6—8).

Similar regressions for some of the elements in relation to the distance from the sea were received by BOATMAN (1961) working with mires within distances smaller than 20 km from the sea (30 km from open sea) in Southwestern Ireland. According to his results (HCl-leachable amounts) Na decreases by ca. 9 μmol and Mg by ca. 11 μmol per g dry matter and 10 km distance from the sea (ca. 0.2 μmol and 6 μmol in the present investigation area). pH was found to increase with increasing distance from the sea. Fe and K showed no change but Ca a slight tendency to increase with distance. The differences in results are seen mainly in the relatively smaller amounts received in the present investigation area. However, opposite results were obtained concerning pH and Ca.

The concentration of elements in mire water in relation to distance from the sea is discussed by e.g. WITTING 1948, MALMER 1961 and SPARLING 1967.

In the present material there is a variation in some peat constituents which thus parallels the variation in the vegetation of the upper hummock levels along the gradient west—east. Considering the other communities investigated, similar relationships are not seen with certainty in the material.

Comparisons between other areas concerning peat chemistry are often difficult to make due to incomplete descriptions of the vegetation of the sampling sites. Different methods of sampling, storing and analysis are also commonly used which further complicate comparisons.

Some hummock samples from Dalarna in Central Sweden reported by SJÖRS (1961) are referable to a vegetation similar both to the *Calluna-Pleurozium-Sphagnum fuscum* variant and to the *Ledum-Pleurozium* variant of the present investigation area (see Table 3 and

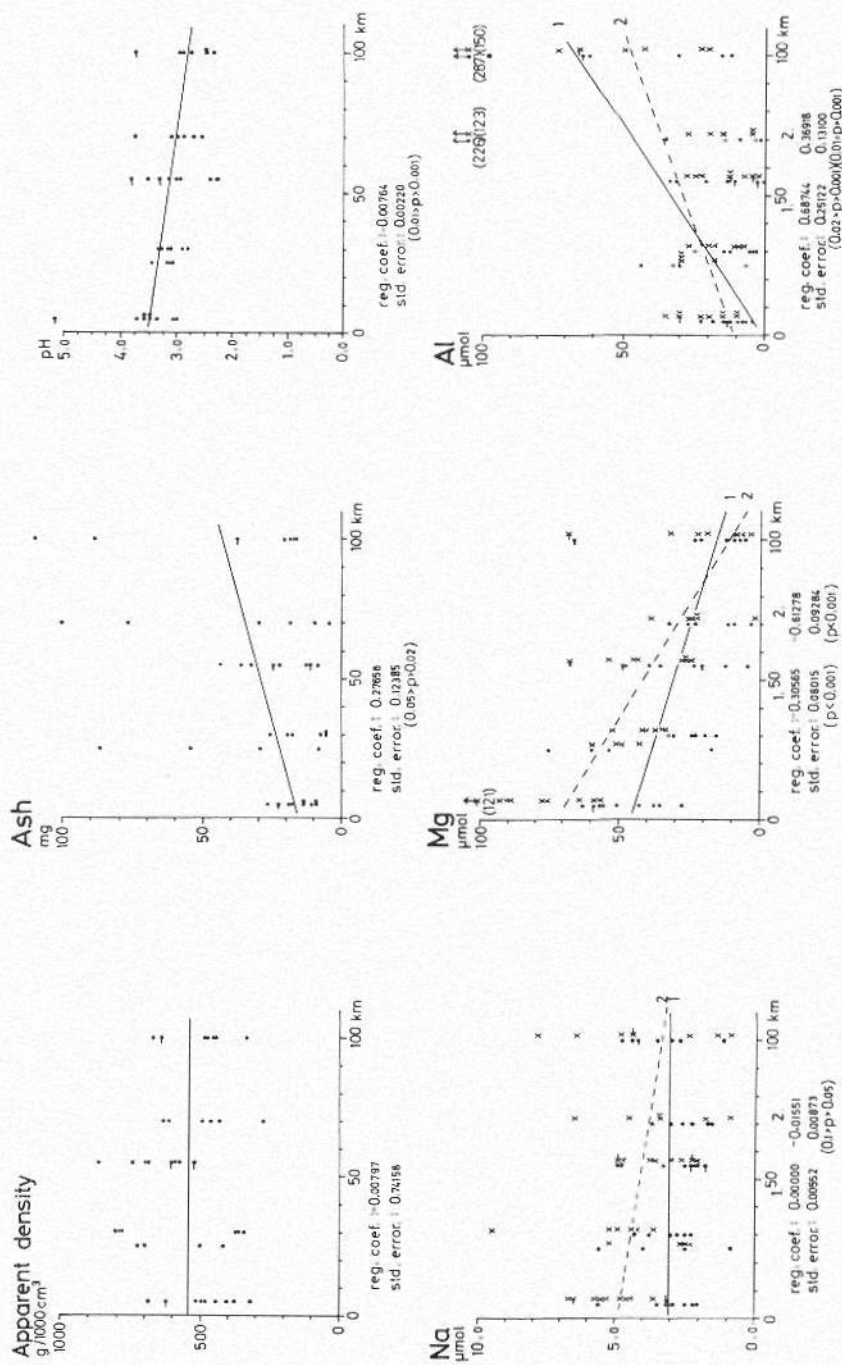


Fig. 5 a.

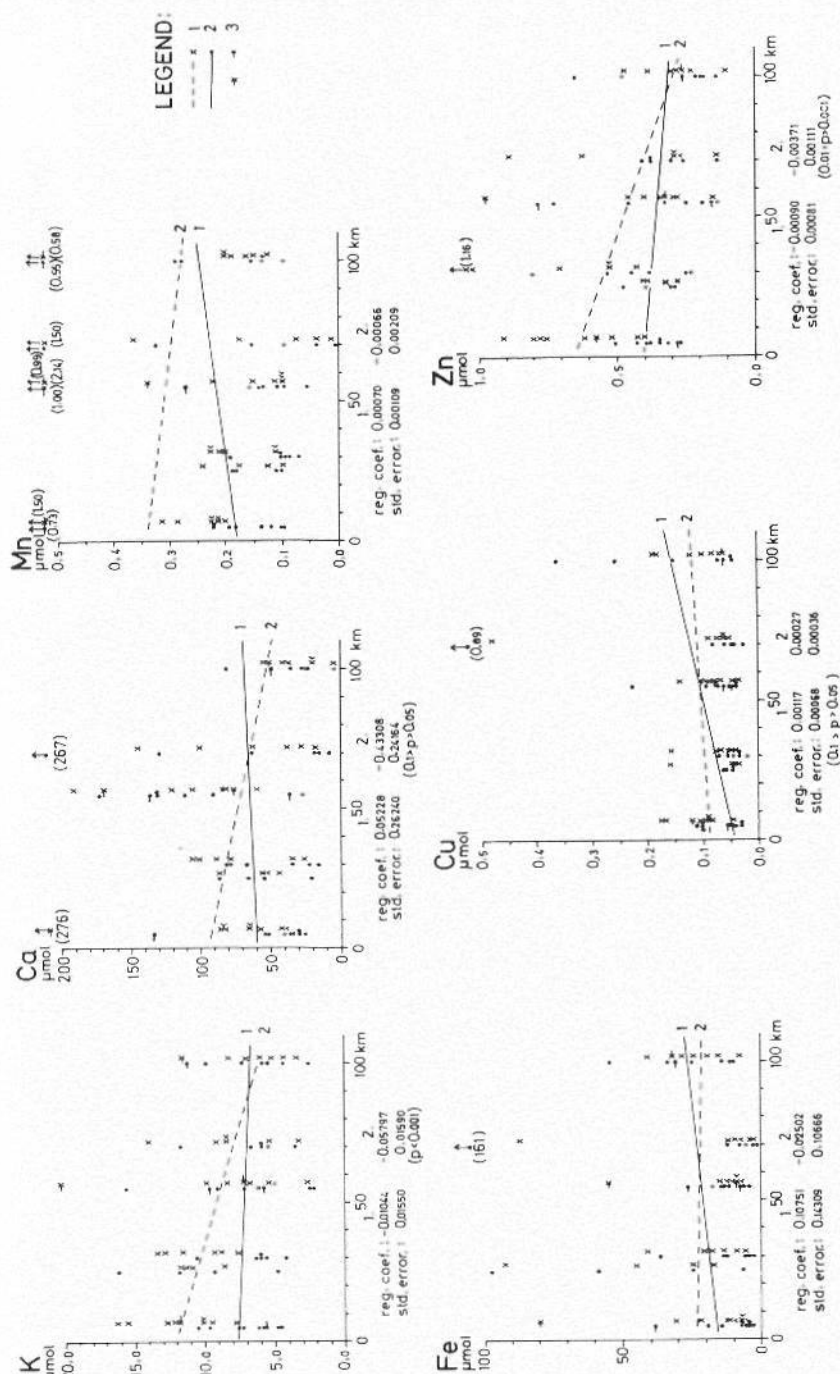


Fig. 5 a-b: Apparent density, pH, total cation and ash contents of surface peat in relation to the distance from the sea (= the Olofjord). The approximate situation and distance are: — Holmvann 5 km, Riksgränsen 25 km, Vassjuaure 30 km, Abisko 55 km, Stordalen 70 km and Tornetråsk 100 km (cf. Fig. 1). Legend: 1. Per g dry matter, 2. Per 10 cm³ fresh peat (N.B. the different numbering in the figures), 3. Fen plants present. Apparent density and pH values refer to the fresh samples. See further in text.

Table 3. Analysis figures of surface peat. Median, range of contents per g dry matter and number of analysed samples shown. The extractable Na, K, Mg and Ca values refer to the NH₄Ac extractable amounts.

Position according to Sjörs 1948, 1950, 1952, PERSSON 1961, SONESSON 1970	Poor vegetation						Intermediate vegetation	Rich vegetation					
	Hummock vegetation			Lawn vegetation					Carpet vegetation	Mud-bottom vegetation			
	Empetrum hermaphroditum - Vaccinium microcarpum association			Carex rot. - Drep. schulzei ass.									
Western communities			Eastern communities			Western communities	Eastern communities	Palud. - Drep. purp. ass.	Scorpidium ass.				
mg, % ₀ , ueq, or umol/g dry matter (Water content % of fresh weight, apparent density g/dm ³ fresh peat)													
Community number	1	2	3	4	5	6	7	8	9	10	11	12	13
Degree of humification (according to von Post's method)	2 1-3 (n=9)	2 1-3 (n=6)	1 1-2 (n=4)	2 1-3 (n=4)	2 2-4 (n=10)	1 1-3 (n=10)	2 1-3 (n=4)	3 3-4 (n=2)	1 1-2 (n=11)	2 1-3 (n=11)	3 2-3 (n=6)	3 2-3 (n=4)	3-3 (n=2)
Apparent density g/dm ³ F.P.	482 320-688 (n=9)	501 321-791 (n=7)	395 277-800 (n=6)	723 522-954 (n=4)	656 414-861 (n=10)	475 273-696 (n=11)	775 664-938 (n=4)	998 992-1003 (n=2)	880 653-1016 (n=11)	973 938-1070 (n=11)	958 827-1097 (n=6)	855 827-1057 (n=4)	951 847-1070 (n=2)
Ash %	2.3 2.0-4.4 (n=8)	2.8 1.1-6.8 (n=7)	2.4 1.0-6.1 (n=6)	5.4 4.1-20.9 (n=4)	4.1 1.4-11.0 (n=10)	2.7 1.1-10.7 (n=11)	3.7 1.3-5.1 (n=4)	6.2 2.8-9.6 (n=2)	3.6 0.6-10.9 (n=11)	8.7 1.9-16.8 (n=11)	19.2 7.0-25 (n=6)	14.0 7.6-20.5 (n=4)	13.5 5.8-21 (n=2)
SiO ₂ mg	7 2-11 (n=9)	7 2-11 (n=6)	9 3-11 (n=4)	37 7-154 (n=4)	22 2-88 (n=8)	9 3-22 (n=10)	31 6-36 (n=4)	26 11-40 (n=2)	10 4-137 (n=11)	21 16-26 (n=2)	146 36-708 (n=6)	96 41-155 (n=4)	93 2-183 (n=2)

Water content %	89	85	89	83	73	86	85	82	83	89	89	89
F.P.	80-92 (n=9)	78-90 (n=7)	82-91 (n=6)	78-87 (n=4)	70-88 (n=10)	79-87 (n=11)	80-88 (n=4)	79-84 (n=2)	75-93 (n=11)	82-95 (n=11)	87-91 (n=6)	87-95 (n=4)
pH direct F.P.	3.5 (n=9)	3.1 (n=7)	3.3 (n=7)	3.6 (n=4)	3.1 (n=10)	3.0 (n=11)	3.1 (n=4)	3.6 (n=2)	3.3 (n=11)	4.1 (n=11)	4.9 (n=6)	4.8 (n=4)
	3.0-3.7 (n=9)	2.8-3.2 (n=7)	3.2-3.5 (n=7)	3.1-3.8 (n=4)	2.3-3.8 (n=10)	2.5-3.8 (n=11)	2.9-3.8 (n=4)	3.6-4.5 (n=2)	2.8-3.6 (n=11)	3.6-4.5 (n=11)	3.3-5.3 (n=6)	4.8-5.7 (n=4)
H ⁺ µeq Ext.	668	897	867	499	812	863	810	547	677	483	253	255
	503-942 (n=7)	783-948 (n=5)	766-1032 (n=3)	360-927 (n=4)	540-870 (n=7)	423-1051 (n=7)	740-889 (n=4)	411-650 (n=2)	518-1612 (n=8)	356-770 (n=11)	213-284 (n=6)	173-638 (n=4)
C.E.C. µeq Ext.	1132	1049	1049	618	—	1063	1009	715	798	759	—	—
	735-1274 (n=4)	—	845-1210 (n=3)	508-1104 (n=4)	—	612-1207 (n=7)	884-1087 (n=4)	569-861 (n=2)	628-1850 (n=8)	601-1126 (n=11)	—	—
N mg Total	9.3	14.2	12.0	13.5	16.5	11.9	18.8	19.1	14.8	17.1	18.3	24.4
	7.1-14.7 (n=9)	8.6-19.3 (n=6)	7.6-18.3 (n=7)	6.9-18.8 (n=4)	8.1-23.0 (n=9)	6.1-21.1 (n=11)	13.4-21.8 (n=4)	15.2-22.9 (n=2)	5.9-20.8 (n=11)	1.7-27.9 (n=11)	8.3-23.6 (n=6)	11.7-36.2 (n=4)
P µmol Ext. (HAc) ..	2.0	—	2.6	2.8	—	1.1	1.4	2.1	1.1	0.7	—	—
	1.0-6.9 (n=4)	—	1.2-3.1 (n=3)	0.4-4.9 (n=4)	—	0.9-4.5 (n=7)	0.6-2.8 (n=4)	1.9-2.9 (n=2)	0.5-3.1 (n=8)	0.4-2.3 (n=11)	—	—
Na µmol Ext.	4	4	—	—	1	—	—	—	—	—	3	3
	3-4 (n=3)	2-6 (n=3)	—	—	1-2 (n=9)	—	—	—	—	—	2-4 (n=6)	2-5 (n=4)
Na µmol Total	6	4	4	4	2	5	3	2	2	3	3	3
	4-7 (n=9)	2-5 (n=6)	3-10 (n=4)	3-6 (n=4)	1-4 (n=10)	2-8 (n=11)	1-7 (n=4)	1-4 (n=2)	1-5 (n=11)	2-4 (n=2)	3-6 (n=6)	2-6 (n=4)
K µmol Ext.	10	8	7	6	5	6	3	2	3	1	4	3
	6-13 (n=7)	5-13 (n=5)	5-7 (n=3)	3-11 (n=4)	2-8 (n=9)	3-14 (n=7)	1-5 (n=4)	2 (n=2)	1-8 (n=8)	1-6 (n=11)	2-6 (n=6)	3-6 (n=4)
K µmol Total	12	11	11	11	6	8	4	4	3	6	32	6
	8-16 (n=9)	8-13 (n=6)	9-13 (n=4)	10-27 (n=4)	3-10 (n=10)	4-20 (n=11)	1-7 (n=4)	3-4 (n=2)	1-9 (n=11)	3-10 (n=2)	12-68 (n=6)	4-11 (n=4)
Mg µmol Ext.	59	29	25	22	15	20	14	32	15	14	25	35
	33-110 (n=7)	16-43 (n=5)	18-30 (n=3)	11-32 (n=4)	1-34 (n=9)	7-51 (n=7)	11-19 (n=4)	7-57 (n=2)	3-33 (n=8)	4-28 (n=11)	14-41 (n=6)	12-60 (n=4)

Table 3. Continued.

Community number	1	2	3	4	5	6	7	8	9	10	11	12	13
Mg $\mu\text{molTotal}$	78 56-121 (n=9)	52 41-59 (n=6)	36 34-47 (n=4)	31 23-43 (n=4)	21 4-44 (n=10)	30 8-68 (n=11)	22 14-24 (n=4)	48 (n=1)	11 7-42 (n=11)	35 32-37 (n=2)	62 54-180 (n=6)	32 12-47 (n=4)	39 32-45 (n=2)
Ca $\mu\text{molExt.}$	49 21-231 (n=7)	53 31-92 (n=5)	42 39-47 (n=3)	46 31-79 (n=4)	54 11-94 (n=9)	32 6-119 (n=7)	46 42-79 (n=4)	31 15-47 (n=2)	53 13-122 (n=8)	39 17-66 (n=11)	178 79-256 (n=6)	111 50-182 (n=4)	237 131-342 (n=2)
Ca $\mu\text{molTotal}$	66 41-276 (n=9)	50 26-101 (n=6)	84 59-106 (n=4)	80 47-128 (n=4)	83 20-151 (n=10)	45 6-190 (n=11)	72 64-109 (n=4)	41 22-59 (n=2)	81 22-124 (n=11)	49 30-67 (n=2)	217 120-356 (n=6)	106 54-225 (n=4)	312 165-455 (n=2)
Fe $\mu\text{molExt. (HAc)}$	0.4 0.2-0.7 (n=7)	0.3 0.2-0.8 (n=5)	0.3 0.2-0.4 (n=3)	1.1 0.3-8.9 (n=4)	0.2 0.1-0.7 (n=9)	0.5 0.3-0.8 (n=7)	1.2 0.1-3.0 (n=4)	0.8 0.8 (n=2)	0.4 0.3-1.8 (n=8)	3.8 0.5-27.2 (n=11)	0.1 0.1-0.4 (n=6)	0.3 0.1-1.5 (n=4)	0.2 0.1-0.3 (n=2)
Fe $\mu\text{molTotal}$	12 8-80 (n=9)	21 6-90 (n=6)	19 13-41 (n=4)	64 34-73 (n=4)	12 8-87 (n=10)	15 1-40 (n=11)	198 27-981 (n=4)	21 15-32 (n=2)	37 5-156 (n=8)	35 7-62 (n=2)	59 26-217 (n=6)	103 53-255 (n=4)	149 77-222 (n=2)
Mn $\mu\text{molExt. (HAc)}$	0.10 0.00-0.64 (n=7)	0.00 0.00-0.82 (n=5)	0.40 0.20-0.82 (n=3)	0.08 0.05-0.15 (n=4)	0.00 0.00-0.10 (n=9)	0.18 0.00-1.01 (n=7)	0.11 0.02-0.27 (n=4)	0.05 0.02-0.08 (n=2)	0.05 0.01-0.11 (n=8)	0.17 0.00-0.31 (n=11)	0.19 0.31-0.07 (n=6)	0.44 1.46-0.05 (n=1)	1.51 0.87-0.36 (n=2)
Mn $\mu\text{molTotal}$	0.2 0.2-1.5 (n=9)	0.2 0.1-0.2 (n=6)	0.2 0.1-0.3 (n=4)	0.6 0.2-0.7 (n=4)	0.1 0.1-0.2 (n=10)	0.2 0.1-2.1 (n=11)	0.4 0.1-0.8 (n=4)	0.4 0.3-0.4 (n=2)	0.2 0.1-0.3 (n=8)	0.7 0.4-0.9 (n=2)	1.7 0.3-4.0 (n=6)	1.1 0.6-1.8 (n=4)	2.5 1.0-4. (n=2)
Cu $\mu\text{molTotal}$	0.10 0.05-0.18 (n=9)	0.05 0.04-0.16 (n=6)	0.07 0.05-0.16 (n=4)	0.12 0.10-0.20 (n=4)	0.13 0.06-0.48 (n=10)	0.09 0.06-0.10 (n=11)	0.15 0.10-0.20 (n=4)	0.14 0.06-0.22 (n=2)	0.08 0.01-0.29 (n=11)	0.10 0.09-0.11 (n=2)	0.60 0.32-0.96 (n=6)	0.31 0.21-1.32 (n=1)	0.30 0.12-0. (n=2)
Zn $\mu\text{molTotal}$	0.62 0.40-0.91 (n=9)	0.46 0.28-1.16 (n=6)	0.62 0.43-0.79 (n=4)	0.14 0.05-0.65 (n=4)	0.30 0.10-0.70 (n=10)	0.29 0.15-0.96 (n=11)	0.25 0.15-0.28 (n=3)	0.08 0.05-0.28 (n=2)	0.08 0.03-0.33 (n=9)	0.23 0.20-0.25 (n=2)	0.64 0.24-0.81 (n=6)	0.34 0.24-0.97 (n=1)	0.28 0.27-0. (n=2)
Al $\mu\text{molTotal}$	20 10-35 (n=9)	24 8-30 (n=6)	19 10-27 (n=4)	77 20-255 (n=4)	39 8-150 (n=10)	20 3-65 (n=11)	83 40-113 (n=4)	87 50-123 (n=2)	28 2-98 (n=11)	29 23-35 (n=2)	276 98-546 (n=6)	131 68-286 (n=4)	117 75-15. (n=2)

SONESSON 1970 p. 43). These samples contain approximately similar amounts of extractable Ca as corresponding samples from the Torneträsk area, even when considering the different calculation bases (loss on ignition - dry matter). MALMER (1962 a) reports lower values from hummock-sites in South Sweden where no species indicating minerotrophic conditions are present. In the peat samples from the "Cladonia series" with *Eriophorum angustifolium* (obligate fen plant according to DU RIETZ 1949, 1954), however, the extractable amounts are similar (about 40 $\mu\text{mol/g}$ D.W.). The "Cladonia series" of communities are best related to the *Calluna - Pleurozium - Sphagnum fuscum* variant (see MALMER 1962 a p. 99, cf. also MALMER & SJÖRS 1955). HOLMEN (1964 p. 165) mentions similar total amounts of Ca to those shown for the Torneträsk area in peats of a partly drained and cultivated mire. These peats refer to "community no. I" which bears some resemblance to the eastern *Ledum - Pleurozium* variant. BELLAMY and RIELEY (1967) reports a total Ca content of approximately 40—70 $\mu\text{mol/g}$ D.W. in peat close to the surface of a *Sphagnum fuscum* hummock in Westmorland, England. The vegetation described is closely related to the *Calluna - Pleurozium - Sphagnum fuscum* variant. All the communities used in this comparison are regarded as ombrotrophic or very poor minerotrophic communities by the authors.

The molar Ca/Mg quotient of peat is often used as an index of the degree of ombrotrophy, being lower than 1.0 in true ombrotrophic sites (see discussions on pp. 106—107). From Fig. 2 D is seen that Mg in excess of Ca was obtained in western sites. However, a few samples referable to the higher levels of the eastern sites show similar values as well.

LOCAL GRADIENTS. Poor—rich. The amounts of Ca, Mn, Cu, Al, ash and SiO_2 are correlated with this gradient. See Table 3. Higher quantities are obtained in peat of the richer communities than in the poorer ones. Acidity also shows a close relationship. However, as shown before (pp. 81—82) at least some of them do not vary independently. The range within each community along the gradient is wide and sometimes possible to relate to other gradients, especially west—east and hummock—mud-bottom (see below). The differences along the gradient poor—rich are still greater when considering the values calculated on a volume or an organic matter basis. This would then result in higher values for the communities with a high content of ash, viz. the richer communities. Data for corresponding poor communities on the northern side of Lake Torneträsk (PERSSON 1962 pp. 66—69) are

similar to those shown here. Considering the intermediate vegetation ("*Calliergon sarmentosum* - *Paludella* vegetation") the extractable amount of Ca in peat is higher (median ca. 250, total range 90—415 μmol per g D.W., $n=19$). The two values reported from the most closely corresponding association to that of Table 3, the "*Calliergon sarmentosum* - *Paludella* association" amounts to approximately 130 and 350 μmol . The vegetational differences along this gradient between intermediate communities on the northern side of Lake Torneträsk according to PERSSON 1961 and 1962 and those investigated in the present investigation area obviously have a parallel in the difference in the amount of Ca (see SONESSON 1970 p. 75). From rich carpet vegetation, referred to the *Scorpidium* vegetation, PERSSON reports Ca values approximately 220—480 μmol ($n=3$) which are slightly higher than those of the mud-bottom variant presented in the table and belonging to the same association.

A close relationship between pH and communities along the gradient poor—rich is obvious. Considering the material sampled during 1960—63 (see p. 74, cf. also values in Table 3 and in Fig. 3) the median value in peat of the *Carex rotundata* - *Drepanocladus schulzei* vegetation accordingly amounted to 4.2, total range 3.6—5.1 ($n=52$), in *Sphagnum riparium* vegetation to 4.8, total range 4.4—4.9 ($n=3$), in *Paludella* - *Sphagnum teres* vegetation to 4.9, total range 4.3—5.8 ($n=63$), in *Drepanocladus procerus* vegetation to 5.0, total range 4.7—5.2 ($n=22$) and in *Scorpidium* vegetation to 5.5, total range 4.8—6.3 ($n=33$).

Hummock—mud-bottom. The variation in contents of in particular Mn, Fe, SiO_2 , Al and ash runs parallel with this gradient as well as with the preceding one. This means that the contents are greater in peat of the richer communities as well as in communities of the lower levels in the sites, even the poor ones. The amount of Zn in peat is higher in western poor sites as well as in peat of the higher levels of such sites in the whole area. Peat of the lower hummock levels and peat of the communities usually occurring in depressions of the hummock-sites contains only about one half to one quarter as much Zn. There is a tendency towards low values in the intermediate—rich mud-bottom sites as well. Relatively large amounts are present in the peat of the intermediate carpet vegetation, however. These differences shown may be due to a varying solubility related to the obvious differences in acidity of the peat (cf. WEAR 1956). The high Zn values in the intermediate carpet peat are puzzling but may be due to the small number of samples.

Elements in Precipitation and in Peat

There are obvious differences between Riksgränsen and Kiruna considering the relative molar amounts of Na and Mg in precipitation (Table 4). At the former locality the Na/Ca quotient is 2.4 while 0.8 at the latter. The Mg/Ca quotients are 0.5 and 0.3 respectively. The relative amounts for K and N are similar at the two localities. There seem to be similar concentrations of Ca and K both at Riksgränsen and at Kiruna when calculated as annual mean; Ca is possibly a little higher at Riksgränsen; however, for Mg and Na about twice and three times the concentrations respectively are recorded at Riksgränsen. Approximately similar values are evident for Ca and K throughout the year at the two localities. However, the concentration of Na and Mg is lower during the growth period especially at Riksgränsen. This indicates a larger amount of sea salts (ERIKSSON 1959 pp. 7—12) during autumn, winter and spring than during summer (cf. SPARLING 1967 p. 4).

However, the total annual supply of elements does not derive from precipitation only. For some elements the contribution from dry deposition may be more than twice as much as that from precipitation (ERIKSSON 1959 pp. 45—48, cf. TAMM 1953 p. 91 and MALMER 1961 pp. 140—142). Even when considering the total annual amounts derived from precipitation only (Table 4) they may not be closely representative of all sites investigated. This is especially apparent for the sites of the Abisko valley where the mean annual precipitation is less than 300 mm (see SONESSON 1970). Also, amounts calculated per mm precipitation may not be strictly proportional due to different wind velocities and different sizes of the particles (ERIKSSON 1959 pp. 22—28, cf. ALLEN et al. 1968 p. 501).

The peat samples used for comparison are those of the higher levels of the hummock-sites mentioned before (pp. 81—82). In western samples the Na/Ca and K/Ca quotients are about the same or only slightly higher than in the eastern samples, while the Mg/Ca quotient is about twice as high in western than in eastern samples.

There are no differences apparent in content in peat of K and Ca when calculated on fresh volume basis but there are increasing contents towards the west apparent when calculations are made on dry weight basis (see p. 84). A tendency of a similar western increase is also seen in precipitation concentration of Ca but not of K (see above).

There seems to be a fairly close relationship between the concentration in peat and in precipitation concerning Mg and Ca but not for

Table 4. Concentration of some elements in precipitation and in surface peat. Pre-precipitation values are annual means as well as means for the growth period calculated from data for the period 1955—1962. The annual amounts are extrapolated. Peat samples refer to samples collected in 1963 and 1969 from the upper levels in some hummock sites. See further in text, pp. 70, 81—82.

	Na		K		Mg		Ca		N						
	g D.W.	cm ³ F.P.	g D.W.	cm ³ F.P.	g D.W.	cm ³ F.P.	g D.W.	cm ³ F.P.	g D.W.	cm ³ F.P.					
In Precipitation															
RIKSGRANSEN (939 mm/year)															
Mean $\mu\text{mol}/\text{m}^2/\text{year}$	32200		3200		6200		13400		5300						
Mean $\mu\text{mol}/\text{mm precip.}/\text{m}^2/\text{year}$	34		3		7		11		6						
Relative values (Ca=1.0)	2.4		0.2		0.5		1.0		0.4						
Mean $\mu\text{mol}/\text{m}^2/\text{June}$ —September	4700		700		1200		3100		1700						
Mean $\mu\text{mol}/\text{mm precip.}/\text{m}^2/\text{June}$ —September	17		3		4		12		6						
Relative values (Ca=1.0)	1.4		0.2		0.4		1.0		0.5						
KIRUNA (513 mm/year)															
Mean $\mu\text{mol}/\text{m}^2/\text{year}$	1900		2000		1900		6000		2200						
Mean $\mu\text{mol}/\text{mm precip.}/\text{m}^2/\text{year}$	10		4		4		12		4						
Relative values (Ca=1.0)	0.8		0.3		0.3		1.0		0.4						
Mean $\mu\text{mol}/\text{m}^2/\text{May}$ —September	1900		900		700		3100		1200						
Mean $\mu\text{mol}/\text{mm precip.}/\text{m}^2/\text{May}$ —September	7		3		2		11		4						
Relative values (Ca=1.0)	0.6		0.3		0.2		1.0		0.4						
In Peat															
WESTERN COMMUNITIES															
Means of medians															
(three communities) μmol	5	3	11	6	8	5	55	38	22	67	50	48	26	850	600
Relative values (Ca=1.0)	0.1	0.1	0.2	0.1	0.2	0.2	0.8	0.8	0.8	1.0	1.0	1.0	1.0	12.7	12.0
Number of samples	19	19	19	19	15	15	19	19	15	19	19	15	15	22	22
EASTERN COMMUNITIES															
Means of medians															
(two communities) μmol	4	3	7	7	5	6	25	22	18	16	64	65	43	1000	900
Relative values (Ca=1.0)	0.1	0.1	0.1	0.1	0.1	0.1	0.4	0.3	0.4	0.3	1.0	1.0	1.0	15.6	14.1
Number of samples	21	21	21	21	16	16	21	21	15	21	21	15	15	22	22

Na, K and N. The K and probably also Na contents in peat (on dry weight basis) are better related to the differences in total annual amounts. N in peat seems to be unrelated to the concentrations as well as to the total annual amounts. The high N values in eastern peat are thus correlated with a low concentration and a low total annual amount from precipitation.

A close relationship between the total annual amounts from precipitation and contents in peat would be apparent for copper since this element is likely to be sorbed almost quantitatively (COLEMAN et al. 1956, RÜHLING & TYLER 1970). However, as seen on p. 84 copper contents have a slight tendency to increase eastwards. The supply by dust of this element is probably greater than that by precipitation. This would accordingly be one indication of a contribution to the mires other than that by precipitation only.

Even supposing an annual peat production of about $1 \text{ dm}^3/\text{m}^2$ as reported from South Sweden (NILSSON 1964 p. 25, see also DURNO 1961) the heavy loss of nutrient derived only from precipitation by run-off (except N) is obvious, this loss being greater in the west than in the east. However, there are evidences of a much smaller hummock peat formation in the Torneträsk area, probably less than $0.5 \text{ dm}^3/\text{m}^2$ and year (see next section, p. 104). Supposing such an annual peat production the great deficit in N supplied by precipitation solely is striking. Such a deficit may, to a large extent, be satisfied by an influx of ammonia directly from the air (TAMM 1953 p. 94, MATTSON et al. 1955 pp. 323—324). Some contribution of animal origin may also be possible (see OSVALD 1925 p. 74, NORDHAGEN 1927—1928 p. 362, MATTSON et al. loc. cit., SONESSON 1970 pp. 19, 22).

Stratigraphy of some Sites

Introduction

The peat profiles shown here (Figs. 6—8) are from Vassijaure, Abisko and Stordalen, respectively. The Abisko site is situated in the central part of the investigation area characterized by soft bedrock and soils rich in calcium while the other two are from parts with hard silicious bedrock and soils poor in calcium. The peat types distinguished correspond to different peat-forming communities. The reconstruction of these is made with aid of the plant remains of the peat. They are named after those present-day communities which they

most closely resemble floristically thereby assuming that they have modern equivalents. No differences are ever seen in the appearance of the macrofossils in relation to corresponding modern plants. The stratigraphical border between the living plant cover and the peat is seldom possible to determine with a high degree of accuracy. The living bryophyte layer is probably only a few centimetres in height whereas most of the living roots of the vascular plants obviously are situated within 30 centimetres level of the bryophyte surface.

The dynamical implications of these profiles will be treated in a future paper (SONESSON in prep.) where also details of these and other profiles will appear. Here only short descriptions will be presented.

Description of the Profiles

V a s s i j a u r e. The profile was located near the middle of a small hummock-site earlier described (SONESSON 1970 p. 94, Figs. 16 A and 17 a—b, near point "71"). The main bryophyte components are indicated in Fig. 6. No remains of exclusive fen plants were found above the 60 cm level. The peat between 70 and 80 cm below the surface (no. 5) was composed of bark and wood, probably of dwarf shrubs, and remains of grass-like species (shoots and leaves of *Carex* species? — cf. the high *Cyperaceae*-pollen frequency immediately above this layer). Sclerotia of *Coenococcum graniforme* were also found. The peat between 120 and 145 cm (no. 7) contained mainly rootlets of *Carex* species and, to a minor extent, also remains of *Equisetum fluviale*. At 105 cm below the surface the lowest finds of apparently living roots were seen. The colour of the peat varied between light yellow and dark brown except between 53 and 60 cm where the peat was blackish and of an amorphous structure with abundant ericaceous twigs. This was the only layer with apparently highly decomposed peat. The remains of bryophytes were sparse but well preserved. Other peat seemed to be only slightly decomposed. The water content was lower than normal. It was not determined in this profile. The contact with the mineral ground (silt and sand) was sharp. No gyttja was seen. The present-day community is: 0. *Empetrum hermaphroditum* - *Vaccinium microcarpum* association: *Vaccinium myrtillus* - *Pleurozium* variant (no fen plants present). The (other) peat-forming communities distinguished are: 1. —27 cm, *Empetrum hermaphroditum* - *Vaccinium microcarpum* association; 2. 27—40 cm, *Carex rotundata* - *Drepanocla-*

dus schulzei association; 3. 40—62 cm, *Empetrum hermaphroditum* - *Vaccinium microcarpum* association; 4. 62—70 cm, *Paludella* - *Sphagnum teres* vegetation; 5. 70—80 cm, dwarf shrub community, probably intermediate; 6. 80—119 cm, *Paludella* - *Sphagnum teres* vegetation; 7. 119—147 cm, *Carex* dominated community; 8. 147—198 cm, *Scorpidium* association.

Abisko. The profile was located near the margin of a big hummock-site, perennially frozen, described earlier (SONESSON 1970 p. 96, Fig. 18 a—b, below point "100", see also SONESSON 1969 Fig. 2 B—C). It reached about half-way down towards the mineral ground. The pollen profile has been published earlier (SONESSON 1968 Fig. 2). The main bryophyte components are indicated in Fig. 7. No remains of exclusive fen plants were found above the 50 cm level (cf. also the high *Cyperaceae*-pollen frequency there). Apparently living roots were not seen below the 30 cm level. The colour of the profile was light brownish, but darker thin strata were seen in the upper, unfrozen level. The present-day community is: 0. *Empetrum hermaphroditum* - *Vaccinium microcarpum* association: *Dicranum elongatum* - *Sphagnum fuscum* variant (no fen plants present). The (other) peat-forming communities distinguished are: 1. —75 cm, *Empetrum hermaphroditum* - *Vaccinium microcarpum* association; 2. 75—90 cm, "*Sphagnum warnstorffianum* - *parvifolium* association" (PERSSON 1961); 3. 90—150 cm, *Scorpidium* association; 4. 150—180 cm, *Empetrum hermaphroditum* - *Vaccinium microcarpum* association.

Stordalen. The profile was located near the margin of a big hummock-site, perennially frozen, described earlier (SONESSON 1970 pp. 96—104, Fig. 19 a—b, below point "40"). It reached about half-way down towards the mineral ground. The main bryophyte components are indicated in Fig. 8. Exclusive fen plant remains were apparent near the surface (*Calliergon stramineum*). The peat between 48 and 93 cm below surface was composed mainly of wood, bark (*Betula*-bark abundant) and remains of grass-like plants (*Carex*? — cf., however, the low frequency of *Cyperaceae*-pollen). Between 93 and 130 cm the peat was composed mainly of *Carex* remains (leaves, rootlets and utricles) but also of stems of *Equisetum fluviatile* and leaves of *Calliergon sarmentosum*. The colour of the profile was greyish-brown except at the level of the frost table where it was blackish brown. The present-day community is: 0. *Empetrum hermaphroditum* - *Vaccinium microcarpum* association: *Cetraria nivalis* - *Dicranum elongatum* vari-

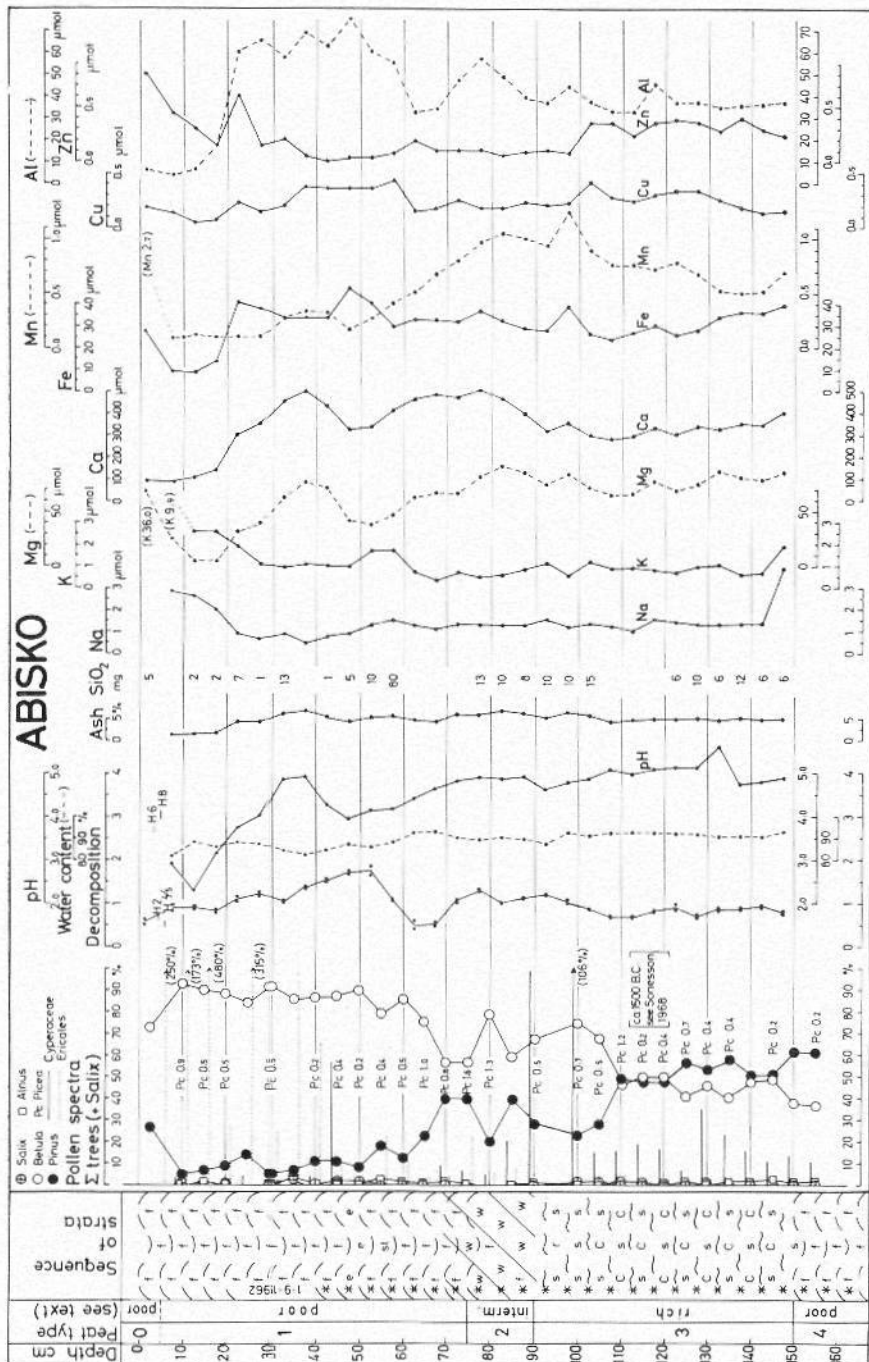


Fig. 7. Stratification of site at Abisko. Total contents of elements are expressed as µmol or mg per g dry matter. Legend in Fig. 8.

ant (no fen plants present). The (other) peat-forming communities distinguished are: 1. —48 cm, *Carex rotundata* - *Drepanocladus schulzei* association; 2. 48—93 cm, fen vegetation with birch in the tree or shrub layer; 3. 93—130 cm, intermediate community probably referable to the *Drepanocladus procerus* vegetation or to some magnocariceta; 4. 130—138 cm, ditto, but may also be referable to the *Paludella* - *Sphagnum teres* vegetation; 5. 138—185 cm, *Scorpidium* association.

Results and Conclusions

Considering the calcium contents, the peat corresponding to the poor *Empetrum hermaphroditum* - *Vaccinium microcarpum* association in the Abisko profile (no. 1) shows a median calcium value (355 μmol , range 83—505 μmol) exceeding those received in peat of present-day rich mire communities (Table 3). In Vassijaure such peat (no. 3) shows values only slightly higher (median 93, range 86—106 μmol) than those received in the corresponding living community. Peats corresponding to the poor *Carex rotundata* - *Drepanocladus schulzei* association (Vassijaure no. 2, Stordalen no. 1) and to the intermediate *Paludella* - *Sphagnum teres* vegetation (Vassijaure nos. 4 and 6) show higher and lower values respectively, in relation to the modern conditions. The three total values referable to "*Sphagnum warnstorffianum* - *parvifolium* association" (PERSSON 1961) in the Abisko profile (no. 2) are more than 50% higher (median 467, range 399—502 μmol) than the two extractable values given by PERSSON 1962 (ca. 180 and 260 μmol per g D.W.). The calcium content of peat corresponding to that of the rich *Scorpidium* association was much lower in Vassijaure (no. 8) but about equivalent to the present-day values in Abisko (no. 3).

Considering the other constituents analysed, the median contents of K are smaller in peats below the 30 cm level than in peats of the modern communities, Na contents are fairly similar but those of other constituents show dissimilarities to modern conditions.

The depth for peat sampling in relation to the bottom layer of the living plant cover never exceeded 30 cm. Usually it was less than 20 cm (see p. 71). This range is certainly reduced during the fossilizing process. Even taking such a stratification into consideration the hypothetical mineral status of the peat-forming communities usually differs much from what is normal for their present-day equivalents. Properly speaking the mineral status should be compared with that in

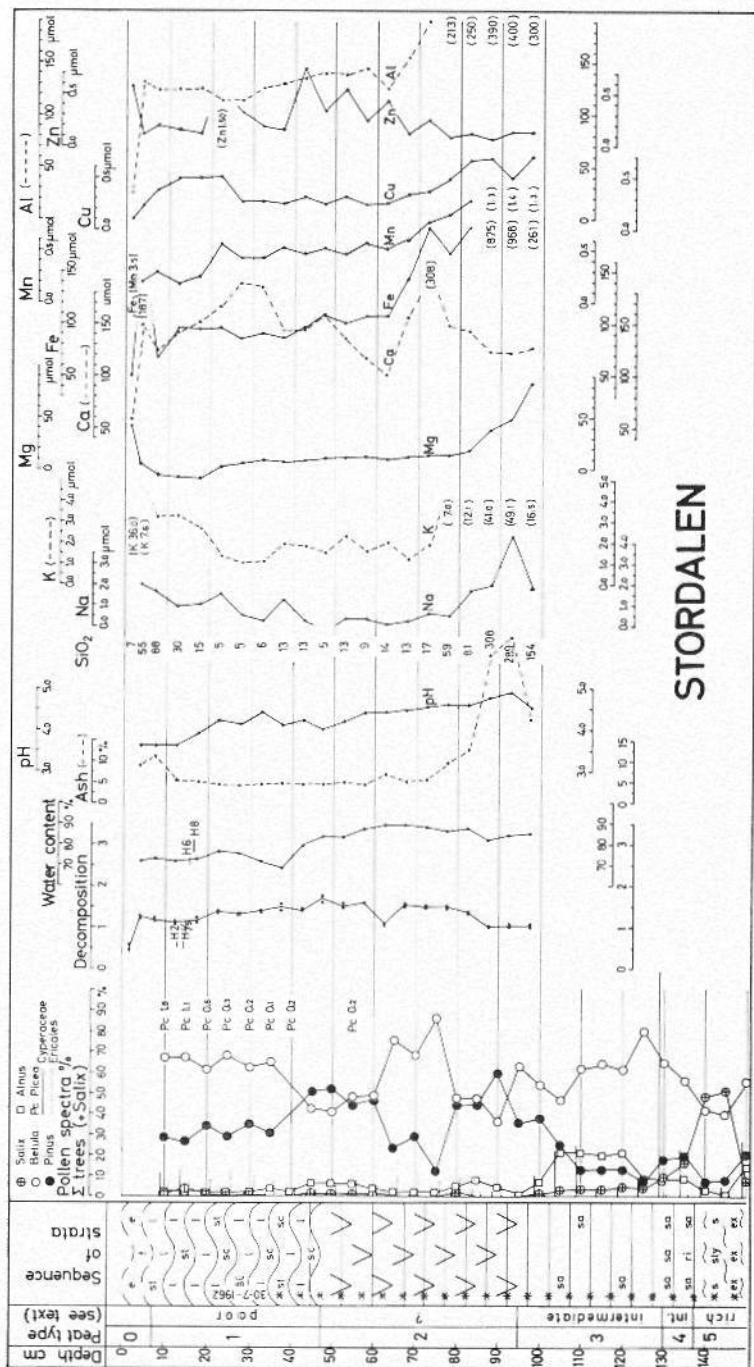


Fig. 8. Stratification of site at Stordalen. Total contents of elements are expressed as μmol or mg per g dry matter. Legend: C = *Calliergon trifarium*, c = *Dicranum cf. elongatum*, ex = *Drepanocladus exannulatus* var. *purpurascens*, f = *Sphagnum fuscum*, l = *Sphagnum lindbergii*, P = *Paludetia squarrosa*, Pl = *Pleurozium schreberi*, r = *Drepanocladus revolvens*, ri = *Calliergon cf. richardsonii*, s = *Scorpidium scorpioides*, sa = *Calliergon sarmentosum*, sc = *Drepanocladus cf. schulzei*, st = *Calliergon stramineum*, sty = *Cinclidium stygium*, t = *Sphagnum teres*, w = *Sphagnum warnstorffii*, * = frost.

living plants as well, since there are probably great differences concerning some constituents in relation to the condition in peat (see KIVINEN 1933, MALMER & SJÖRS 1955, MALMER 1958, 1962 b, BELL 1959). However, the superficial samples probably contain much living matter as well which render them to some extent intermediate between those of the peat proper and the living plant cover. This would make the comparisons more justified.

The comparisons made show either that quite different nutrient conditions for the peat-forming communities in comparison with modern conditions once prevailed or that great changes in peat chemistry have occurred during the development of the sites. So many different ecotypes/physiological races with ecologic conditions deviating so greatly from their present-day equivalents, now extinct 8000 years ago or less, seem improbable. The great changes are more likely to be secondary, with the exception of those of the superficial peat.

The most obvious changes in the cation content are seen in the minerogenous strata, at the mineral ground, at the frost table (in the eastern profiles) and in the superficial layers. Such changes may have arisen in different ways: —

1. The addition from the environment can have been altered, e.g. by flooding of water rich in electrolytes or by an increased supply of air-borne matter. Such an altered addition may arise if the climatical conditions change. According to the present material the great chemical changes are apparently not related primarily to the great changes in the pollen spectra nor to the great changes in the peat types of the sites. This is especially apparent in the profile of the Abisko site (see also Fig. 2 in SONESSON 1968). This is situated close to a minerotrophic site partly covered with rich mire vegetation (SONESSON 1970 Fig. 18 a—b). An obvious rise in the level of the subsoil water table more than 3500 years ago resulted in a flooding of the poor hummock peat (no. 4). Half a metre of rich fen peat was then produced (no. 3). This stratigraphical change took place at the end of pollen zone T 3, viz. at the end of a period with a relatively continental climate (SONESSON 1968, 1970 p. 18). The high calcium values near the permafrost table in the Abisko site (about 300—500 μmol) have smaller equivalents in Stordalen (about 150—200 μmol) and in Torneträsk (30—60 μmol). This changed course of the Ca curves (as well as in Mg but not in e.g. K) is allied to obvious changes in the pollen spectra and in the macrofossil content in Stordalen but not in Abisko (not investigated in Torneträsk). The peat-forming community no. 1 in Stordalen was

wet-growing but whether more wet-growing than the preceding one (no. 2) is uncertain. If there has been a flooding of these frost table layers too it must have been of a short duration in the Abisko site since any evidence of wet-growing communities above ca. 70 cm level is not found. Some of the changed course may also be the result of a rising frost table altering the concentrations of elements in peat water and drainage water. The lower strata will then successively be incorporated into the frozen peat. A precipitation of colloidal matter in the water (cf. MALMER 1963, INGRAM 1967) due to freezing and or a changed redox potential may also be possible. This would increase the exchange capacity of the peat. An increased decomposition due to repeated thawing and freezing (regelation) seems probable too. However, the relationship between the extinction values for NaOH soluble matter in the peat and the cation contents is not very close and is in some cases ambiguous (see e.g. the Abisko profile: level 30—70 cm). The possibility of some addition through migration of small mineral particles in the peat can not be excluded (cf. ROWLEY & ROWLEY 1956) but such a contribution is probably slight only (GODWIN 1934).

The superficial changes in Vassijaure (Fig. 6) may be due to a previous temporarily increased influence of water (cf. peat type no. 2) but these changes are quite obvious even below the highly decomposed layer between 53 and 60 cm (see further below).

The hydrographical conditions of a mire may be altered due to dynamical changes within the mire vegetation without a corresponding regional change (POST & SERNANDER 1910). However, there are more obvious signs of flooding also in the lower strata of some profiles investigated indicated by the abundance of mineral soil (sand—gravel) within limited strata. This was seen for example in the profiles at Stordalen (see SONESSON 1970 Fig. 19 a—b) and in some profiles of sloping fens from the northern side of Lake Torneträsk (unpublished). It is possible that some of the strata discussed are synchronous indicating regional hydrological changes. The superficial increase in several of the curves evident in all profiles is related to the same pollen zone (T 4) but it obviously begins at different times during this period.

There is no certain evidence of a changed supply of air-borne matter in the present material. The Mg/Ca, K/Ca and Na/Ca quotients are most similar to modern conditions (see Table 3) in layers close to the surface and in those rich in (secondary) ash. In other layers they are usually lower, which is most likely due to secondary alterations in the contents. On the whole the Na/Ca quotients are highest throughout

the whole profile in the westernmost site investigated (cf. BOATMAN 1961).

The ash content of the two eastern profiles below the surface is high throughout (as is also evident in the unpublished Torneträsk profile), much higher than that reported for ombrotrophic peat, e.g. from South Sweden (see MATTSON et al. 1955, OLAUSSON 1957, ASSARSSON 1961, MÖRNSJÖ 1968). Some of it is probably due to a previously higher contribution of secondary ash, since low peat production and decomposition (see further below) alone are obviously insufficient to explain the high content. Neither is there any evidence of great differences in decomposition of the superficial peat layers. At least some of these high ash and aluminium contents may be due to flooding rather than to an altered supply of air-borne matter.

2. The addition from the environment can have been unchanged even although there has been an unequal peat production during the development of the site. In the Vassijaure profile the average annual peat accumulation between 80 and 120 cm (no. 6) amounted to 0.7 mm. The content of many elements in this peat is also relatively low. The obvious increase in the upper peat layers is allied to a much smaller annual peat accumulation (about 0.2 mm). Some of the lowest values of the profile are apparent in layer no. 7 which has a similar low accumulation. However, contents only related to the quantity per unit of time from environment are not probable (cf. pp. 93—95).

3. Differences in the degree of humification may also have been important during the development in affecting the mineral content of the peat. However, in the layer between 53 and 60 cm in the Vassijaure profile, which obviously is highly decomposed, a correspondingly great alteration in content is not obvious. Neither is any alteration in ash content evident. The course of the Cu-curve is especially instructive. Of the divalent elements investigated copper is likely to be retained most strongly by the colloids (COLEMAN et al. 1956, RÜHLING & TYLER 1970).

4. A great mineral content may arise in peat where living organic tissues present have sorbed the elements from adjacent peat (see MATTSON et al. 1944 p. 105) and or directly from the atmosphere. This is probably the main reason for the increasing contents in the superficial layers. Much of the elements essential for the living organisms, e.g. K, Mg, Ca, Mn and Zn, are continuously retained in such peat (possibly also elements such as Na, cf. GOODMAN & PERKINS 1959 p. 467). A capillary transport of the components in the peat (ASSARSSON 1961)

as well as in the plant cover (MALMER 1962 b) may be of importance too. This superficial increase is obvious above the 20 cm level in the eastern sites but as low as at ca. 75 cm in the western, which approximately corresponds to the differences in root depths found (pp. 96—98). The frost table is usually situated between 30—50 cm in the eastern hummock-sites but normally no frost is present in the western ones during summer (see SONESSON 1970 pp. 31—35). The hummock communities of the eastern and the western hummock-sites are usually different (SONESSON *op. cit.*).

The Gradient Ombrotrophy—Minerotrophy in the Investigation Area

It seems improbable that the elevated parts of most of the eastern hummock-sites nowadays are influenced by free water other than precipitation water normally. A free water table on the frost table of such structures has not been observed other than temporarily after prolonged rain and as an obviously secondary result of previous digging. Influence of minerotrophic subsoil water is more possible on many western hummock-sites since they are unfrozen and often occupy a lower position than the adjacent terrestrial sites. The occurrence of obligate fen plants is more abundant in western than in eastern hummock-sites. Whether such plants are always related to minerotrophic conditions in the substrate is unknown, however, since there is a lack of investigations into the distribution along the gradient ombrotrophic—minerotrophic sites in Northern Fennoscandia.

However, temporary minerotrophic conditions of the present-day bog vegetation of the upper levels in some of the eastern sites may result during years when the frost table is lowered more than normal. This is likely to occur during unusually cool and rainy summers when an altered thermal diffusivity of the superficial peat cover would result. During the period in which these poor mires have been studied (since 1960) a considerable variation in weather has been experienced. However, any consistent change in the usual position of the frost table has never been apparent. Thus depths to the frost table exceeding 50 cm in the elevated structures of such sites have been measured only rarely (normal range during growth period 30—50 cm, see SONESSON 1970 p. 31). Most of the subterranean parts of the mire communities are obviously located at a level less than 30 cm below surface. Sparse, apparently living roots were, however, often found in the cores close to and below the frost table in the eastern sites, in

a few cases as deep as 70 cm (SONESSON 1970 p. 30). Much deeper occurrence was observed in the western unfrozen sites (cf. e.g. p. 96 in this paper).

When deducing whether the conditions in the sites are functionally ombrotrophic or minerotrophic to the plant cover neither the floristic composition of the present-day community nor that of the underlying peats would give conclusive evidence in all cases (cf. SONESSON 1970 pp. 27—31, 38, 74—79). A similar discrepancy between the floristic composition and chemistry of the peat was also obvious in Northern Finland (KIVEKÄS & KAILA 1957) and in South Sweden (MÖRNSJÖ 1968).

The Ca/Mg quotients (on equivalent basis) are often discussed as an index of ombrotrophy—minerotrophy, being less than 1.0 in true ombrotrophic sites (see e.g. MATTSSON et al. 1944, BOATMAN 1957, OLAUSSON 1957, SJÖRS 1961, MÖRNSJÖ 1968). The low ratios are considered to be related to a correspondingly low ratio in the salts supplied by precipitation (MATTSON et al. 1955 p. 323). However, Ca/Mg quotients of ombrotrophic peats lower than 1.0 are also recorded from the interior of Fennoscandia (see e.g. MALMER 1962 a and MÖRNSJÖ 1968) where the equivalent of Ca has been in excess of Mg in precipitation as long as continuous recording of chemical data of precipitation has been carried out (since 1955, cf. p. 70). Such relationship of precipitation may be a recent phenomenon only due to an enrichment of calcium from human activities (cf. e.g. MATTSON et al. 1955 p. 364) but may also be a primary condition. A great excess of air-borne Mg from dust in these parts of Fennoscandia seems less probable.

The presence of constituents in ombrotrophic peat which are common in mineral soil has been widely discussed mainly as a result of the often obvious greater ash content of the surface peat than in lower strata. It may be due to the contribution from the terrestrial surroundings by air-drift. This contribution is supposed to have increased recently. However, since some of these constituents are important in living tissues, they may be retained continuously by e.g. the plant cover too, and are not or are only slightly incorporated in the peat proper. This would also explain some of the increase towards the surface. As pointed out by HOLMEN (1964 p. 175): “. . . the air-borne matter must be important because most of the ash is composed of silica and aluminium compounds, which probably cannot reach an ombrotrophic site in considerable quantities in any other way than through the atmosphere . . .”. Obviously both possibilities should be taken into consideration. See POST 1925, MALMER & SJÖRS 1955, MATTSON et al. 1955, KAILA & KIVEKÄS 1956, OLAUSSON 1957, ERIKSSON 1959, ASSARSSON 1961, MALMER 1962 b, CHAPMAN 1964, BELLAMY & RIELEY 1967, MÖRNSJÖ 1968.

Ca/Mg quotients lower than 1.0 are rarely measured in surface peats of the investigation area except in the westernmost sites (Table 3, Fig. 2 D). Considering the present chemical stratigraphical material all quotients investigated exceed 1.0 also in such peat which obviously is ombrotrophic, judging from its floristic composition as well as its altitudinal position in the sites. The lowest ratios were always recorded in the superficial peat samples.

It is shown that Ca/Mg quotients are different in living and in dead *Sphagna* or peat and that there are differences between the species in this respect (ANSCHÜTZ & TESSNER 1954, MALMER & SJÖRS 1955, PUUSTJÄRVI 1955, 1956, KIVEKÄS & KAILA 1957, BELL 1959, MALMER 1962 b). Obviously the Ca/Mg quotient is not a function of the contribution of air-borne salts only. Changes in the relative content of the mineral constituents arise during fossilization, and such changes may not be the same or of the same magnitude in all sites with an ombrotrophic position.

Considering the chemistry of hummock surface peat in a west—east direction there is an obvious gradient in acid-base status. The lower pH in eastern than in western peat seems more likely to be an effect of different redox potentials than of differences in decomposition and peat production (see PERSSON 1962 pp. 33—36, MALMER 1962 a pp. 191—194, 1962 b p. 24, CLYMO 1964 p. 429). In the elevated parts of the eastern hummock-sites normally no free water is present during the growth period. However, in corresponding western sites the water level is much raised after the snow thaw and after prolonged rain. The sparse snow over eastern sites sharply contrasts with the deep and lasting cover over western sites (SONESSON 1969). Obviously there ought to be better reducing conditions near the surface in western than in eastern sites (cf. SPARLING 1967 pp. 1, 12). This is allied to great differences in the cation supply and cation concentrations in precipitation which would also cause a higher pH in peat of the western than in the eastern sites. The effect of this supply is seen e.g. in the higher contents of Ca and Mg in the west.

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Wiborgia apterophora R. Dahlgr., a New Species of Leguminosae from the Cape Province

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ABSTRACT

DAHLGREN, H.: *Wiborgia apterophora* R. Dahlgr., a New Species of Leguminosae from the Cape Province. — Bot. Notiser 123: 112—114, Lund.

Wiborgia apterophora R. DAHLGR. sp. nov., Leguminosae, is described and illustrated. It deviates from all the previously known species of the genus *Wiborgia* by its small, relatively thin-walled and inflated fruits, which lack a prominent wing on the upper (placental) margin. The winged fruit has previously been considered a generic character for *Wiborgia*. In other features the new species does not differ particularly from the other species of the genus. It is known only from the Giftberg Mountain, Vanrhynsdorp Division, Cape Province, South Africa.

Wiborgia apterophora R. DAHLGR. sp. nov.

Type collection: Cape Prov., Vanrhynsdorp Div., Giftberg. In sand at edge of lands, alt. 2,000 ft. 14.10 1953. E. ESTERHUYSEN no. 22,042 (BOL., holotype).

Shrublet, decumbent, with slender, somewhat angular, reddish-brown branches sparsely and adpressedly puberulous on the younger parts. — *Leaves* with prominent tubercular base, exstipulate, with a flattened petiole only 1—2 mm long and adpressedly pubescent, and with three linear-spathulate leaflets usually $5-9 \times 0.8-1.3$ mm large, with narrow puberulous base and acute—apiculate apex; basal half of laminae often canaliculate-compressed, distal half slightly canaliculate—flat; laminae smooth, subglabrous. — *Flowers* usually 2—6, in sparse racemes terminating the branchlets. — *Pedice* slender, usually 1.5—2.5 mm long, short-sericeous. — *Bract* and *bracteoles* (the latter situated ca. 1—2 mm from the pedice base) caducous, generally falling off before anthesis, subulate-linear, ca. 0.6—1.2 mm long (the bracts larger than the bracteoles), \pm pubescent. — *Calyx* tube campanulate, somewhat shorter on the upper than on the lower side, ca. 2.0—2.2 mm long and almost equally wide, glabrous, rather smooth; lobes short, the upper and lateral four ones broadly triangular and ca. 0.5 mm in length, the lowest nar-

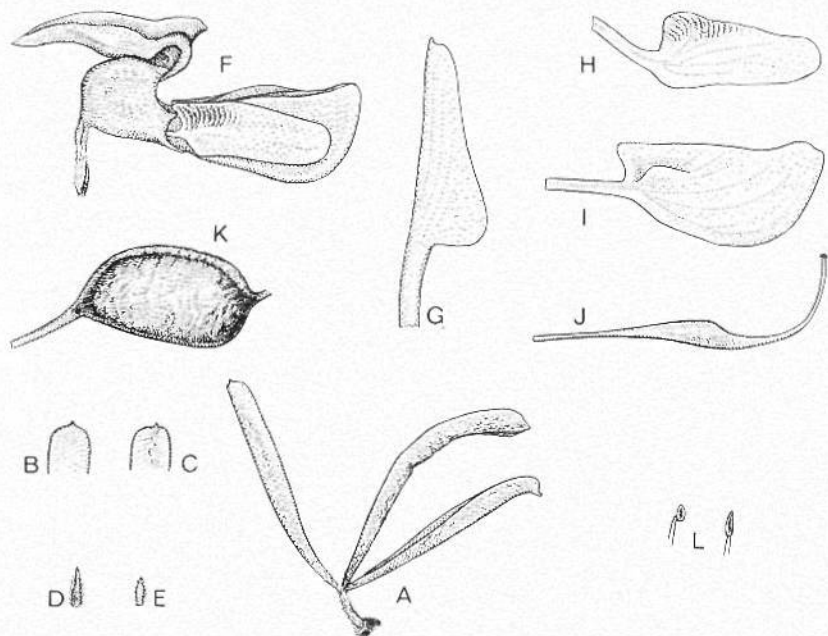


Fig. 1. *Wiborgia apterophora* R. DAHLGR.; ESTERHUYSEN no. 22042. All details $\times 5$. — A: Leaf. — B—C: Upper and lower side of leaflet apex. — D—E: Bract and bracteole from flower bud. — F: Flower. — G: Vexillum (early stage). — H: Ala petal. — I: Carina petal. — J: Pistil — K: Fruit. — L: Short and long anther.

rowly triangular and ca. 0.7—0.8 mm long. — *Petals* delicate, partly pale brown—pink, glabrous. — *Vexillum* with a claw ca. 2 mm long and a somewhat triangular lamina (see Fig. 1 G) ca. 5.5×4 mm large, twisted backwards at an early stage. — *Alae* with claws ca. 2 mm long and laminae $4-4.5 \times 2$ mm large, often twisted in the flowering stage; basal broadest parts of laminae with undulate transverse folds on the upper half. — *Carina* with claws ca. 2 mm long and laminae ca. 5.5×2.5 mm large; laminae with rather prominent upper basal ears and distinct lateral spurlets; the upper sides only slightly curved (see Fig. 1 I) and the apex obtuse. — *Pistil* with long stipe and slender style; ovules 2. — *Fruit* with a stipe up to 2 mm long, ovoid, somewhat inflated, excl. stipe and style (and in lateral view) ca. 4×2 mm large, more than 2 mm thick, glabrous, wingless, but with a broad obtuse ridge on the placental side. Fruit walls thinner and more fragile than in the other species of the genus. Seed solitary.

Fruticulus decumbens, ramulis adpresse puberulis, fusco-purpureis. Petiolus 1—2 mm longus, pubescens. Foliola lineare spathulata, plerumque 5—9 × 0.8—1.3 mm, subglabra, truncata cum acumine (apiculata). Inflorescentia racemosa, sparsa, fere 2—6-flora, Pedicellus 1.5—2.5 mm longus, breviter sericeus. Bractea et bracteolae deciduae, lineares vel late subulatae, 0.6—1.2 mm longae. Tubus calycis campanulatus, extus glaber; lobi breviter triangulares, 0.5—0.7 mm longi. Petala pallide rosea, glabra. Lamina vexilli anguste triangularis, 5.5 × 4 mm, apiculata; unguis ca. 2 mm longus. Laminae alarum ca. 4—4.5 × 2 mm. Laminae carinae lunatae, obtusae, ca. 5.5 × 2.5 mm. Fructus longe stipitatus, ovoideus, ca. 4 × 2 mm (stipite et stylo excl.), > 2 mm crassus, fere inflatus, glaber, apterophorus, supra late et obtuse crasso-cristata. — Typus speciei: ESTERHUYSEN no. 22042 (BOL holotypus).

W. apterophora differs from the other species in the genus mainly in the fruits, which are exceptionally small, turgid, and thin-walled, and which lack a prominent wing on the placental side. In the previously known *Wiborgia* species the fruits are larger, hard, ± compressed, and provided with a marked or even broad wing on the upper side. Sometimes the lower side is winglike as well, and in certain species the fruits bear winglike appendages also on the sides (see DAHLGREN 1963 fig. 80 K on p. 265). Thus they could be classed as samaras.

Morphologically *W. apterophora* comes closest to *W. obcordata* THUNB.

The genus *Wiborgia* is geographically most frequent and variable on the lowlands between the Malmesbury and Vanrhynsdorp Divisions, but ranges into Little Namaqualand in the northwest and past Swellendam in the southeast. It is important in the vegetation of the sandy lowland areas west and north of the Cedarberg Mountains.

The problems of specific delimitation in the genus are great because of the vegetative similarities between the species, the variability of the fruit shape, and the shortness of collected material with flowers as well as fruits. The difficulties partly lie in combining flower and fruit material.

The genus contains approximately 10 species.

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Studies in the Genus *Allium* III

Wind Dispersal of *Allium* Bulbs

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ABSTRACT

EKBERG, L.: Studies in the Genus *Allium* III. Wind Dispersal of *Allium* Bulbs. — Bot. Notiser 123: 115—118, Lund.

Under certain circumstances, bulbs of *Allium stocksianum* BOISS., which grows in subdesertic conditions, may be dispersed by the wind. They are well protected against drying out by thick layers of reticulate-fibrous tunics. The same kind of bulb tunics occur in many unrelated species growing under similar conditions and are considered to be an adaptive feature.

INTRODUCTION

SERNANDER (1906) pointed out several methods of wind dispersal (anemochori) in *Allium*. He recognized three types of diaspores:

1. Seeds (from ballistic anemochors).
2. Capsule surrounded by the persistent membranous tepals and with a part of the pedicel.
3. The whole inflorescence.

SERNANDER considers the two first alternatives as the more important. Examples of all the types are found in the *Allium* species of Central and South West Asia. Examples of the second type are: *A. cucullatum* WENDELBO and *A. mirum* WENDELBO both of sect. *Thaumasio-prason* WENDELBO and *A. spirophyllum* WENDELBO of sect. *Scordon* C. KOCH.

The third type is also important. Good examples are *Allium cristophii* TRAUTV. of sect. *Acanthoprason* WENDELBO and the species of sect. *Kaloprason* C. KOCH, such as *A. caspium* (PALL.) M.B., *A. protensum* WENDELBO and *A. schubertii* ZUCC., where not only the inflorescence but also the short, somewhat inflated and fistular scape form the diaspor.

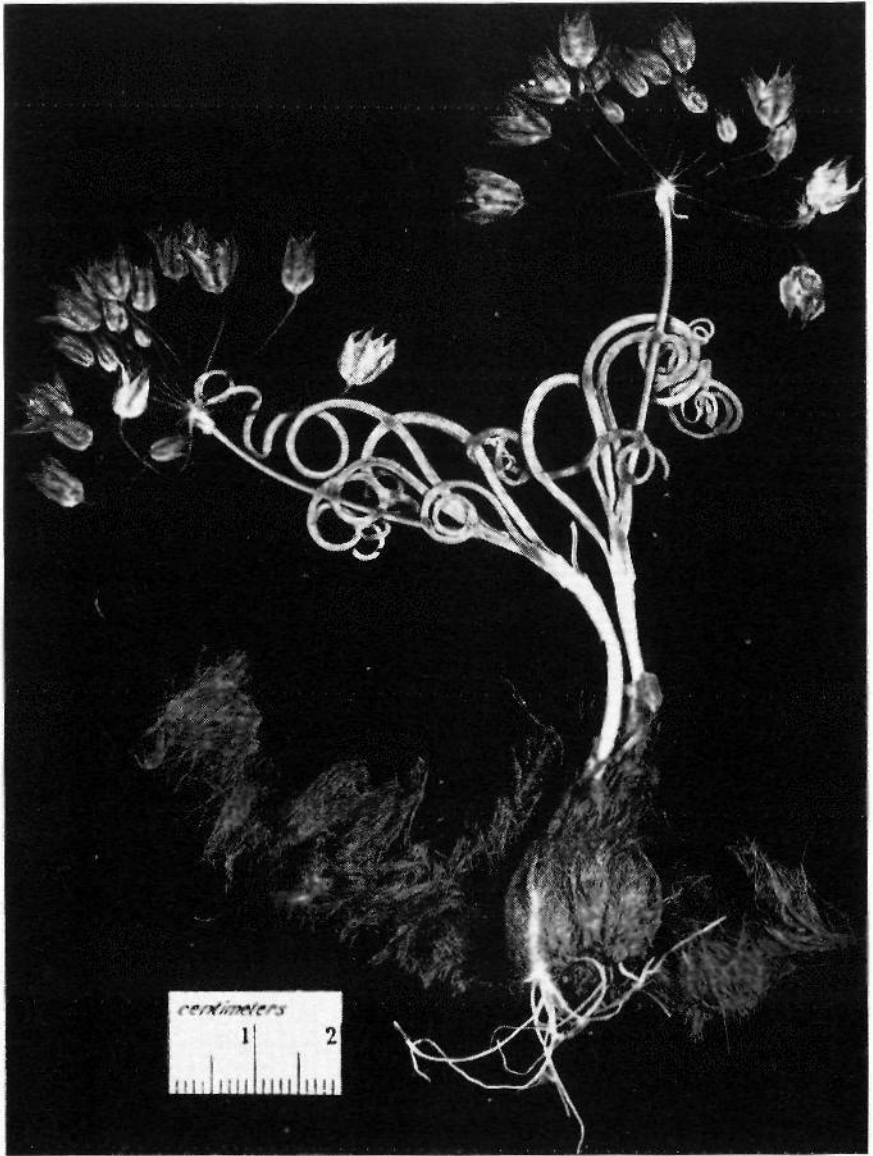


Fig. 1. *Allium stocksianum* Boiss. W 7247. The reticulate-fibrous bulb tunics are partly unrolled to show their thickness and texture.

A possible fourth type of anemochori in *Allium* is described below:

4. The diaspores are either a single bulb or a few bulbs in a cluster.

WIND DISPERSAL OF BULBS IN ALLIUM STOCKSIANUM

During a plant collecting expedition in Afghanistan in 1969 the very characteristic *Allium stocksianum* BOISS. (Fig. 1) was collected in many places. It grows in subdesertic conditions in South Afghanistan at altitudes between 750 and 1800 m and is usually found on slopes of small gravelly hills with a very sparse vegetation. Between Kajkai and Khumari in the province of Helmand, bulbs of *A. stocksianum* (HEDGE & EKBERG W. 7212) were found lying on the ground which was rich in gravel and small stones. The bulbs were, as is typical for the species, enclosed in a thick brown coat consisting of many tunics of reticulate fibres that must give good protection against desiccation. They were fresh and seemed to be in a good condition. In several cases there were a few bulbs within each coat due to vegetative reproduction from the main bulb. Parts of the fibrous tunics were found on the ground in many places showing that the bulbs must have blown along the surface. During this movement it is possible that bulbs are loosened from the cluster, analogous to seeds falling out from a moving inflorescence (type 3) above. Most probably the bulbs are washed out of the ground by heavy winter rains or have come to the surface as a result of strong wind erosion. In places where the soil accumulates the bulbs may again be covered and thus find good growing conditions.

FIBROUS BULB TUNICS IN ALLIUM; A CASE OF ADAPTIVE CONVERGENCY

The thick layers of fibrous tunics covering the bulbs of *Allium stocksianum* apparently may be seen as an adaption to more or less desert-like conditions and is known in many species of *Allium*. The importance of the outer tunics in *Allium* systematics is testified by, e.g., VVEDENSKY (1965 p. 113) but it must not be overemphasized as most probably we have here a case of adaptive convergence. The systematic value of the outer tunics are more on a specific level. Examples of Southwest Asiatic species with fibrous tunics, belonging to different sections are: *A. borszczowii* REGEL, *A. hamrinense* HAND.-MAZZ., *A. longicollum* WENDELBO and *A. viride* GROSSH. of sect. *Allium*; *A. fibriferum* WENDELBO of sect. *Megaloprason* WENDELBO; *A. pogonotepalum* WENDELBO and *A. scabriscapum* BOISS. & KY. of sect. *Rhizirideum* KOCH; and *A. callidictyon* C. A. MEY., *A. desertorum* FORSK., *A. ionandrum*

WENDELBO, *A. registanicum* WENDELBO, *A. sindjarense* BOISS. & HAUSSKN., *A. stocksianum* BOISS. of sect. *Scordon* C. KOCH.

The tunics mainly consist of the basal parts of leaf-sheaths which split up into a reticulate or a reticulate-fibrous pattern. Due to the dryness of the climate the tunics do not decay and will accumulate from year to year. Undoubtedly the thick coat of tunics that is found in the species mentioned above must be important as a protection against desiccation of the bulb. In subgenus *Melanocrommyum* (WEBB & BERTH.) WENDELBO, the main part of the tunic consists of the old storage cataphyll which has been sucked out. This cataphyll is surrounded by remains from the leaf-sheaths from the last year.

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Studies in *Montia* L., *Claytonia* L. and Allied Genera

IV. The Genus *Crunocallis* Rydb.

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ABSTRACT

NILSSON, Ö.: Studies in *Montia* L., *Claytonia* L. and Allied Genera. IV. The Genus *Crunocallis* Rydb. — Bot. Notiser 123: 119—148.

Crunocallis RYDB. (subfam. *Montioideae*, *Portulacaceae*) an American genus related to *Montia* L. and *Claytonia* L. The genus is described and its relationship to *Montia* and *Claytonia* is discussed. With the aid of a series of characters it has been possible to give the genus a natural circumscription and delimitation against the other genera. It agrees in several respects with *Montia* to which it shows a close relationship. The remaining genera of *Montioideae* are more different. The two species, *C. chamissoi* (LEDEB.) RYDB. and *C. calcicola* (STANDL. & STEYERM.) Ö. NILSS., are described. *C. chamissoi* has a western distribution in North America, from Alaska to southern California and New Mexico. The species shows vegetative reproduction by stolons and bulblets. Some anatomical and morphological structures and the different types of reduction in the inflorescence have been discussed in detail. *C. calcicola* is a local endemic of Guatemala. It shows a great resemblance to *C. chamissoi*, differing in a dwarfish habit, smaller leaves and flowers, and a reduced inflorescence. Originally it was described as a *Montia* species. In the descriptions particular attention has been paid to gross morphology, but additional characters of anatomy and pollen morphology have been considered.

The most important characters in distinguishing *Crunocallis* from *Montia* are: 1. the perennial habit, 2. the stolons, 3. the type of stem branching, 4. stomata, with subsidiary cells, on both sides of the leaves, 5. five almost free, equal tepals, 6. five stamens, 7. extrorse—laterorse anthers, 8. the presence of a style, 9. a three-sulcate capsule dehiscing to half of its length. Among the characters in common of the two genera the following are important: 1. decussate leaves, 2. scorpioid cymes in terminal or pseudolateral position with similar reductions, 3. similar seeds, 4. similar pantocolpate pollen grains.

INTRODUCTION

This paper is a contribution to the author's studies in the subfam. *Montioideae* (*Portulacaceae*) previously published under the title Stu-

dies in *Montia* L. and *Claytonia* L. and Allied Genera (NILSSON 1966, 1967).

The generic difficulties of delimitation in the subfam. *Montioideae* have caused serious taxonomical confusion. The subfamily comprises perennial and annual herbs with pentamerous flowers and a superior ovary with basal placentation. The fundamental floral structures are comparatively uniform, whereas the vegetative parts and the pollen grains exhibit great diversity. The species involved are usually ordered in *Claytonia* or *Montia* in current floras and manuals, but not consistently in the same genus. The present study is intended to give the genera more definite limits and present their natural relationship based on a thorough examination of their morphology, anatomy, pollen morphology, cytology and other characteristics.

The subfam. *Montioideae* (sensu PAX & HOFFMAN 1934 p. 257) can be divided into two main groups. One group (the *Claytonia* group) is composed of the genus *Claytonia*, and to this group the genus *Lewisia* PURSH of the subfam. *Portulacoideae* probably can be added (cf. NILSSON 1966 p. 266, 1967 pp. 327, 337). The other group (the *Montia* group) comprises the genera *Mona* Ö. NILSS., *Maxia* Ö. NILSS., *Naiocrene* (TORR. & GRAY) RYDB., *Neopaxia* Ö. NILSS., *Montia* L., *Limnalsine* RYDB., *Crunocallis* RYDB., and perhaps also the more deviating genus *Montiastrum* (GRAY) RYDB. The two main groups of *Montioideae* appear to represent two different evolutionary lines, quite distinctive for a long time, at present divergent in several important characters (cf. NILSSON 1967). In the *Montia* group the morphological differences between some taxa, particularly in their vegetative parts, have become more accentuated than in the *Claytonia* group and therefore it is natural to treat the segregates as separate genera. The genus *Crunocallis* has two species.

MATERIAL AND METHODS

Herbarium material has been used for this study. No living material has been available. Experience from parallel investigations on living material from related genera is considered, however. The material used covers almost the entire distribution area of the genus (cf. Appendix p. 144). No complete herbarium revision is made. Material (but not the entire material of all herbaria) from the following herbaria has been studied: BM, C, CAN, COLO, E, F, GB, GH, JE, LD, LE, M, MT, POM, PRC, S, SMC, UPS, US, W, WRSL (the abbreviations follow Index Herbariorum, Ed. 5, 1964). To the directors and keepers of these herbaria I would like to express my gratitude.

Anatomical and pollen grain preparations have been made of herbarium specimens.

The illustrations of organ details are camera lucida drawings made from full preparations in which the vascular system has been stained with safranin and the surrounding tissue made transparent with lactic acid. The dry material was boiled with water before the preparations were made. In the study of the inflorescences the accompanying drawings are highly simplified.

CRUNOCALLIS RYDBERG Bull. Torrey Club 33: 139. 1906

Claytonia L. p.p. in SPRENGEL 1825 p. 790; *Claytonia* (§, sect.) *Alsinastrum* TORR. & GRAY 1838 p. 201, p.p.; *Claytonia* sect. *Alsinastrum* TORR. & GRAY sensu FENZL in LEDEBOUR 1843 p. 151; *Claytonia* sect. *Alsinastrum* TORR. & GRAY sensu V. POELLNITZ 1932 p. 209, p.p. (*Claytonia* § *Limnia* ** *Alsinastrum* TORR. & GRAY sensu GRAY 1887 p. 282.)

Montia L. p.p. in GREENE 1891 p. 180; *Montia* (sect.) *Limnia* L. p.p. sensu ROBINSON in GRAY 1897 p. 273; *Montia* sect. *Alsinastrum* (TORR. & GRAY) PAX & K. HOFFMANN 1934 p. 259; *Montia* sect. *Montia* sensu SWANSON 1966 p. 232, p.p.

Type species: *Crunocallis chamissoi* (LEDEB.) RYDB. (cf. RYDBERG 1932 p. 313).

Perennial, glabrous, somewhat succulent, stoloniferous herbs of moderate or dwarfish size, sometimes forming loose mats by means of vegetative propagation. *Aerial stems* terete, slender, rooting at base, with one branch from alternating nodes, withering after fruiting. *Stolons* axillary from the stem base, filiform, rather long, terminating with buds or bulblets, with small opposite scales, starch-storing and hibernating. *Leaves* simple, decussate along aerial stems and branches, entire, flat and \pm horizontally directed, sessile or shortly petiolate, oblanceolate—obovate or spatulate, pinnately veined; leaf apex with a distinct, swollen hydathode. Stomata on both sides of the leaf; subsidiary cells two, usually distinct, one on each side, parallel to the guard cells; guard cells with a very minute or lacking internal ledge; epidermal cells square—rounded with straight or usually slightly undulating side walls, cuticle thick, smooth except along leaf-margins where wrinkled. *Inflorescences* a few (1—4), terminal or often pseudo-lateral and axillary, scorpioid cymes with few flowers and a scarious, small bract opposite the lowermost pedicel, varying with regard to development of peduncle, axis, internodes and number of flowers. *Pedicels* evenly recurved after anthesis. *Involucral leaves* two, opposite, equal sized, obtuse or retuse, the outer clasping the inner one, shorter than the capsule, persistent. *Tepals* five, equal, 2—3

times longer than the involucre, \pm obovate, obtuse—emarginate, petiolate, all shortly, laterally connate at base, white—pink. *Stamens* five, about 2/3 of tepal length, free from each other but shortly adnate to the tepals at the base; anther medifixed, extrorse or somewhat laterorse; tepals and stamens fading rapidly after the anthesis. *Style* of ovary length or longer, falling off after anthesis. *Style branches* three, with the stigmatic area confined to the inner side, diverging during anthesis. *Capsule* obovoid—pear shaped, at base three-sulcate, grooves ending at top with a small bulge (when dry); valves three, dehiscing to the grooves, becoming reflexed and involute. *Ovules* three. *Seeds* obovoid, compressed with a rounded top without keel, about 1—1.3 mm long, with a distinct attachment plate and a small, flat, whitish strophiole; testa colliculate with distinct, low, blunt, rounded tubercles in concentric rows. *Pollen grains* spherical, pantocolpate, sexine tectate, punctate and spinulate or smooth (NPC = 763). Chromosome number unknown. (The generic characters in common are usually not repeated in the descriptions of the species.)

Discussion

The discussion will mainly concern *Crunocallis chamissoi*, which is a well-known species with a wide distribution in western North America. *C. calcicola* was recently described and has not yet appeared in floras or monographs.

SPRENGEL (1825 p. 790) placed the species in *Claytonia*. It was treated in this genus until 1891, when it was transferred by GREENE to *Montia*. TORREY and GRAY (1838) established within *Claytonia* four "sections" in one of which, named *Alsinastrum*, they placed *C. chamissoi* together with *C. flagellaris* BONG. FENZL in LEDEBOUR (1843) retained *C. chamissoi* within section *Alsinastrum* but transferred *C. flagellaris* to another section. According to HOLM (1905 and 1913), *C. chamissoi* was the only species of section *Alsinastrum*. In his monograph of the genera in *Montioideae*, VON POELLNITZ (1932) kept *C. chamissoi* in section *Alsinastrum* but added *C. halli* GRAY which is a *Montia* species (*Claytonia chamissoi* var. *tenerrima* GRAY as a synonym), and in that he followed HOWELL (1893 p. 37).

In current floristic works and manuals the species has been variously placed in *Montia* or *Claytonia*. The same is true of several other species

in *Montioideae*. This has made the limit between the two genera diffuse (cf. NILSSON 1966 p. 265).

In 1906 RYDBERG erected the new genus *Crunocallis* for this species. His reasons were: "This genus has the flowers of *Claytonia*, but the general habit of *Montia*; the mode of propagation and the seeds are different from both." His generic conception has been followed here.

SWANSON (1966 p. 232) emphasized the habit and life-forms and pollen morphology of the species in *Montioideae*, while floral characters were somewhat neglected. He retained only the two genera *Montia* and *Claytonia*, the latter of which he gave a natural limitation. The genus *Montia* was subdivided into four sections. The species here in question was placed in the section *Montia*, together with *M. fontana* L., *M. australasica* (HOOK. F.) PAX & HOFFM., and *M. howellii* S. WATS. In this way he conglomerated species which have very vague characters in common and do not show any closer relationship (cf. NILSSON 1967).

Crunocallis belongs to the second main group of *Montioideae* (cf. p. 120) and is definitely separate from *Claytonia* (cf. NILSSON 1966 pp. 467—368; 1967 pp. 325—326; SWANSON 1966 p. 231).

Among the genera of the second group, *Montia* and *Crunocallis* have a particular position. They have a closer affinity to each other than to the remainder. The following morphological features in common may be emphasized: 1. the decussate leaves, 2. the scorpioid inflorescence, 3. the shape of seeds, 4. the pantocolpate pollen grains (the colpus length is different, cf. NILSSON 1967). The characters in common are important, and it may seem doubtful whether the two genera should be kept separate or treated as sections of *Montia*. However, there are other reasons to treat them as separate genera, as will be advocated below.

The most important characters distinguishing *Crunocallis* from *Montia* are, 1. the perennial habit, 2. the mode of vegetative propagation by stolons, 3. the type of stem branching with one branch per node, 4. stomata (with subsidiary cells) on both sides of the leaf, 5. the recurving of the pedicels after anthesis, 6. five almost free, equal tepals distinctly longer than the involucrem, 7. five stamens, 8. extrorse—laterorse anthers with two-celled thecae, 9. the presence of a style with stigmatic areas only on the inner sides of the style branches, 10. a three-sulcate capsule dehiscing to half of its length (cf. p. 142). Of these characters the floral ones must be considered with regard to the predominant autogamy in *Montia* with its consequent floral reductions. However, *Crunocallis calcicola* seems to be autogamous too and in this

species the floral reductions follow a somewhat different pattern to that of *Montia*. Rarely reduced flowers with three stamens may occur in species which normally have five stamens per flower. This phenomenon is common to the whole family. But in *Montia* and some other genera the flowers regularly have three stamens.

It is evident that *Montia* and *Crunocallis* are the most closely related genera within *Montioideae*. Compared with the other genera of the subfamily, some more original morphological features seem to have been preserved in *Crunocallis*, e.g., the perennial habit and the complete flower with five large, equal tepals, five stamens, and a long style. The *Montia* species seem to be more advanced — they are mainly annuals with a rapid life cycle and have reduced flowers well adapted to autogamy. This view is confirmed when the distribution of the two genera is compared. *Montia* is an almost cosmopolitan genus. *Crunocallis* is endemic in North—Central America where the subfamily has its widest differentiation. It seems reasonable to assume that *Crunocallis* originated more recently in this area: the original area of *Montia* is very uncertain.

Key to the Species of *Crunocallis*

- A. Stolons with bulblets, aerial stems usually 8—15 cm long, leaves 1—7 cm long, 0.2—2.7 cm broad, inflorescences normally with a peduncle and axis, flowers about 0.6—1.5 cm wide, white—pale pink, anthers with parallel thecae 1. *C. chamissoi* p. 124
- B. Aerial stems 1—6 cm long, often branched from base, leaves 0.5—1.7 cm long, 0.2—0.6 cm broad, inflorescences without peduncle and axis, flowers about 0.3—0.5 cm wide, bright pink, anthers with thecae diverging at base 2. *C. calcicola* p. 138

1. *Crunocallis chamissoi* (LEDEB.) RYDBERG Bull. Torrey Club 33: 139. 1906 ("Chamissonis")

Claytonia Chamissoi LEDEBOUR in SPRENGEL 1825 p. 790. — *Claytonia Chamissonis* "ESCH(SCHOLTZ) in litteris! LEDEB. SPRENG." in CHAMISSO 1831 p. 562. (Non "*Claytonia chamissoi* LEDEB." sensu DE CANDOLLE 1828 p. 363.)

Montia Chamissonis (LEDEB.) GREENE 1891 p. 180. — *Montia Chamissoi* (LEDEB.) DURAND & JACKSON 1903 p. 282. — *Montia Chamissoi* (LEDEB.) ROBINSON & FERNALD in GRAY 1908 p. 388.

Original collection: Unalaska, ESCHSCHOLTZ (LE lectotype; isotypes in C. S. and GIL, some of the original specimens were sent to A. GRAY). ("Type locality: Unalaska", cf. PIPER 1906 p. 250.)

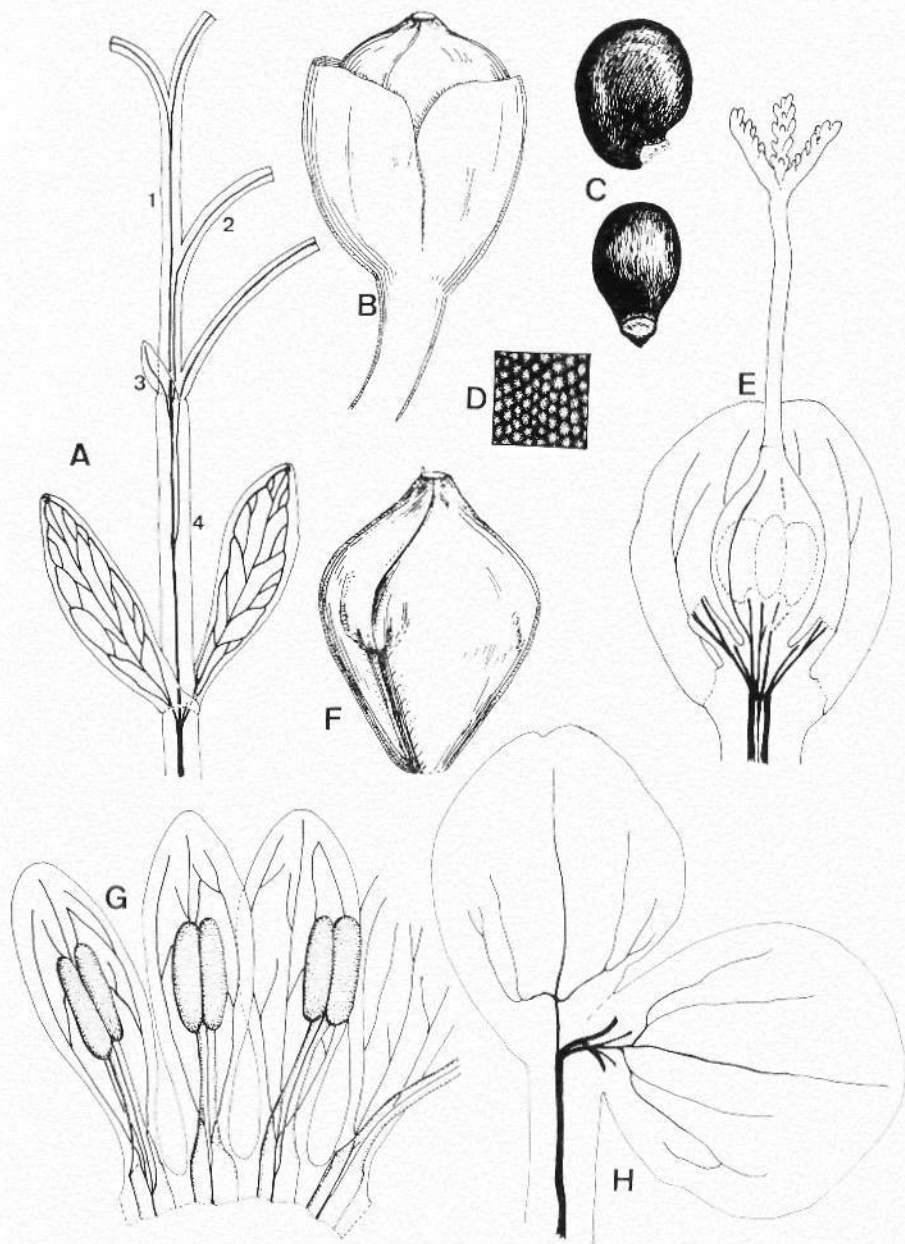


Fig. 1. *Crunocallis chamissoi*. — A: Top of aerial stem with a pair of leaves and a terminal inflorescence: 1. axis, 2. pedicel, 3. bract, 4. peduncle. — B: Involucre and capsule. — C: Seeds, the upper in lateral view. — D: Part of testa. — E: Pistil. — F: Capsule. — G: Part of perianth with stamens. — H: Involucre, the upper leaf is the inner one.

Claytonia stolonifera C. A. MEYER 1829 p. 139, tab. 3. (Amer. Ross., Sitcha, MERTENS; LE lectotype; GH, LD isotypes.)

Claytonia aquatica NUTTALL in TORREY & GRAY 1838 p. 201 — corrected to *Claytonia Chamissonis* in TORREY & GRAY 1840 suppl. p. 676. (Oregon, NUTTALL; GH lectotype.)

(*Claytonia chamissoi* var. *tenerrima* GRAY is a *Montia* sp.)

The use of "in" instead of "ex" in the auctors of *Claytonia Chamissoi* is somewhat uncertain, but it is probable that SPRENGEL obtained information and the specific name from LEDEBOUR, who had the original material at hand, and that SPRENGEL then redacted the text (cf. Int. Code Bot. Nomenclature 1966, Art. 46). In this way the established use of LEDEBOUR as auctor can be preserved.

Moderately sized herb. *Subterranean stem* usually short, up to 15 cm long, about 1—2 mm thick, \pm horizontally and shallowly creeping with fibrous adventitious roots particularly from the nodes, short-lived and soon withering in the distal part, rarely branched and with one or occasionally a few aerial stems. *Aerial stem* erect, ascending, decumbent or sometimes in part creeping or floating, 2—32 cm long (usually 8—15 cm), 1—3 mm thick, weak and somewhat sappy, usually with no or a few lateral branches at the top (cf. p. 130), sometimes rooting at basal nodes, length and numbers of internodes variable (0.5—8 cm long and 2—21 respectively on flowering stems). *Stolons* one at each node of the stem-base (Fig. 2 A), spreading shallowly in the ground, usually branched, filiform, 0.3—1 mm thick, usually 10—30 cm but up to 50 cm long, occasionally very short, 0.4—1 cm long (Fig. 2 F), internodes of variable length, 0.5—12 cm long, often pinkish or white, ending with small pointed buds or bulblets; with thin, usually small, 1—4 mm long, ovate, subacute, opposite, semiamplexicaul scales, scales sometimes replaced by ordinary leaves on supraterranean parts, transitions between stolons and normal branches occurring sometimes (cf. p. 131). *Bulblets* terminal on stolons (Fig. 2 A, D, E), solitary, ovoidal, 2.5—7 mm long, 2—5 mm thick, white or pinkish, scaly, with 3—7 pairs of opposite, closely set, fleshy scales on a short axis (cf.

Fig. 2. *Crunocallis chamissoi*. — A: General habit of plant, somewhat simplified. — B: Diagrammatic drawing of A showing type of branching. — C: Diagrammatic drawing of stem part, to show position of lateral branches marked with X; M indicates the main stem. — D: Growing bulblet with main shoot and lateral stolons. — E: Growing bulblet with main shoot and adventitious roots. — F: Portion of stem base with a subsessile bulblet. — G: Two flowers, the left in "male phase", the right in "female phase" (further explanation in text). — H: Variation in tepal shape.

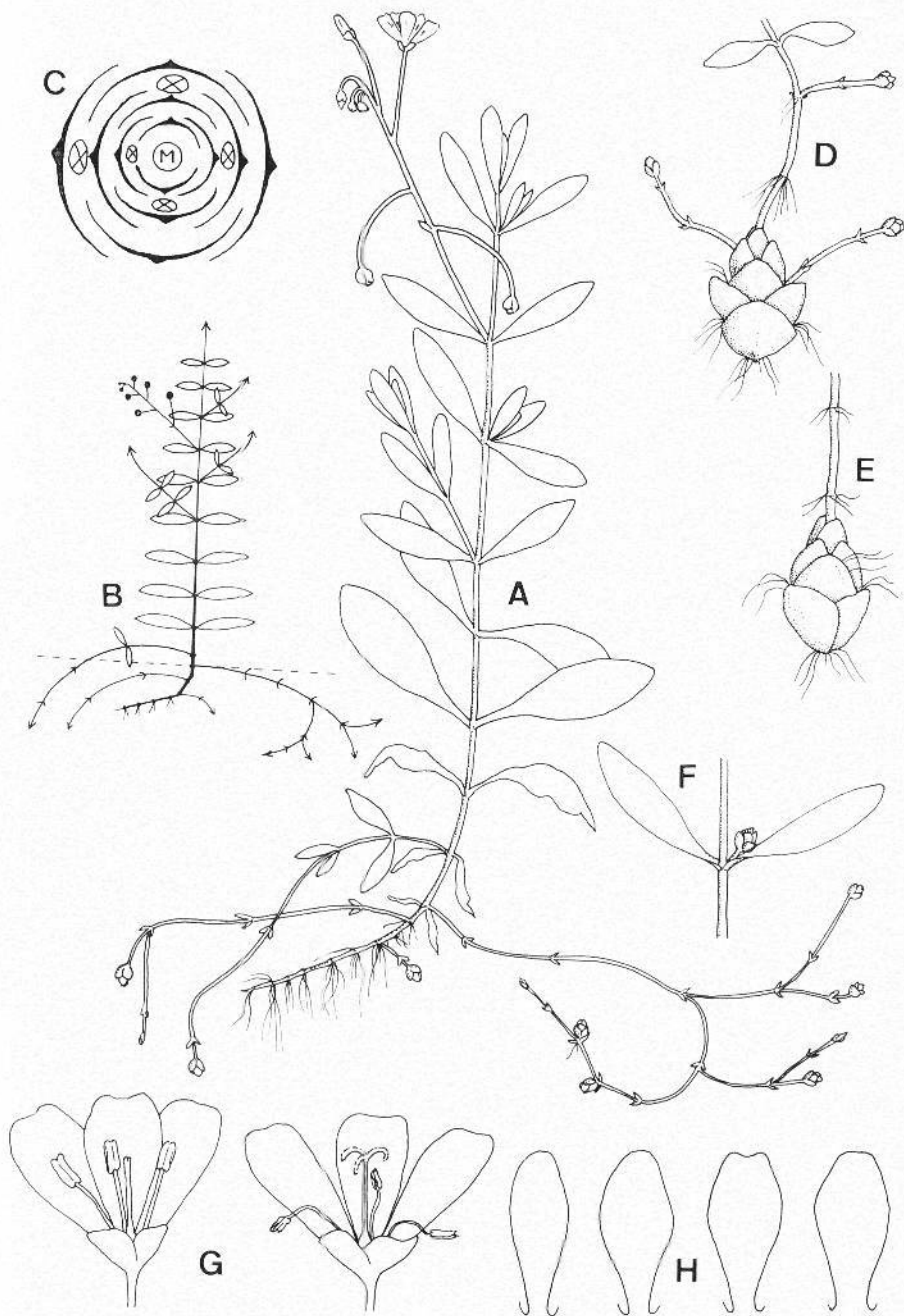


Fig. 2.

p. 133). *Leaves* 2—21 pairs (usually 4—10 pairs) on flowering stems, the lowermost often withered at anthesis, oblanceolate, narrowly elliptic or obovate, the basal ones often spathulate (Fig. 3 A), 1—7 cm long, 0.2—2.7 cm broad, longer or shorter than the internodes, sessile or the lower subsessile or often shortly petiolate; petiole winged, shorter than blade; pinnately veined with the first branches from or near leaf-base (Fig. 1 A); leaf-base slightly dilated, almost half-clasping, sometimes with narrow scarious margins; leaf-apex acute—obtuse, hydathode often dark on dry leaves. Stomata on both leaf-sides, somewhat sparser and sunken on the upper (ventral) side; subsidiary cells usually distinct (Fig. 3 F); cuticle particularly thick on the upper side of the leaf. *Inflorescences* 1—3 (rarely more), each with usually 2—8 flowers, occasionally one or up to 13, axis usually elongate, straight, erect, often with two flowers in anthesis simultaneously (cf. p. 134, Figs. 1 A, 4). *Peduncle* 0.5—5 cm long, rarely very short or missing. *Bract* one (very rarely two), obtuse—acute, ovate, c. 2 mm long, scarious or occasionally leaf-like, opposite the lowermost pedicel. *Pedicels* at anthesis 0.5—2 cm long, thin, erect, after anthesis up to 4 cm long, recurved from the base and bow-like, becoming straight and erect again at maturity (cf. p. 134). *Involucral leaves* ovate—broadly ovate, 1.5—3 mm long, obtuse or the inner often retuse, both growing somewhat after the anthesis, usually shorter than the capsule (Fig. 1 B, H). *Tepals* 3.5—9.5 mm long, 1.5—5 mm wide, of about equal size and shape, 2—3.5 times as long as the involucrem, flat, ascending or patent at the anthesis, obovate-pandurate, obtuse, retuse or slightly emarginate, shortly petiolate, petioles all laterally connate in the basal half up to c. 0.5 mm, white or pale pink (Figs. 1 G, 2 H). *Stamens* 2.5—6.5 mm long, filaments at base dilated and adnate to the tepals, free part of filaments 2—5.5 mm long; anther often lavender in colour, dorsifixed, 1—2 mm long, 0.5—1.5 mm broad with parallel sides, extrorse (Fig. 1 G); flower protandrous. *Style* thin, 1.5—4 mm long, about twice the ovary length, not sharply set off from ovary, falling off after anthesis from a distinct point (Fig. 1 E). *Style branches* three, rather short with sparsely set, low papillae on the inner face, extended and diverging during the late phase of anthesis (cf. p. 134). *Capsule* 2—3.5 mm long, three-sulcate at base, grooves of about half the length of the capsule (Fig. 1 F). *Ovules* three, all of which only sometimes developing to seeds. *Seed* 1.0—1.3 mm long, blackish (Fig. 1 C, D). *Pollen grains* 44—47 μ in diameter, colpi 16—18 μ long, tectum almost smooth.

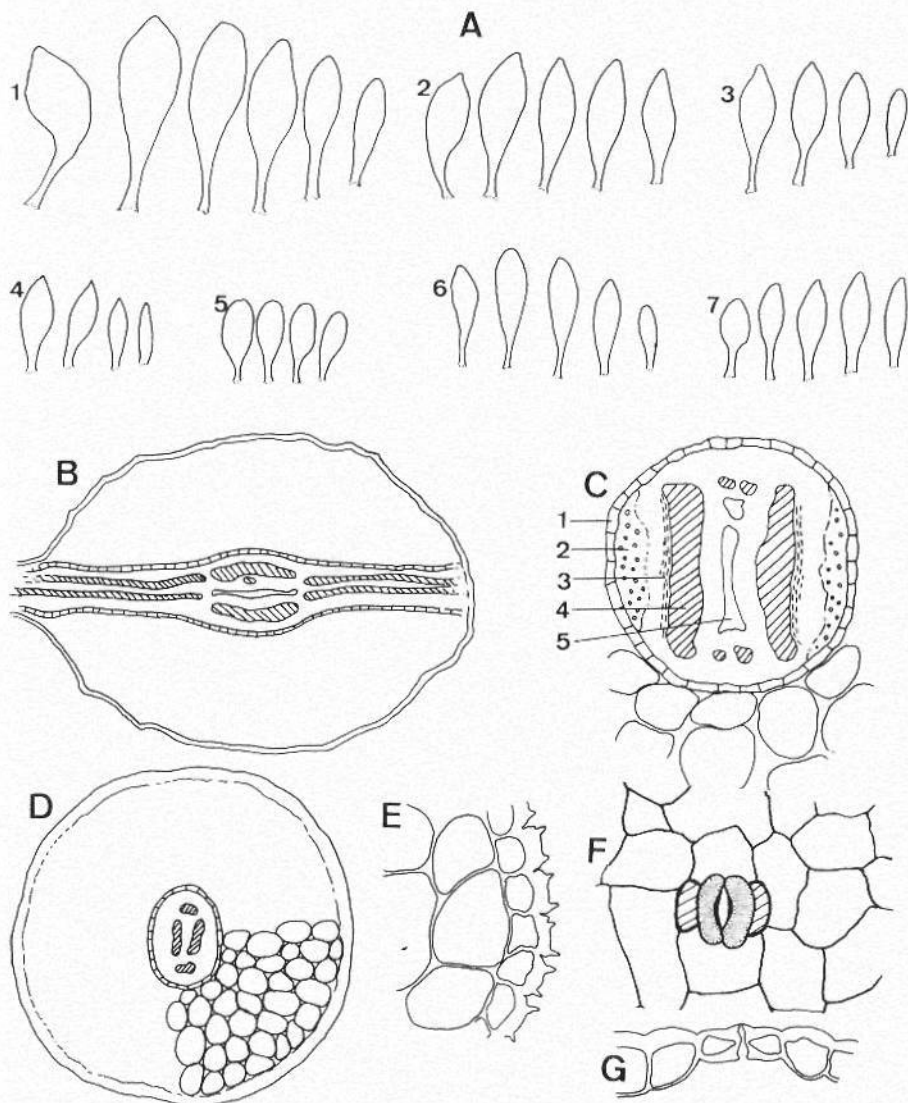


Fig. 3. *Crunocallis chamissoi*. — A: Variation in leaf shape; 1—7 leaf series of different specimens, the left leaf is the lowermost. — B: Cross-section of the aerial stem at a node. — C: The stele of aerial stem; 1. endodermis, 2. fibre cells, 3. cambium, 4. xylem part of vascular bundle, 5. hollow of pith. — D: Cross-section of stolon with epidermis, starch-storing cells in cortex and the stele. — E: Stolon, portion of epidermis. — F: Part of ventral leaf epidermis with stoma; hatched cells are subsidiary cells, spotted cells are guard cells. — G: Section of stoma.

Discussion, with Morphological and Anatomical Comments

Crunocallis chamissoi is a geophyte with a rather wide variation in its vegetative parts. Variable features are: the number and length of internodes, the shape and size of leaves (Fig. 3 A), the number and length of stolons, the branching, the number and position of inflorescences, and flower size. Alterations also occur in the inflorescences, e.g., in the number of flowers and length of internodes. However, the variation does not seem to be confined to certain geographical areas or ecological niches. It appears mainly modificative. The plants have the same high phenotypic plasticity everywhere and thus the species can be regarded as comparatively uniform within its entire area. Different specimens evidently belonging to the same clone may differ in, e.g., the leaf shape and the development of the inflorescences. The plant follows the general pattern of modification, i.e., in moist and shady places the plants are tall, branched, with long internodes, large leaves and the inflorescence is long and many-flowered. On the other hand, plants on open and drier places are smaller with short internodes and smaller leaves and the inflorescences are often solitary and few-flowered, and the flower are often deeper pink.

MODE OF BRANCHING. The branching of the stem is usually confined to two different regions (Fig. 2 B). The basal part (often near the ground) is usually more ramified than the top, but the stem part in between is normally unbranched. The basal branches are mainly stolons.

In the apical part of the stem the first inflorescence often terminates the main shoot while a lateral branch continues the growth of the vegetative shoot. In this case the inflorescence acquires a pseudolateral position (Fig. 2 A). Thus the apical part of the shoot can have a sympodial type of branching. The same opinion is expressed by HOLM (1905 p. 29), who says that the shoot is not monopodial but terminated by an inflorescence. In other plants the shoot may be terminated by an inflorescence which has a truly terminal position (Fig. 1 A).

The remaining part of the shoot seems to have a monopodial type of branching with a main stem with lateral branches. The monopodial branching is evident in the growth of the bulblets. The axis of the bulblet is terminated by a bud. After hibernation this bud develops and its internodes elongate. The direct continuation of the axis of the bulblet forms the main stem of the new plant (Fig. 2 E). If side branches

develop from the bulblet they have a later and weaker development, forming only stolons (Fig. 2 D).

The branching of the shoot almost always follows a distinct pattern. As a rule only one branch develops at each node. The leaves are decussate. The branching become four-sided (in herbarium specimens usually two-sided). Two branches in succession are at right angles. Two branches in a row above each other are separated by four internodes (Fig. 2 C). Also the "lateral" inflorescences are included in this type of branching. The mode of branching in *Montia* is different. In this genus there are often two opposite branches at each node. This has been seen only very occasionally in *Crunocallis* specimens. Such "secondary" branches are usually very short and delicate, however; normally they never develop.

STEM ANATOMY. The anatomy of the aerial stem shows a great resemblance to that of other members of the subfamily (Fig. 3 B). The epidermis has a rather thick cuticle which is prominently wrinkled. The cells are long and have straight side walls. The stomata are sparse. Inside epidermis there is a thick parenchymatous cortex. Its thin-walled cells are rather short with obtuse ends and have a rounded outline in cross section. This tissue is open and assimilatory. Its innermost part is differentiated as an endodermis of thin-walled cells with distinct Casparian dots. In the stele (Fig. 3 C) there are two broad, strap-like, collateral vascular bundles, and two thinner ones in an alternating position. These bundles change places in the following internode; the smaller ones are replaced by the broader. Immediately inside the endodermis, opposite the larger bundles, there are some thick-walled fibrous cells. The bundles are surrounded by a sheath of parenchymatous cells. A cambium is present. The centre of the pith is usually hollow. The stem lacks collenchymatic and stereomatic tissues (cf. HOLM 1905 p. 35). The aerial stem withers after fruiting.

STOLONS. The stolons can be regarded as basal, subterranean, lateral branches (long shoots) with a function in vegetative reproduction. The internodes of the stolons are often long and the stolons are often many-branched (Fig. 2 A). The branching follows the system of the stem. The leaves of the stolons are usually very small and scale-like. The stolons and the scales are white or pinkish. The stolons normally lack adventitious roots. The development of stolons can start in connection with the growth of the bulblets in the spring. At the time of flowering often a rich system of stolons has developed. Flowering

specimens with up to 12 many-branched stolons occur, but the usual number is 2—5. The length of the stolons is variable. Stolons longer than 50 cm are not met with in the herbarium material, but the stolons are often very delicate and may easily be broken. Occasionally there occur in the basal leaf axils very short stolons, c. 0.5 cm long, with a terminal bulblet (Fig. 2 F). The terminal, small buds continue the growth of the stolons.

The lowermost aerial branches can be transformed into stolons. In such a branch the supraterranean part has ordinary green leaves while the subterranean part is stolon-like with scaly leaves and bulblets. Such transitions are not uncommon. The reverse condition, with stolons passing over into aerial branches, does not occur.

According to HOLM (1905 p. 31), the vegetative propagation starts at a very early stage in the plant's life, already in the same year when the seed has germinated. The first stolon can develop from an axil of the cotyledons.

HOLM also described a seedling. It was provided with a pair of minute, hairy, epigeic cotyledons. The primary root was long but very thin and sparsely ramified. Its duration was not more than one season. Then the root was replaced by adventitious roots which lacked secondary thickness growth and were not contractile.

The anatomy of the stolons is similar to that of the aerial stem. It differs in some details (Fig. 3 D). The cuticle is wrinkled but also provided with two distinct longitudinal ribs, one at each cell margin. In cross section the two ribs look like two small lateral horns (Fig. 3 F). The epidermis lacks stomata. The cortex consists of closely packed starch-storing cells of the same form as in the aerial stem. The starch grains are rather large, obtusely angled. No thick-walled fibrous cells occur inside the endodermis. There is no cambium and thus no secondary growth. The pith is narrow and not hollow (cf. HOLM 1905 p. 35). The stolons are annual but probably hibernate and can continue growth by the buds.

LEAVES. The leaf has a distinct palisade tissue in the upper (ventral) side and an open pneumatic tissue in the lower. No mechanical tissue occurs. The guard cells of the stomata have a rather distinct upper ledge but the lower one is lacking or is very low (Fig. 3 G). According to HOLM (1905 p. 36) the mestome bundles are surrounded by a thin-walled parenchymatous sheath.

BULBLETS. The bulblets develop terminally on the stolons. They are short shoots with small scaly opposite leaves closely set on a short axis. The axis is terminated by a minute bud hidden by the scales. The two basal scales are thin and membranous and remain on the stolons when the bulblets are shed. The remaining scales are fleshy and starch-storing (blue with iodine).

The bulblets are organs for hibernation and vegetative reproduction. They can become separated from the stolons. After anthesis the bulblets have a continuing growth. In spring they are considerably larger than on flowering specimens. At "germination" adventitious roots are formed at the nodes of the bulblet and they force a way out between the scales (Fig. 2 E). The apical bud starts growing. From the original short shoot a long shoot is formed which develops into the new plant. Usually only one plant is formed from a bulblet. Sometimes lateral branches may develop from the bulblet; these become new stolons (Fig. 2 D).

One flowering specimen with 27 bulblets has been recorded in a herbarium specimen. Probably they may be more numerous but the stolons are easily broken and the bulblets come loose easily.

The bulblets seem to have their main importance in local reproduction. However, it is reasonable to assume that loose bulblets can be transported by water or otherwise and play some rôle in long distance dispersal.

Small simple hairs sometimes occur on the scales of the bulblets. According to HOLM (1905 p. 36), the cotyledons and lowermost leaves of the seedlings are hairy too. *C. chamissoi* is the only species in the subfamily where hairs of any type occur.

The epidermis of the bulblet scales has no stomata. The mesophyll is represented by a compact homogeneous tissue of starch-storing cells. Only three vascular bundles occur in the scale, one median and two lateral.

INFLORESCENCES. The inflorescences exhibit numerous irregularities (Fig. 4). One type, here called the normal type, is found in about 75 % of the investigated material. One specimen can have more than one type of inflorescence. In such specimens the lowermost inflorescence is often of normal type while the remainder can be reduced. The irregular inflorescences usually can be interpreted as derived from the normal type.

The normal type is a pseudolateral or terminal scorpioid cyme. The inflorescence has a stalk, here called peduncle, which is the basal part

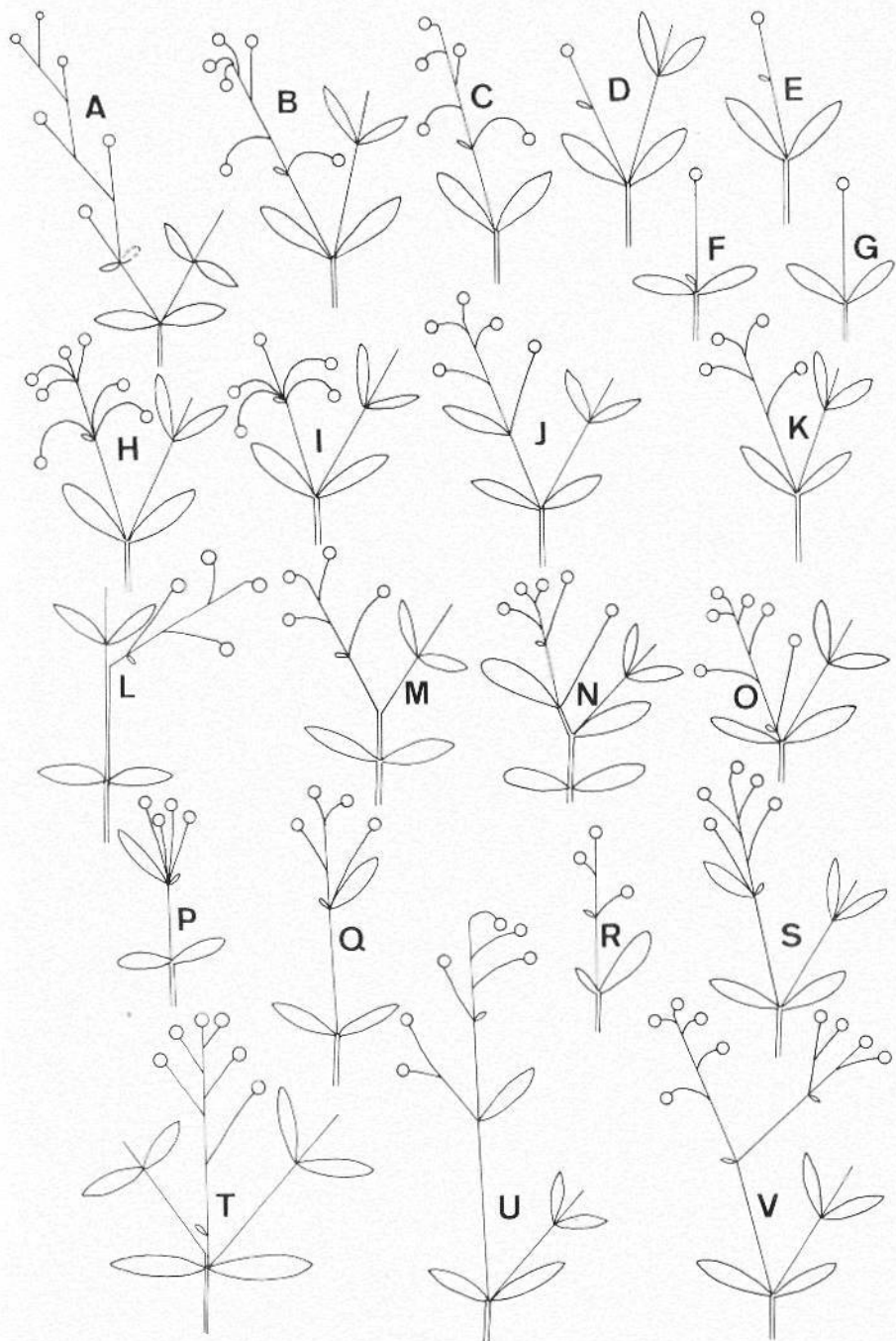
of the pedicel of the lowermost flower (Fig. 1 A:4). Its length is variable but usually it is as long as the leaf of the axil. The lowermost flower of the inflorescence has a minute scaly bract in an opposite position (Fig. 1 A:3). Other bracts are lacking. In the inflorescence the basal parts of the pedicels form a sympodial axis which is \pm straight and elongate (Fig. 1 A:1), but coiled while in bud. The number of flowers varies; usually they are 3–6.

Fig. 4 A—E shows the normal type of inflorescence and a hypothetical explanation of it, and a number of irregular inflorescences (Fig. 4 D—V). The latter are often reduced forms of the normal type, but in some inflorescences additional organs can occur — some examples of irregular inflorescences: the internodes of the axis are not developed, the flower can be a single one, the bract can be absent, another opposite usually leaf-like bract can occur, the normal bract can be leaf-like, transitions between ordinary leaves and scaly bracts occur, the peduncle can be very short, only very rarely is it entirely lacking. The different reductions and additions can be combined in several ways and coalescences and additional branching can also cause irregularities. Some of the most anomalous inflorescences cannot be accurately explained. Several of the irregularities in the inflorescence of *C. chamissoi* occur also in some *Montia* species. However, in this genus the peduncle is consistently lacking.

According to HOLM (1905 p. 28), the inflorescence is a regular cyme (a dichasium) at least in the lower portion of the stem, here called in pseudolateral position. HOLM is of the opinion that, while one lateral branch becomes a few-flowered leafless monochasium, the other branch develops as a vegetative shoot. However, terminal inflorescences with two lateral vegetative branches at base can occur (Fig. 4 T), which makes HOLM's explanation less probable.

ANTHESIS. In inflorescences with several flowers there may be two (or three) in anthesis simultaneously. The filaments in the upper flower are straight and the anthers dehiscing. The style is short and

Fig. 4. *Crunocallis chamissoi*, variation in inflorescences, highly simplified. — A: Hypothetical explanation of the normal inflorescence type. — B—C: The normal type. B: in pseudolateral position; C: in terminal position. — D—G: Reductions in flower number. F: with short peduncle; G: without bract. — H—I: Reductions in the internodes of axis. — J: Leaf-like bract. — K: Without bract. — L—N: Coalescences of different types. — O: Reduction of peduncle. — P—Q, S: Additional bracts. — R: Leaf size reduction in normal leaves. — T: Additional lateral vegetative branch. — U—V: Branched inflorescences.



the style branches converge firmly. In the lower flower the filaments are usually slack and the anthers empty. The style has grown and reached the same height as the anthers of the upper flower. The stigmatic areas become exposed because the style branches have diverged. The flowers are protandrous.

The protandry follows a pattern which has been thoroughly examined in other species of the subfamily. The flowers can be expected to have a rather short duration, probably only 2 or 3 days. During the "male phase" of the anthesis the stigma is probably not receptive. At the end of the "female phase" the style drops. Then the flower withers rapidly. The ripening of the fruit is also rapid. In an inflorescence with 8 flowers the lowermost capsule had dehisced while the apical flower was still in bud. The seeds are probably actively thrown away some distance, as in other species with a similar type of capsule.

FLOWERS. According to SWANSON (1966 p. 231), *C. chamissoi* has sometimes a sympetalous and asymmetrical corolla and the stamens are frequently reduced to three. He also says that the flower only sometimes is unreduced. These statements seem to be somewhat overemphasized. The tepals are laterally united at the base but only for a very short distance (cf. p. 128). In *Montia* the tepals are often united for half their length, but the perianth has also one median very deep slit. The tepals of *Crunocallis chamissoi* can be slightly unequal in size and rarely also in shape. Two tepals are then smaller than the remainder; in one case the larger ones were 8.7 mm long while the smaller were 8.5 mm long. Such small differences occur in most genera of the subfamily and can usually be ignored. In *Montia* the difference in size is much more obvious. No flowers with originally three stamens have been observed by the present author in the material studied; thus it cannot be a frequent condition. However, during the late phase of the anthesis the stamens have often faded and sometimes one to all can be lost.

SEEDS. The formation of seeds is often very sparse and irregular in *C. chamissoi*. In 148 examined capsules 42 had ripe or ripening seeds. In the remainder the ovules had failed to develop. Self-pollination is probably effectively prevented by the protandrous system, which is proved in other species. But cross-pollination may take place without any obstacles. Either pollination is not forthcoming in full or the development of the seeds is prevented by other causes. When seeds are developed, often only one or two of the three ovules develop. It is

a common condition that plants with an effective vegetative reproduction have a reduced sexual one.

According to BRANDEGEE (1894 p. 87), the cotyledons have an accumbent position in the seeds.

Distribution and Habitat

Crunocallis chamissoi is a North American species with its main distribution in the mountainous areas of the west. It occurs from the Aleutian Islands and Alaska in the north to southern California, Arizona and New Mexico in the south. It also has some isolated localities east of the mountains in Manitoba and in the driftless area of Iowa and Minnesota. The southernmost localities are in California in the San Jacinto, Palomar and San Bernardino Mts. In the United States the species occurs in the Rocky Mts., particularly on the eastern slopes, in the Sierra Nevada and Cascade Range. It has an almost continuous distribution in the following states: California, Arizona, New Mexico, Nevada, Utah, Colorado, Oregon, Idaho, Wyoming, Washington, and Montana (cf. RYDBERG 1932 p. 314 and HITCHCOCK et al. 1964 p. 239). The area is widest south of the Canadian border, along a line from Colorado to California, and there the species is rather common (cf. Appendix). North of the Canadian border the distribution area becomes narrower and follows the coast from northern British Columbia to Alaska. In Alaska it occurs mainly in the western coastal districts but also in the Mt. McKinley area. From the Kodiak Island it follows the Aleutian Islands to their westernmost point, the Attu Island (cf. HULTÉN 1968 p. 409). A general map, Fig. 5, shows the distribution of the species.

The distribution area of *C. chamissoi* in North America is rather similar to that of some other species of subfam. *Montioideae*, e.g., *Claytonia sibirica* L. and *Naiocrene parvifolia* (MOQ.) RYDB. However, most of these species do not extend their distribution so far north and south and they usually lack eastern outpost localities. Phytogeographically *Crunocallis chamissoi* has many parallels in other groups of flowering plants in western North America (cf. HULTÉN 1968).

In the southern part of its distribution *C. chamissoi* occurs in the mountains from the foothills to middle elevation, usually below the timberline; in Sierra Nevada from an elevation of 1200 m to about 3000 m, in Nevada from 2000 m up to 3700 m, in Oregon from 750 m

to 2000 m. In Alaska the species has localities on seashores probably only a few meters above sea level, but also in the mountains of the Alaska Range at an altitude of 1000 m.

C. chamissoi grows predominantly in wet habitats; stream and creek banks, moist meadows, marshes, open moist woods, sandy and moist seashores, and in springs and shallow water, also in brackish water. The species prefers comparatively open habitats where, however, it usually occurs in the shade of scattered trees or bushes, e.g., aspen, willows, yellow and Jeffrey pines, etc. The plant may form loose mats on naked soil, but more occasionally in a closed, high-grown vegetation.

Flowering Period: In the south (California) the flowering of the species may start in May and continue till September. In Alaska flowering usually begins in late May and ends in August.

2. ***Crunocallis Calcicola*** (STANDL. & STEYERM.) Ö. NILSSON *Grana Palynol.* 7: 359. 1967

Montia calcicola STANDLEY & STEYERMARK 1944 pp. 48—49.

Original collection: Guatemala, Dept. Huehuetenango, Cerro Chémal summit of Sierra de los Cuchumatanes, alt. 3700—3800 m, Aug. 8, 1942. J. A. STEYERMARK no. 50508 (F holotype).

Dwarfish herb, forming loose mats. *Subterranean stem* rather short, up to 10 cm long, slender, 1—1.5 mm thick, shallowly creeping, with fibrous adventitious roots both from nodes and internodes, often many-branched and usually with several aerial stems. *Aerial stems* erect—ascending, often branched from base, short, 1—6 cm long, 1—2 mm thick with lateral branches or small buds in the lowermost axils, internodes 2—6, 2—7 mm long (Fig. 6 A). *Stolons* spreading shallowly beneath the ground, sparsely branched or unbranched, often pinkish, 0.3—0.7 mm thick, up to 10 cm long, internodes c. 1—2 cm long, ending with minute pointed buds (bulblets not observed), with thin, 0.8—1.6 mm long, ovate, acute, opposite, semiamplexicaul scales, scales sometimes replaced by small ordinary leaves (Fig. 6 A), transitions between stolons and normal branches occurring sometimes. *Leaves* 2—6 pairs, the lowermost \pm withered at anthesis, somewhat succulent, sessile or subsessile with an indistinct broad petiole, shorter than the blade, leaves 0.5—1.7 cm long, 0.2—0.6 cm broad, longer than the internodes, oblanceolate—narrowly elliptic or basal ones narrowly spatulate; leaf-base distinctly widened, half-clasping, often with narrow scarious margins; leaf-apex subacute. *Stomata* with two, rather distinct sub-

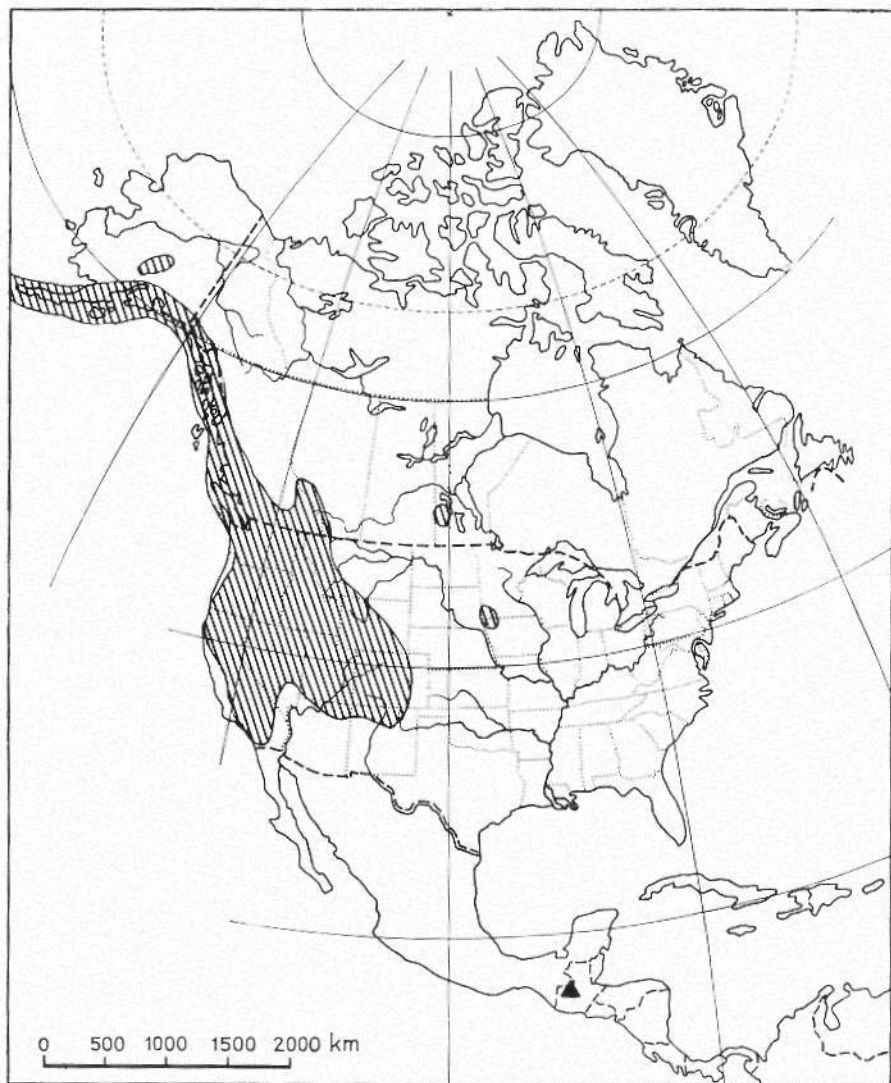


Fig. 5. General distribution of *Crunocallis chamissoi* in North America, hatched areas; outside the map the distribution continues to Attu in the Aleutian Islands. ▲ marks out the locality of *C. calcicola* in Guatemala.

sidiary cells; epidermal cells with slightly undulating side walls. *Inflorescences* 1—3, pseudolateral and axillary, with 1—4 flowers, axis and peduncle lacking (Fig. 6 B, C). *Bract* one, c. 2—3 mm long, scarious, often with a green apical point, ovate, acute, opposite the first flower.

Pedicels at anthesis 3—7 mm long, \pm erect, after anthesis up to 10 mm long, recurving like a bow. *Involucral leaves* broadly ovate, 1.5 mm long, the outer clasping the inner at least at the base, obtuse or slightly emarginate, both growing somewhat after anthesis, distinctly shorter than the capsule (Fig. 6 E). *Tepals* 2—3 mm long, 0.8—1.0 mm broad, of about equal size and shape, 1.5—2 times longer than the involucre, ascending in anthesis, obovate, subacute—obtuse with a short petiole, tepals connate at base to about 1/7 of their length, bright pink (Fig. 6 D). *Stamens* of about equal length, c. 1.5—1.7 mm long, filaments with a broad base adnate to tepals; anther medifixed, 0.3—0.5 mm long, \pm cordate or square with pointed lobes \pm diverging at the base, somewhat laterorse; flower probably autogamous (Fig. 6 D). *Style* rather thick and short, c. 0.5 mm long, about as long as the ovary, and distinctly set off from the ovary (Fig. 6 H). *Style branches* three, short, with rather closely set long papillae on their inner side, extending and diverging in late anthesis. *Capsule* 1.5 mm long, at base three-sulcate, grooves of about half capsule length (Fig. 6 G). *Ovules* three, all of which usually develop to seeds. *Seed* 1.0—1.2 mm long, 1 mm broad, glistening, dark chestnut brown—blackish. *Pollen grains* 46—49 μ in diam., minutely spinulate.

Discussion

Crunocallis calcicola may be regarded as a diminutive *C. chamissoi*. Among the characters in common some can be emphasized. The two species are perennial geophytes with a very effective subterranean propagation by means of stolons and stems. The anatomy and morphology of the stolons show great resemblances, e.g., in the starch-storing tissue and epidermis (cf. p. 131). But no bulblets of *C. calcicola* have been seen. The anatomy and morphology of the stem and leaves and the type of branching are similar. The flowers, capsules, seeds, and pollen grains are also similar in several respects.

There exist, however, some important morphological differences which make it appropriate to treat the two taxa as separate species. *C. calcicola*

Fig. 6. *Crunocallis calcicola*. — A: Portion of a plant, somewhat simplified, 1. stem, 2. stolon, 3. bud, 4. inflorescence, the flowers are cut off. — B: Highly simplified drawing of a branch with inflorescences. — C: Branch with inflorescences, 1. scarious bract, 2. pedicel, 3. lateral branch, 4. semiscarious bract. — D: Tepals and stamens. — E: Involucre and capsule. — G: Capsule. — H: Pistil.

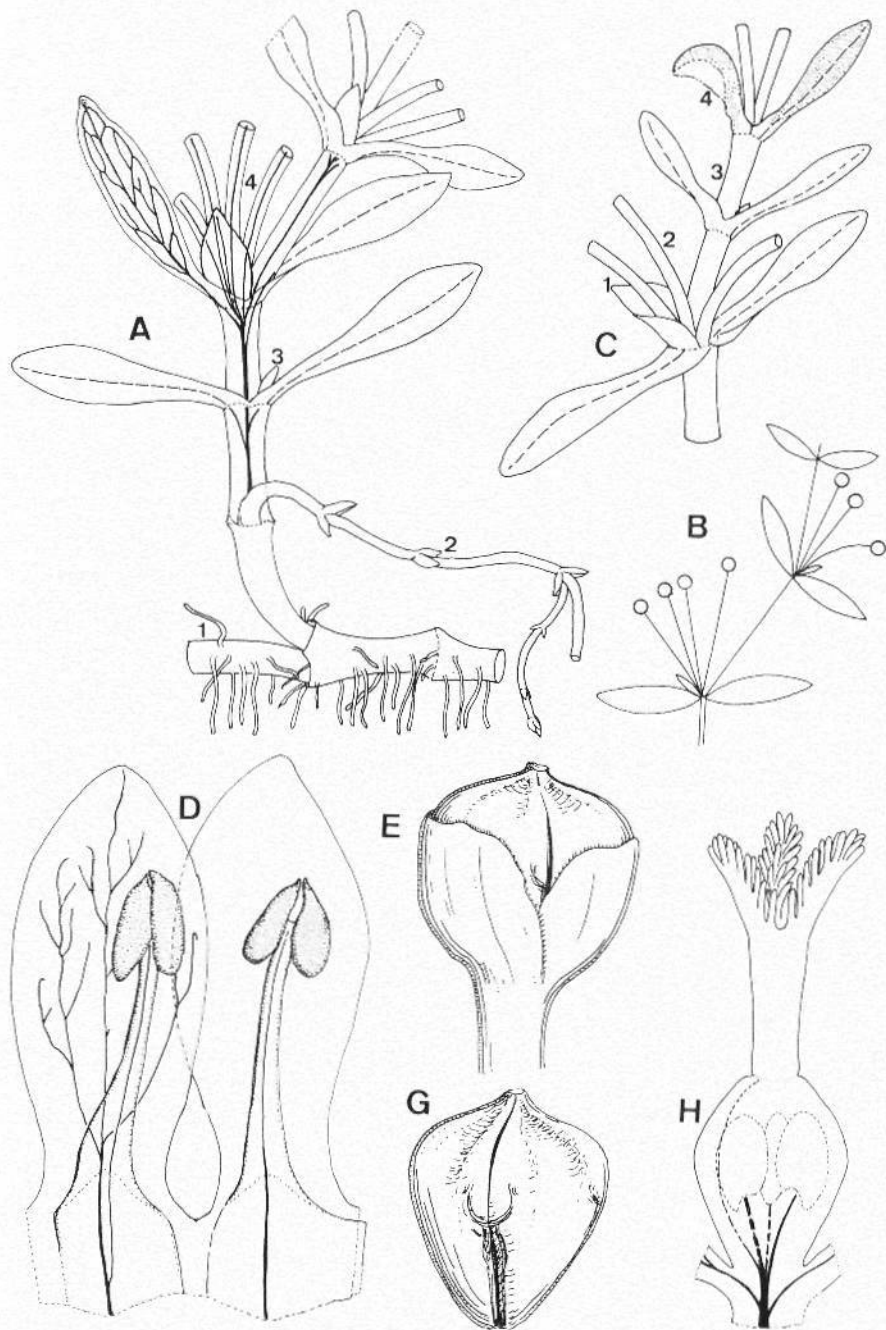


Fig. 6.

is a dwarfish herb with a many-branched subterranean stem. The inflorescence is always in pseudolateral position and lacks both axis and peduncle (cf. p. 133), both of which normally occur in *C. chamissoi*. The flower exhibits several diverging characters, some of which, however, may be regarded as different adaptations in consequence of the allogamy of *C. chamissoi* and the probably predominant autogamy of *C. calcicola*.

STANDLEY and STEYERMARK (1944 p. 49) referred *C. calcicola* to the genus *Montia*. It is obvious that *C. calcicola* has some resemblance to several *Montia* species, e.g., in general habit, leaf arrangement, inflorescence and small flowers. However, there are several important characters which make it natural to place the species in *Crunocallis*. Some characters of the *Montia* species are given below for comparison (cf. also p. 123). — The plants are mainly annual without hibernating stems or stolons. The stem has often a different type of branching with two lateral branches from each node. The stomata lack subsidiary cells and are restricted to the upper side of the leaves. The pedicels become hook-like after anthesis. Usually the tepals are distinctly unequal in size and they are united up to about half their length. The perianth has a characteristic deep median slit. The stamens are normally three and there is usually no style. The anthers are introrse. The capsule is usually not sulcate and its valves become separated almost to the base. There are some small pollen morphological differences too in, e.g., colpus length (cf. NILSSON 1967 pp. 351—352).

The material of *C. calcicola* is sparse. About 30 specimens have been examined. At present only two collections are known. Therefore nothing definite can be said of the intraspecific variation. It is not impossible that the taxonomic rank of *C. calcicola* might be altered when more extensive material becomes available.

In the collections, both fruiting and flowering specimens are present. There is only one flower in anthesis in the same inflorescence. Flowers and almost ripe fruits can be present simultaneously in an inflorescence or on a flowering stem.

Distribution and Habitat

Crunocallis calcicola is known at present only from Guatemala in Central America. It seems to be a local endemic plant restricted to the Sierra de los Cuchumatanes in the department of Huehuetenango. The

species has been collected in two places, 1. Cerro Chémal, and 2. Tojquia. Another collection from Guatemala referred to this species, Volcán Tajumulco, Dept. San Marcos, 1940, J. A. STEYERMARK no. 35596 (F), is incorrectly determined.

The species must have been isolated from closely related species for some considerable time in this mountainous area. The southernmost localities of *C. chamissoi* are in southern California. The only other member of the subfamily occurring in Guatemala is an annual *Claytonia* species.

C. calcicola grows in alpine areas at an altitude of 3700—3800 m. In STANDLEY and STEYERMARK (1944 p. 49) the altitude of the collection STEYERMARK 50127 is assigned to 2700 m, but on the original label the altitude is 3700 m. The species occurs on Mt. Cerro Chémal in woods of *Juniperus standleyi*. In the alpine area of Tojquia it grows in limestone bluffs.

Flowering period: August.

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APPENDIX

List of material examined.

Crunocallis chamissoi (LEDEB.) RYDB.

USA. ALASKA: Unalaska, ESCHSCHOLTZ (LE). — Unalaska, CHAMISSO in itin. (GH). — Ex Unalaska, det. LEDEBOUR (C). — Unalaska, ex herb. KLATT (S). — Amer. Bor., ESCHSCHOLTZ, ex herb. LEDEBOUR (S). — Amer. Ross., Sitcha, MERTENS (LE). — Sitcha, MERTENS (GH, LD, LE). — Shumagin Islands, Popof Island, 1899, T. KINCAID (S). — Lake Ilimna Region, 1902, M. W. GORMAN 123 (BM). — Kodiak Island, vicinity of Karluk, 1903, C. RUTTER 219 (C). — Baranof Island, Haanus Bay, 1917, E. P. WALKER 1175 (C). — Kodiak Island, Three Saints Bay, 1931, W. J. EYERDAM 322 a (BM, GB, LD, S). — Aleutian Islands, Umnak Island, Nikolski, 1932, E. HULTÉN 5729 (S). — Aleutian Islands, Attu, 1932, E. HULTÉN 6821 (S). — Aleutian Islands, Unimak Island, False Pass, 1932, W. J. EYERDAM 2038 (S), EYERDAM 2057 (C, S), EYERDAM 2107 and 2157 (S). — Seward, 1934, F. W. WENT 276 (LD). — Meier's R. H., RICHARDSON Hwy 175, 1935, J. P. ANDERSSON 2076 (LD, S). — Kodiak Island, near cannery, 1936, I. W. HUTCHISON 296 (BM). — Seward, 1937, E. SCAMMAN 547 (GH). — Seward, 1939, J. P. ANDERSSON 5651 (S). — Haines, 1946, M. WILLIAMS & L. STONEHOUSE (S). — King Salmon, beach of Naknek River, 1952, W. B. SCHOFIELD 2270 (S). — King Salmon, margin of Naknek River, 1952, W. B. SCHOFIELD 2598 (COLO). — Alaska Range, Tangle Lakes, along Denali Hwy c. 20 miles W of Paxson's, 2900 feet, 1953, G. SMITH 2092 (S).

ARIZONA: Willow Spring, 1874, J. T. ROTHROCK 219 (GH). — Willow Spring, 1890, E. PALMER 570 (C, GH, S). — Bill William's Mt., 1893, H. H. RUSBY 534 (S).

CALIFORNIA: Soda Springs, 2700 m, 1863, W. H. BREWER 1707 (GH). — Yosemite, 1872, A. GRAY (GH). — Sierra Co., 1874, J. G. LEMMON 27 (GH). — Near Truckee, 1878, SORME (C). — Nevada Co., Soda Springs, 2300 m, 1881, M. E. JONES (POM). — San Bernardino Mts., Bear Valley, 1882, S. B. & W. F. PARISH 1492 (BM, GH, S). — Emigrant Gap, 1882, M. E. JONES 2628 (BM, LE, POM). — Yosemite Valley, 1886, H. N. BOLANDER 374 b (GH). — Tulare Co., Long Meadow, 3000 m, 1888, E. PALMER 197 (BM). — Alpine Co., Twin Lakes, c. 3000 m, 1892, G. HANSEN 546 (BM, WRSL). — Alpine Co., Cahle Lake, c. 3000 m, 1892, G. HANSEN (JE). — Plumas Co., 1893, M. E. P. AMES (GH). — Goose Lake Valley, 1895, R. M. AUSTIN 470 (POM). — Lassen's Peak, 2000 m, 1897, M. E. JONES (BM, POM). — San Jacinto Valley, along creeks of Tamarack Valley, 1901, H. M. HALL 2362 (E). — Natural Bridge Meadow, 1700 m, 1904, CULBERTSON 5027 (POM). — Tuolumne Co., Tuolumne Meadows near Soda Springs, 1800 m, 1907, R. A. WARE 2655 c (GH). — Fresno Co., Kearsarge Pass, 1910, J. CLEMENS (POM). — Yosemite Nat. Park, Yosemite Valley, 1300 m, 1911, L. R. ABRAMS 4447 (GH, POM). — Tahoe City, Lake Tahoe Region, 1912, A. EASTWOOD 438 (GH). — Humboldt Co., Buck Mt., near the summit, c. 2000 m, 1913, J. P. TRACY 4169 (E). — Calveras Co., Lake Tahoe Region, Mt. San Joaquin, c. 3000 m, 1916, H. M. EVANS (F). — Fresno Co., Tamarack Meadows near Dinkey Grove of Big Trees, 2800 m, 1917, A. L. GRANT 1189 (POM). — San Bernardino Mts., Huntsacker Flats, 1700 m, 1919, P. A. MUNZ & D. M. JOHNSTON 2907 (POM). — Sutter Co., 1 mile below Susko Meadow, 1921, H. M. EVANS (F). — San Bernardino Mts., Bear Valley 2 miles E of Bluff Lake, 1922, P. A. MUNZ 5619 (POM). — San Jacinto Mts., Tahquits Valley, 2400 m, 1922, P. A. MUNZ 5994 (POM). — San Bernardino Co., San Bernardino Mts., Bluff Lake, 2400 m, 1922, P. A. MUNZ 10440 (POM). — San Diego Co., Palomar Mts., near Doane Valley, 1600 m, 1924, P. A. MUNZ 8307 (POM). — Tuolumne Co., Aspen Valley, 2100 m, 1932, L. BENSON 3764 (POM). — Ventura Co., Mt. Pinos, head of Bitter Creek, 2800 m, 1933, J. A. EWAN 7764 (POM). — Tuolumne Co., Pine Crest Recreation Area, Stanislaus Nat. Forest, 1934, I. L. WIGGINS 6797 (LD). — Siskiyou Co., Siskiyou Mts., Jayne's Canyon, 2100 m, 1935, L. C. WHEELER 3705 (GH). — San Bernardino Co., San Bernardino Mts., Bluff Lake, 2500 m, 1936, C. B. VOLF 8046 (GH). — San Bernardino Co., San Bernardino Mts., near South Fork, 2400 m, 1937, J. ROOS 334 (POM). — Modoc Co., between Likely and Jess Valley, 1940, A. EASTWOOD & J. T. HOWELL 8076 (GH). — Mono Co., Sierra Nevada, Mammoth Lakes Post Office, 2500 m, 1942, L. BENSON 11238 (POM). — Inyo Co., Sierra Nevada, Onion Valley W of Independence, 3000 m, 1942, A. M. ALEXANDER & L. KELLOGG 3191 (GH). — Madera Co., Pumice Flat Forest Service Campgd. along upper San Joaquin River, 7800 feet, 1956, E. K. BALLS 10957 (S). — Mono Co., White Mountain Road, at Campito Meadow, 10600 feet, 1963, R. M. LLOYD 3173 (C).

COLORADO: nr. 7887 (LD). — N. Sierra Blanca, J. D. HOOKER & A. GRAY (GH). — Ute Pass, 1861, FLACES (C). — Rocky Mts., 1862, C. C. PARRY (GH). — Rocky Mts., 1862, E. HALL & J. P. HARBOUR 84 (GH). — Rocky Mts., 1868, G. VASEY 88 (GH). — Alpine, 1872, C. C. PARRY (GH). — Georgetown, 2800 m, 1878, M. E. JONES 345 (BM, GB, POM). — Boulder Co., 1881, J. I. MET. (COLO). — Montes, 2000 m, 1886, A. EASTWOOD (LD). — Palmer Lake, 1887, A. EASTWOOD (COLO). — Bear River Flats, 2000 m, 1892, C. S. CRANDALL (GH). — Rancho, Como, 1892, E. L. HUGES 9 (GH). — Colorado Mts., about the head waters of Clear Creek, near Empire, 2800 m, 1892, H. N.

PATTERSON 174 (GH). — Moon's Ranch, 2800, 1894, C. S. CRANDALL 101 (GH). — Moon's Ranch, 14 miles W of Livermore, 2300 m, 1894, C. J. BAKER (POM). — Larimer Co., Moon's Ranch, 1894, C. J. BAKER (POM). — Steamboat Springs, 1894, C. F. BAKER (POM). — El Paso Co., Ute Pass, 1896, BILTMORE 1983 a and 1983 b (S). — Boulder Co., 1896, F. J. MOSLEY 278 (COLO). — Beaver Creek, 3200—4000 m, 1898, 14 (LD). — Long's Peak, aspen zone, 8600 feet, 1899, T. HOLM (S). — Buffalo Park, 1901, W. C. FERRIL (COLO). — Magnolia, 1800 m, 1901, H. N. WHEELER 351 (COLO). — Eldora, 1902, F. RAMALEY B 12 (COLO). — Cumbers, 1902, W. C. FERRIL (COLO). — Grant, 1904, W. M. HUESTIS (COLO). — Near Florissant, 1800 m, 1905, F. RAMALEY 1360 (COLO). — S Boulder Canyon, 1906, W. W. ROBBINS 1630 (COLO). — Lake 1/4 mile below Tolland, 2900 m, 1907, F. RAMALEY & W. W. ROBBINS 3377, (COLO). — Tolland, 1909, F. RAMALEY & W. W. ROBBINS (COLO). — Park Lake, Lindland, 1910, W. W. ROBBINS 7827 (COLO) and 1913, ROBBINS 10141 (COLO). — Loveland, 3000 m, 1919, P. A. MUNZ 3224 (POM). — Estes Park, 1924, W. PENFOUND 363 (COLO). — Larimer Co., Rocky Mt. Nat. Park, Longs Peak Valley, 2500 m, 1928, W. KIENER 2146 (COLO). — Boulder Co., 3 miles below Ward on left hand, 1932, H. W. CAMPBELL 98 (COLO). — Boulder, Estes Park, 2300 m, 1933, H. LENANDER (S). — Cuchara Valley, above Cuchara Pass, 3500 m, 1934, B. M. STIGALL (COLO). — San Luis Valley, Almosa Canyon, 2900 m, 1936, F. RAMALEY 15810 (COLO). — San Luis Valley, Rock Creek Canyon near Monte Vista, 3000 m, 1936, F. RAMALEY 15632 (COLO). — Chaffee Co., Four Mile Creek, 8 miles NE of Buena Vista, 3200 m, 1936, R. C. ROLLINS 1388 (GB). — Deep Creek, near Creede, 2900 m, 1937, B. K. STEWART 820 (COLO). — Deep Creek, 2 miles S of Creede c. 3000 m, 1937, B. K. STEWART 855 (COLO). — Estes Park, Fall River, 1937, C. H. KNOWLTON (GH). — Deep Creek, near Creede, 2900 m, 1938, B. K. STEWART 1285 (COLO). — Middle St. Vrain Canyon, 1939, H. L. ZOBEL (SMU, UPS). — San Luis Valley, Parlin-Saguache Hwy E of Cochetopa Pass, 3000 m, 1939, F. RAMALEY & W. GAMBILL JR. 16933 (COLO). — Wason, 3000 m, 1939, B. K. STEWART 1454 (COLO). — Clear Creek Co., near edge of Echo Lake not far below timberline, Mt. Evans, 1941, U. T. WATERFALL 3381 (GH). — Larimer Co., Rocky Mt. Nat. Park, Beaver Park, 1947, E. WHITEHOUSE 18922 (SMU). — Grand Co., near Tabernash, A. Petersen's Ranch, 1947, E. WHITEHOUSE 19034 (SMU). — Boulder Co., Wagoner's Tahosa Valley on Branch of N St. Vrain, 1/2 mile S of Meeker Lodge, 2700 m, 1949, L. BOUGERE 1793 (SMU). — Boulder Co., trail from Wild Basin River S to Thunder Lake, Rocky Mt. Nat. Park, 2900—3200 m, W. A. WEBER 5744 (SMU). — Routt Co., Trail from Columbine to summit of Hahn's Peak, 2500—3500 m, 1951, W. A. WEBER 6903 (COLO). — El Paso Co., along Black Squirrel Creek near its head, NE of Colorado Springs, 1953, L. S. ROSE & W. A. WEBER 8492 (COLO). — Boulder Co., Front Range Trail, above Nederland, 8500 feet, 1962, G. N. JONES 33962 (S).

IDAHO: Latah Co., Little Pottalch River, 1892, D. L. Mc DOUGAL 398 (S). — Latah Co., 1892, J. H. SANDBERG (GH). — Latah Co., head of Little Pottalch River, 1892, J. H. SANDBERG et al. (BM, GH, POM). — Near Keltchum, 1892, A. J. MULFORD (GH). — Washington Co., Goose Creek, 1800 m, 1899, M. E. JONES (POM). — St. Anthony, 1901, E. D. MERRILL & E. N. WILCOX 860 (GH). — Owyhee Co., Jordan Valley, 1911, J. F. MACBRIDE 960 (GH, POM, SMU). — Owyhee Co., House Creek, 1912, A. NELSON & J. F. MACBRIDE 1802 (E, GH, S, SMU). — Blain Co., Corral, 2000 m, 1916, J. F. MACBRIDE & E. B. PAYSON 2942 (E, GH, POM). — Fremont Co., Buffalo

River, 1934, G. N. JONES 5183 (GH). — Idaho Co., near Cottonwood, 1937, J. H. CHRIST 7553 (SMU). — Idaho Co., about 1/2 mile N of New Meadows, 1938, F. G. MEYER 1462 (BM, GH). — Adams Co., 4 miles W of New Meadows, 1946, M. & G. B. OWNBEY 2757 (S, SMU).

MINNESOTA: Queen's Bluff, Dresbach, 1889, J. M. HOLZINGER (POM). — Base of Queen's Bluff, 1895, J. M. HOLZINGER (COLO, GH, POM). — Winona Co., 1896, J. M. HOLZINGER (GH), 1897, HOLZINGER (SMU). — Winona Co., Queen's Bluff, 1919, C. O. ROSENDAHL 3839 (GH).

MONTANA: Gallatin Co., West Yellowstone, 2200 m, 1920, E. B. PAYSON 1935 (GH).

NEVADA: Reno, F. H. HILLMAN (POM). — Harallat Mts., 2000 m, 1868, S. WATSON (GH). — Esmeralda Co., White Mts., 400 m, 1888, W. H. STOCKLEY 590 (GH). — Reno, foothills, 2000 m, 1897, M. E. JONES (POM). — Ormsby Co., Kings Canon, 1700—2000 m, 1902, C. F. BAKER 901 (GH, POM). — Jarbidge, 2300 m, 1912, A. NELSON & J. F. MACBRIDE 2056 (GH). — Washoe Co., Thomas Canyon, 2700 m, 1912, P. B. KENNEDY 1877 (GH). — Washoe Co., Lemmon Valley, 2000 m, 1913, P. B. KENNEDY 2088 (E, GH). — Duch Creek, Schell Creek Mts., 1924, M. E. JONES (POM). — Esmeralda Co., Chiatovitch Creek, White Mts., 2450 m, 1931, V. DURAN 3079 (C, E, GH, LD, POM, PRC, S). — Nye Co., Monitor Range, Toiyabe Nat. Forest, Scuffe Pasture, head of Baily Creek, Table Mt., 3100 m, 1945, B. MAGUIRE & A. H. HOLMGREN 25732 (GH, W).

NEW MEXICO: Colfax Co., Intervals, 1896, O. ST. JOHN 85 (GH). — Rociada, 1905, J. E. DANDELIN (GH). — Pecos River Nat. Forest, mouth of Pouchuelo Creek, 2800 m, 1908, P. C. STANDLEY 4092 (GH).

OREGON: Ex herb. J. A. LOWELL 1201 (GH). — C. A. GEYER 531 (BM). — Oregon 1866, NUTTALL (GH). — Banks, Shunap, 1872, M. W. HARRINGTON (GH). — Grant's Pass, 1881, T. HOWELL (C). — Waldo Co., Grant's Pass, 1884, T. HOWELL (GH). — Malheur Co., near Harper Ranch, 750 m, 1896, J. B. LEIBERG 2111 (BM, GH, POM, S). — Klamath Co., Keno, 1920, M. E. PECK 9348 (GH). — Klamath Co., Swan Lake Valley, 1923, E. I. APPLGATE 3559 (LD). — Josephine Co., Bolar Lake, Siskiyou Mts., 1700 m, 1935, J. W. THOMPSON 12505 (LD). — Lake Co., 4 miles N of Lakeview, 1940, C. L. HITCHCOCK 6738 (POM). — Crook Co., Indian Creek just N of Big Summit Prairie, Ochoco Mts., between Prineville and Mitchell, 1700 m, 1953, A. CRONQUIST 7375 (LD, S).

UTAH: 10 miles N of Fish Lake, 3000 m, M. E. JONES 5831 (BM, POM). — Uinta Mts., 2000 m, 1869, S. WATSON 184 (GH). — Fish Lake, 1882 and 1894, M. E. JONES (POM). — Utah Co., Mt. Timpanogos, Wasatch Mts., 2200 m, 1927, A. O. GARRETT 3655 (LD). — Blacksmith Forks Canyon, 1800 m, 1932, B. & R. MAGUIRE 3351 (GH, POM). — Garfield Co., Pleasant Creek Channel, near Wild Cat R. Sta., E Face Aquarius Plateau, Powell Nat. Forest, 1932, H. DIXON 646 (F).

WASHINGTON: J. G. Cooper (GH). — Cimcoe Mts., 1880, T. J. HOWELL (GB). — Roy, 1889, O. H. ALLEN 93 (GH). — Falcon Valley, 1890, W. N. SUKSDORF 958 (GH). — Pullman, 1893, C. V. PIPER 1712 (GH). — Spokane Co., near Rock Creek, 750 m, 1893, J. H. SANDBERG & J. B. LEIBERG 88 (BM, C, GH, S). — Whitman Co., Pullman, 1897, A. D. E. ELMER 818 (POM). — Kittitas Co., N of Ellensburg, 1932, J. W.

THOMPSON 8361 (C, GH, LD). — Asotin Co., 1/2 mile W of Anatone Butte, 10 miles SW of Anatone, 1500 m, 1949, A. CRONQUIST 5927 (COLO, S, SMU).

WYOMING: Pole Creek, 1895, A. NELSON 1337 (S). — Green Iop, 1897, A. NELSON 3250 (BM, POM). — Yellowstone Nat. Park, Yancey's, 1899, A. & E. NELSON (BM, GH, POM, S, UPS, WRSL). — Head of Lake Sybille, 1894, A. NELSON 309 (GH). — Albany Co., Chug Creek, 1900, A. NELSON 7343 (COLO. GH, LD, POM, S). — Big Horn Co., Canon Creek, 1901, L. N. GOODING 401 (GH). — Yellowstone, 2600 m, 1907, E. O. ESSIG (POM). — Dale Creek, 1908, J. CLEMENTS (GH). — Hawk's Ranch, 25 miles S from Laramie, 1918, J. R. CHURCHILL (GH). — Yellowstone Park, Gibbon River 1921, K. M. WIEGAND et al. 875 (F). — Yellowstone Park, Hayden Valley, 1925, P. H. HAWKINS (MT). — Albany Co., Douglas Creek., Medicine Bow Mts., 1929, G. J. GOODMAN 899 (M). — Albany Co., Along Crow Creek, Laramie Mts., 1934, C. L. PORTER 1469 (S). — Albany Co., in the vicinity of Vedawoo Glen, Laramie Mts., 2800 m, 1935, R. C. ROLLINS 993 (GH). — Albany Co., Pole Mt., Region, 2800 m, C. L. PORTER 4023 (GH, SMU, UPS), PORTER 4029 (S).

Canada. BRITISH COLUMBIA: Vancouver Island, 1875, J. MACOUN (CAN). — Vancouver Island, vicinity of Comoy, 1893, J. MACOUN (BM). — Vancouver Island, Comoy 1893, J. MACOUN (GH). — Vancouver Island, Somas River, Alberni, 1916, J. K. HENRY & W. R. CARTER 9050 (GH). — Vancouver Island, Alberni, Sproat Lake Falls, 1917, W. R. CARTER 149 (GH). — Vancouver Island, Sproat River, near Sproat Lake, 1907, C. O. ROSENDAHL 1937 (C, GH).

Crunocallis calcicola (STANDL. & STEYERM.) Ö. NILSS.

Guatemala: Dept. Huehuetenango, Tojquia in Sierra de los Cuchumatanes, 1942, J. A. STEYERMARK 50127 (F, US).

Studies in Galápagos Plants VIII¹

Chromosome Numbers of Some Endemic Species

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ABSTRACT

ELIASSON, U.: Studies in Galápagos Plants VIII. Chromosome Numbers of Some Endemic Species. — Bot. Notiser 123: 149—154, Lund.

Chromosome counts of seven species of endemic plants of various families in the Galápagos archipelago are reported. The following somatic numbers have been found: *Pleuropetalum darwini* HOOK. F. (*Amaranthaceae*) $2n=34$, *Nolana galapagensis* (CHRISTOPH.) JOHNST. (*Nolanaceae*) $2n=24$, *Scalesia affinis* HOOK. F. (*Compositae*) $2n=68$, *S. crockeri* HOWELL $2n=68$, *S. hopkinsii* ROBINS. $2n=68$, *S. microcephala* ROBINS. $2n=68$, *Lecocarpus foliosus* DECAISNE (*Compositae*) $2n=22$.

MATERIAL AND METHODS

Chromosome counts were made from root tips of plants, about two years of age, grown in green-house conditions in the Botanic Garden of Göteborg. The plants were grown from seeds collected in the Galápagos during the years 1966 and 1967.

The method used was a modification of that described by ÖSTERGREN and HENEEN (1962). Excised root tips were pretreated for three hours with a solution of 8-hydroxy-quinoline (concentration 0.002 mols/litre), and fixed for one minute in Carnoy (three parts alcohol, one part glacial acetic acid). After hydrolysis in 1 N HCl for eight minutes at 60°C, the roots were stained in Schiff's reagent for three hours, and then left for two hours in a solution of 5% pectinase to make the cells more easily separable. After treatment in 45% acetic acid for twenty minutes, the root tips were squashed on a slide under a cover slip of Vipolon plastic. The preparations were sealed by the application of a rubber solution around the edges of the cover slip. The rubber solution was left dry for some hours. The slides were left in acetone over night to dissolve the plastic cover slip. After removal of the rubber frame and the plastic cover slip, the slides were transferred to a mixture of equal parts of acetone and xylol, and then to xylol. The preparations were mounted in DPX under a glass cover slip.

This method yielded good results for the genera *Scalesia* and *Lecocarpus*. In *Pleuropetalum* and *Nolana* the chromosomes were very faintly stained.

¹ Contribution No. 118 from the Charles Darwin Foundation for the Galápagos.

although sufficiently so to make counts possible. A closer study of the structure of the chromosomes has not been possible.

The drawings were made by camera lucida.

RESULTS

Pleuropetalum darwinii HOOK. F. — Fig. 1 A

SEED COLLECTION: ELIASSON 1271, Isla Isabela, Volcán Alcedo, near the geyser on the southern inner slope of the crater, alt. c. 900 m, 12 Feb. 1967.

CHROMOSOME COUNT: $2n=34$. It was possible to count the number in five cells. All counts originate from one plant.

The species is endemic to Galápagos and known from the islands of Isabela, San Salvador and Santa Cruz. It is a shrub 1—2 m tall. The genus comprises five species in Central America and tropical South America. I have been unable to find any previous reports of the chromosome number in this genus. Within the family (*Amaranthaceae*) the same somatic number ($2n=34$) has been reported in several species of *Amaranthus* (cf. e.g. SHARMA & BANIK 1965).

Nolana galapagensis (CHRISTOPH.) JOHNST. — Fig. 1 B

SEED COLLECTION: ELIASSON s.n., Isla Santa Cruz, south side, Turtle Bay, alt. 0—10 m, 11 May 1967.

CHROMOSOME COUNT: $2n=24$. Counts were made in six cells, all from one plant.

This endemic species is rather wide-spread in the archipelago and grows on shell sand near sea level, forming rounded shrubs about one meter in diameter. The main distributional area of the genus (and the family *Nolanaceae*) is the coastal regions of Chile and southern Peru. JOHNSTON (1936), in his monographic treatment of the family, recognizes 57 species of *Nolana*, but according to WILLIS (1966) the genus should comprise about 80 species. The Galápagos plant sets the extreme northern limit for the genus.

The chromosome number of *Nolana galapagensis* agrees with the number found by previous authors (CAMPIN 1925, WHYTE 1929, SAUNDERS 1930, DATTA 1933, SUGIURA 1936) in the mainland species "*N. atriplicifolia*", "*N. grandiflora*", "*N. prostrata*" and "*N. tenella*". Since no author combinations have been cited in the works mentioned, it is not quite clear on what species the counts have been made. JOHNSTON (1936) gives the following synonymy (valid names in bold face):

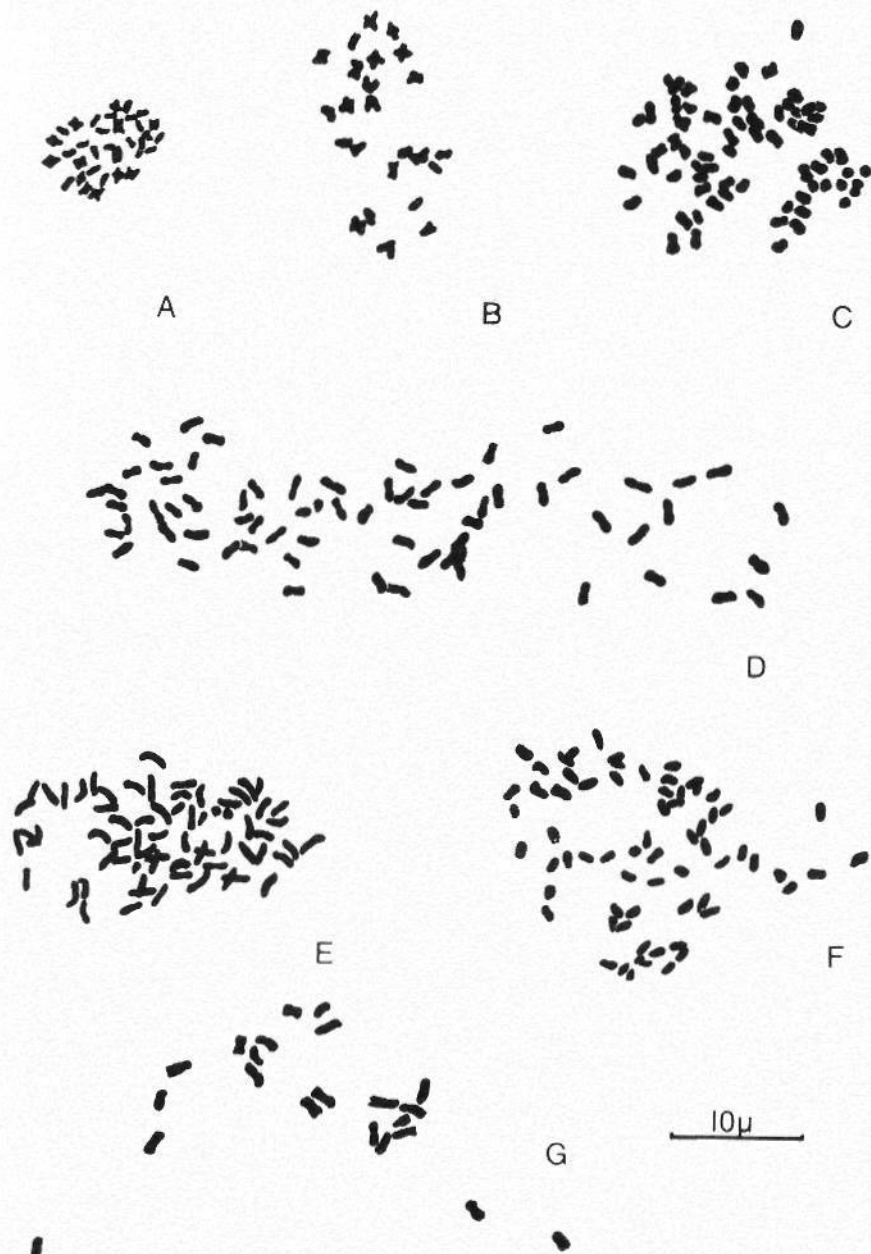


Fig. 1. Squashed chromosome plates. — A: *Pleuropetalum darwinii* HOOK. F. — B: *Nolana galapagensis* (CHRISTOPH.) JOHNST. — C: *Scalesia affinis* HOOK. F. — D: *S. crockeri* HOWELL. — E: *S. hopkinsii* ROBINS. — F: *S. microcephala* ROBINS. — G: *Lecocarpus foliosus* DECAISNE.

N. paradoxa LINDL. = *N. atriplicifolia* D. DON = *N. grandiflora* LEHMANN, while *N. grandiflora* HERZOG = **N. acuminata** MIERS. and *N. prostrata* L. = **N. humifusa** (GOUAN) JOHNST. *N. paradoxa* and *N. acuminata* are both Chilean, while *N. humifusa* is Peruvian. *N. tenella* LINDL. is considered by JOHNSTON (op. cit. p. 81) to be of garden origin and a chance hybrid of *N. humifusa* and *N. paradoxa*.

Scalesia ARN.

Scalesia is an endemic genus of the *Compositae* (*Heliantheae* - *Verbesininae*). HOWELL (1941), in his monograph of the genus, treats eighteen species, but the delimitation of several taxa is still unsatisfactory, especially concerning the species with lobed leaves.

Chromosome counts have been made previously by ONO (1967 a), who counted 68 chromosomes in somatic cells of *S. affinis* HOOK. F. and *S. pedunculata* HOOK. F. He (1967 a, b) also discussed the systematic relationship of the genus from the data of chromosome numbers.

I have counted chromosomes in *S. affinis* and in another three species not previously investigated in this respect. In all of them the somatic number was found to be 68.

Scalesia affinis HOOK. F. — Fig. 1 C

SEED COLLECTION: ELIASSON s.n., Isla Santa Cruz, Academy Bay, alt. c. 10 m, Nov. 1966.

CHROMOSOME COUNT: $2n=68$. Counts were made in ten cells, all from one plant.

The species forms a shrub or small tree, up to 3 m tall, and is distributed on the islands of Fernandina, Floreana, Isabela and Santa Cruz. Specimens from different islands are somewhat divergent, and three subspecies have been distinguished (cf. HARLING 1962).

Scalesia crockeri HOWELL — Fig. 1 D

SEED COLLECTION: ELIASSON 1990, Isla Santa Cruz, north-east side, Punta Carrión, alt. 5—10 m, 21 April 1967.

CHROMOSOME COUNT: $2n=68$. Counts were made in eight cells, all from one plant.

The species forms a low shrub about 1 m tall. It is restricted to lava cliffs close to the sea on the north-east side of Santa Cruz and on the associated islands of Baltra and Seymour.

Scalesia hopkinsii ROBINS. — Fig. 1 E

SEED COLLECTION: ELIASSON 2146, Isla Pinta, south side, alt. 200 m, 17 May 1967.

CHROMOSOME COUNT: $2n=68$. Counts were made in about twenty cells, all from one plant.

The species forms shrubs or small trees, up to 3 m tall. In a restricted sense, the species is known only from the island of Pinta, but the delimitation from other species with deeply lobed leaves is not altogether satisfactory.

Scalesia microcephala ROBINS. — Fig. 1 F

SEED COLLECTION: ELIASSON 1301, Isla Isabela, Volcán Alcedo, on the eastern slope of the volcano, alt. 800 m, 13 Feb. 1967.

CHROMOSOME COUNT: $2n=68$. Counts were made in seven cells, all from one specimen.

A small tree, 2—4 m tall. This species forms low-growing forests at high levels on the islands of Fernandina and Isabela.

Lecocarpus foliosus DECAISNE — Fig. 1 G

SEED COLLECTION: ELIASSON s.n., Isla Floreana, Floreana Peak, alt. 350 m, 22 Nov. 1966.

CHROMOSOME COUNT: $2n=22$. Counts were made in six cells, all from one plant.

A monotypic genus of the *Compositae* (*Heliantheae* - *Melampodinae*), restricted to the island of Floreana. This low shrub, up to 1 m tall, grows on lava fields near the shore as well as on the inner parts of the island.

Chromosome counts have hitherto been published for only a few genera within this subtribe, but the basic number 11 has not been found previously. The genera closest related to *Lecocarpus* seem to be *Melampodium* L. and *Acanthospermum* SCHRK. The only chromosome counts hitherto in these genera seem to be those of TURNER and FLYR (1966), who found $n=10$ in two species of *Melampodium*.

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Studies in South African Liliaceae

III. The Genus *Rhadamanthus*

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ABSTRACT

NORDENSTAM, B.: Studies in South African Liliaceae. III. The Genus *Rhadamanthus*. — Bot. Notiser 123: 155—182, Lund.

In the present revision of the genus *Rhadamanthus* SALISB. (*Liliaceae-Scilleae*) all three previously described species are recognized, viz. the type species *R. convallarioides* (L. F.) BAK., *R. urantherus* DYER, and *R. cyanelloides* BAK. Six new species are added, viz. *R. montanus* B. NORD., *R. arenicola* B. NORD., *R. secundus* B. NORD., *R. platyphyllus* B. NORD., *R. fasciatus* B. NORD., and *R. albiflorus* B. NORD. The genus is closely allied to *Urginea*, from which it differs chiefly by the mode of dehiscence of the anthers. *Rhadamanthus* is confined to southern Africa, and most species occur in arid regions.

INTRODUCTION

The genus *Rhadamanthus* was established by SALISBURY in his posthumously published fragment of 'The genera of plants' (SALISBURY 1866). The genus was originally monotypic, including only *Hyacinthus convallarioides* L. F. Among the many new genera proposed in this work, the only one subsequently accepted by BAKER was *Rhadamanthus* (BAKER 1871). In 'Flora Capensis' BAKER added a second species but hesitatingly, viz. "*R. ? cyanelloides*" BAKER (1897). A third species, *R. urantherus* DYER, was described in 1934.

The present study was initiated during my stay in South Africa in 1962—64, when I experienced some difficulties to name properly a few small bulbous lilies, which I had brought into cultivation (in Kirstenbosch, and later in the Botanical Garden of Lund, Sweden). One of my plants appeared to be a very distinct new species of *Rhadamanthus*, characterized by its two flat and broad leaves. The other two collections were less clear-cut, however, and I finally realized that a revision of all available material of this small genus was necessary. This study was accelerated by a request from Professor MERXMÜLLER

of Munich to examine the South West African material of the genus as well as some other collections of obscure affinity within the tribe. The investigation gave the surprising result, that my own three collections represented as many undescribed species and that another three new species would have to be added.

The affinities of *Rhadamanthus* are very clearly with the large genus *Urginea*. The chief difference is found in the mode of anther dehiscence. The anthers of *Rhadamanthus* are said to open by apical pores. A more correct description is that the anthers dehisce incompletely by introrse longitudinal slits. When the sutures reach down below the middle of the thecae, as in *R. fasciatus* and *R. albiflorus*, the difference from the complete dehiscence in *Urginea* may seem trifling.

Some other characters may be thought of as typical of *Rhadamanthus*, e.g. the constantly hysteranthous leaves, the slender peduncle, the spurred bracts, the pendulous gamophyllous and bell-shaped perigons, and the black discoid seeds with a firm endosperm. All these characters occur in species with complete anther dehiscence, however, and thus have little diagnostic value in the present classification. The importance of a gamophyllous perigon as a generic character was stressed by COMPTON, who defined the monotypic genus *Urgineopsis* from *Urginea* on this single character (COMPTON 1930). Two years earlier DUTHIE had distinguished a section *Pseudurginea* of four *Urginea* species with tepals united at the base (DUTHIE 1928). ADAMSON (1942) in a discussion of this character concluded that *Urgineopsis* must be included in *Urginea*. Until the generic limits within the South African *Scilleae* have been revised, *Rhadamanthus* is best retained as a genus. In its present circumscription the genus gives the impression of a natural group of species, with the exception of *R. cyanelloides*. When better known the latter species certainly will have to be excluded.

The present revision will serve to illustrate our incomplete knowledge of several species. Rootstock, leaves, capsules and seeds are unknown in *R. cyanelloides*, and in other species information is lacking in one or more of these respects. It is recommendable to study the plants in cultivation. They readily set fruits and seeds and are probably autogamous. Other aspects needing further study include pollen morphology, cytology and bulb anatomy.

The revision is based on herbarium material from the following herbaria (abbreviations according to LANJOUW and STAFLEU 1964 with the addition of WHK): B, BM, BOL, G, GRA, K, L, LD, M, NBG, PRE, S, SAM, UPS, W, WHK (= South West African Herbarium, Windhoek, South West Africa).

RHADAMANTHUS SALISB.

SALISBURY 1866 p. 37; BAKER 1871 p. 434; BENTHAM & HOOKER 1883 p. 808; BAKER 1897 p. 444; THONNER 1915 p. 128; PHILLIPS 1926 p. 151; KRAUSE 1930 p. 341; PHILLIPS 1951 p. 190.

Caudex a thinly tunicated bulb; bulb scales sometimes only loosely imbricated or even separate and stalked, apically (especially the inner ones) often produced into short or rarely elongated papyraceous sheaths; these distinctly or obscurely fasciated with \pm raised cross-bars. Roots several, fibrous.

Leaves hysteranthous, radical, erect or spreading, 1 or 2 or several—numerous, filiform—linear or ovate—oblong, glabrous or pubescent.

Scape solitary, simple, erect, leafless, glabrous or minutely puberulous—scabrid with numerous small hairs or excrescences arranged in several longitudinal rows.

Inflorescence a lax to subdense, few- to many-flowered, often somewhat unilateral bracteate raceme. Bracts membranous, shorter than the pedicels (in one species of equal length); lower bracts usually distinctly spurred basally. Pedicels erecto-patent—spreading, \pm curved near the apex (upwards in bud and fruit, downwards during anthesis).

Perigon campanulate—subglobose; tepals half-closed to almost spreading during anthesis, subequal or somewhat unequal, midribbed, connate basally or up to above the middle, seldom free from the base.

Stamens enclosed. Filaments basally adnate to the perigon or almost free, shorter to somewhat longer than the anthers. Anthers often somewhat connivent around the gynoeceium (in *R. cyanelloides* permanently connate into a cone), yellow—greenish, basifixed—medifixed, dehiscing introrsely with incomplete longitudinal slits, which remain apical and pore-like or proceed down to the middle of the theca or somewhat more; thecae basally rounded or apiculate—caudate, glabrous or barbellate.

Ovary sessile, globose—ovoid—subquadrate, often trilineate and somewhat triquetrous, glabrous or papillate—puberulous. Style columnar—subclavate, thick and short (seldom longer than the ovary) or lacking; stigma capitate and faintly trisulcate or crateriform with shallowly lobed margin.

Capsule ovoid—subglobose, somewhat triquetrous, often carrying the withered perigon as a hood, glabrous, with a somewhat glistening surface, loculicidally three-valved.

Seeds several—many, flattened, discoid, black or blackish brown; testa thin and papery, finely reticulate—rugulose, often wrinkled or folded. Endosperm firm, whitish.

Type species: *R. convallarioides* (L. F.) BAK.

Species 9, one of which (*R. cyanelloides*) may have to be excluded upon further study.

Distribution: Arid parts of South and South West Africa and montane habitats in southwestern Cape. From Central South West Africa in the north to Stellenbosch—Swellendam—Oudtshoorn Divisions in the south, and in the interior reaching eastwards to Bloemfontein. The deviating species *R. cyanelloides* has also a distinct distribution, being known only from Komgha Division in the Eastern Cape Province.

Key to the Species of *Rhadamanthus*

1. Anthers connate to a cone, dehiscing with small apical pores. Tepals free from the base. Scape stout, 40—60 cm long 9. *R. cyanelloides*
1. Anthers free, dehiscing with apical slits sometimes reaching below the middle of the theca. Tepals basally connate. Scape \pm slender, rarely up to 40 cm long.
 2. Bulb scales separate, stalked. Raceme curved to the north, distinctly secund. Pedicels very short (1—2 mm long) 5. *R. secundus*
 2. Bulb scales sessile, loosely or densely imbricate to a normal bulb. Raceme erect, all-sided or somewhat unilateral. Pedicels 3—15 mm long.
 3. Anthers basally rounded and glabrous.
 4. Scape quite glabrous and smooth throughout, basally surrounded by a twisted, distinctly cross-barred sheath. Filaments free from the base 7. *R. fasciatus*
 4. Scape puberulous or minutely scabrid, at least basally. Sheaths, if present, not twisted and only faintly cross-barred. Filaments basally adnate to the perigon.
 5. Filaments very short (0.5 mm long or shorter), curved. Flowers white, expanded 8. *R. albiflorus*
 5. Filaments almost as long as the anthers or longer (0.8—1.5 mm long). Flowers brownish—pinkish, subglobose or campanulate.
 6. Scape distinctly puberulous throughout or nearly so. Pedicel usually shorter than perigon 1. *R. convallarioides*
 6. Scape minutely scabrid (or rarely puberulous) in the basal part only, otherwise smooth. Pedicel usually longer than perigon 2. *R. montanus*
3. Anthers basally caudate, apiculate, or barbellate.

7. Anthers basally barbellate. Filaments papillate—puberulous. Leaves 2, broad and flat, densely and shortly velutinous above 6. *R. platyphyllus*
7. Anthers basally apiculate or caudate. Filaments glabrous. Leaves several, filiform—linear, glabrous.
8. Bulb scales loosely imbricate with separate tips. Scape glabrous. Anthers basally apiculate 4. *R. arenicola*
8. Bulb scales densely imbricate. Scape puberulous throughout. Anthers basally caudate 3. *R. urantherus*

1. *Rhadamanthus convallarioides* (L. f.) BAK.

BAKER 1871 p. 434; DURAND & SCHINZ 1895 p. 373; BAKER 1897 p. 444; COMPTON 1931 p. 277. — *Hyacinthus convallarioides* L. f.; LINNÉ FIL. 1781 p. 204; THUNBERG 1794 p. 64; WILLDENOW 1799 p. 168; THUNBERG 1823 p. 326; ROEMER & SCHULTES 1829 p. 584; KUNTH 1843 p. 305. — Orig. coll.: THUNBERG, karroo below Roggeveld (Herb. THUNBERG 8519, *H. c. m.* THUNB., UPS lectotype; herb. LINNAEUS 438: 12, *H. c. m.* L. f., LINN; ex herb. ALSTROEMER, S; ex herb. MONTIN, S).

The species was founded on a THUNBERG collection, the locality of which is given in THUNBERG 1823. MASSON's specimens in BM were no doubt collected at the same occasion. In selecting a lectotype I have been in a dilemma. The sheet in the Linnean Herbarium of London, with the name in the handwriting of the younger LINNAEUS, may seem most suitable. However, on the sheet in THUNBERG's herbarium DYER has written "type!" and he has also in print expressed his opinion that the sheet in Uppsala represents "the type" (DYER 1934). Since it is not known who first proposed the species, THUNBERG or LINNÉ FIL. (or perhaps his father), there is no reason to depart from DYER's suggestion.

The combination *R. convallarioides* has always been ascribed to SALISBURY (1866). According to the present rules of nomenclature (Art. 33) the combination was not validly published by SALISBURY, who merely cited *Hyacinthus convallarioides* under his new genus *Rhadamanthus*. Instead, the combination must be ascribed to BAKER (1871).

Illustr.: Fig. 1 A—D. (JACQUIN 1797 refers to *R. montanus*). — Map 1.

Bulb subglobose—ovoid, 1.5—3 cm in diam., with silvery white or greyish thin outer tunics. Basal sheaths (withered leaf bases) short, laxly and faintly transversely banded, apically normally pink—pale purplish. *Leaves* several (c. 4—10), erect, filiform, 4—10 (—15) cm long and c. 1 mm thick, glabrous, green, c. 3—5-ribbed when dry, acute or subacute. *Scape* erect, often gently flexuous, 8—25 cm long, 0.8—2 mm thick near the base, densely puberulous up to below the raceme or sometimes higher up with patent or somewhat deflexed short and stiff acute hairs, brown or pale brownish to straw-coloured (rarely

reddish or purplish brown). *Raceme* 2.5—10 (—12) cm long, somewhat unilateral, lax to fairly dense, 5—25-flowered. *Bracts* deltoid—ovate, 1—2 mm long, acute—acuminate, lower ones spurred with a 0.5—1.5 mm long spur. *Pedicels* \pm patent, some curved during anthesis to form a subsecund raceme, (2—) 3—10 mm long, usually about equalling the perigon in length or slightly shorter, glabrous or rarely minutely and laxly scabrid-puberulous. Flowers nodding, normally several in flower simultaneously. Perigon broadly campanulate. *Tepals* narrowly oblong-ovate or narrowly elliptic-oblong, 7—10 mm long, 2.5—3 mm wide, connate for 2—3 mm basally, obtuse, pale brownish to pinky white with a darker midrib, puberulous-tipped. *Filaments* inserted 1.7—2 mm above the perigon base; the free parts linear to oblong, 1.5—2 mm long, 0.2—0.4 mm wide, flat. *Anthers* rich or orange yellow, 1.5—2 mm long, 0.7—1 mm wide, dehiscing with apical slits down to 1/3 or 1/2 of the theca length, basally rounded, glabrous. *Ovary* narrowly ovoid, 2.5—4 mm long, 1.7—2 mm wide, glabrous (or microscopically papillate), distinctly 3-lined. *Style* columnar—subclavate, 1.5—2.5 mm long, 0.4—0.6 mm wide; stigma capitate, shallowly trilobate. *Capsule* subglobose, slightly triquetrous, trilineate, c. 5 mm long and broad, dull green with a somewhat glittering golden yellow tinge. *Seeds* many, 2—2.5 mm long, c. 1.5 mm wide, \pm obovate, black, somewhat wrinkled and finely reticulate.

Flowering period: Oct.—Dec.

COLLECTIONS

CAPE PROVINCE. L. Namaqualand Div.: Near Garies, XI. 1939, ESTERHUYSEN 2610 (BOL). — Vanrhynsdorp Div.: Klaver, X. 1944, LEIPOLDT (BOL, K, PRE); cult. in Kirstenbosch. XII. 1945 (NBG). — Clanwilliam Div.: Clanwilliam, hills near the village, 200 ft, LEIPOLDT 547 (BOL) — Behind Synnotts Location, Clanwilliam, 360 ft, XII. 1897, LEIPOLDT 660 (GRA) — Pakhuis Pass, XII. 1934, SALTER 5025, grown at Bolus Herb., leaves added VIII. 1936, flowers XII. 1936 (BOL), grown in Mr. PILLANS' garden, leaves added VIII. 1935, flowers XI. 1935 (BOL) — Rondegat, X. 1938, L. BOLUS, herb. BOL 30630 (BOL) — 10 miles NW by N of Clanwilliam, slopes to Olifants River, X. 1958, ACOCKS 19758 (PRE) — Slope of Kafferskraal off National Road, c. 20 miles S of Clanwilliam, 1000—1500 ft, XI. 1963, TAYLOR 5550 (PRE) — Pakhuis Pass, X. 1964, colour photo and leaves from cult., HARDY 1749 (PRE). — Calvinia Div.: Lokenburg, between Nieuwoudtville and Boter Kloof, XII. 1946, LEIGHTON 2359 (BOL) — Lokenburg, flowered in cult., XI. 1956, ACOCKS 18203 (PRE). — Sutherland Div.: Koedoes Mountains, X. 1950, H. HALL 284 (NBG). — Laingsburg Div.:

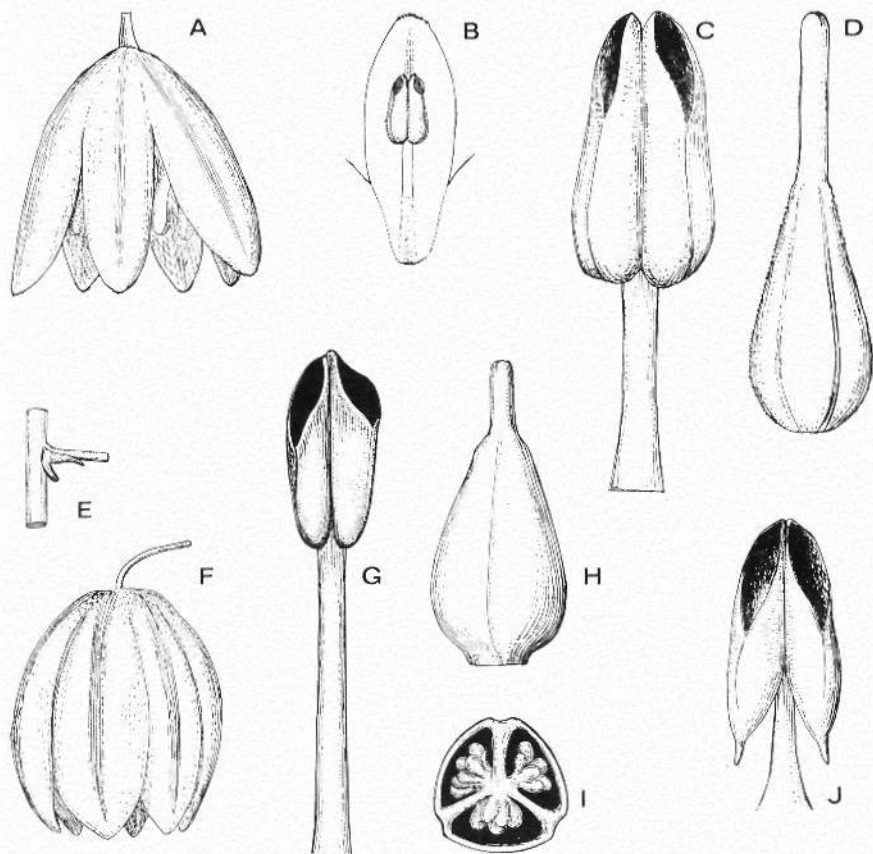


Fig. 1. A—D: *Rhadamanthus convallarioides* (TAYLOR 5550). — A: Flower, $\times 5$. — B: Tepal and stamen, $\times 5$. — C: Stamen, $\times 20$. — D: Gynoecium, $\times 10$. — E—I: *R. montanus* (NORDENSTAM 3398). — E: Bract, $\times 5$. — F: Flower, $\times 5$. — G: Stamen, $\times 20$. — H: Gynoecium, $\times 10$. — I: Ovary, transverse section, $\times 10$. — J: *R. urantherus* (BARKER 126), stamen, $\times 20$.

Whitehill, XI. 1935, leaves added XI. 1936, COMPTON (BOL) — Whitehill Karroo, XI. 1944, COMPTON 16387 (BOL), grown in Karroo Garden, XI. 1944 (NBG). — *Sine loco*: THUNBERG (LINN, UPS), ex herb. ALSTROEMER (S), ex herb. MONTIN (S) (Karoo below Roggeveld, fide THUNBERG 1823) — MASSON (BM) — Bolus Herb., flowered in cult. XI. 1940, L. BOLUS (BOL).

This species was already by JACQUIN (1797) confused with another species more common in the southwestern mountain districts of the Cape (see further under *R. montanus*).

R. convallarioides is found in karroo and dry aspects of fynbos ("near fynbos" and "arid fynbos"), and it grows on stony slopes as well as in sandy soil. The distribution ranges from L. Namaqualand in the north to Clanwilliam in the south and eastwards to the karroo parts of the Wittebergen in Laingsburg Division. Most localities recorded are from low altitudes (below 500 m s.m.).

2. *Rhadamanthus montanus* B. NORD., sp. nov.

Hyacinthus convallarioides auct. non L. F.; JACQUIN 1797 p. 42.

Orig. coll.: ESTERHUYSEN 11456, Cape Province, Stellenbosch Div., Jonkershoek Twins, ledges, NE side, 3000—4000 ft, 12.II. 1945, leaves added VI. 1945 (BOL holotype, K, NBG).

Illustr.: Fig. 1 E—I; JACQUIN 1797, Plate 81. — Map 2.

Bulbus subglobosus—ovoideus vel pyriformis tenuiter tunicatus. Vaginae inconspicuae vel destitutae indistincte transverse paucistriatae. Folia pauca—numerosa erecta filiformia—linearia glabra. Scapus erectus prope basin scabridiusculus (raro minutissime puberulus) cetera glaber plerumque cupreus vel rufescens. Bracteae inferiores distincte calcaratae. Pedicelli filiformes glabri. Tepala elliptico-oblonga obtusa dilute fusca — rubella brunneo-costata basi connata. Antherae luteae glabrae, thecis desuper ad medium fere dehiscentibus basi rotundatis. Filamenta antheras longitudine aequantia vel eis paulo longiora. Ovarium anguste ovoideum trilineatum glabrum in stylum columnarem vel subclavatum productum. Semina complanata nigra—fuscoatra splendentia.

Bulb subglobose—ovoid or pyriform, 1.5—4 (—5) cm in diam., with light grey or transparent tunics. Basal sheaths inconspicuous or lacking, with or without a few faint cross-bars. *Leaves* few—many (from 3—4 up to c. 25), erect, filiform—linear, 3—10 cm long (in cult. rarely up to 25 cm), 0.8—2 (—2.5) mm thick, semiterete, 5—7-ribbed (when dry) or indistinctly veined, green or slightly glaucous, glabrous, rarely minutely scabrid along the veins, obtuse—subacute. *Scape* straight or somewhat flexuous, 5—30 (—40) cm long, 0.7—2.5 mm thick near the base, glabrous to the naked eye but under the microscope minutely scabrid with small excrescences on the basal half only, usually reddish brown. *Raceme* 2—18 (—22) cm long, c. 5—50-flowered, almost all-sided or somewhat one-sided. *Bracts* ovate-acuminate or triangular-cuspidate, 1—2 mm long with 0.5—1 (—2) mm long spur, upper ones shorter and indistinctly spurred, often purplish and with somewhat dentate margins. *Pedicels* erecto-patent—patent, 3—15 (—18) mm long, glabrous. Flowers nodding, but mature capsules erect on curved or erecto-patent pedicels. Perigon campanulate—subglobose. *Tepals*

4.5—8 mm long, 1.5—3 mm wide, elliptic-oblong, pale brown to creamy pink with brown median stripe, obtuse, basally connate for 1—2.5 mm. *Filaments* inserted c. 1 mm above the perigon base; the free parts linear, flat, 0.8—2 mm long. *Anthers* 1—1.6 mm long, yellow, dehiscing to about the middle of the theca. *Ovary* narrowly ovoid—subconical, 1.8—3 mm long, trilineate, glabrous. *Style* columnar—subclavate, 1—1.5 mm long. *Capsule* subglobose—broadly ovoid, subtriquetrous, 4—6 (—7) mm long and broad, dull or pale green to purplish with a somewhat glistening golden linge. *Seeds* many, flattened, narrowly oblong—elliptic-obovate or somewhat broadly lunate in outline, 2.5—4.2 mm long, 1.5—2 mm wide; testa easily wrinkled or deformed, glossy dark blackish brown—black with a minutely and faintly rugulose surface.

Flowering period: Nov.—Jan.

COLLECTIONS

CAPE PROVINCE. C I a n w i l l i a m D i v.: Pakhuis, Heuning Vlei, XII. 1941, ESTERHUYSEN (NBG) — Pakhuis, summit of peak, XII. 1941, ESTERHUYSEN 7423 (BOL) — Summit of Pakhuis Peak, 3500 ft, XII. 1948, ESTERHUYSEN 14953, grown at Bolus Herb., flowers added I. — II. 1950 and 1951, XII. 1951, 1953 and 1954, leaves added VI. 1949, capsules and seeds added I.—II. 1949 (BOL, 2 sheets, on one of which 3 scapes of *R. platyphyllus* have been erroneously mounted) — Cedarberg, Wolfberg, XII. 1953, leaves added V. 1954, ESTERHUYSEN 22474 (BOL). — C e r e s D i v.: Visgat, XII. 1946, ESTERHUYSEN 13391 (BOL) — Onderboschkloof, I. 1948, ESTERHUYSEN 14298 (BOL) — Above Witels Kloof, off Michell's Pass, XII. 1948, grown at Bolus Herb., leaves added VI. 1949, ESTERHUYSEN 14738 (BOL) — Elands Kloof, Cold Bokkeveld Mts., 3500 ft, III. 1951, flowers added I. 1952 and 1953, leaves added IV. 1953, ESTERHUYSEN 18449 (BOL) — Michell's Pass, N slope, XI. 1952, ESTERHUYSEN 20724 (BOL). — P i k e t b e r g D i v.: Piketberg, upper W slopes of Levant Hill, XII. 1963, NORDENSTAM 3398, also grown in Kirstenbosch and Lund (S). — W o r c e s t e r D i v.: In convalle flum. Hex, 1700 ft, I. 1908, leaves added IV.—VII., BOLUS 13210 (BM, K) — Du Toits Kloof, above Elands Kloof stream, XII. 1943, grown at Bolus Herb., leaves added IX. 1945 and 1946, ESTERHUYSEN 9694 (BOL) — Stettynsberg, 4000 ft, XII. 1944, leaves added VI. 1946, ESTERHUYSEN 11445 (BOL) — Waaihoek Mts., lower parts of Jan du Toits Kloof, I. 1949, ESTERHUYSEN 15065 (BOL, K, UPS) — Elandskloof, off Du Toits Kloof, XII. 1952, leaves added V.—VI. 1953, ESTERHUYSEN 20983 (BOL). — P a a r l D i v.: Near French Hoek, I. 1932, SALTER 1935, flowered in cult. I. 1933 (BOL), leaves added VII. 1932 (BM, BOL) — Bains Kloof, I. 1940, HENRY, NBG 1001/34 (NBG) — Bains Kloof, N side of Sebastians Kloof, V. 1940, ESTERHUYSEN (BOL), NBG 407/40, flowered in Kirstenbosch II. 1945 (NBG) and I. 1951 (NBG) — Slanghoek Mts., Observation Peak, 3500 ft, II. 1943, ESTERHUYSEN 8614 (BOL) — Groot Drakenstein

Mts., Devil's Tooth, XII. 1943, flowered at Bolus Herb. I. 1946, ESTERHUYSEN 9518 (BOL) — Bailey's Peak, Bains Kloof Mts., 3000—3500 ft, II. 1954, leaves added at Bolus Herb. XI. 1954, ESTERHUYSEN 22738 (BOL, K, PRE). — Stellenbosch Div.: Banhoek, I. 1941, COMPTON 10346 (NBG) — Jonkershoek Twins, NE side, 3000—4000 ft, II. 1945, ESTERHUYSEN 11456 (BOL, K, NBG) — Emerald Dome (?), in pot at Bolus Herb. marked 4/44, XII. 1945, ESTERHUYSEN, herb. BOL 30627 (BOL) — Guardian Peak, summit, 4600 ft, I. 1955, ESTERHUYSEN 24132 (BOL) — Langrivier, Jonkershoek, 3700 ft, below twin peaks, II. 1966, KERFOOT 5675 (NBG). — Ladismith Div.: Seven Weeks Poort, LEWIS, NBG 2671/32, flowered in Kirstenbosch XII. 1939 (NBG). — Prince Albert Div.: "Prince Albert", NEETHLING, NBG 1447/16, flowered in Kirstenbosch I. 1923 (BOL). — Sine loco: Kirstenbosch, nursery, II. 1932, herb. BOL 30631 (BOL) — Bolus Herb. in tin, I. 1936, leaves added XI. 1936, herb. BOL 30626 (BOL).

R. montanus is no doubt closely allied to *R. convallarioides*, from which it differs in several morphological details as well as in ecology and distribution. In the latter species the basal sheaths are usually distinct, laxly fasciated and apically pink or purplish, and the scape is distinctly puberulous for the greatest length and more or less pale coloured. In *R. montanus* the sheaths are lacking or inconspicuous and only faintly fasciated, and the scape is minutely scabrid in its basal part and typically coppery or reddish brown in colour.

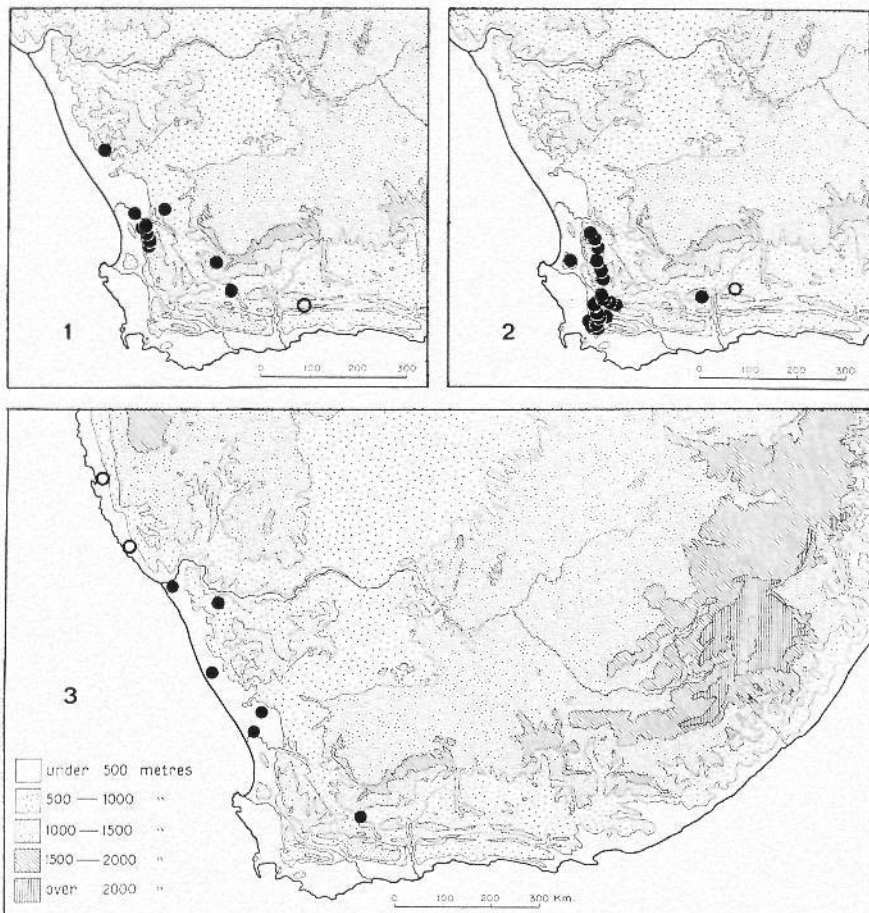
In its present circumscription *R. montanus* is the most variable species of the genus. The variation is considerable especially in size of flowers and floral details and in length of scape and pedicels. Very gracile and small-flowered specimens occur in the northernmost part of the distribution area, viz. the Cedarbergen. In a few of these collections the leaves are minutely scabrid, whereas in other regions only quite smooth leaves have been observed.

R. montanus is a montane species of the western Cape mountain districts with essentially fynbos vegetation. The species ranges from Cedarbergen in the north to Stellenbosch in the south and eastwards to about Gamka River. It grows in shallow soil on stony slopes and especially on rock ledges and in pans on boulders, at altitudes mostly between 600 and 1500 m s.m.

3. *Rhadamanthus urantherus* DYER

DYER 1934 text to Plate 3247. — Orig. coll.: BARKER, Cape Province, Oudtshoorn Div., 1 mile E of Oudtshoorn, 1932, hort. Kew 933/32, flowers added III. 1933, leaves X. 1933 (K holotype).

Illustr.: Fig. 1 J; DYER 1934 Plate 3247. — Map 1.



Maps 1—3. — 1. *Rhadamanthus convallarioides* (●) and *R. urantherus* (○). — 2. *R. montanus* (○ = inexact locality). — 3. *R. arenicola* (●) and *R. secundus* (○).

Bulb subglobose—ovoid, 2—3.5 cm long, 1.5—3 cm in diam., with grey—brownish outer tunics. Basal sheaths short, greyish, laxly transversely banded. *Leaves* filiform, erect, several (2—8 fide DYER), 4—6 cm long, c. 0.5 mm wide, subterete, green, glabrous, obtuse—subacute. *Scapae* erect, 12—20 (in cultivation—30) cm long, 0.7—1.5 mm thick near the base, pale brownish, minutely puberulous throughout. *Raceme* gracile, lax, c. 5—10 (—12) cm long, c. 10—25-flowered. *Bracts* 1—1.7 mm long, triangular-ovate, acuminate; spur distinct, linguiform, 0.5—1.5 mm long (in upper bracts shorter or obsolete). *Pedicels* (erectopatent—) spreading, slender, filiform, 3—12 mm long, minutely and

sometimes indistinctly scabrid-puberulous. Flowers nodding. Perigon subglobose, half-closed, 5—6 mm in diam. Tepals basally connate (for c. 0.8—1 mm), elliptic-oblong, c. 4 mm long and 2—2.5 mm wide, light brown with somewhat darker midrib; apex rounded, minutely and sparsely puberulous. *Filaments* basally adnate to the perigon; the free parts linear from a broader base, c. 1 mm long. *Anthers* 1.5—1.7 mm long (incl. tails), yellow, basally distinctly and acutely caudate, dehiscing with apical pore-like slits reaching down to the middle of the theca or less. *Ovary* pyriform—bluntly conical-ovoid, somewhat triquetrous, 2—2.5 mm long, 1.3—1.5 mm wide, puberulous, without produced style, apically truncate with shallowly three-sulcate stigma. *Capsules* and *seeds* unknown.

Flowering period: March—Apr.

COLLECTIONS

CAPE PROVINCE. Oudtshoorn Div.: 1 mile E of Oudtshoorn, 1932, BARKER, hort. Kew 933/32, flowers added III. 1933, leaves X. 1933 (K); Oudtshoorn, IV. 1933, BARKER 126 (BOL p.p., K).

R. urantherus in habit resembles slender and small-flowered forms of *R. convallarioides* and *R. montanus* but is on closer examination readily distinguished by the caudate anthers and the puberulous ovary without a produced style. The scape is puberulous throughout, in contrast to *R. montanus*, and also in contrast to the probably closely related *R. arenicola* which has a glabrous scape.

The sheet in BOL is heterogeneous, only the two left specimens belonging to *R. urantherus*. The other specimens consist of inflorescences and leafy bulbs pertaining to *R. montanus* and have evidently been added by mistake from some other material cultivated at the Bolus Herbarium.

The single locality known lies within the Little Karroo, and the bulbs were said to be growing "amongst stones". It is quite possible that this easily overlooked species will be found in other karroo areas as well.

4. *Rhadamanthus arenicola* B. NORD., sp. nov.

Orig. coll.: PILLANS, herb. BOL 18253, Cape Province, L. Namaqualand Div., 0.5 mile S of Walle Kraal, sandy ridge, X. 1924 (BOL holotype).

Illustr.: Fig. 2 A—F. — Map 3.

Bulbus ambitu fere globosus; bulbi squamae imbricatae, apicibus distinctis roseis vel dilute purpureis leviter fasciatis. Folia filiformia plura erecta glabra. Scapus erectus glaber. Flores nutantes in racemo laxo dispositi; pedicelli longitudine flores superantes. Tepala ad medium vel ultra connata subinaequalia obtusa—truncata. Antherae basi apiculatae. Ovarium ovoideum. Styles brevissimus, stigmatе crateriformi.

Bulb ± globose in outline, 2.5—5 cm in diam.; bulb scales somewhat loosely imbricate, ovate—lanceolate, 1—3 cm long, 0.5—1.5 cm wide, brown when dry (white—pinkish when fresh?), apically pink—purplish blue and ± acuminate with a linear-subulate laxly and indistinctly cross-banded sheath. *Leaves* erect, filiform, several, a few cm long, glabrous. *Scape* (5—) 10—15 cm long, 1—1.5 (—2) mm thick basally, glabrous, dark brown to light greyish brown. *Raceme* lax, all-sided, c. 8—25-flowered, 3—7 cm long. *Pedicels* ± patent and curved downwards (after anthesis straight and spreading, finally curved upwards or erecto-patent), 4—10 mm long. *Bracts* ovate—subdeltoid, 1—2 mm long and 1—1.5 mm wide, acute—acuminate or short-cuspidate, few-toothed or subentire, shortly spurred. Perigon campanulate or subglobose and half-closed, 3—4 mm long and wide. *Tepals* elliptic-oblong, connate to about the middle or slightly more, 3.5—4 mm long, 1.3—2 mm wide, subequal, whitish or light brown, with a brown midrib, obtuse—truncate or somewhat cucullate. *Filaments* adnate to the perigon for c. 0.8—1 mm; the free parts narrowly oblong—linear from a broader base, flat, c. 1 mm long. *Anthers* 1—1.2 mm long, dehiscing with apical slits down to c. 1/3 from the apex, basally apiculate (=with a short acute basal appendage). *Ovary* ovoid, 2—2.5 mm long, 1.5—1.8 mm wide, subtriquetrous, minutely papillate. *Style* obsolete or short, up to 0.5 mm long; stigma crateriform, concave with auriculate lobed margin. *Capsule* ovoid—rounded, 4—5 mm long. *Seeds* narrowly oblong, complanate, 3.7—4 mm long, 1—1.5 mm wide, shiny black, coarsely wrinkled and finely rugulose.

Flowering period: Oct.—Nov.

COLLECTIONS

CAPE PROVINCE. L. Namaqualand Div.: Sandy depression N of Witbank, X. 1926. PILLANS 5562 (BOL) — 0.5 mile S of Walle Kraal, X. 1924, PILLANS, herb. BOL 18253 (BOL) — 18 miles S of Violsdrift, VI. 1963, flowered in Kirstenbosch XI. 1963, NORDENSTAM 2847 (S). — Vanrhynsdorp Div.: Ebenezer, stony dry hills, below 500 ft, XI., DRÈGE (*Hyacinthus*

convallarioides c") (L, S) — 11 miles S of Nuwerus on Vanrhynsdorp road, H. 1968, KERS 2204 (S). — Laingsburg Div.: Matjesfontein, sandy flats, X. 1921, FOLEY 121 (PRE).

Some of these collections are incomplete and only with some hesitation referred to this species (DRÈGE, KERS, NORDENSTAM).

In this species the bulb scales are more loosely imbricated than in the preceding species. This tendency has reached an extreme development in the following species, *R. secundus*. The relationship between *R. arenicola* and *R. secundus* is further enhanced by some other features in common, e.g. the glabrous peduncles, the strongly gamophyllous perigon, and the basally apiculate anthers. The closest affinity, however, appears to be with *R. urantherus*. From the latter, *R. arenicola* is sufficiently distinct by its peculiar bulbs, its glabrous scape, and its shorter and less distinctly caudate anthers.

R. arenicola seems to prefer sandy habitats and is hitherto known from a few localities from Matjesfontein in the south up to northern Little Namaqualand.

5. *Rhadamanthus secundus* B. NORD., sp. nov.

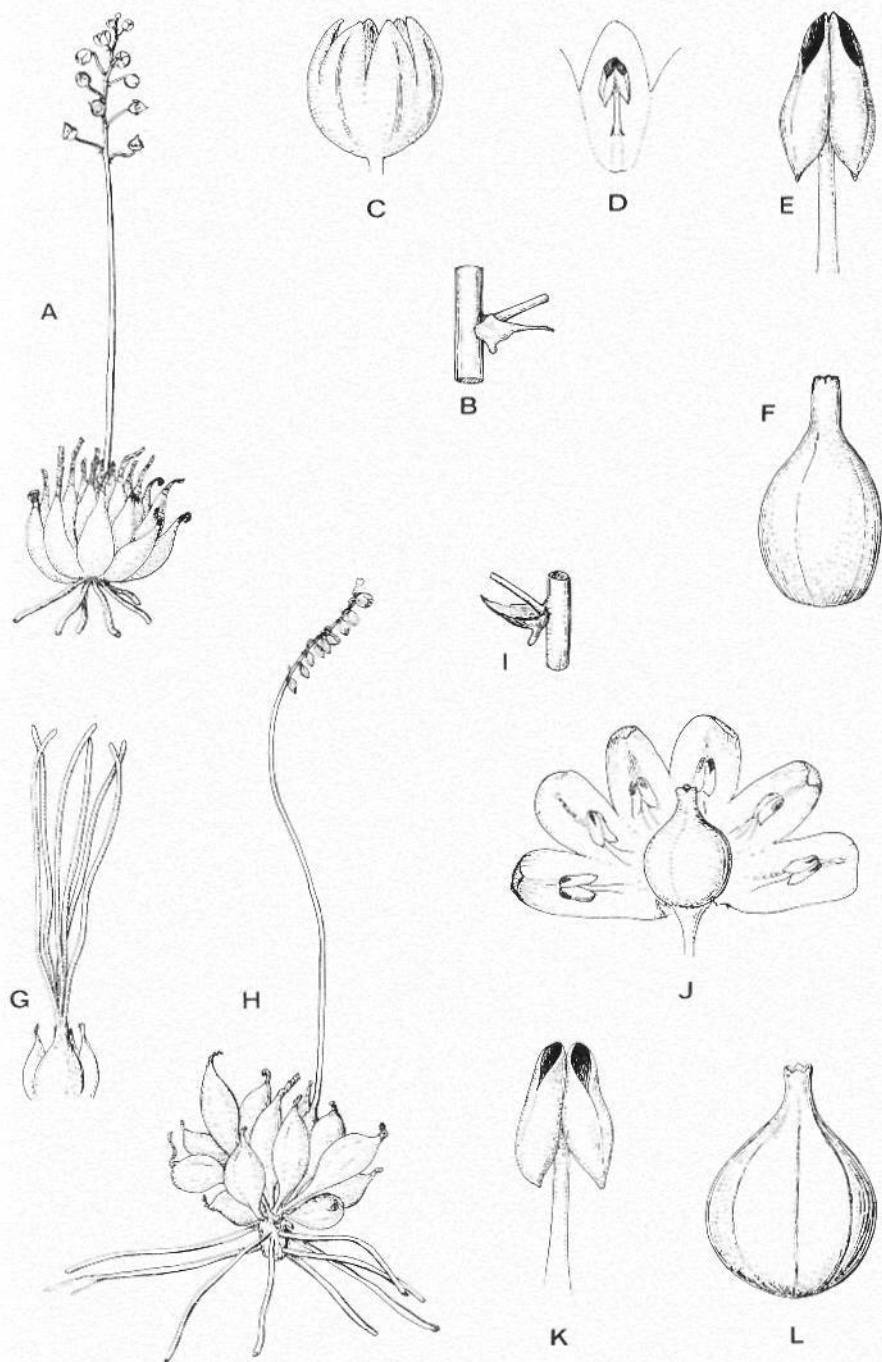
Orig. coll.: GIESS 2350, S.W. Africa, Distr. Lüderitz-Süd, Kavisberge, 30.IX. 1959 (M holotype, WIK).

Illustr.: Fig. 2 G—L. — Map 3.

Bulbi squamae discretae fusiformes stipitatae carnosae e rhizomate brevi enatae. Folia plura lineari-filiformia glabra. Scapus glaber erectus ad septentriones versus distincte curvatus. Bractae ovatae acutae vel breviacuminatae basi breviter calcaratae. Flores brevipedicellati in racemo subdenso secundo dispositi. Tepala ultra medium connata subinaequalia obtusa—truncata. Antherae basi apiculatae. Ovarium subglobosum. Stylus brevis, stigmatе crateriformi.

Bulb scales several—numerous, separate (except perhaps the most central scales) and forming a lax rosette, stalked from a short rhizome, clavate or ellipsoid—fusiform, carnosе (probably very juicy and pellucid), whitish or somewhat pinkish, c. 1.5—4 mm long and 1—2 cm wide, apically tapering or contracted to a \pm withered pinkish membranous subhyaline sheath with a few faint cross-bars. Roots fibrous,

Fig. 2. A—F: *Rhadamanthus arenicola* (A—B: PILLANS 18253, C—F: FOLEY 121). — A: Habit, $\times 0.5$. — B: Bract, $\times 5$. — C: Flower, $\times 5$. — D: Tepal and stamen, $\times 5$. — E: Stamen, $\times 20$. — F: Gynoecium, $\times 10$. — G—L: *R. secundus* (G: DINTER 6492, H—L: GIESS 2350). — G: Leaves, $\times 0.5$. — H: Habit, $\times 0.5$. — I: Bract, $\times 5$. — J: Flower, laid out, $\times 5$. — K: Stamen, $\times 20$. — L: Gynoecium, $\times 10$.



numerous from the rhizome, long and somewhat thickish. *Leaves* several—many, mainly from the central bulb scales (central bulb?), erect, often somewhat flexuous, narrowly linear-filiform, 5–8 cm long, 1–1.5 mm wide, green, glabrous, flattish (?), faintly 5-veined, obtuse—subacute. *Scape* erect, distinctly curved towards the north, 8–15 cm long, c. 1.5 mm thick, terete, glabrous, basally straw-coloured, upwards light brown or purplish. *Raceme* fairly dense and spike-like, distinctly secund, 2.5–5 cm long, c. 10–25-flowered. *Bracts* ovate, 1–2 mm long (lowermost bracts often larger), acute or short-acuminate, basally shortly spurred; spur up to 0.5 mm long. *Pedicels* \pm patent, straight or curved, 1–2 mm long. Perigon campanulate, open for a short time (subglobose in bud, acutely lachrymiform after anthesis), 4–5 mm long and up to 4.5 mm in diam. *Tepals* connate to above the middle; the free lobes ovate—ovate-oblong, 1.5–2 mm long, obtuse—truncate and often somewhat cucullate, brownish with green median stripe, whitish membranous margins and rosy tips. *Filaments* inserted 1.5–1.8 mm above the perigon base, linear from a dilated base, 1–1.5 mm long. *Anthers* c. 1 mm long, light yellow, basally apiculate, dehiscing with apical oblique pores c. 1/3 the length of the theca. *Ovary* subglobose, 2–2.5 mm wide and long, glabrous; style very short, c. 0.5 mm long; stigma concave with minutely auriculately lobed margin. Capsule and seeds unknown.

Flowering period: Sept.

COLLECTIONS

SOUTH WEST AFRICA. Distr. Lüderitz-Süd: W side of Buchberge, VII. 1929, DINTER 6492 (B, BOL, M, S) — Kosisberge, IX. 1959, GIESS 2350 (M, WHK).

In gross morphology this peculiar species looks very different from its congeners. The close agreement in floral morphology especially with *R. arenicola* removes any doubt above the relationship, however.

The complete separation of the bulb scales is a very unusual feature in the family. A similar and probably homologous type of caudex exists in *Drimia haworthioides* BAK. (cf. MARLOTH 1913 p. 101).

The inflorescence is more distinctly secund than in any other species of the genus. Because of the short pedicels the raceme is almost spike-like in appearance, and it always leans gently to the north. This constant inclination of the stem towards the sun is not a unique case.

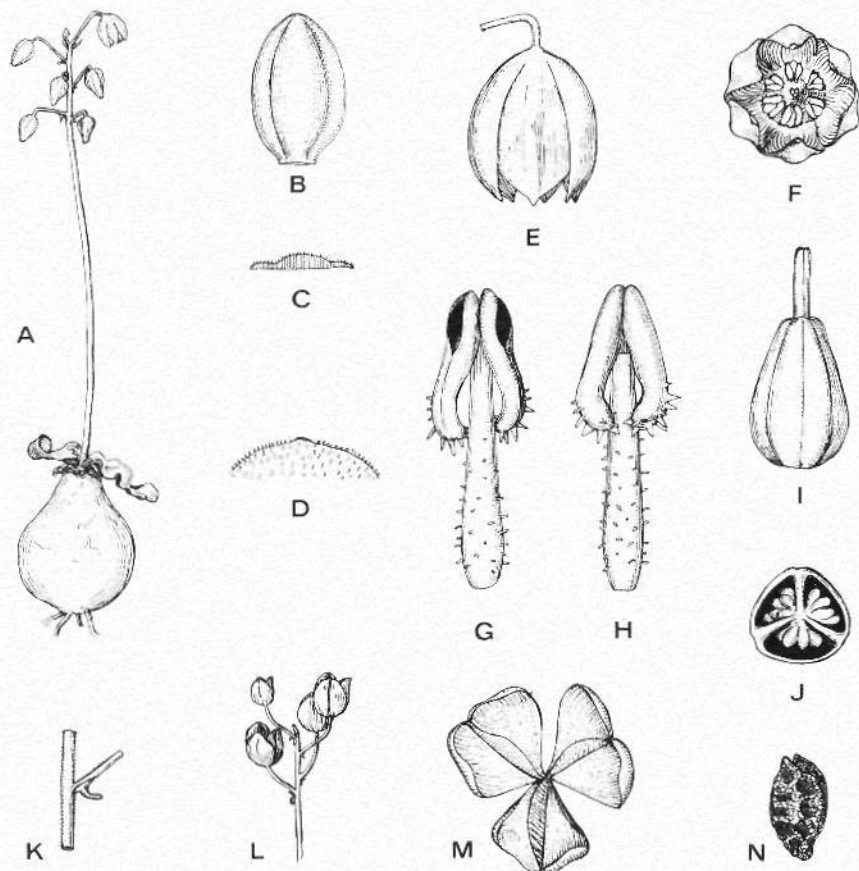


Fig. 3. *Rhadamanthus platyphyllus* (NORDENSTAM 3394). — A: Habit, $\times 1$. — B: Leaf, dorsal view, $\times 2$. — C: Leaf transect, $\times 2$. — D: Leaf surface near apex, $\times 5$. — E: Flower, $\times 5$. — F: Flower, dorsal view, $\times 5$. — G: Stamen, adaxial view, $\times 20$. — H: Stamen, abaxial view, $\times 20$. — I: Gynoecium, $\times 10$. — J: Ovary, transverse section, $\times 10$. — K: Bract, $\times c. 2.5$. — L: Raceme in fruit, $\times 1$. — M: Capsule, dehiscent, dorsal view, $\times 5$. — N: Seed, $\times 5$.

Another example is afforded by the famous *Pachypodium namaquanum* (*Apocynaceae*) of the same phytogeographical region.

R. secundus is known only from the southernmost part of South West Africa, where it has been found twice in Namib coastal desert mountains. DINTER's collection has bulbs and leaves only, and Mr. GIESS' specimens are in flower and leafless. It is not proved, but very likely, that the two collections are conspecific.

6. *Rhadamanthus platyphyllus* B. NORD., sp. nov.

Orig. coll.: ESTERHUYSEN 18135, Cape Province, Clanwilliam Div., Cederberg Tafelberg, 3500—4000 ft, 16.XII. 1950, leaves added IV. 1951 (BOL holotype).

Illustr.: Fig. 3 A—N. — Map 4.

Bulbus subglobosus vel ovoideus leviter tunicatus. Folia duo subopposita patentia plana late ovata—elliptico-oblonga integerrima supra dense et minute velutina apice obtusa—rotundata. Scapus dense puberulus sanguineus vel rufus. Pedicelli filiformes scabridiusculi vel glabrati. Flores sanguinei—rubelli—dilute carnei. Tepala basi vel ad medium fere connata. Antherarum thecae basi divergentes barbellatae. Filamenta papillata—puberula. Ovarium ovoideum—subquadratum glabrum, in stylum columnarem productum.

Bulb subglobose—ovoid, 2—3.5 (—4) cm in diam., up to 4 (—5) cm long, whitish—light brownish, soft and fleshy. *Leaves* usually 2, subopposite (the base of the first leaf encloses that of the second), horizontally spreading, broadly ovate—elliptic—elliptic-oblong, 1—4 cm long, 0.6—2.5 cm wide, completely entire, flat, dull green, usually with two longitudinal impressed furrows, indistinctly veined, minutely and densely velutinous on the upper surface, glabrous below, with obtuse—rounded apex. *Scape* 3—15 (—30) cm long, 0.5—1.5 mm thick basally, densely and shortly papillate-hirsute with patent or somewhat declined papilliform hairs in straight lines, usually reddish brown or purplish red. *Raceme* moderately dense, 1.5—10 (—12) cm long, 5—50-flowered, all-sided. *Bracts* ovate-triangular—lanceolate, acute—acuminate, 1—1.5 (—2.5) mm long, distinctly spurred; spur up to 1.5 (—2) mm long. *Pedicels* filiform, erecto-patent—spreading, 3—10 mm long, minutely scabrid-papillate or glabrate. Flowers nodding, but capsules finally erect. Perigon urceolate—subglobose. *Tepals* connate for 1/4—1/2 of their length, ovate-oblong—narrowly elliptic-oblong, 3.5—6 mm long, 1.2—2.5 mm broad, reddish brown—creamy pink with a broad purplish—green median stripe, with puberulous obtuse and sometimes subcucullate tips. *Filaments* adnate to the perigon for c. 0.7 mm; the free parts 1—1.5 mm long, whitish, laxly papillate-puberulous with spreading hairs. *Anthers* yellow, 1—1.8 mm long, with basally diverging thecae, dehiscing with apical pore-like slits 1/3—1/2 of the theca length, basally barbellate with spine-like or papilliform excrescences. *Ovary* ovoid—subquadrate, 1.8—2 mm long and 1.2—1.5 mm wide, light green, glabrous. *Style* columnar, terete, c. 1 mm long, white. *Capsule* 4.5—7 mm long and broad, broadly ovoid—subglobose, subtriquetrous, somewhat glossy golden green or purplish brown. *Seeds*

compressed, unequally elliptic-oblong to reniform, 3—4 mm long, 1.2—1.5 mm wide, shiny black, irregularly folded and wrinkled and finely reticulate.

Flowering period: (Nov.—)Dec.—Jan.

COLLECTIONS

SOUTH WEST AFRICA. Rehoboth Distr.: Areb, Granitkuppe, 1929, WETTSTEIN 244 (M, PRE).

ORANGE FREE STATE. Bloemfontein Div.: Mazelspoort, steep side of hills, XI. 1952, MOSTERT 720 (PRE).

CAPE PROVINCE. Clanwilliam Div.: Elands Kloof, E end, XII. 1940, ESTERHUYSEN 3985 (BOL) — Below Cederberg Tafelberg, 3500—4000 ft, XII. 1950, leaves added IV. 1951, ESTERHUYSEN 18135 (BOL) — Welbedacht Cave, Cederberg, 3500—4000 ft, IV. 1952, ESTERHUYSEN (BOL). — Piketberg Div.: Twenty Four Rivers Kloof, near Saron, XII. 1950, ESTERHUYSEN 17948 (BOL) — Piketberg, Levant Hill, upper W slopes, XII. 1963, NORDENSTAM 3394 (S) — Piketberg Mtn., on top, IX. 1965, flowers added I. 1966, fruits II. 1966, BARKER 10308 (NBG). — Ceres Div.: Ezelsfontein, lower N slopes of Hex River Mts., IX. 1952, flowers added XII. 1954, fruits I. 1955, ESTERHUYSEN 20331 (BOL, K). — Paarl Div.: Paarlberg, 2000—3000 ft, XI.—XII., DRÈGE ("*Hyacinthus convallarioides* e") (G). — Worcester Div.: Kloof on S slopes of Du Toits Peak, 2500—3000 ft, XII. 1949, leaves added IV.—VI. 1950, fruits II. 1950, ESTERHUYSEN 16631 (BOL, K) — Fairy Glen Kloof, at foot of Audensberg Ridge Peak, I. 1950, leaves added VI. 1951, ESTERHUYSEN 16675 (BOL) — N end of Du Toits Peak, 3000—3500 ft, X. 1951, flowers added I. 1952, ESTERHUYSEN 18924 (BOL) — Blaauwkop, near Keeromsberg, lower W slopes, XII. 1951, leaves added VIII. 1952, ESTERHUYSEN 19627 (BOL). — Robertson Div.: Klaasvogds, at foot of Langeberg, I. 1954, flowers added I. 1955, leaves VI. 1955, fruits II. 1955, ESTERHUYSEN 22686 (BOL).

R. platyphyllus is a very characteristic species. The flat and broad leaves are unique in the genus as are also the barbellate anther bases and the papillate filaments. The leaves are nearly always two in number and have a minutely velvety upper surface. The scape is pubescent throughout its length, and even the pedicels are puberulous, though sometimes indistinctly so, or glabrescent.

The distribution of *R. platyphyllus* is remarkable. The main range falls within the fynbos region of the western Cape, and here the species in its ecology much resembles *R. montanus*. (On the Piketberg I have found both species growing together). In addition there are two widely distant localities known, one in South West Africa and one

in the Orange Free State. The material from these two outpost localities is certainly meagre, but I have discovered no significant differences from the Cape forms.

R. platyphyllus grows in shallow sandy soil on rock ledges and cliffs, among stones on slopes, and in rock pans and shallow basins, mainly in situations with a northern or western aspect.

7. *Rhadamanthus fasciatus* B. NORD., sp. nov.

Orig. coll.: LEISTNER 1983, Cape Province, Kimberley Div., Nooitgedacht, c. 10 miles SE of Barkly West, c. 3800 ft., 15.X. 1960 (PRE holotype, LD).

Illustr.: Figs. 4 (photograph), 5 A—C. — Map 5.

Bulbus ovoideus—pyriformis tenuiter tunicatus. Vaginae albae—argenteae conspicue fusco-fasciatae denique productae torsivae. Folium solitarium linearifiliforme glabrum. Scapus erectus glaber. Bractae breviter vel indistincte calcaratae. Tepala elliptico-oblonga obtusa basi connata. Antherae flavovirentes, thecis basi rotundatis glabris desuper usque infra medium dehiscentibus. Ovarium subglobosum—ovoideum glabrum, in stylum columnarem productum.

Bulb ovoid—pyriform, up to 4 cm long and 3 cm in diam., with a thin brownish—greyish skin. Basal sheaths white—silvery grey, eventually 3—10 (—13) cm long and spirally twisted around the scape base, distinctly cross-barred with firm and raised brown stripes. *Leaf* solitary, linear-filiform, glabrous. *Scape* (6—) 10—25 cm long, 1—1.5 mm thick basally, glabrous, usually brownish. *Raceme* often elongate, lax to moderately dense, 3—11 cm long, all-sided, c. 10—30-flowered. *Bracts* deltoid—broadly ovate, often somewhat irregularly and coarsely dentate, 1—1.5 mm long, minutely and often obscurely spurred basally, acute. *Pedicels* patent or nearly so, 5—11 mm long and c. 0.2 mm thick, terete, glabrous. Flowers nodding, at least in bud, becoming more erect during and after anthesis. Perigon broadly campanulate. *Tepals* connate basally (for c. 1—1.5 mm), elliptic-oblong, 3.5—5.5 mm long, 1.7—2.8 mm wide, whitish to pale yellow or light brownish pink with a brown median stripe, obtuse, puberulous-tipped. *Filaments* free, narrowly oblong but somewhat tapering above, 1—1.7 mm long, 0.2—0.5 mm wide, flat, white—pinkish. *Anthers* 1.8—2.3 mm long, 0.7—1 mm broad (near the base), green or greenish yellow, basally rounded, glabrous, dehiscing with apical slits which eventually proceed down to below the middle of the theca. *Ovary* subglobose—ovoid, c. 2 mm long and 1.8 mm wide, glabrous. *Style* columnar, c. 1.5 mm long and 0.4 mm thick. *Capsule* and *seeds* unknown.

Flowering period: Aug.—Oct.



Fig. 4. *Rhadamanthus fasciatus* (LEISTNER 2400 from Kenhardt). Photograph by courtesy of the Botanical Research Institute, Pretoria, South Africa. The scale is in inches.

COLLECTIONS

SOUTH WEST AFRICA. Windhoek Distr.: Farm Binsenheim, VIII. 1956, VOLK 11078 (M). — Rehoboth Distr.: Blässkranz, X. 1939, VOLK 922 (M). — Maltahöhe Distr. (?): Damas, X. 1939, VOLK 788 (M) (Probably also Rehoboth Distr.). — Keetmanshoop Distr.: Klein Karas, X. 1923, DINTER 5071 (B).

CAPE PROVINCE. Kenhardt Div.: Kakamas, XI. 1930, FULLER 0 26 (PRE) — Gannapoort, 22 miles SE of Pofadder, flowered in Pretoria X. 1961, LEISTNER 2400 (PRE, photograph in S, see Fig. 4). — Hay Div.: Top of Langebergen at Bergenaars Pad, X. 1936, ACOCKS in herb. HAFSTRÖM 1098 (PRE, S) — Leeuwfontein, X. 1936, HAFSTRÖM 1074 (S). — Herbert Div.: Ruigtefontein, X. 1936, ACOCKS 1617 (PRE). — Kimberley Div.: Nooitgedacht, c. 10 miles SE of Barkly West, c. 3800 ft, X. 1960, LEISTNER 1983 (LD, PRE). — Prieska Div.: Prieska, X. 1910, BRYANT 846 (PRE).

Only after some hesitation I refer this new species to *Rhadamanthus*, since it takes a position somewhat transitional to the related genus *Urginea*. In herbaria the species may be found under this genus, and WILMAN (1946 p. 290) cites it as "*Urginea* sp." The anthers dehisce by longitudinal slits, which often eventually reach below the middle or even to near the base of the theca. The dehiscence is never complete, however, and the opening remains somewhat "pore-like", having its greatest width near the top of the anther (Fig. 5 C).

This species is insufficiently known, since information about leaves, capsules and seeds is incomplete or lacking. From leaf remains and label annotations it seems that a solitary hysteranthous leaf is developed. In this connection it should be mentioned, that a minor part of the collection GIESS 9040 (S. W. Africa, Rehoboth Distr., Nabitsaus at Gr. Aub. in herb. M and WHK) may belong to this species, viz. altogether two bulbs, each carrying a single filiform leaf and with the characteristic cross-banded sheaths of *R. fasciatus*. The major part of this collection consists of fruiting specimens, which cannot be referred to this species, by characters of stem puberulence and bract shape (*Urginea* sp. ?).

The perigon of *R. fasciatus* is furnished with small rectangular cells (visible in microscope after soaking in hot water), which reflect the light and add a certain brilliance to the otherwise fairly dull coloured flowers. Similar but more distinct and almost scale-like bodies occur on the basal sheaths (like in some other species of the genus).

R. fasciatus is restricted to South West Africa and adjacent parts of the northern Cape Province and Griqualand West. The species grows in rock fissures or in shallow soil, usually in a brown sandy loam, on rocks of dolomite, diabas or quartz.

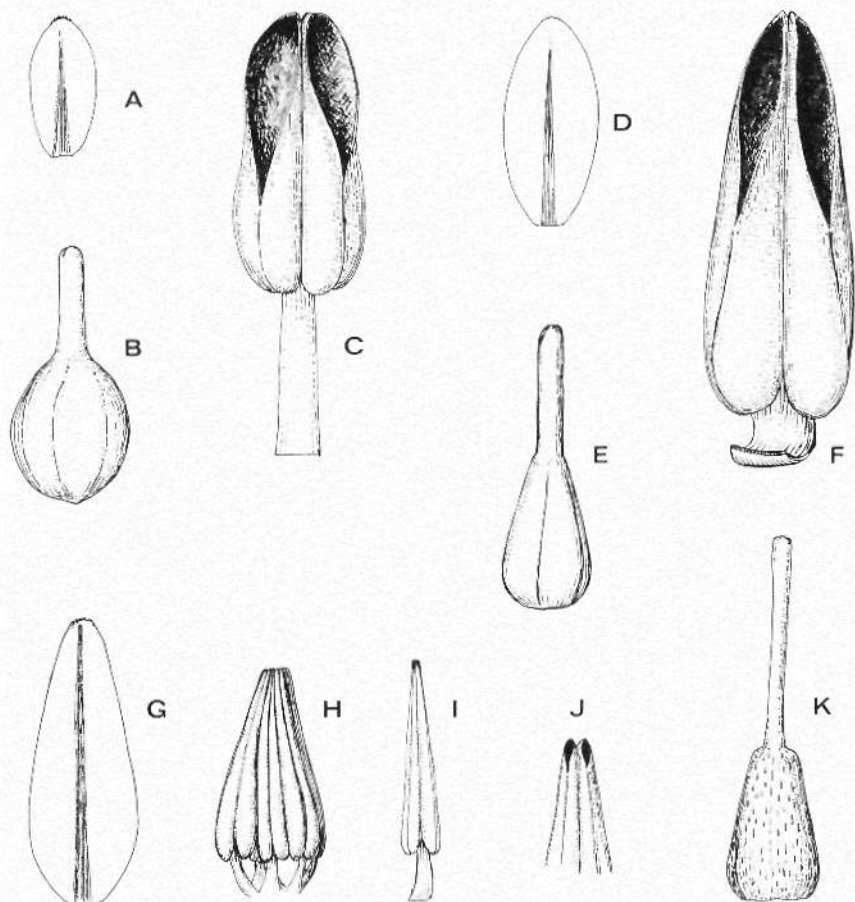


Fig. 5. A—C: *Rhadamanthus fasciatus* (LEISTNER 1983). — A: Tepal, $\times 5$. — B: Gynoecium, $\times 10$. — C: Stamen, $\times 20$. — D—F: *R. albiflorus* (ACOCKS 23242). — D: Tepal, $\times 5$. — E: Gynoecium, $\times 10$. — F: Stamen, $\times 20$. — G—K: *R. cyanelloides* (FLANAGAN 573). — G: Tepal, $\times 5$. — H: Stamen cone, $\times 5$. — I: Stamen, $\times 5$. — J: Top of anther, $\times 20$. — K: Gynoecium, $\times 10$.

8. *Rhadamanthus albiflorus* B. NORD., sp. nov.

Orig. coll.: ACOCKS 23242, Cape Province, Swellendam Div., Hesquaspoort, c. 800 ft, 20.XII. 1962 (PRE holotype).

Illustr.: Fig. 5 D—F. — Map 5.

Bulbus ovoideus—pyriformis. Vaginae albae leviter et rare fasciatae. Scapus erectus dense et minute scabrido-puberulus saltem in dimidio inferiore. Bractee inferiores distincte calcaratae. Perigonium late campanulatum, tepalis per

anthesin subpatentibus elliptico-oblongis obtusis albidis conspicue fusco-costatis basi connatis. Filamenta brevissima. Antherae flavae, thecis desuper tandem infra medium dehiscentibus. Ovarium oblongo-ovoideum glabrum, apice in stylum columnarem productum.

Bulb ovoid—pyriform, 2—3 cm long, 1.5—2.5 cm wide, with silvery white—greyish thin tunics. *Leaves* unknown. Basal sheaths thin and papery, up to 2 cm long, whitish, faintly longitudinally striate, sparsely and rather indistinctly transversely banded. *Scape* straight or gently flexuous, 12—25 cm long, 0.7—1.2 mm thick in the basal part, reddish brown, densely scabrid-puberulous in the basal half or sometimes higher up with short and spreading or slightly deflexed whitish hairs. *Raceme* moderately dense to fairly lax, 2—6 cm long, c. 6—15-flowered. *Bracts* ovate-triangular, 1—2 mm long, acute—acuminate, distinctly (at least the lower ones) spurred with an up to 1 mm long lingulate or sub-cylindric spur. *Pedicels* erecto-patent—almost spreading, filiform, 3—9 mm long, glabrous. Flowers nodding. Perigon broadly campanulate to almost flat. *Tepals* connate to c. 1/4 (or c. 1.5 mm), elliptic-oblong, c. 5.5 mm long and 2.5 mm wide, white with a distinct brown midrib, obtuse. *Filaments* short, adnate to the perigon for c. 0.5 mm; the free parts only 0.3—0.5 mm long, 0.4—0.5 mm wide, broadly oblong, flat, curved towards the gynoeceum. *Anthers* yellow, 2.5—2.7 mm long, c. 1 mm wide, glabrous, rounded at the base, dehiscent with apical slits down to or below middle of the thecae. *Ovary* ovoid-oblong, c. 2 mm long and 1.3 mm wide, glabrous. *Style* columnar, c. 1.8 mm long. *Capsule* and *seeds* unknown.

Flowering period: Dec.

COLLECTION

CAPE PROVINCE. Swellendam Div.: Hesquaspoort, c. 800 ft, XII 1962, ACOCKS 23242 (PRE).

The remarkably short filaments at once distinguish this species from all its congeners. The open, almost flat flowers and the white tepals with sharply contrasting brown midribs also serve to characterize the species.

R. albiflorus was found, according to its collector's note, in marginal fynbos on northern aspect and was said to be fairly frequent. It is an urgent task to recollect the species and to study it in cultivation in order to obtain information about leaves, capsules and seeds.

9. *Rhadamanthus cyanelloides* BAK.

BAKER 1897 p. 444. — Orig. coll.: FLANAGAN 573, Cape Province, Komgha Div., grassy valleys near Prospect Farm, 2100 ft, XII. 1889 (K holotype, PRE). — (FLANAGAN 573 in BOL was according to the label collected in 1895, certainly in the same locality).

Illustr.: Fig. 5 G—K. — Map 4.

Subterranean parts and *leaves* unknown. *Scape* erect, 40—60 cm long, 2—3 mm thick basally, glabrous, straw-coloured—brownish. *Raceme* 4—6 cm long, all-sided, 12—20-flowered. *Bracts* ovate-acuminate and with one lateral tooth or lobe on each side (hence 'tricuspidate'), c. 4 mm long, submembranous, the lower ones distinctly spurred with a narrowly cylindrical spur up to 5 mm long, upper ones not spurred. Bracteole present, axillary, 1—2 mm long, filiform-subulate or almost linear, membranous. *Pedicels* erecto-patent, (3—) 5—10 mm long, straight, glabrous. Flowers \pm erect. *Tepals* biseriate (outer 3 distinctly overlapping inner 3), free from the base, almost patent during the anthesis, oblong—narrowly ovate-oblong, c. 7.5 mm long and 2.5—3 mm wide, with a distinct brown midrib, obtuse and minutely puberulous at the apex. *Filaments* free, 1—1.5 mm long, flat, ovate-oblong, widest (0.6—0.7 mm) near the base. *Anthers* yellow, 5—6 mm long, 1 mm wide or less at the base, evenly tapering upwards, permanently connate into a narrow cone surrounding the gynoeceum, dehiscing by small introrse apical pores. *Ovary* oblong-ovoid, c. 2 mm long and 1.2 mm broad, glabrous, marked with numerous small longitudinal streaks. *Style* columnar, c. 3 mm long. *Capsule* and *seeds* unknown.

Flowering period: Dec.

COLLECTIONS

CAPE PROVINCE. Komgha Div.: Prospect Farm, 2100 ft, XII. 1889, FLANAGAN 573 (K, PRE) — Near Komgha, 2000 ft, XII. 1895, FLANAGAN 573 (BOL).

This enigmatic species was with a question mark referred to *Rhadamanthus* by BAKER, who added: "Most likely a new genus". I am inclined to share this view, but it seems inadvisable to describe a new genus on the basis of the limited and incomplete material available. BAKER's laconic description, "rootstock, leaf, fruit and seeds

unknown", is unfortunately still valid. The species should be searched for and further studied, preferably in cultivation.

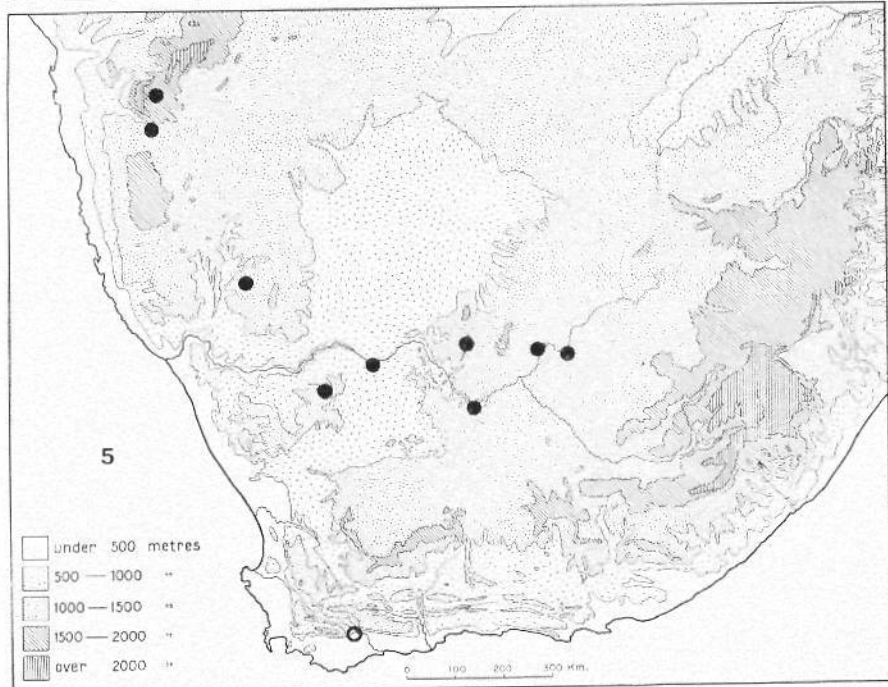
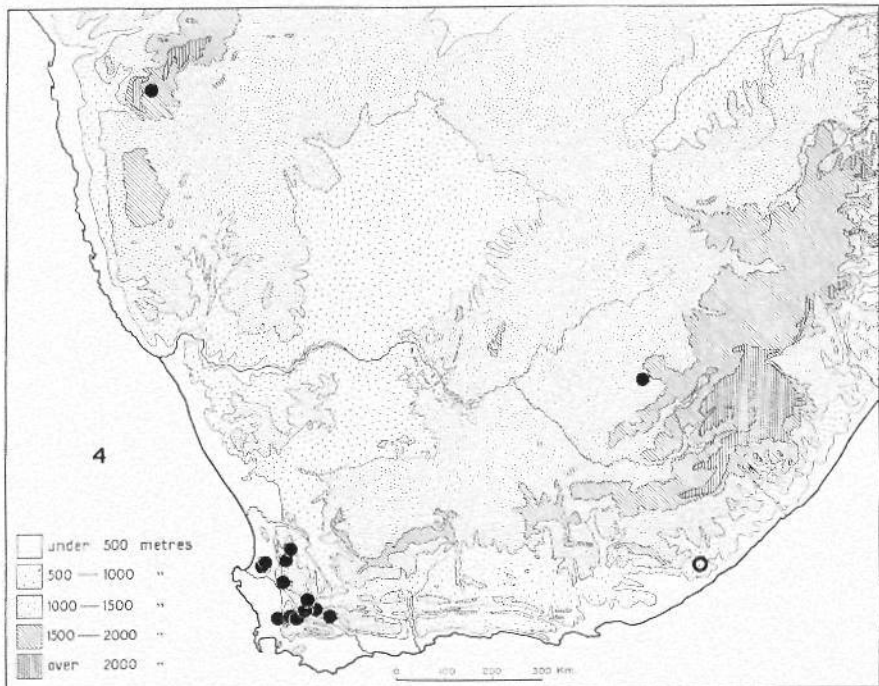
The most striking differences from other *Rhadamanthus* species are the long and stout scape, the presence of bracteoles, the polyphyllous biseriate perigon, and especially the connate anthers forming a cone around the pistil and dehiscing by quite small apical pores.

The single locality lies in the neighbourhood of Komgha in the eastern Cape.

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Maps 4—5. — 4. *Rhadamanthus platyphyllus* (●) and *R. cyanelloides* (○). —
5. *R. fasciatus* (●) and *R. albiflorus* (○).



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Notes on the Biomass and Productivity of Below-ground Organs of a South-Swedish Hay-Meadow

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ABSTRACT

NILSSON, J.: Notes on the Biomass and Productivity of Below-ground Organs of a South-Swedish Hay-Meadow. — *Bot. Notiser* 123: 183—194, Lund.

A preliminary report on the distribution of organic matter and its turnover in a South-Swedish hay-meadow is given. About 94% of the organic matter in the ecosystem consists of humus. The below-ground biomass is about five times as the above-ground biomass. Roots and rhizomes are concentrated in the upper layers of the soil. In five of the six sites 87—97% of the below-ground organs is found in the upper 30 cm.

The below-ground productivity has been determined as the difference between maximum and minimum values of biomass of monthly samplings. The variation of biomass is very regular, with the peak value at the end of June. There is then a gradual decrease with minimum values in the spring. The difference between highest and lowest values is of the order 1100 g/m² (11 t/ha). This is approximately 50% of the maximum dry matter measurement, suggesting a turnover for the "root system" as a whole every second year, although certain parts may persist for a longer or shorter period.

INTRODUCTION

Many studies on terrestrial vegetation have, during later years, dealt with the productivity of ecosystems. Most of them concern the above-ground plant parts only. This may be ascribed to the difficulty in sampling below-ground stems and roots. The quantity of roots and their vertical distribution is of great importance to the above-ground production. In addition, the below-ground parts play an equally important role in their effects upon the soil, especially its content of organic matter. An understanding of the cyclic processes associated with root growth and decay is of special importance in studying hay-meadows, as most of the aerial components are removed each year.

Our knowledge of these processes in established grass-swards is scanty. MILNER and HUGHES (1968 p. 4) write: "The studies of BRAY (1963) and DAHLMAN and KUCERA (1965) are among the few which

have been concerned with the dynamics of root production and its effect on estimates of net primary production."

The purpose of this paper is to present preliminary data on the dynamic aspect of below-ground organs in a South-Swedish hay-meadow. I prefer to use the concept of below-ground organs instead of roots, as this includes rhizomes and bulbs. These fractions ought to be separated in further studies, because of their different functions in the ecosystem (WEINMANN 1961).

The data presented in this paper have been obtained in connection with a research on the temporal variation of some mineral nutrients in the soil. Consequently sampling methods have not been chosen especially for the investigation of below-ground organs. However, the study has produced valuable ideas of how to investigate "root systems". The figures presented below also give valuable information on the below-ground biomass in hay-meadows. The studies will be continued using more adequate methods.

LOCATION AND DESCRIPTION OF THE STUDY AREA

The studies have been carried out on the island of Höö (lat. $56^{\circ}39'$, long. $3^{\circ}53'$ W Stockholm), located in Lake Möckeln in the southern part of the province of Småland, South Sweden. The mean annual precipitation is approximately 700 mm. The soil-type is a brown-earth, lying on a diabase. There is a low content of clay ($<10\%$). A more detailed description of chemical and physical properties of the soil will be given in a later paper.

Only hay-meadows, which are still managed, have been investigated. The meadows have never, as far as is known, been manured. They are mowed practically every year, as a rule in July. In August and September they are grazed by bullocks. These meadows have probably been used for hay production since the 16th century and perhaps even earlier. It is a fundamental ecological problem how the productivity of these meadows has been maintained during hundreds of years, without manuring. The hay-meadows occupy an area of about 6 ha, divided into several smaller parts by arable lands and pastures. There is a variation in vegetation within the area. This is caused among others by the variation in exposure and supply of oozing water which leads to differences in water content and chemical properties of the soil. Most of the investigations have been done in six homogeneous sample points, whose most important species are shown in Table 1.

Table 1. The main species on the six sample points. The first figure represents the small square frequency and the second the characteristic degree of cover (see MALMER 1962 pp. 48—49).

Sample point	1	35	4	20	15	13
Exposure	S	W	SW	E	NW	NW
Slope angle	20°	20°	5°	5°	10°	20°
Number of species (in 20 m ²)						
a) grasses	10	11	12	13	11	11
b) herbs	25	28	31	29	28	34
<i>Helianthemum chamaecistus</i>	100.4	—	—	—	—	—
<i>Hieracium pilosella</i>	91.2	—	—	—	—	—
<i>Festuca ovina</i>	100.4	91.3	—	18.1	9.1	27.1
<i>Trifolium medium</i>	27.4	100.5	100.5	100.3	100.2	9.1
<i>Leontodon hispidus</i>	36.1	9.1	9.1	100.2	18.1	9.1
<i>Lathyrus montanus</i>	—	91.1	82.1	100.1	82.1	100.2
<i>Primula veris</i>	—	55.1	100.3	82.1	64.1	64.1
<i>Centaurea jacea</i>	—	—	100.4	9.1	—	—
<i>Deschampsia flexuosa</i>	—	18.1	18.1	—	100.1	100.2
<i>Hypericum maculatum</i>	—	55.2	64.1	100.1	100.4	73.2
<i>Convallaria majalis</i>	—	27.1	—	—	100.4	100.3
<i>Anemone nemorosa</i>	—	—	—	9.1	100.2	100.2
<i>Potentilla erecta</i>	—	—	9.1	18.2	73.1	100.3

A more detailed description of the vegetation is under preparation. In addition to the six previously mentioned sampling points, a few measurements have been made at other points within the area.

METHODS

A core sampling method was used to make quantitative determinations of the below-ground organs. Steel cylinders with an inner diameter of 7 cm and a height of 10 cm were used.

In the six sites, three successive 10 cm levels were investigated about once a month during the periods 1.5—8.11 1965 and 8.3—21.5 1966. In addition, three samples were taken at each level to a depth of 90 cm in September 1966.

The fresh soil samples were sieved (meshes 2 mm). Some smaller roots will pass the screen during this procedure. STEEN (1957 a) estimated this quantity to be 5 % of the total below-ground biomass. After most of the fine earth was sieved, the screen refuse was washed with water (meshes 0.6 mm). Some very fine roots passed through the sieve. This part was not collected, but occasional measurements showed that its quantity was very low in comparison with the total mass (about 1 %). As the clay content is low, the rinsing was easy to perform. No dispersing agent was used. After washing, the below-ground organs were dried at 80°C and weighed. Values of living organic matter were not corrected to combustible material only. Thus they include the inorganic content, if not otherwise mentioned.

When easily distinguishable, dead roots and rhizomes were separated. In many cases it was not possible to do this visually. A more objective method

to separate dead and living material ought to be used in future studies. Unfortunately, there are no suitable methods available for this as yet. The dead fraction seems to be of low importance in the studied samples.

The greatest deviation from the mean value by triplicates for the whole profile at the sampling in September 1966 was as follows: 2 %/o, 7 %/o, 1 %/o, 3 %/o, 5 %/o, 5 %/o (cf. SCHURMAN & GOEDEWAAGEN 1965 p. 42). This indicates that there is an even distribution of the below-ground organs in these hay-meadows. However in further studies a larger sample must be taken.

The content of carbon in soil has been determined by wet combustion (JANSSON & VALDMAA 1960). In order to convert organic carbon measurements to estimates of organic matter, the factor 1.72 is generally adopted. Some scientists have raised objections against the use of this conversion factor (cf. SILVERBERG 1957 p. 15). It seems obvious that the factor must be determined for each soil type and horizon under consideration. I have multiplied the carbon values by 2.00. This conversion factor has been calculated on my own material according to HOWARD (1966). Most values lay between 1.97 and 2.03. In some samples, with a deviating mineralogical composition, higher values have been received. This is ascribed to mineral destruction, which has been verified by ignition at different temperatures.

pH has been determined on fresh fine earth with glass electrode in extracts of water. A volume ratio soil/liquid 1:1 was used.

THE DISTRIBUTION OF ORGANIC MATTER IN THE ECOSYSTEM

The total mass of below-ground organs at the sampling in September 1966 (total profile) varied between 916 and 1839 g/m² (Table 2). Many authors, in studying grassland vegetation, have reported values of the same order, of which some are gathered in the following Table.

Author Year of publication	STEEN 1957 a, b	OLOFSSON 1963	LINKOLA & TIIRIKKA 1936	KMOCH 1952	DAHLMAN & KUCERA 1965
Number of sample points	4	13	7	104	1
Below-ground organs 0—30 cm, g/m ²	840—1760	1110—2350	440—1690	170—6400	1190—1620

The relative distribution of organic matter on above-ground biomass, below-ground biomass and humus is almost equal in the six sample points. Mean values from these points are represented in Fig. 1. Figures on biomass from each point in turn represent mean values from three sampling occasions, 1.7, 22.7 and 20.8 1965. For below-ground biomass values from September 1966 for the level 30—90 cm are added.

About 94 %/o of the organic matter in the meadow consists of humus. The variation within the points was 91.8 %/o to 95.2 %/o. 99 %/o of the organic matter in the ecosystem is found in the soil. The below-ground

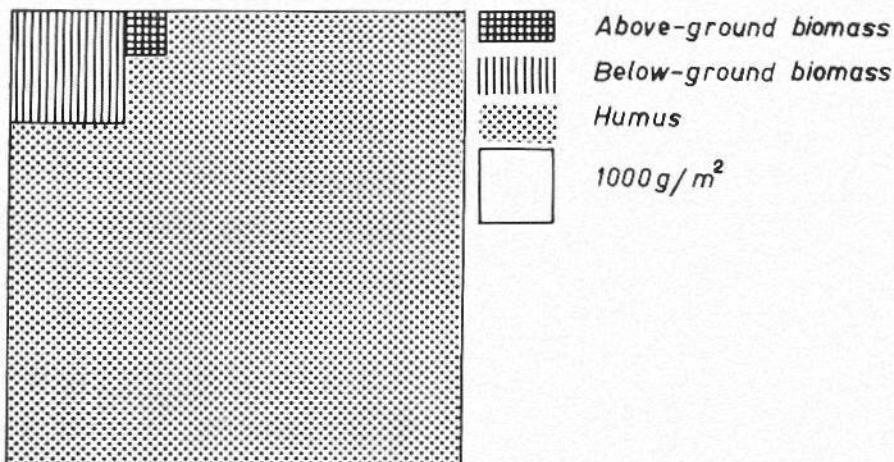


Fig. 1. The distribution of organic matter on above-ground biomass, below-ground biomass and humus (level 0—90 cm). Mean values from six sites.

organs constitute only a small part of the total organic matter. On the other hand, its quantity is generally several times greater than that of the aerial parts. It makes up 4.0—7.1 % (mean 5.4 %) in the six sites, and above-ground biomass constitutes 0.5—1.3 % (mean 0.9 %). In real figures the mean values correspond to 1.9 kg/m² and 0.33 kg/m² respectively.

The quotient below-ground organs/above-ground organs varies between 3.1 and 9.3. It decreases with increasing pH (cf. KMOCH 1952).

THE VERTICAL DISTRIBUTION OF BELOW-GROUND ORGANS

The quantities of roots and rhizomes at different levels of the profiles are seen in Table 2. The greatest concentration occurs in the top 10 cm. In the uppermost 30 cm 87—97 % of living below-ground organs are found. Only site 35 shows a lower value (66 %). This is ascribed to special conditions in the profile with a marked concentration of humus at 50—80 cm. The reason for this is not known.

In the samples taken monthly only the upper 30 cm have been studied. Calculated on the quantities in this layer, the below-ground organs in the level 0—10 cm constitute 77—82 %. Again site 35 is characterized by a lower value (69 %).

The vertical distribution of below-ground organs seems to show a

Table 2. The below-ground plant biomass in the soil profiles in September 1966. Dry matter, g/m².

Depth cm	Sample point					
	1	35	4	20	15	13
0—10	991	860	683	879	812	993
10—20	158	234	226	83	54	289
20—30	61	126	41	51	22	234
30—40	22	119	13	30	20	126
40—50	13	92	18	19	5	28
50—60	17	87	9	12	2	19
60—70	14	122	3	17	1	16
70—80	2	120	2	6	—	9
80—90	2	79	2	—	—	6
Σ 0—90	1280	1839	997	1097	916	1720

general picture in most grasslands, with a high concentration in the upper part of the soil profile. This is shown by STEEN (1957 a, b) and OLOFSSON (1963) in Sweden, LINKOLA and TIIRIKKA (1936) in Finland, KMOCH (1952) and KLAPP (1943) in Germany and many others in northern Europe. A very good survey is given by TROUGHTON (1957 p. 43). The great concentration in the upper parts may be ascribed to at least three facts. Many species have a very dense "root-system", which does not penetrate very deep. Most grasses belong to this group. A second reason is, that roots are much thicker in their proximal parts, even if they do not function as absorbing organs. Further, the rhizomes are restricted to the upper parts of the soil.

BELOW-GROUND PRODUCTIVITY

The below-ground biomass at the monthly sampling occasions are given in Fig. 2. In order to reduce the effect of non-homogenities the mean values for the six sites have been calculated.

There is regular variation, which cannot be due to sampling errors. The same tendency is maintained at all sample points. At some points there are some irregularities, which, at least to a large degree, may be ascribed to heterogenities.

The below-ground biomass increases from May to the end of June. Then there is a gradual decrease until the following spring. At corresponding dates 1965 (22.5) and 1966 (21.5) the quantity of subterranean organs is almost the same. Sampling has not been done often enough to follow small fluctuations. It is impossible to say if the real maximum is reached during the last days of June, or some weeks be-

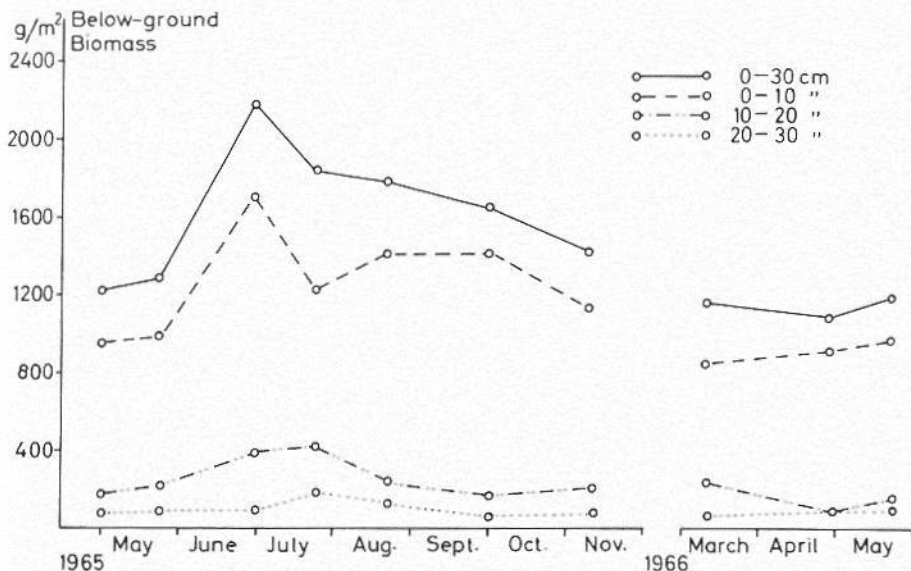


Fig. 2. The variation of below-ground biomass during a year for different levels (g/m^2). Mean values from six sites.

fore or after. Similarly, no autumn increase has been recorded (cf. KÖNEKAMP & ZIMMER 1955 p. 164, KMOCH et al. 1958 p. 131). The decrease during the summer and autumn means that the decomposition is greater than the production of new organic matter.

Deducing root productivity from the biomass change probably gives a too low value. The increase in biomass between two sampling occasions is interpreted as the production of new living organs. This method will give an underestimation, as a consequence of inter alia the following reasons.

1. There is a simultaneous dying off. When there is a decrease in biomass eventual production of new roots is masked, and consequently there is an underestimation of the productivity. This is especially relevant in studying grass-swards, as the rhythm varies between species.

2. Additional growth may still occur after the period of greatest recorded measurement. More frequent samplings would increase the probability of assessing the greatest mass of below-ground biomass.

In some cases a variation in biomass may be ascribed to translocation of carbohydrates up in the growing top or down to below-ground organs (cf. TROUGHTON 1957 p. 51, WEINMANN 1961).

The difference between the highest and the lowest mean values is of the order 1100 g/m^2 (11 t/ha). Summing the different levels gives a difference, 1300 g/m^2 (13 t/ha) (Table 4). The corresponding increase in aerial organs is about 3300 g/m^2 (3.3 t/ha). This means that the below-ground increase in biomass is three to four times that of the above-ground. The total productivity is of the same order in this meadow as in temperate forests. BRAY (1963) gives values of 7.8–15.6 t/ha for arboreal species.

The variation in biomass at different levels is seen in Fig. 2. The maximum value is in the uppermost level reached at the end of June. At lower levels there is a delay in the increase of biomass. This may be ascribed to lower and more constant temperatures. As the maximum growth of below-ground organs is not quite simultaneous at different levels, it is not advisable to treat the whole soil block to the appropriate depth as a unit. It ought to be cut off in separate layers.

Additional measurements have also been made at another site (31). This sampling point is very wet. *Carex panicea*, *Menyanthes trifoliata* and *Cirsium palustre* are dominating species. The below-ground biomass is given in the following Table.

Date	22.5	29.6	23.7	20.8	1.10	8.11	8.3	27.4	21.5
below-ground organs $\text{g/m}^2 \cdot 10 \text{ cm}$	1950	1300	1070	990	940	1330	—	1040	1980

The picture of variation is principally regular, but it has a different rhythm to that of the other drier sites. Peak values are obtained in the middle of May both years. It ought to be pointed out, that there was soil frost only two weeks in November. During the summer and autumn there is a gradual decrease, so that the quantity in October is about half that of May 22. Next spring a great increase was registered. In this wet site, the peak of below-ground production precedes that of the above-ground. The "root" horizon is about 15 cm in this site, so that the given values approximately give the total productivity. This amounts to about 1000 g/m^2 .

The fact that the quantity of below-ground organs in grassland varies during the year, seems to be a general opinion (cf. TROUGHTON 1957). Three types of yearly variation may be distinguished. A common opinion is that the production of roots precedes the development of the above-ground parts (STUCKEY 1941, KÜBLER 1954). Some studies have shown that the greatest production of below-ground and aerial

organs are simultaneous (KÖNEKAMP & ZIMMER 1955, KMOCH et al. 1958). Finally other authors find that the increase in root biomass is greatest after the grasses have flowered, even during winter (KAUTER 1933, TROUGHTON 1951). Site 31 in my investigation belongs to the first group, and the other sites to the second group.

LYR and HOFFMANN (1967) have summarized our knowledge of the growth periodicity of tree roots. Even with trees different growth patterns are to be seen. In most cases, the largest annual increment is recorded in spring and early summer.

Most statements in literature regarding the quantity of below-ground yearly production concern single species one or two years after planting (BRAY 1963, LIETH 1962). The greatest value in BRAY's list (op. cit.) fall on *Beta* with 6.6—13 t/ha. Cereals and some meadow species reported vary commonly from 1—5 t/ha (cf. my values of 10 t/ha). Only a few reports deal with established grass-swards.

KÖNEKAMP and ZIMMER (1955) found 2.2 t/ha, and KMOCH et al. (1958) 2—3 t/ha. For prairie vegetation 4.3 t/ha is reported (DAHLMAN & KUCERA 1965). The biomass in early spring amounted to 4.8, 4.8 and 11.9 t/ha respectively.

THE BELOW-GROUND ORGANS AND THE HUMUS CONTENT

In hay-meadows most of the above-ground biomass is removed by mowing and grazing. Renewal of the humus content of the soil thus has to occur by the death of roots, rhizomes and microorganisms. Net annual increment and turnover value are given in Table 3. Annual increment in the three levels represents the difference between the high and low seasonal totals of the entire below-ground biomass in each layer.

The ratios of annual estimated production to the maximum total root mass, or turnover values, were greater for the deeper profile levels. For 0—30 cm the turnover value is 0.50. This suggests that about half of the "root system" as a whole is replaced each year, although certain parts may persist for a longer or shorter period. It is a rough estimate. The vegetational composition is not identical in the different sites, and the rhythm of root production is therefore not quite the same. This means that some of the turnover may be levelled out, if the mean from several sites is used. This is clearly seen in Table 3. The turnover value of all the single sites are greater than the turnover value, based on the mean. In this table it is seen that on average about 60 % of the

Table 3. Relation between the annual increment and the maximum total biomass at different levels in the soil (g/m²).

Site	Depth cm	Period of greatest difference	Maximum below-ground organs g/m ²	Annual increment g/m ²	Turnover value
Mean values of the six sites					
	0—10	June—March	1700	850	0.50
	10—20	July—April	420	330	0.79
	20—30	July—Oct.	180	120	0.67
	0—30	June—April	2180	1100	0.50
The individual sites					
1	0—10	June—March	1690	1040	0.62
	10—30	June—Nov.	460	280	0.61
35	0—10	May—Aug.	1900	980	0.52
	10—30	June—May	1040	830	0.80
4	0—10	June—April	1270	930	0.73
	10—30	July—May	340	230	0.68
20	0—10	Aug.—April	1530	850	0.56
	10—30	July—April	580	450	0.78
15	0—10	June—Nov.	1770	990	0.56
	10—30	July—April	670	570	0.85
13	0—10	June—March	2260	1660	0.73
	10—30	July—Oct.	620	520	0.84

biomass is replaced each year. Even this value is certainly too low, as turnover in root hairs has probably been only partially registered.

In these well-drained soils the quantities of both humus and below-ground biomass decrease with depth (cf. Table 3—4). The amount of biomass decreases more rapidly than that of humus. Moreover, there is no correlation between the humus content and the annual increase of below-ground biomass (Table 4). The quotient between these components increases with depth. This may be due to several reasons. Organic matter will be washed down in the soil, partly as alluviation, partly

Table 4. The relation between humus content and annual combustible increment of organic matter (mean values from the six sites, g/m²).

Depth cm	Humus g/m ²	Annual increment g/m ²	Ratio of total humus to annual growth
0—10	7690	773	10.0
10—20	3930	294	13.4
20—30	3050	107	28.5
0—30	14670	1174	12.5

as colloids. In the deeper layers the temperatures are lower. Hence there is decreased microbial activity. Perhaps also the way of mineralization is different. The activity of earthworms leads to a net downward transport of organic matter.

ACKNOWLEDGEMENTS

I wish to express my gratitude to Professor NILS MALMER, Head of the Department of Plant Ecology, and to Dr. FOLKE ANDERSSON for offering valuable criticism of the manuscript. I also want to thank Mrs. MAJ-LIS GERNERSSON, who has done the carbon determinations.

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21 FEBRUARI. Professor PER WENDELBO, Göteborg, höll föredrag om »Släktet *Allium* på det iranska höglandet». — Inledningsvis behandlades släktets utbredning och systematiska ställning. *Allium* har sitt geografiska centrum i Flora Iranica-området och angränsande delar av Sovjetunionen; i Flora Iranica urskiljer föredragshållaren ca. 135 arter, medan VVEDENSKY's bearbetning för Flora SSSR (1935) upptar 226 arter. Totalutbredningen omfattar större delen av norra halvklotet från Etiopien till subarktiska trakter. Enligt föredragshållaren talar övervägande skäl, bl.a. cytologiska och embryologiska, för att *Allium* placeras i familjen *Liliaceae*.

De odlade arterna *Allium sativum*, *A. porrum* och *A. cepa* antas ha uppkommit ur vildväxande former i Centralasien, där både vilda och odlade *Allium*-arter spelar stor roll i den dagliga kosten, t.ex. i Afghanistan.

Större delen av föredraget upptogs av en redogörelse för olika utbredningstyper i Flora Iranica-området, vilka exemplifierades med arter och sektioner av *Allium*. Kartbilderna kompletterades med landskapsbilder från föredragshållarens färder i området samt närbilder av blommande *Allium*-arter.

28 MARS. Universitetslektor KJELD HOLMEN, Köpenhamn, höll föredrag om »Grönlands botaniska utforskning, speciellt i 1700- och 1800-tallet». — De första botaniska uppgifterna från Grönland härstammar från missionären HANS EGEDE, som bosatte sig vid nuvarande Godthåb i samband med den danska kolonisationen under tidigt 1700-tal. Hans son PAUL EGEDE insamlade ett herbarium, som nu utgör den äldsta växtsamlingen i Köpenhamns Botaniska Museum. I ett arbete av den tyske missionären DAVID CRANZ från 1770 finns den första systematiskt uppställda artlistan över Grönlands växter.

I början av 1800-talet gjordes omfattande insamlingar av den tyske mineralogen K. L. GIESECKE, som reste i Västgrönland för Grönlandske Handels räkning samt av M. WORMSKIÖLD, elev till Flora Danicas redaktör J. W. HORNEMANN. En annan av HORNEMANNs elever, JENS VAHL, gjorde 1828—36 betydande insamlingar längs hela Västgrönlands kust, bearbetade själv sitt material och beskrev flera nya arter. Svensken S. BERGGREN deltog i A. E. NORDENSKIÖLDs expedition till Västgrönland och utgav den första omfattande listan över Grönlands mossor.

Under 1800-talets sista decennier leddes Grönlandsforskningen av den år 1878 bildade »Komision for ledelsen av de geologiske og geografiske undersøgelser i Grønland». Vegetationsbeskrivningar började utges och olika expeditioner trängde allt längre upp längs nordostkusten.

9 MAJ. Ordföranden höll parentation över föreningens bortgångne hedersledamot professor NILS SYLVÉN.

Ordföranden meddelade att föreningen erhållit en donation på 1.000:— kronor från en person som önskade förbli anonym. Beloppet skall enligt styrelsens beslut läggas till SVANTE MURBECKS fond.

Föreningen beslöt enhälligt utse professor HENNING WEIMARCK till hedersledamot.

Fil. lic. UNO ELIASSON, Göteborg, höll föredrag med rubriken »Något om Galapagosöarnas vegetation och flora». — Som Regnellstipendiat har föredragshållaren tillbringat ca. 9 månader på denna ögrupp, tillhörig Ecuador och belägen omkring 1.000 km väster om Sydamerikas fastland. Öarna antas ha uppkommit genom vulkanisk aktivitet; flertalet har ännu verksamma vulkaner och täcks till stora delar av sterila lavafält.

Efter en exposé över öarnas unika djurliv övergick föredragshållaren till en beskrivning av flora och vegetation och valde därvid att skildra tre exkursionsmål, nämligen öarna Santa Cruz, Isabela och Fernandina. Floran omfattar totalt ca. 600 kärleväxter, varvid 35 % är endemer. Fyra endemiska släkten förekommer, samliga kompositar.

På de högre öarna kan man urskilja olika vegetationszoner. Innanför den egentliga strandzonen följer på Santa Cruz ett brett torrbälte med endemiska *Cereus*- och *Opuntia*-arter. Det endemiska compositsläktet *Scalesia* spelar en framträdande roll i skilda vegetationstyper. På 400—500 meters höjd förekommer fuktig skog av *Scalesia pedunculata* med rik epifytvegetation av mossor och ormbunkar. Ovanför skogsbältet följer på Santa Cruz trädlösa gräsmarker.

Öarna Isabela och Fernandina är krönta av vulkankratrar med tät vegetation. Fernandinas krater hade nyligen ett utbrott, varvid vegetationen på de inre sluttningarna förstördes och kraterbotten sänktes från 700 till 900 m under randen.

8 JUNI. Under ledning av docent ÅKE PERSSON och docent HANS RUNEMARK företogs en exkursion med privata bilar till Söderåsen med deltagande av 29 personer. Sedan den märkliga Odensjön beskådats, fortsatte färden till Skogvångshus, där HANS RUNEMARK demonstrerade *Polystichum braunii*, som förekommer i ett 60-tal exemplar längs en bäck i en bokskogssluttning tillsammans med den på avstånd snarlika *Dryopteris filix-mas*.

Fram till 1500- och 1600-talen var Söderåsens sluttningar beväxna med skogar av ek och bok, som emellertid successivt avverkades och kom att ersättas av öppna betesmarker med ljunng och en. Dessa marker nådde sin största utbredning vid mitten av 1800-talet; under senare tid har allt större områden planterats med gran. Gillastigs fälad är det största kvarvarande området av fuktig ljunghed kring Söderåsen; dess karaktär är i hög grad beroende av betning. Här kunde bl.a. följande arter studeras: *Arnica montana*, *Dactylorhiza maculata*, *Erica tetralix*, *Juncus squarrosus*, *Pedicularis silvatica*, *Plantanthera bifolia*, *P. chlorantha*, *Succisa pratensis*, *Trichophorum caespitosum* ssp. *germanicum*, och *Valeriana dioeca*.

Från platsen för Skärälids gamla turisthotell vandrade sällskapet längs bäcken in i den smala och branta Skärälidsdalen. Söderåsens djupa dalgångar

är troligen sprickdalar, som förstörats genom erosion och sannolikt var täckta av stillaliggande is under sista istiden. På de flesta ställen har rasmarkerna invaderats av hedbokskog eller *Quercus petraea*. På nordvända sluttningar finns en rik kryptogamflora, där inslaget av nordliga och västliga arter är påfallande. Bland levermossorna märks *Bazzania trilobata*, *Mylia taylora* och *Porella leavigata*, varav den sistnämnda har sin enda svenska lokal i Skäralidsdalen. Busklavarna *Cladonia alpestris* och *C. bellidiflora* har här sina sydligaste förekomster i Sverige.

Kulturpåverkan i Skäralidsdalen har beskrivits av ÅKE PERSSON i en uppsats i Skånes Natur 56(2), 1969. Dalen har i nästan hela sin längd utnyttjats för slätter och bete. På gamla slättermarker återfinns man nu ett trädskikt som huvudsakligen består av ask samt i någon mån ek, rönn, avenbok och apel. Örterna, bl.a. *Hypericum maculatum*, *Lathyrus montanus* och *Potentilla erecta*, utvisar att marken tidigare varit öppen. Slätterna torde ha upphört strax efter sekelskiftet, varefter ängen ännu någon tid utnyttjades för bete. På fuktigare partier finner man nu högörtäng med bl.a. *Aegopodium podagraria*, *Cirsium oleraceum*, *Filipendula ulmaria*, *Thalictrum aquilegifolium* och *Trollius europaeus*. Skogsavverkning i själva dalen har skett först på 1910-talet. På de gamla hyggena har boken nu i stor utsträckning ersatts av björk, rönn och avenbok.

Som avslutning på dagens botaniska studier besöktes Anderstorps enskog, som demonstrerades av markägaren. Ett område på 8 hektar domineras här helt av en och områdets karaktär vidmakthålles genom röjning samt betning av nötkreatur. Skogen domineras av högväxta, rakstammiga pelarenar, men enstaka plymförmiga eller krypande exemplar förekommer.

28 SEPTEMBER. I klart och kyligt höstväder företogs en exkursion till Hallandsåsen med deltagande av 21 personer förutom ledarna, fil. kand. LENNART LINDGREN och docent HANS RUNEMARK. I anslutning till den statliga bokskogsutredningen har LINDGREN gjort en översiktlig vegetationsanalys av det svenska bokbeståndet, som totalt omfattar ca. 43.000 hektar, varav 10.000 ha i Malmöhus län och 27.000 ha i Kristianstads län. Arealen minskar årligen med ca. 800 ha. Enbart vid oktoberstormen 1967 fälldes vid ett och samma tillfälle ca. 900 ha bokskog. Huvuddelen av denna areal har nu planterats med gran. Utredningen föreslår att ca. 4.000 ha avsättes som naturreservat, medan ytterligare en del kan komma att skyddas på annat sätt.

Olika typer av bokskog studerades vid Lärkesholmssjöns norra del i Örkel-ljunga, vid Stavershult i Rössjö socken och på åsens nordsluttning i Hasslövs socken i Halland. Vid Lärkesholmsåns utlopp i Ö. Spång kunde ett praktfullt bestånd av *Osmunda regalis* studeras.

Till följd av den torra sommaren och hösten var svampfloran mager, men på åsens sydsluttning norr om Rössjöholmssjön kunde RUNEMARK demonstrera bl.a. följande arter: Vitgul, vit, rodnande och ringlös flugsvamp, honungsskivling, svavelgul och tegelröd slöjkskivling, föränderlig tofsskivling, rynkad och blekviolett spindelskivling, stinksvamp, strecknagelskivling, rotnagelskivling, lökbroskskivling, blodsopp, lärksopp, Karl Johansvamp, sammetsopp och rutsopp.

31 OKTOBER. Fil. lic. ÖRJAN NILSSON höll föredrag om »Sydsvenska vildrosor». — Släktet *Rosa* är nordhemisfäriskt och förekommer huvudsakligen i tempererade trakter. Enligt modern uppfattning innehåller det ca. 150 arter. I Sverige har föredragshållaren urskiljt 16 vilda och naturaliserade arter (jfr. serien »Drawings of Scandinavian Plants» i Bot. Notiser 1967).

Efter en genomgång av den viktigare systematiska litteraturen och en redogörelse för *canina*-gruppens säregna fortplantningsmekanism presenterade föredragshållaren de sydsvenska *Rosa*-arterna i ord och bild. Material för bestämning bör helst insamlas strax före fruktmognaden och bör omfatta en del av årsskottet samt ett nyponbärande skott.

Arterna *Rosa rugosa*, *R. camtschatica* och *R. rubrifolia* anses med säkerhet vara införda; den förstnämnda är nu helt naturaliserad på sandiga och steniga stränder i södra Sverige, trots att den började uppträda på sådana lokaler först under 1920-talet.

21 NOVEMBER. Föreningen förrättade val av styrelse för 1970. Valda blev: Docent HANS RUNEMARK, ordförande; docent SVEN SNOGERUP, vice ordförande; fil. lic. ARNE STRID, sekreterare; fil. kand. JIMMY Persson, vice sekreterare; övriga ledamöter: fil. lic. FOLKE ANDERSSON, trädgårdsmästare JOHN KRAFT, fil. lic. LENNART LINDGREN, fil. lic. ÖRJAN NILSSON, docent SUNE PETTERSSON och direktör HELGE RICKMAN. — Till revisorer valdes fil. mag. ULF OLSSON och fil. lic. TORGNY VON WACHENFELDT; till revisorssuppleanter fil. mag. LENNART ENGSTRAND och fil. kand. MATS GUSTAFSSON.

Docent HANS RUNEMARK höll föredrag om »Floran på de egeiska öarna». — Den centralegeiska arkipelagen, som omfattar ett 30-tal bebodda och ca. 200 smärre, obebodda öar, utgör resterna av en landbrygga som fram till tidig Pleistocen förenade södra Grekland och södra Turkiet.

I området förekommer ca. 1.300 arter av högre växter, ett för Medelhavsområdet tämligen lågt antal. Många arter torde ha dött ut i samband med klimatfluktuationer under och mellan de nordeuropeiska istiderna.

Enligt föredragshållarens framställning kan man i nutiden urskilja följande floristiska element: 1) Mesofil flora, 2) *Radiola/Isoëtes*-samhället, 3) Macchia, 4) Frygana eller garigue, 5) Klippflora, 6) Småöflora och 7) Egentlig strandflora. Gariguen med kuddformiga, låga buskar utgör den dominerande vegetationstypen. Den slumpmässiga utbredningen av många garigue- och klipparter, ett förhållande som torde stå i samband med lokalt utdöende under klimatiskt ogynnsamma perioder, belystes med utbredningskartor.

Den nu avslutade inventeringen av de cykladiska öarnas flora har tjänat som bas för mer detaljerade experimentella undersökningar över variationen inom enskilda arter och artgrupper.

13 DECEMBER. Fil. lic. ÖRJAN NILSSON föredrog revision av räkenskaperna för 1967, varvid ansvarsfrihet beviljades kassören.

Föreningen beslutade om ändring av paragraf 3 i stadgarna. Sista meningen utgår och i stället tillkommer: »Hedersledamöter, korresponderande ledamöter och ständiga medlemmar erhåller kostnadsfritt föreningens organ Botaniska Notiser. Årligen betalande medlemmar erbjuds Botaniska Notiser till ett reducerat pris».

Med. kand. C. H. JUHLIN visade sina båda färgfilmer »Skånsk orkidé» och »Väderövallfart». — Den förra visar med ett fåtal undantag samtliga skånska orkidéer, varav åtskilliga rariteter, medan den senare skildrar en försommar-exkursion till Hallands Väderö.

Arne Strid

Avdelningen för Systematisk botanik,
Lunds Universitet, Lund

Announcement

Key to the species of *Aspalathus*

A limited number of reprints of "Comprehensive key to the species of *Aspalathus* (Leguminosae)" in *Botaniska Notiser* 122: 512—548, is available at a price of Sw. Kr. 3. They should be useful especially as a complement to the "Revision of the genus *Aspalathus*" published in *Opera Botanica* vol. 4, 6(2), 8(1), 10(1), 11(1), 21, and 22, and in *Botaniska Notiser* 121: 165—208. The order can be placed with Mrs. E. NORDSTRÖM, Institute of systematic botany, Ö. Vallgatan 18, S-223 61 Lund, Sweden.

THE EDITOR

Berichtigung

In unserem Artikel über die Flora des Njuonjevare-Gebietes (*Bot. Notiser* 122: 284—293) soll der zweite Satz des zweiten Abschnittes auf Seite 290 lauten: Nach SONESSON (1967 S. 279) ist dies das einzige bisher bekannte Vorkommen in Moorvegetation im Torneträsk-Gebiet.

KURT LINDBERG und BERIT RING

Brief Articles and Reports

(Smärre meddelanden)

***Stellaria nemorum* ssp. *glochidosperma* Found in Småland, South Sweden**

(*Stellaria nemorum* ssp. *glochidosperma* funnen i Småland)

ABSTRACT. — In connection with an inventory of beechforests in Sweden, *Stellaria nemorum* ssp. *glochidosperma* has been found in the province of Småland, South Sweden. This subspecies is not earlier known from that part of the country.

Under arbete med en växtekologisk inventering av bokskogar i Sverige har en lokal för *Stellaria nemorum* ssp. *glochidosperma* konstaterats i Småland. Lokalen i fråga är en bokskog — Mårås kronoskog — c. 4.5 km N Hyltebruk i Jönköpings län. Skogen som helhet var närmast av *Oxalis acetosella*-typ med vissa mera hedartade partier. Inom ett mindre område var vegetationen betydligt rikare och där återfanns underarten tillsammans med bl.a. *Milium effusum* och *Viola riviniana*.

Stellaria nemorum L. har två subspecies: ssp. *nemorum* (*S. montana* PIERR. 1880, *S. nemorum* ssp. *montana* MURB. 1899) och ssp. *glochidosperma* MURB. 1891.

Enligt HULTÉNS atlas (1950) är ssp. *nemorum* mycket vanlig i Norge och Balticum. Även i Mellansverige och södra Finland är den på vissa ställen vanlig. I Skåne finns enligt WEIMARCKS flora ett tiotal lokaler. I Danmark är den sällsynt. För ssp. *glochidosperma* råder det motsatta förhållandet. Den är vanlig i Danmark och Skåne, men förekommer norrut endast på ett fåtal lokaler (Blekingekusten, Göta älv-dalen, Kinnekulle, norra Öland). Ssp. *glochidosperma* är vanlig art i skånska ängsbokskogar och dominerar i vissa fall fältskiktsvegetationen.

LENNART LINDGREN

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***Hierochloë alpina* (Gramineae) $2n=66$ in Northern Finland**

ABSTRACT. The chromosome number $2n=66$ was found in a collection of *Hierochloë alpina* from Enontekiö parish, Finland. From different parts of the distribution area of the species the number $2n=56$ was previously known.

Previous reports give the chromosome number $2n=56$ of *Hierochloë alpina* (SWARTZ) ROEMER & SCHULTES (BOWDEN 1960 p. 551, Canada: Baffin Island, Southampton Island, Essex Co.; FLOVIK 1938 p. 301, Spitsbergen: HEDBERG 1967 p. 310, Canada: Baffin Island; JOHNSON & PACKER 1968 p. 414, Alaska: Ogotoruk; JØRGENSEN, SØRENSEN & WESTERGAARD 1958 p. 12, Greenland: Nugsuaq, Clavering Island; KNABEN & ENGELSKJØN 1967 p. 15, Norway: Troms; LÖVE & RITCHIE 1966 p. 432, Canada: Southampton Island; SOKOLOVSKAJA 1960 p. 44, USSR: Sachalin Island; SOKOLOVSKAJA 1963 p. 49, USSR: Kamchatka; SOKOLOVSKAJA & STRELKOVA 1960 p. 373, USSR: Kolguev Island; TATEOKA 1954 p. 46, Japan; WEIMARCK unpubl., Greenland: S. Strømfjord; ZHUKOVA 1967 p. 984, USSR: Wrangel Island). The related *H. monticola* (BIGELOW) LÖVE & LÖVE is reported to have $2n=63$ (JØRGENSEN, SØRENSEN & WESTERGAARD 1958 p. 12, Greenland: Narssarsuaq; LÖVE & LÖVE in LÖVE & SOLBRIG 1964 p. 201, USA: New Hampshire; WEIMARCK 1967 p. 499 and unpubl., USA: New Hampshire, Greenland: Narssarsuaq, Frederikshåb, Godthåb).

H. alpina plants from Northern Finland, Enontekiö parish, Markkina (collection B D R) are aneuploid, $2n=66$. The collection is apomictic and male meiosis is disturbed as is also the case with collections studied from Greenland (WEIMARCK unpubl.). Morphologically the plants are not deviating from the normal within the taxon. Whether *H. alpina* shows more cytological anomalies in Northern Fennoscandia is now subject to further investigation.



Mitosis in root tip of plant BDR 3. Excised root treated in 0.0125% colchicine for 20hr at $+4^{\circ}\text{C}$, fixed in absolute alcohol : glacial acetic acid 3:1, Feulgen stained and squashed according to ÖSTERGREN & HENEEN (1962). Photomicrograph with Nikon Microflex AFM on Leitz microscope. $\times 1500$.

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Botanical Literature

(Botanisk Litteratur)

HEGNAUER, R.: *Chemotaxonomie der Pflanzen. Eine Übersicht über die Verbreitung und die systematische Bedeutung der Pflanzenstoffe.* Band 5. Dicotyledonae: Magnoliaceae — Quinaceae. — Birkhäuser Verlag, Basel and Stuttgart 1969. 506 pp. Price FR 98.00.

Volume 5 of the basic, encyclopedic work "Chemotaxonomie der Pflanzen" by HEGNAUER was announced to be the last publication in the series. It follows the same general plan presenting families in alphabetical order. *Magnoliaceae* to *Quinaceae* are described in terms of morphology and taxonomy, with anatomical notes, discussions, and conclusions. Obviously the publication will be continued with one or more volumes. Extensive appendices of chemical notes at the end of each volume indicate the fast evolution of plant biochemistry. Die Nachträge in volume 5 was completed in July 1968. It would be valuable if the complete work was followed by supplementary books or a new edition within a few years.

"Chemotaxonomie der Pflanzen" could be looked upon as a plant catalogue of micromolecules (in the sense of non-polymeric substances) in extant plants. Alkaloids, phenolic compounds, essential oils, cyanogenic compounds, fatty acids and saponins are some of these plant constituents, which are found in many families. Most of these compounds are believed to be metabolically inert, non-adaptive and regarded as good taxonomic characteristics in phenetic and to a degree phylogenetic classification of the plant kingdom.

"Von den Inhaltstoffen der Familie wissen wir noch viel zuwenig, um deren systematischen Wert ermessen zu können". HEGNAUER often asks for an enlarged and intensified investigation of the nature and distribution of substances in different plant groups. The thoroughness of the chemical analysis is satisfactory in less than 5% of the phanerogames. Nevertheless this set of books is a reliable, rich source of well verified notes on the occurrence and biogenesis of many organic substances. However, many of these chemical characteristics have not yet found use in any plant taxonomic problem.

The present chaos resulting from the more or less unnatural systems of ENGLER, WETTSTEIN, HUTCHINSON, PULLE, LEMÉE, CRONQUIST, TAKHTAJAN and others, each with strongly divergent taxonomic opinions have made it impossible to follow one system. HEGNAUER, however, follows LEMÉE's ideas of subfamily divisions and family range confinement. At the family and other levels the angiosperm systems of WETTSTEIN and HUTCHINSON is almost always

compared. Other interpretations are also commented upon in the conclusion following the discussion of each family.

HEGNAUER is well aware of the ambiguity of homonymous and synonymous plant names. Many other biochemists, however, do not have information enough of this nomenclature. Several chemical analyses have been published using scientific plant names without attributing author notations. Synonymous species even have been the object of a comparative analysis by different scientists with accompanying meaningless dispute. For that reason, especially at the species level, the plant systematist ought to check the nomenclature and avoid any ambiguities concerning the validly published plant names. In HEGNAUER's work this check is facilitated by many references to the botanical as well as the chemical literature. A cumulative index of plant names and chemical compounds would make it easier to use a serial book of this kind.

Sometimes the chemical characteristics will support a system arranged on morphological groups. In other cases the phytochemistry does not support any taxonomic interpretations at all. Too little is known about the relationship between biogenesis and morphogenesis. In the attempt to get out a natural system, it is not always suitable merely to put new chemical characteristics into the "morphological" systems. It may only cause confusion.

A presumptionless systematization of the angiosperms based exclusively on the "invisible characteristics" of plant chemistry may produce results valuable to the study of evolution. Furthermore one should give priority to the so-called microevolution research and also increase the chemical investigations of genetically well-known plant populations. Such primary research will be fundamental to macroevolution theories based upon chemical characteristics.

"Chemotaxonomie der Pflanzen" is one of the best publications of the relationship of plant taxonomy and phytochemistry and is filled with new ideas for future research in these disciplines.

ULF OLSSON

BRIGGS, G. E.: Movement of water in plants. — Blackwell Scientific Publications, Oxford 1967. X+142 pp. Price 32s.6d.

Professor G. E. BRIGGS, professor emeritus of botany at the University of Cambridge, gives in his book physical and physiological aspects on the movement of water through a plant. According to the introduction the book is intended for plant physiologists who have a knowledge of plant anatomy and of the usual experimental procedures for measuring water absorption, movement in the plant and transpiration.

The first and even the greatest part of the book deals very thoroughly with the effects of different factors on the water potential and upon the movement of water. In recent years attempts have been made to apply a terminology based on physical chemistry to cell water relations. These attempts have had some influence on professor BRIGGS. Unfortunately this influence has got him to mix the new and the old terminology. This and the fact that there are no explanatory figures in the book, have made this part unnecessarily hard to read. The author's personal point of view in the subject is, however, very

interesting. According to him the concept of matric potential is quite unnecessary. He also contests the point of "some modern writers" who "seem to imply" that the movement of water is "merely a question of gradients of water potential and the appropriate resistances".

In the second part of the book the concepts discussed in the first part are used to describe the movement of water through plants. The presentation is clear but rather brief. In chapter 5 for instance only the stomatal transpiration is discussed and moreover only the effects on transpiration of the variably layer of undisturbed air outside the stomata and of the stomatal aperture.

The book is impaired by rather many mistakes in form of missing words and letters in the wrong order.

LENNART PERSSON

ROBERTSON, R. N.: *Protons, Electrons, Phosphorylation, and Active transport*. — Cambridge University Press 1968. VII + 96 pp. 17 figs. Price £ 1.6.0.

R. N. ROBERTSON, professor of Botany at the University of Adelaide is a well-known authority and specialist on salt uptake in plants. In this book — based on a series of lectures by the author — he consciously puts his own personal point of view on several important biological processes. Starting from Mitchell's chemiosmotic hypothesis postulating a separation of positive and negative electrical charges in normal mitochondria and chloroplasts which is responsible for the formation of ATP from ADP and inorganic phosphate in a reversal of the pH-sensitive ATP-ase reaction he suggests that the principle of separation of protons and electrons from hydrogen atoms of water or organic molecules is a general and fundamental biological process. Thus, he discusses charge separation and ion movement in chloroplasts and mitochondria and the phenomenon of active ion transport into living cells. The discussion is based on about 170 modern references.

The book is suggestive and also very legible for the advanced student or the scientist of physiology or biochemistry. The arrangement of the subject is not that of a text-book. Important but also controversial concepts such as the kinetic analysis of salt uptake or the possible presence of a dual-mechanism for salt uptake are just referred to and the uncertainty of those theories as well as of the main ideas of charge separation which are discussed in detail is not always quite clear.

However, as a contribution by an authority to the debate on the motive force for active transport of substances in cells the book is inspiring and we are once more reminded of the important and necessary statement that we always must be looking for mechanisms of active transport instead of for the mechanism.

SUNE PETTERSSON

Bot. Notiser, vol. 123, 1970

HEATH, O. V. S.: *The Physiological Aspects of Photosynthesis*. — Stanford University Press, Stanford 1969. VII+310 pp., 142 figs. Price \$ 8.50.

Enormous amounts of original research papers, congress proceedings and review articles are being produced in the field of photosynthesis. While I am writing this the three volumes (totalling about 2000 pages) of "Progress in Photosynthesis Research" from last year's congress in Tübingen is just being distributed. Nevertheless, it has been annoyingly difficult to find modern textbooks suitable to put into the hands of students. For Scandinavian readers there has been the little book by P. HALLDAL ("Fotosyntesen"), but for those wanting to learn a little more there has been a large gap to the very specialized literature. Now there are suddenly two books supplementing one another in an excellent way. One of them ("Photosynthesis" by E. RABINOWITZ and GOVINDJEE) deals mainly with the molecular aspects, i.e. the physics and chemistry of photosynthesis. The other one, with which this review is concerned, deals with the physiological aspects, i.e. relates the properties and activities of the whole plant to the process.

The first chapter, dealing with the structure and pigments of chloroplasts, falls a little outside the main topic, but forms a natural introduction. Several of the current and partly conflicting ideas about the submicroscopic structure are described and the chapter also contains some nice and well reproduced electron micrographs.

The next chapter is called "The diffusion paths". The physical relations are appropriately described without the vagueness that often results from the idea that biologists cannot be made to understand even simple mathematical formulae. If some immaterial objection should be raised against the treatment, it would be against the parallel drawn between a pressure (or concentration) difference and a potential difference (p. 43). As it is stated it is correct, and even instructive, but there is a slight danger of misunderstanding which could have been removed. It might have been pointed out that in thermodynamical terms a potential difference corresponds to a difference in *logarithms* of concentrations or pressures.

The third chapter and parts of other chapters, concern methods of investigation. Stressing the methodology in this field is motivated, since the kind of results obtained is largely determined by the choice of methods. This is particularly obvious when dealing with the difficult question of respiration intensity in light, which fills a whole chapter. The scientist should (whenever possible) know exactly what he is measuring.

I have only minor objections. I think that the discussion of light measurement from a broad band source (p. 100) could have been made a little clearer, perhaps even by introducing the feared integral sign. In the chapter about "Interaction of factors" the mathematical relations are not always unambiguous. For example, formula 4.2 (p. 114) reads

$$Y = f(A) + f(B) + f(C) + \dots + k.$$

A mathematician would probably write it

$$Y = f_A(A) + f_B(B) + f_C(C) + \dots$$

with the subscripts indicating that the f 's represent different functions. The addition of a k at the end is meaningless, since the form of the functions is not specified and may include constants. I also consider it an unnecessary monstrosity to introduce a fictitious "effective length" L_{it} (p. 124) for the photochemical and biochemical phases to explain the overall kinetics of photosynthesis.

In the chapter on chlorophyll content and light absorption reference could have been made to the work of P. LATIMER and others regarding the general optical properties of living matter and other scattering materials. The only statement touching this is that Beer's law "would not be expected to apply exactly".

In the final chapter "Physiology in future work" the author makes a plea for the survival of "botanical plant physiology, as distinct from the biochemical and biophysical sorts". He feels the squeeze between the biochemists and biophysicists on the one hand and ecology and practical agriculture, horticulture and forestry on the other. He argues that there is still work for the plant physiologist who is "primarily a botanist and therefore unfortunately knows less of biochemistry, biophysics and mathematics than the specialists in those subjects". This may be true, although I would like to stress the word "unfortunately". In any case, the whole book shows that plant physiology certainly is not dead.

L. O. BJÖRN

RICHTER, G. *Stoffwechselphysiologie der Pflanzen*. — Georg Thieme Verlag, Stuttgart 1969. X + 437 pp., 102 figs. Price DM 12.80.

The author starts out with the nuclear fusion in the sun which drives all life, and continues with the energetics of biochemical reactions and the basic nature of enzyme action. This is all dealt with in a very simple way, without touching any kinetics.

For the rest of the book the author has selected a few of the most important topics in plant biochemistry, and deals with them in rather great detail, starting out from scratch. These topics are photosynthesis and CO_2 -assimilation, respiration, structure and synthesis of nucleic acids, proteins, isoprenoids, lipids and porphyrins. One chapter deals with the assimilation of nitrogen, sulfur and phosphorus. And last, but not least, the most abundant chemical compound of living organisms, water, has got its own little chapter.

I think the author's choice of topics, and the disposition of the book is very well made. Also the treatment of the material is worth praise. There are particularly two features I would like to emphasize. The first is that the structural aspects of biochemistry are not neglected. The famous α -helix is there of course, like in all other books. The reader also learns about the multi-enzyme-complex in fat synthesis, about the importance of structure in the respiratory chain, and the structure of the photosynthetic apparatus gets 16 pages. There could have been more about the structure of proteins and of the polysaccharides of the cell wall, but then something else of importance might have had to be excluded.

The other general feature that I consider of great value is that the methods of investigation are worked into the subject. The student becomes familiar with the principles of chromatography and gel filtration, separation of cell organelles by density centrifugation, autoradiography, spectrophotometry and manometry.

My main objection against the book is that there are no references. Whatever reasons there may be for this, it seriously hampers the students who become particularly interested in some special topic and want to dig deeper into it. Those students may be few, but they are the ones worth writing good books for.

Of course one can find particular points to criticize here and there, but they are all of minor importance. I do not consider the experimental setup in figure 59 very suitable for studying fluorescence. I suppose the author has never tried it. Furthermore it is an oversimplification to claim that the emission from a leaf is identical (in spectral composition) to the fluorescence of *pure* chlorophyll. — In describing the methods of oxygen determination, polarography might have been mentioned, perhaps in place of Winkler's method which is very little used to-day.

The book is written in such a way that not much prior knowledge of chemistry (or of anything else for that matter) is required to understand it after careful reading. Nevertheless, the student may need more time than he anticipates to digest the seemingly small volume. There is no dead talk, there are lots of facts, but the author also pauses for the connexions between the details.

In summary: A very nice book.

L. O. BJÖRN

BUTENKO, R. G.: *Plant Tissue Culture and Plant Morphogenesis*. — Israel Program for Scientific Translations, Jerusalem 1968. X 296 pp., 104 figs. Price \$ 12.75.

This book is translated from a Russian original published in 1964. It is both a manual for "tissue culture" (in fact of organs, calli and cell suspensions) and a review of scientific results obtained with such cultures.

There is much valuable advice to be found in the book, but since there is no subject index a reader must take his time. The photographic reproductions are extremely bad. In the copy obtained for review four pages are left without print.

I have found few factual errors. On p. 32 it is claimed that isolated roots (in contrast to some other materials) need sucrose in the medium. This is correct only for a few plants. *Equisetum* roots are reported to use only sucrose, and roots of dicotyledons generally grow better on sucrose than on glucose. Roots of conifers and monocotyledons generally grow at least as well on media containing glucose as on those with sucrose. Wheat roots can be grown on glucose, but not at all on sucrose media. For some kinds of roots there are also reports of positive results with other carbohydrates.

It is recommended to incubate cultures in complete darkness if no illumination is required for special reasons. It could have been mentioned in this connection that excised roots generally require some light for continued growth; in complete darkness cell divisions cease after a couple of weeks.

Cytokinins seem to be a neglected topic in this treatise. There is, at the beginning of the book, a section entitled "Growth factors — synthetic and natural". This section deals with the effects of different auxins and plant extracts. Kinetin or cytokinins are not at all mentioned here. Although it is mentioned that corn steep water contains growth factors, nothing is said regarding their nature. This is somewhat surprising, since some of C. O. MILLER's work on the "kinetin-like factor in maize" is included in the bibliography. The nature of zeatin was, in fact, fairly well realized at the time of printing of BUTENKO's Russian edition, and it was also known that fruitlets of different species contain substances with kinetin-like activity. In the short section on "The effect of kinetin" (p. 135) BUTENKO states that "kinetin has not been detected in biological specimens, and it may be an artefact". This is true, but at least something should have been mentioned about the natural counterparts, the cytokinins.

The increasing flow of translations of Russian scientific literature is a welcome substitute (but no more) for our lacking knowledge of an important language of science. The translations, particularly of journals, are often of low standard. In this particular case the translator, Dr. M. ARTMANN, seems to have made an unusually good job.

L. O. BJÖRN

ROUND, F. E. Introduction to the lower plants. — Butterworths, London 1969. XII + 170 pp. Price £ 1.

Almost the whole plant system is referred to here as the "lower plants", only the gymnosperms and angiosperms being left aside. Thus the material is extremely heterogeneous, indeed. However, the book gives a well-balanced account of the chosen topic with many interesting details and modern aspects, and it has been a pleasure for me to study it. A criticism must therefore be rather peripheral.

The illustrations are simple and easy to understand. Possibly the *Isoetes* plant (p. 133) should have been drawn in a manner not hiding the corm.

The systematic disposition is mainly a conventional one with the exception of the rank of some algal groups. The lichens are treated as a separate group not included in the fungi, a somewhat disputable matter. Apart from this, matters of controversion are rare. In many cases the author has valuable practical aspects on his subject, stressing the everyday contact with the lower plants, but I regret the existence in a text-book from 1969 of an unreserved recommendation of controlling *Venturia* attacks by mercury-containing fungicides.

The notes on practical study at the end of each chapter are valuable. Perhaps the review questions are, too, but I think many of them can hardly be answered without a teacher's preparation and guidance. Moreover, each group

by necessity has been dealt with in a fairly small space. The major trends, although easily found by the more experienced reader, tend to be obscured by the details. I am afraid that the student really using the book as an "Introduction" cannot organize the subject without help. A great many anatomical, morphological and other terms are also introduced without being explained.

A better checking of terms is also recommended for the second edition. Most errors are of no real importance but some are in fact disturbing. Some examples: p. 44: the gametes of *Phaeophyta* are stated to be formed in sporangia (should be gametangia); p. 47: egg cells in terminal sporangia (should be oogonia); p. 78: cleistocarp (should be cleistothecium); pp. 92, 93: Spanish moss is stated to be an *Usnea* (rather a *Bromeliaceae*, *Tillandsia usneoides*); p. 139: the sporangiophores (of the *Sphenophyta*) are terminal (should be the strobili); p. 142: sporophyll types (in the *Sphenophyta*) (should be sporangiophore types).

In conclusion it must be said that it is a most stimulating and useful book. A direct continuation on gymnosperms and angiosperms would be very welcome.

GUNNAR WEIMARCK

Fotofloran. — Läromedelsförlagen, Uniskol, Lund 1969. 262 sidor. Pris 27.50 kr.

En ny och annorlunda flora har kommit ut från Läromedelsförlagen, Uniskol, i Lund. Lektor LORENTZ BOLIN, med tidigare erfarenhet från floraarbete, står för planläggning och bildorganisation i Fotofloran. 691 svenska växter presenteras här i färg, fördelade på 836 bilder. 95 % av bilderna har BOLIN själv tagit under ett par års intensivt arbete över hela Sverige. Kvalitén på bilderna är genomgående mycket hög. Vissa växter presenteras mycket illustrativt med flera bilder, t.ex. blomma och frukt.

Urvalet av arterna tycks vara mycket genomtänkt även om man kan ifrågasätta om vildtulpan och kronlilja är berättigade.

Fotofloran stiger ytterligare i värde genom de utmärkta texter som ÖRJAN NILSSON skrivit till varje art. Texterna har näst göras ganska komplicerade, men är ändå mycket innehållsrika och kompletterar bilderna förtjänstfullt. Exempelvis har många intressanta kulturhistoriska notiser fogats till, liksom upplysningar om giftighet och fridlysning. Text och bild följs åt helt vilket underlättar florans användning.

I slutet av florans ger ÖRJAN NILSSON med egna teckningar på nio sidor en översikt av växternas morfologi som är mera komplett än i någon tidigare fältflora.

Men det är inte bara bildmaterialet som gör florans intressant. Ett nytt och mycket viktigt grepp i takt med tiden är att växterna grupperats efter sin växtmiljö: kulturmarker, ängsmarker, torra, steniga och sandiga marker, skogsmarker, fuktiga marker, sjöar och stränder, havsstränder, fjällmarker. Träd, buskar och ris behandlas dock för sig, vilket kanske inte är helt konsekvent men ändå praktiskt riktigt.

Grupperingen av växterna är också noga genomtänkt och några grava anmärkningar går knappast att göra. Genom grupperingen har floran blivit ett enkelt hjälpmedel för den som ej är så bevandrad i systematik.

Grupperingen efter miljö borde dock följts upp med kompletterande bilder över de miljöer som omnämnes.

Inom zoologien har man sedan länge haft fälthandböcker för olika miljöer av typ »Vad jag finner på havsstranden». För växterna har det hitintills inte funnits någon motsvarighet i Sverige, vilket onekligen varit en stor brist. Man kan väl misstänka och hoppas att Fotofloran nu röjt vägen för nya grepp i denna riktning.

För botanisten är det naturligtvis inte tillfredsställande att »endast» 691 av Sveriges ungefär 1300 arter finns representerade. Floran vänder sig dock enligt förlaget i första hand till skolorna och man får nog säga att artstocken är lagom stor.

Floran ingår i en serie »Slå upp» från samma förlag som nu är under utgivning och som i första omgången behandlar ämnena geografi och biologi (där utöver de traditionella ämnena även ekologi och naturvård kommer att bli viktiga inslag). En intressant satsning som har alla förutsättningar att slå igenom.

Priset — 27,50 kr — för en så genomarbetad fältflora med 836 högklassiga färgfotografier är verkligen anmärkningsvärt lågt.

Slutsummering: En utmärkt fältflora som torde finna en mycket bred publik.

LENNART LINDGREN

LEVRING, T. H., HOPPE, H. A. & SCHMID, O. J.: *Marine Algae. A Survey of Research and Utilization.* — Cram, De Gruyter and Co., Hamburg 1969 421 pp. with 118 figures. DM 140.—.

Numerous books on algae have been published during the last decade. Nevertheless, there has been a great demand for a new treatise of the algae, especially their utilization. The present book by LEVRING — HOPPE — SMID fills this gap.

The book comprises three parts: 1. The vegetation of the sea and the classification of the algae written by LEVRING; 2. Marine algae as raw material written by HOPPE and SCHMID, and 3. Commercial products written by SCHMID.

LEVRING first gives a short, but very interesting survey of algal ecology, partly based on his own researches. He gives a view of the ecological factors and their influence on the algal vegetation. This review is extremely valuable as it is the first time the advances in marine botanical ecology have been summed up in this way. Further on he gives a comprimized review of the algal system, essentially the bentic forms, but also the phytoplankton and the freshwater algae. He uses with some modifications the system adopted by SMITH. However, some modern aspects could have been used, for instance concerning the systematics of the siphonous green algae. This chapter is, however, chiefly a base for the following chapters on the utilization of the algae.

The chapter on marine algae as raw material is a unic review of all algae,

which can be of economic importance. An account of the biochemical composition, of the distribution, and of the commercial products is given for 160 genera.

The part on commercial products is a comprehensive summary of all known algal products and their different names, the chemical composition, the use and also an estimation of the total productions of each kind. The last chapter gives a review of miscellaneous product in algae such as pigments, vitamins, antibiotics, and enzymes.

Each chapter ends with a generous literature list, which is of outmost importance.

The book is illustrated with many diagrams, drawings and photographs. In some cases the printing quality of the illustrations are insufficient.

As a summary can be stated that the book is extremely valuable to all students of algae and to Institutions working on algal products. It completes the algal literature in a new field that earlier have been nearly impossible to get a general view of.

TORGNY VON WACHENFELDT