With the compliments of the author

A CONTRIBUTION TO THE ECOLOGY OF THE ESTONIAN DECIDUOUS FOREST

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T. LIPPMAA

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1. Introduction.

The following investigations were carried out on the Estonian Islet of Abruka (58^{0} 9' north latitude and 22^{0} 30' eastern longitude from Greenwich). The total area of this islet together with the adjacent islets of Vahase and Kassemaa is 15.25 km^2. From north-west to south a ridge about 5—6 m. high makes the backbone of the islet. This part of it is covered with a luxuriant lime tree forest which is the most northern forest of this kind in this part of Europe. On both sides — west and east of the ridge — the lime-tree forest is followed by a marshy wood formed by ash, birch, spruce and alder. This borders on semi-natural vegetation — a cleared wood — which is used as a meadow ("wooded meadows").

The sea-shore is low and loamy, usually covered with salt meadows dominated by *Juncus Gerardi.* Especially in the northern part of the island and on the islet of Kassemaa this vegetation is predominant.

The core of the islet is formed by Kaugatoma lime-stone. Yet everywhere on the islet this limestone is covered with glacial and postglacial deposits such as loam, sand, gravel, stones and erratic blocks.

The age of the island is about 2000 years. First the above-mentioned ridge stretching from north-west to south emerged from the sea. This ridge contains a great many erratic blocks and stones. Some of them rise above the surface, while the majority is buried in a very stony and gravelly soil.

Little by little phanerogamous vegetation took foot on the emerged soil, first halophytes like *Crambe maritima* L., *Cakile maritima* L., *Honckenya peploides* Ehrh., *Aster tripolium* L., *Triglochin maritima* L., *Plantago maritima* L., etc. later *Festuca rubra* L., *Ostericum palustre* Bess. and other non-halophytic species as demonstrated in a previous paper of the author's (Lippmaa, 1934).

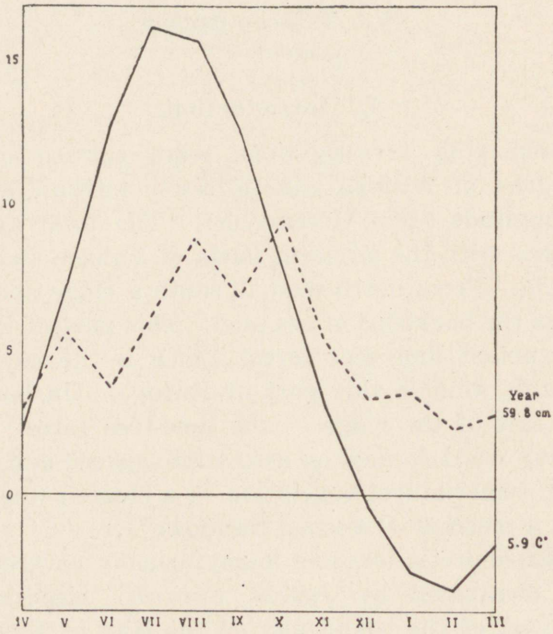


Fig. 1. The range of temperature and precipitation (hydrotherm figure) for the Island of Abruka (Estonia).

The secular raising of the land in this part of the Baltic sea still being in progress, practically every stage of this evolution can be observed. So, for instance, in the western part of Abruka a low stony ridge (the so-called "Laherahk" Cape) has a vegetation which certainly stands very near the former vegetation of the principal ridge of the island covered to-day with lime-tree forest.

This vegetation of Laherahk is rich in calciphilous species and is closely related to the vegetation of the Estonian and Swedish ålvars. What changes took place during the development of this ålvar-vegetation into the luxuriant lime-tree forest are best seen in a comparison of both e. g. the ålvar-vegetation of Laherahk and the lime-tree forest of the central part of Abruka. This comparison is the task of the following chapters.

In the preceding lines a short description of the island has been given. It seems useful to add now some data concerning the general climatic conditions on the island.

The hydrotherm figure for the Island (fig. 1) shows that the distribution of the average precipitation (59.8 cm.) is unequal. The bulk of it falls in August, September and October. The winter, spring and the first part of the summer are relatively dry, often even very dry. The difference between individual years is evident even if we take only the five years from 1932 to 1936.

	Jan.	Febr.	March	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
1932:	4.4	1.3	1.4	3.9	2.9	1.8	2.8	**6.4**	**9.2**	**11.0**	2.1	1.6	48.8
1933:	3.5	2.8	2.0	2.0	5.6	0.7	4.9	4.9	3.0	3.8	4.0	1.1	38.3
1934:	3.0	1.6	4.5	2.2	4.0	2.4	3.6	**8.9**	4.3	**10.7**	**6.8**	3.2	55.2
1935:	2.1	3.9	2.1	4.4	3.3	3.8	**8.8**	**14.4**	**11.5**	**16.8**	1.8	4.5	77.4
1936:	5.3	3.9	4.2	3.6	3.8	1.9	**10.4**	**9.2**	4.5	7.5	4.9	3.7	62.9

The 60-year average of temperature is as follows:[1]

[1] For the peninsula of Sõrve, about 40 km. SW from Abruka (Frisch, 1934). For the islet of Abruka itself no data are available.

	Jan.	Febr.	March	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Aver.	— 2.5	— 3.3	—1.9	2.4	7.7	13.1	16.4	15.6	12.7	7.7	3.1	—0.3	5,9
Max.	1.3	0.8	2.2	6.3	12.0	18.2	20.8	18.7	14.9	11.5	5.9	5.7	7.6
Min.	—11.7	—10.8	—8.1	—0.1	5.2	10.8	13.4	13.6	10.8	5.5	1.3	—3.2	4.7

The average air humidity (Frisch, 1934) for the year is 85 p. c. (86 p. c. in the morning and evening, 82 p. c. at midday), the lowest average observed being 77 p. c. (13^h, July), the highest — 90 p. c. (7^h, March).[1]

2. Calciphilous vegetation on immature soil.

On the low western ridge (Laherahk) the development of vegetation has reached a stage of relative stability. The moss-cover is almost continuous. This cover is formed by a number of calciphilous or indifferent species together with numerous seedlings belonging to species occurring in the herb layer. The floristic composition of the moss society (*Stereodon—Camptothecium—Thuidium* soc.) is given in the following table:

	2m.^{2}	2m.^{2}	2m.^{2}	2m.^{2}	2m.^{2}
Cladonia sylvatica (L.) Hoffm.	4.2—5	—	—	—	+.2
Stereodon cupressiforme Brid.	3.2—3	3.2—3	2.2	1.2	1.2—3
Camptothecium lutescens Bryol. eur.	1.2	3.2—3	4.2—5	3.2—3	2.2
Thuidium abietinum Bryol. eur.	+.1	2.1—2	2.1—2	3.2—3	1.1
Peltigera rufescens (Weis) Humb.	2.2	2.2	+.2	2.2	2.2—3
Dicranum scoparium (L.) Hedw.	1.2	1.2	3.2—3	—	—
Rhodobryum roseum (Weis) Limpr.	2.1—3	—	1.1—2	—	—
Cladonia furcata (Hds.) Schrad.	1.2	—	1.1	+.1	2.2
Bryum spp.	+.2	1.2	+.2	2.2	+.2
Climacium dendroides Web. et Mohr.	1.1	2.1—2	—	+.1	3.1—3

[1] Vilsandi, on the western coast of the Island of Saaremaa (Frisch, 1934).

	2 m².	2 m².	2 m².	2 m².	2 m².
Dicranum Muehlenbeckii Bryol. eur.	+.2	—	—	—	—
Cetraria aculeata (Schreb.) Th. Fr.	—	+.1	+.1	—	—
Thuidium Philiberti Limpr.	—	+.1	+.1	—	1.1
Tortula ruralis (L.) Ehrh.	—	+.2	—	2.1—2	—
Hylocomium proliferum (L.) Lindb.	—	—	+.1	2.1—2	—
Rhytidiadelphus squarrosus (L.) W.	—	—	+.1	—	—
Cladonia pyxidata (L.) Fr.	—	—	—	—	+.2
Ceratodon purpureus (L.) Brid.	—	—	—	—	+.1
Silene nutans L. s.[1]	+.1	+.1	+.1	+.1	+.1
Anthyllis vulneraria L. s.	+.1	+.1	+.1	+.1	+.1
Thymus serpyllum L. s.	—	+.1	+.1	+.1	+.1
Achillea millefolium L. s.	—	—	+.1	—	+.1
Galium boreale L. s.	+.1	+.1	+.1	+.1	+.1
Chrysanthemum leucanthemum L. s.	—	—	+.1	—	+.1
Rumex acetosa L. s.	—	—	—	+.1	—
Filipendula hexapetala Gil. s.	+.1	+.1	+.1	—	—
Euphrasia sp. s.	+.1	—	+.1	+.1	—

This society contains a number of lichens. Some of them — especially *Cladonia sylvatica* — have to be considered as destructive for the *Stereodon — Camptothecium — Thuidium* society. In this moss community the seedlings of the superimposed herb layer have to struggle for their lives. Yet they are here only transitory members. It seems very likely that in this early stage of their life the influence of these flowering plants upon the moss society is insignificant.

The superimposed herb society has the following floristic composition:

	10 m.²	10 m.²	10 m.²
Thymus serpyllum L.	5.5	4.2—5	4.5
Seseli libanotis (L.) Koch.	2.2	2.2	1.2
Trifolium montanum L.	3.1—2	2.1	3.2
Filipendula hexapetala Gil.	2.1—2	+.1	+.2
Centaurea scabiosa L.	2.2	2.2	1.2
Anthyllis vulneraria L.	3.2	3.2	3.2

[1] s = seedlings and young plants.

	10 m².	10 m².	10 m².
Avena pratensis L.	2.1	1.1	2.1
Galium boreale L.	2.1—2	2.1—2	2.1—2
Galium verum L.	2.1—2	1.2	2.1—2
Campanula persicifolia L.	1.1	2.1	1.1
Primula veris (L.) Huds.	1.2	1.2	2.2
Geranium sanguineum L.	+.2	+.2	+.2
Phleum Boehmeri Wibel.	1.1	+.1	1.1
Avena pubescens Huds.	1.1	+.1	+.1
Pimpinella saxifraga L.	1.2	1.2	—
Silene nutans L.	+.2	+.2	+.2
Arabis hirsuta (L.) Scop.	+.1	+.2	+.2
Potentilla reptans L.	+.1	+.1	+.1
Fragaria viridis Duch.	+.2	+.2	+.2
Veronica spicata L.	+.2	+.2	1.2
Medicago lupulina L.	+.1	+.2	+.1
Ranunculus bulbosus L.	+.1	—	—
Draba incana L.	—	+.1	—
Centaurea jacea L.	2.2	2.2	—
Hieracium pilosella L.	2.1—2	1.2	—
Festuca rubra L.	2.1	2.2	2.1
Achillea millefolium L.	+.1	2.1—2	2.1—2
Briza media L.	1.1	2.1	1.1
Linum catharticum L.	2.1	2.1	2.1
Chrysanthemum leucanthemum L. . . .	1.1	1.2	1.2
Carex verna Chaix	+.2	—	+.2
Festuca ovina L.	+.2	—	+.2
Trifolium pratense L.	+.1	—	+.2
Plantago media L.	1.2	+.2	+.2
Stellaria graminea L.	+.1	+.1	—
Allium oleraceum L.	+.1	+.1	1.1
Luzula campestris DC.	+.2	+.2	1.1
Allium scorodoprasum L.	+.1	—	+.1
Taraxacum sp.	+.2	—	+.2
Ranunculus polyanthemus L.	+.1	+.1	+.2
Poa irrigata Lindm.	+.1	+.1	—
Poa angustifolia L.	+.1	—	—
Artemisia campestris L.	+.2	+.2	+.2
Carex panicea L.	+.2	—	—
Plantago lanceolata L.	+.2	+.2	1.2
Vicia cracca L.	+.1	+.1	1.1
Rumex acetosa L.	—	+.2	—
Polygala amarella Crantz	—	+.1	—

Fig. 2. The calciphilous ålvar-like vegetation of Laherahk (Abruka, Estonia).

Fig. 3. Thermographs in the *Stereodon — Camptothecium — Thuidium* and *Filipendula hexapetala — Trifolium montanum* societies on Laherahk.

	10 m².	10 m².	10 m².
Cerastium caespitosum Gil.	—	+.1	+.1
Heracleum sibiricum L.	—	+.1⁰	+.2⁰
Sesleria uliginosa Čelak.	—	+.2	+.2
Sedum acre L.	—	—	+.2
Rhinanthus major Ehrh.	—	—	+.1
Crataegus curvisepala Lindm. s.	+.1	—	—
Rhamnus cathartica L. s.	+.1	—	—

As seen from the analysis this vegetation is close to the *Scabiosa columbaria — Avena pratensis* society described by Pastak (1935) on the western shore of the Island of Saaremaa. It belongs to the *Filipendula hexapetala — Trifolium montanum* society, which is widely spread over the whole north and north-west of Estonia on the shallow ålvar-soils covering the silurian and ordovician lime-stone rocks. It is certainly of interest to notice that this vegetation is related floristically to the vegetation of the Russian steppes, that is, to the vegetation of the northern ones named by Alechin the multicoloured mixed steppes ("stepy krasochnovo raznotraviya"). In a description of these steppes Alechin mentions the following species as being of importance: *Bromus erectus, Briza media, Phleum Boehmeri, Trifolium montanum, Filipendula hexapetala, Galium verum, Hieracium pilosella, Ranunculus polyanthemus, Avena pubescens, Poa angustifolia, Festuca rubra, Chrysanthemum leucanthemum, Vicia cracca, Lotus corniculatus, Primula veris, Anthyllis vulneraria,* etc. Of course together with them grows many a species which does not occur in Estonia, viz. *Stipa*-species, *Salvia pratensis, Pedicularis comosa, Carex humilis, Veratrum nigrum,* etc.

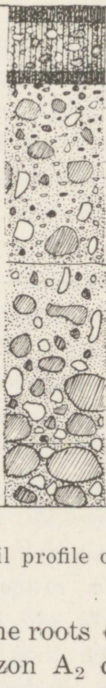
In the Russian mixed steppe the grass layer societies are also combined with a moss layer society as in our case. There it is the *Thuidium abietinum* society formed by a pure and uninterrupted carpet of this moss.

The general climatic conditions in the northern Russian steppes and on the Islet of Abruka being without any doubt very different, the question arises how are we to explain this striking similitude of vegetation.

The soil conditions are summed up on fig. 4. In this typical profile the surface soil (horizon A_1) consists of a dark dusty humus mixed with coarse sand. This horizon contains the

Percentage of soil components in sieved

(2 mm mesh) soil.



Depth in cm.	Water	Humus	$CaCO_3$	Coarse sand	Fine sand	Silt	Clay
3	9.88	38.7	0.78	92.2	3.5.	1.1	3.2
		7.6	11.43	98.8	0.7	0.4	0.1
15							
20	0.40	1.6	13.12	96.9	1.5	0.6	1.0
		1.5	14.72	97.2	2.2	0.4	0.2
	0.72						
70	2.05		9.49	97.4	1.3	1.0	0.3
102							
160	5.91		7.85	98.1	1.0	0.8	0.1
165	17.31		3.53				
175	30.71		4.38				

Fig. 4. Soil profile of the ålvar vegetation of Laherahk (27th July 1937).

bulk of the roots of the herbaceous species. Under this horizon lies horizon A_2 containing less humus. This is a soil rich in stones and gravel, the proportion of gravel to sieved soil[1] being about 3 to 1. The narrow horizon A_3 contains more humus than A_2.

The subsoil, or horizons B and C, are very stony, the first being rich in gravel, the second more sandy. As seen from fig. 4 the water distribution in the soil is unexpected. The

[1] The diameters of the sieve openings are 2 mm.

minimum of the water content lies between 15 cm. and 70 cm. (only 0.40 to 2.0 p. c. water in July). In both directions upwards and downwards from this dry horizon the water content increases, being on the 27th July about 10 p. c. in the uppermost humus horizon as well as in the subsoil at a depth between 160 and 165 cm. At this time the water table was 180 cm. above the soil surface.

Further remarkable peculiarities of this soil are (1) the high humus percentage of the uppermost layer (mild humus); (2) the coarseness of the soil; (3) the very high percentage of calcium carbonate in all the soil horizons except the uppermost humus layer which still contains about 0.8 p. c.

The pH of this soil varies with the depth. For horizon A_1 the average is 7.12 (individual results: 7.16; 7.21; 7.00). In the subjacent horizon A_2 6.08 was measured. The subsoil is pronouncedly alkaline and gave for horizons A_3, B and C 7.20, 7.30 and 7.50.

The results of the studies concerning the soil conditions might be summarized as follows:

The soil of the *Filipendula hexapetala* — *Trifolium montanum* society is in summer extremely dry. Only the uppermost layer of humus contains about 10 p. c. of water even in the dryest time of the summer. From about 10 cm. to 100 cm. the subsoil contains only 0.40 to 2—3 p. c. of water. This poverty of water is due to the coarse structure of the relatively young soil having emerged from the sea after being washed for ages by the waves. The subsoil is very rich in lime. This explains the high percentage of calciphilous and neutrophilous species found in both the moss society and the herb society.

The climatical conditions of the habitat turned out to be quite different from the general climatic conditions of the islet. They are different even in the moss society and the herb society.

To prove this some results of the observations made on the islet in the summer of 1937 are summed up in the following tables.

Temperature in the *Stereodon — Camptothecium — Thuidium* society.

	8^h	10^h	12^h	14^h	16^h	18^h	20^h	22^h	24^h	2^h	4^h	6^h	8^h	
25. July	—	32.2	34.0	32.5	31.0	29.0	21.8	18.0	17.5	17.0	16.9	17.3	18.3	26. July
26. July	18.3	26.5	35.1	33.7	27.0	21.6	16.9	15.2	15.8	16.0	16.0	16.8	19.0	27. July
8. Aug.	24.5	30.3	34.8	36.9	30.0	26.8	21.2	17.5	16.6	16.4	15.4	15.7	27.0	9. Aug.
9. Aug.	27.0	29.0	37.1	35.0	28.5	24.7	21.0	19.8	20.0	19,8	19.6	19.8	—	10. Aug.
Average	23.3	29.5	35.2	34.5	29.1	25.5	20.2	17.6	17.5	17.3	17.0	17.4	21.4	

Temperature in the *Filipendula hexapetala — Trifolium montanum* society.

	8^h	10^h	12^h	14^h	16^h	18^h	20^h	22^h	24^h	2^h	4^h	6^h	8^h	
25. July	—	28.0	28.3	28.0	27.0	26.1	21.1	17.9	17.3	16.4	16.4	17.1	18.7	26. July
26. July	18.7	23.0	29.0	30.1	22.5	18.2	16.1	14.1	15.3	16,0	16.0	16.3	18.4	27. July
8. Aug.	24.5	28.0	29.6	31.0	29.0	25.5	22.7	17.0	16,0	15,3	15.5	15.7	27.0	9. Aug.
9. Aug.	27.0	26.6	31.1	29.2	26.0	23.7	21.1	20.2	20,2	20,1	20.0	20.3	—	10. Aug.
Average	23.4	26.4	29.5	29.6	26.1	23.4	20.2	17.3	17.2	16.9	17.0	17.3	21.4	

	8^h	10^h	12^h	14^h	16^h	18^h	20^h	22^h	24^h	2^h	4^h	6^h	8^h
Camptothecium—Thuidium society .	23.3	29.5	35.2	34.5	29.1	25.5	20.2	17.6	17.5	17.3	17.0	17.4	21.4
Filipendula—Trifolium society . .	23.4	26.4	29.5	29.6	26.1	23.4	20.2	17.3	17.2	16.9	17.0	17.3	21.4
Difference	—0.1	+3.1	+5.7	+4.9	+3.0	+2.1	0	+0.3	+0.3	+0.4	0	+0.1	0

For four summer days the average temperature in the moss community is distinctly higher than in the herb society.

Although the density of covering in the hemicryptophytic community (*Filipendula hexapetala — Trifolium montanum* society) is not very high, there is a pronounced difference in the light intensity in this community and in the subjacent one. The measurements were made by using the Lange photo-element and were expressed in Lx.

The range of light intensity in the *Stereodon — Camptothecium — Thuidium* society.

Time	7^h—8^h	9^h—10^h	11^h—12^h	13^h—14^h	15^h—16^h	17^h—18^h	19^h—20^h
25. July			53.600	52.600	8.400	27.900	6.800
27. July		43.100	66.200	20.000	17.200	6.200	4.800
8. Aug.	22.400	34.100	47.700	53.300	45.800	22.100	8.800
9. Aug.	14.700	40.100	49.500	55.100	43.000	22.000	4.400
Average	18.500	39.100	54.200	45.300	28.600	19.500	6.200

The range of light intensity in the *Filipendula hexapetala — Trifolium montanum* society.

Time	7^h—8^h	9^h—10^h	11^h—12^h	13^h—14^h	15^h—16^h	17^h—18^h	19^h—20^h
25. July			64.000	64.200	10.000	39.500	9.900
27. July		52.700	75.600	23.500	20.000	8.000	5.200
8. Aug.	27.900	43.500	54.900	59.600	49.500	27.500	12.300
9. Aug.	23.200	46.100	58.000	60.100	47.700	29.100	5.400
Average	25.600	47.400	63.100	51.800	31.800	26.000	8.200

Thus the light intensity in the moss society is about 0.8—0.9 of that in the herb society. Only in the evening is it less — 0.75. Therefore all the species of the moss society are true heliophytes with high light resistance, the only exception being *Rhodobryum roseum* which occurs here in spots protected from the direct sunlight. The colour of this moss carpet poor in chlorophyll is olive-brown or olive-green.

Also the species of the *Filipendula hexapetala — Trifolium montanum* society often show in their foliage a low percentage of chlorophyll. The occurrence of red cell-sap (anthocyanines) is very common, especially during the drought. It was found so in the following species: *Avena pratensis, A. pubescens, Phleum Boehmeri, Briza media, Festuca rubra, F. ovina, Poa irrigata, P. angustifolia, Thymus serpyllum, Galium boreale,* *Veronica spicata, Libanotis montana, Centaurea scabiosa, C. jacea, Pimpinella saxifraga, Campanula persicifolia, Geranium sanguineum.*

The air humidity in the habitat of the societies under consideration is distinctly less than the average air humidity (cf. p. 34). This is evident from observations made with the Assmann psychrometer in July and August.

Air humidity in the habitat of the *Stereodon — Camptothecium — Thuidium* society.

	8^h—9^h	10^h—11^h	12^h—13^h	14^h—15^h	16^h—17^h	18^h—19^h
4. July		56	43	44	53	68
25. July		43	34	40	68[1]	95
26. July		63	43	38	61[1]	96
27. July	83	67	60	76	94[1]	95[1]
8. Aug.	79	60	40	53	71	80
9. Aug.	82	59	55	69	76	84

Air humidity in the habitat of the *Filipendula hexapetala — Trifolium montanum* society.

	8^h—9^h	10^h—11^h	12^h—13^h	14^h—15^h	16^h—17^h	18^h—19^h
4. July		70	47	53	56	66
25. July		58	56	61	79[1]	80
26. July		57	52	56	62[1]	84
27. July	82	71	63	80	84[1]	86[1]
8. Aug.	78	65	66	66	66	78
9. Aug.	81	69	64	70	74	82

The air in the habitat of the moss society is very dry. In summer during the daytime a saturation deficit of 50—70 p. c. is not at all exceptional. The influence of the dryness of the air on the moss society is however softened by the superimposed hemicryptophytic community which protects the moss community from wind. This was proved by measurements of the rate

[1] It rained.

of evaporation. Measurements made with the Iwanoff phyto-atmometer show clearly that the difference in the evaporation rate in the moss and hemicryptophyte societies is relatively small, the values being almost regularly less in the moss community.

Evaporation rate (in cm.^{3} per hour) in the habitat of the *Stereodon — Camptothecium — Thuidium* society.

	9^h	11^h	13^h	15^h	17^h	19^h	Average for day	night
25. July		0.42	0.34	0.26	0.06	0.10	0.24	0.04
26. July	0.22	0.32	0.40	0.26	0.04	0.00	0.20	0.01
27. July	0.10	0.38	0.22	0.05	0.02	0.00	0.13	0.01
8. Aug.	0.18	0.21	0.37	0.35	0.05	0.07	0.21	0.02
9. Aug.	0.21	0.34	0.45	0.27	0.05	0.06	0.23	0.02
Average	0.18	0.33	0.36	0.24	0.04	0.05	0.20	0.02

Evaporation rate (in cm.^{3} per hour) in the habitat of the *Filipendula hexapetala — Trifolium montanum* society.

	9^h	11^h	13^h	15^h	17^h	19^h	Average for day	night
25. July		0.68	0.80	0.57	0.07	0.07	0.40	0.13
26. July	0.15	0.54	0.62	0.42	0.04	0.02	0.28	0.05
27. July	0.12	0.53	0.29	0.09	0.13	0.02	0.19	0.06
8. Aug.	0.25	0.39	0.38	0.34	0.09	0.05	0.25	0.02
9. Aug.	0.25	0.35	0.51	0.37	0.10	0.05	0.27	0.03
Average	0.19	0.50	0.52	0.36	0.09	0.04	0.28	0.06

The much lower evaporation rate of the moss society as compared with the herb society is due a great deal to the influence of dew, this being often abundant on open places like the habitat of the societies under consideration.

The habitat conditions of the societies reviewed might be summarized as follows:

Stereodon — Camptothecium — Thuidium society.

Soil. Subneutral humus (30—40%) mixed with coarse sand, relatively decalcified. In summer very dry.

Filipendula hexapetala — Trifolium montanum society.

Soil. The uppermost layer rich in humus (30—40%), deeper very rich in sand, with a pH of 7,1. In summer extremely dry.

Climate. Temperature in summer in daytime about 30° (fine weather). Light about 0.8—0.9 of the light in the open. Air humidity in daytime (July) about 35—60 p. c. Often abundant dew cover in the night and early morning. Average daily evaporation about 0.22 ccm. per hour (fine weather).

Climate. Temperature in summer in daytime about 27° (fine weather). Full sunlight. Air humidity in daytime (July) about 50—70 p. c. Often abundant dew cover in the night and early morning. Average daily evaporation about 0.30 ccm. per hour (fine weather).

3. The forest vegetation and its ecology.

A detailed analysis of the societies of the deciduous forest of Abruka is to be found in a previous paper of the author's ("Une analyse des forêts de l'île estonienne d'Abruka (Abro) sur la base des associations unistrates", Acta Inst. et Horti Botan. Univers. Tartuensis, Vol. IV, Fasc. 1—2). Five superimposed societies occur: (1) *Ulmus — Acer — Tilia* society, (2) *Corylus avellana* society, (3) *Lonicera xylosteum — Ribes alpinum* society, (4) the variants of the *Galeobdolon — Asperula — Asarum* union and (5) *Rhytidiadelphus triquetrus — Eurhynchium striatum* society.

The floristic composition of the first is as follows:

Ulmus — Acer — Tilia society.

	1	2	3	4[1]
Tilia cordata Mill.	4.1—3	2.1	3.1—3	4.3—1
Ulmus montana With.	3.1—2	3.1	—	2.1
Acer platanoides L.	+.1	+.1	1.1	1.1
Sorbus aucuparia L.	1.1	+.1	1.1	+.1
Populus tremula L.	1.1	+.1	—	—
Corylus avellana L.	—	2.1	2.1	+.1
Pyrus malus L.	—	+.1	—	—
Betula verrucosa Ehrh.	—	+.1	1.1	—
Salix caprea L.	—	—	+.1	1.2
Quercus robur L.	—	+.1	—	—

[1] Each square is 400 m^2.

Fig. 5. The *Corylus avellana* society on the Islet of Abruka containing abundant *Crataegus curvisepala* Lindm.

Fig. 6. The *Ulmus — Acer — Tilia* society, the *Corylus avellana* society and the *Mercurialis perennis* society in the lime-tree forest on Abruka.

The forest trees on the islet attain a height of about 20—25 m. Even the usually bushy hazel frequently reaches in the forest an altitude of 10—15 m. The growth of the trees is luxuriant and exceptional for a northern forest.

Under the dense canopy of the *Ulmus* — *Acer* — *Tilia* society the subjacent communities — the *Corylus avellana* society and *Lonicera xylosteum* — *Ribes alpinum* society — are ordinarily more or less scantily developed. These communities enjoy their full development in places with a destroyed tree-layer society (fig.5). The floristic composition of the *Corylus avellana* society has been found in a favourable place to be as follows:

Corylus avellana society.

Corylus avellana L.	5.3
Crataegus curvisepala Lindm. . . .	3.3
Sorbus aucuparia L.	+.1
Salix caprea L.	+.1

The *Lonicera xylosteum* — *Ribes alpinum* society on the islet is formed chiefly by scattered bushes of *Lonicera xylosteum* and *Daphne mezereum.*

The aspect of the *Mercurialis* society and the *Asperula* society depends in the first place upon the dominating species. Both, *Mercurialis perennis* as well as *Asperula odorata,* are species with a high power for conquering soil and holding it. As *Mercurialis* is higher in growth than *Asperula* and the foliage of *Mercurialis* is much larger the soil is more shaded under this species than below *Asperula*. It seems that *Asperula odorata* prefers lower ground. Therefore the moisture-liking *Sanicula europaea* is mostly to be found together with this species.

The results of the numerous analyses communicated below prove that both societies — *Asperula odorata* society and the *Mercurialis perennis* society — belong to the same plant union — the *Galeobdolon* — *Asperula* — *Asarum* union (cf. Lippmaa, 1938).

In the lime-tree forest the moss layer is scanty. Here the mosses never form large carpets, but only scattered patches of different sizes. The floristic composition of the *Rhytidiadelphus — Eurhynchium* society is as follows:

Rhytidiadelphus — Eurynchium society.[1]

	1	2	3	4	5
Rhytidiadelphus triquetrus (L.) Warnst.	3.2—3	3.2—3	5.4	+.2	3.3
Eurhynchium striatum (Spruc.) Bryol. eur.	3.2—3	2.2—3	+.1	5.3	2.2
Mnium undulatum (L.) Weis. .	1.1—2	+.1	+.1	1.1—2	2.2
Plagiochila asplenioides (L.) Dum.	+.1	—	+.2	—	+.1
Rhodobryum roseum (Weis) Limpr.	+.1	+.1	+.1—2	+.1	+.1
Mnium medium Bryol. eur. . .	—	+.1	+.1	—	+.1
Hylocomium proliferum (L.) Lindb.	—	+.1	+.1	—	—
Dicranum scoparium (L.) Hedw.					
Dicranum majus Turn.	—	+.2	—	—	—
Thuidium recognitum (Hedw.) Lindb.	—	—	+.2	+.2	—
Pleurozium Schreberi (Willd.) Mitt.	—	—	+.1	—	—
Cirriphyllum piliferum (Schreb.)	—	—	+.1	—	—
Grout	—	—	+.1	+.1	+.1
Mnium cuspidatum (L.) Leyss.					
Brachythecium rutabulum (L.)	—	—	—	+.2	—
Bryol. eur.	—	—	—	+.2	—
Mnium stellare Reich.	—	—	—	+.2	—

In the lime-tree forest the *Rhytidiadelphus — Eurhynchium* society occurs in isolated patches. In mixed woods with dominating *Picea excelsa* this moss cover often forms extended carpets. That the determining factor of such distinct behaviour is not founded on a difference in light intensity is proved by the fact that the light intensity in both habitats investigated was nearly the same.

Careful examination of soil conditions in the lime-tree forest in places with a moss cover and on those without it showed that there is no difference either in the water content

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[1] The size of each square is 2 m^2.

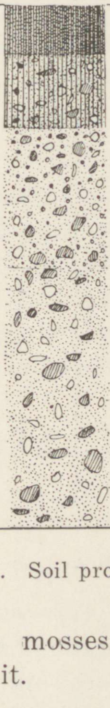
Characteristics and companions:	*Asperula odorata* society.[1]										*Mercurialis perennis* society.[1]									
Asperula odorata L.	5.5	5.5	5.5	5.5	5.5	4.5	5.5	4.5	5.5	5.5	1.1	+.1	2.2	1.1	+.1	—	—	—	—	+.1
Mercurialis perennis L.	+.1	+.1	—	—	—	+.1	—	+.1	—	+.1	5.5	5.5	5.5	5.5	5.5	5.5	5.5	5.5	5.5	5.5
Carex digitata L.	+.1	+.2	+.2	1.2	1.2	2.2	2.2	1.2	—	1.2	+.2	—	+.2	+.2	—	—	+.2	—	+.2	+.2
Hepatica triloba Gil.	2.1	+.1	1.1	1.1	2.1	2.1	2.1	1.1	3.1	2.1	2.1	1.1	3.1	1.1	1.1	2.2	1.1	2.1	+.1	1.1
Sanicula europaea L.	+.1	+.1	1.1	+.1	—	+.1	+.2	+.2	—	+.1	—	—	—	—	—	—	—	—	+.1	—
Orobus vernus L.	1.1	1.1	+.1	+.1	1.1	2.1	1.1	—	+.1	—	—	+.1	+.1	+.1	+.1	+.1	+.1	+.1	+.1	+.1
Dentaria bulbifera L.	+.1	1.1	+.1	+.1	+.1	+.1	—	—	+.1	+.1	—	—	+.1	+.1	—	—	—	—	—	—
Actaea spicata L.	+.1	—	—	—	—	—	—	—	—	—	+.1	—	—	—	—	—	—	—	—	—
Viola mirabilis L.	—	—	—	1.2	+.2	+.1	+.1	+.1	+.1	+.1	+.1	—	+.2	—	—	—	—	—	—	—
Allium ursinum L.	—	—	+.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bromus Beneckenii (Lge.) Syme	—	—	—	+.1	—	1 spec.	+.1	–	—	—	—	—	—	—	—	—	—	—	+.1	—
Aegopodium podagraria L.	1.1	1.1	+.1	+.1	+.1	+.1	+.1	+.1	1.1	1.1	1.1	+.1	1.1	+.1	1.1	2.1	+.1	+.1	1.2	+.1
Oxalis acetosella L.	1.1	1.1	1.1	1.1	1.1	2.5	2.5	+.1	2.1	2.1	2.1	2.5	+.1	+.1	+.1	1.3	+.1	+.1	1.1	+.1
Majanthemum bifolium F. W. Schm.	1.1	1.1	2.1	1.1	1.1	2.1	2.1	+.1	2.1	2.1	2.1	2.1	+.1	1.1	1.1	2.1	2.1	+.1	1.1	1.1
Aspidium filix mas (L.) Sw.	+.2	+.2	+.2	+.2	—	1.2	1.2	+.2	1.2	+.2	+.2	—	1.2	1.2	+.2	+.2	+.2	+.2	—	1.2
Milium effusum L.	1.1	+.1	+.1	1.1	+.1	+.1	1.1	+.1	+.1	1.1	+.1	+.1	+.1	—	—	+.1	+.2	—	+.1	+.1
Geum urbanum L.	+.1	—	+.1	+.1	+.1	—	+.1	+.1	1.1	+.1	+.1	1.1	+.1	+.1	+.1	+.1	1.1	+.1	+.1	+.1
Veronica chamaedrys L.	+.1	+.1	+.1	1.1	+.1	+.1	+.1	+.1	1.1	+.1	+.1	+.1	+.1	—	+.1	+.1	+.1	+.1	+.1	+.1
Poa nemoralis L.	+.2	+.2	1.2	+.2	2.2	+.2	1.2	+.2	+.2	2.2	+.2	+.2	+.2	+.2	+.2	+.2	+.2	+.2	+.2	+.1
Vicia sepium L.	+.1	+.1	+.1	+.1	+.1	+.1	+.1	+.1	1.1	+.1	+.1	+.1	+.1	+.1	+.1	+.1	+.1	—	—	+.1
Luzula pilosa (L.) Willd.	+.2	—	+.2	+.2	+.2	+.1	+.2	+.2	+.2	+.2	—	—	+.1	—	—	+.2	+.2	+.2	—	+.2
Viola Riviniana Rchb.	+.1	+.1	1.1	1.2	+.1	1.1	+.1	1.1	+.1	+.1	+.1	+.1	+.2	+.1	+.1	+.1	+.1	+.1	+.1	+.1
Ranunculus cassubicus L.	+.1	+.1	+.1	+.1	+.1	+.1	+.1	—	+.1	—	—	+.1	—	+.1	—	+.1	—	—	—	+.1
Fragaria vesca L.	—	—	+.2	+.2	+.2	+.1	+.1	—	+.1	+.1	+.1	—	+.1	+.1	+.1	+.1	+.1	+.1	+.1	+.1
Carex Pairaei F. Schultz	—	—	+.2	—	—	—	+.2	—	+.2	—	+.2	+.2	—	+.2	+.2	—	—	+.2	—	—
Primula veris L. em. Huds.	—	—	+.1	—	—	1.2	+.2	1.2	—	+.2	+.1	+.1	—	+.2	+.2	+.1	—	+.1	+.2	—
Festuca gigantea Vill.	—	—	—	—	—	+.1	+.2	—	—	—	+.1	+.1	1.1	—	+.1	+.1	+.1	—	—	—
Stachys silvaticus L.	—	—	—	—	—	—	—	+.1	—	—	+.1	—	—	+.1	—	—	—	—	—	—
Urtica dioeca L.	+.1	—	+.1	—	—	—	—	—	—	—	—	1.1	—	—	—	—	+.1	—	—	—
Geranium Robertianum L.	+.1	+.1	+.1	+.1	—	—	—	—	+.1	—	—	+.1	—	—	—	—	+.1	—	+.2	—
Lactuca muralis (L.) Fries	—	—	—	—	+.2	+.1	+.1	—	+.1	+.1	—	+.1	+.1	—	—	—	—	—	—	+.1
Trientalis europaea L.	+.1	+.1	—	1.1	+.1	+.1	—	—	—	+.1	—	+.1	+.1	—	+.1	+.1	1 spec.	—	—	+.1
Convallaria majalis L.	—	—	—	—	+.1	1.1	1.1	—	—	—	—	+.1	—	+.1	+.1	+.1	+.1	+.1	+.1	—
Polygonatum officinale All.	—	—	—	+.1	—	—	—	—	—	—	—	1 spec.	—	—	—	—	—	+.2	—	—
Melampyrum pratense L.	1 spec.	—	+.1	+.1	1.1	+.1	+.1	—	+.1	—	—	—	—	—	—	+.1	+.1	—	—	—
Rubus saxatilis L.	+.1	+.1	—	—	+.1	+.1	+.1	+.1	+.1	—	—	—	—	—	+.1	—	—	—	—	+.1
Campanula trachelium L.	+.1	—	+.1	+.1	—	+.1	+.2	—	+.1	+.1	—	—	—	—	—	+.1	—	—	+.1	+.1
Aspidium euspinulosum Asch.	1 spec.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ranunculus polyanthemus L.	1 spec.	—	—	—	—	1 spec.	—	—	+.2	+.2	—	—	—	—	—	—	1 spec.	—	—	—
Polygonatum multiflorum All.	—	+.1	+.1	—	—	1.1	+.1	+.1	—	+.1	—	—	—	+.1	—	—	+.1	+.1	+.1	+.1
Paris quadrifolia L.	—	—	—	+.1	—	+.1	—	+.1	—	—	—	—	—	—	—	—	—	—	—	+.1
Aspidium dryopteris (L.) Baumg.	—	—	—	+.2	+.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pteridium aquilinum Kuhn.	—	—	—	1 spec.	1.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Melica nutans L.	—	—	—	+.2	+.2	+.2	1.2	—	+.1	+.2	—	—	—	—	—	+.2	+.1	+.1	+.2	—
Chaerefolium silvestre (L.) Sch. u. Thell.	1 spec.	—	—	—	—	+.1	+.1	—	—	+.1	—	—	+.1	—	—	1 spec.	—	—	—	—
Agropyrum caninum P. Beauv.	—	—	—	—	—	—	+.1	—	—	—	—	—	—	—	—	—	—	—	—	—
Brachypodium silvaticum R. et Sch.	—	—	—	—	—	—	+.1	—	—	—	—	—	—	—	—	—	—	—	—	—
Geranium silvaticum L.	—	—	—	—	—	—	+.2	—	—	+.1	—	—	—	—	—	—	—	—	—	—
Platanthera chlorantha Rchb.	—	—	1 spec.	+.1	+.1	—	1 spec.	+.1	—	—	—	—	—	—	—	—	—	—	—	—
Hieracium Hjeltii Norrl.	—	—	—	—	—	—	—	—	—	+.1	—	—	+.1	—	—	—	—	—	—	—
Epilobium montanum L.	—	—	—	—	—	—	—	—	—	—	+.1	—	—	—	—	—	—	—	—	—
Satureja vulgaris (L.) Fritsch	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1 spec.	—	—	—	—	—
Transitory companions:																				
Acer platanoides L. seedl.	+.1	+.1	+.1	+.1	1.1	+.1	+.1	+.1	1.1	1.1	+.1	+.1	+.1	+.1	1.1	1.1	+.1	+.1	+.1	+.1
Corylus avellana L. „	+.1	+.1	+.1	—	—	—	—	+.1	+.1	—	+.1	+.1	—	+.1	—	+.1	—	—	+.1	—
Fraxinus excelsior L. „	+.1	+.1	—	—	+.1	1.1	1.1	1.1	+.2	+.2	+.1	—	+.1	+.1	+.1	+.1	+.1	+.1	+.1	+.1
Tilia cordata Mill. „	—	—	—	—	1 spec.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Daphne mezereum L. „	—	—	—	—	1 spec.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Quercus robur L. „	—	—	—	+.1	—	—	—	+.1	+.1	—	—	—	—	—	—	—	—	—	—	—
Ulmus montana With. „	—	—	—	+.1	—	+.1	—	+.1	—	+.1	—	—	—	—	—	—	—	—	+.1	—
Populus tremula L. „	—	—	—	+.1	+.1	—	—	—	—	+.1	—	—	—	—	—	—	—	—	—	—
Sorbus aucuparia L. „	—	—	—	—	—	—	+.1	+.1	+.1	—	—	—	+.1	—	—	+.1	+.1	+.1	—	—
Accidentals:																				
Galium mollugo L.	—	—	—	—	1 spec.	—	+.1	—	—	—	—	—	—	—	—	+.1	—	—	—	—
Solidago virgaurea L.	—	—	—	—	1 spec.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Helleborine latifolia Druce	—	—	—	—	1 spec.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Carex silvatica Huds.	+.2	+.2	+.2	+.2	—	—	—	—	+.2	+.2	—	+.1	+.1	—	—	—	—	—	—	—
Deschampsia caespitosa P. Beauv.	+.2	—	—	—	—	—	—	—	+.2	+.2	—	—	—	—	—	—	+.2	—	—	—
Scrophularia nodosa L.	+.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Filipendula ulmaria (L.) Max.	1 spec.	—	—	—	—	—	—	—	—	—	—	—	—	+.1	—	—	—	—	—	1 spec.
Equisetum pratense L.	+.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dactylis glomerata L.	—	—	+.1	+.1	+.1	—	—	—	+.1	+.1	—	—	—	—	+.1	+.1	+.1	—	—	+.1
Heracleum sibiricum L.	—	—	—	—	—	1 spec.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hypericum quadrangulum L.	—	—	—	—	—	—	—	—	—	1 spec.	—	—	—	—	—	—	—	—	—	—

[1] Each square is 20 m^2.

of the soil, or in the pH, or in the humus content of the uppermost soil horizon.

The determining factor is very simple. The places suitable for the moss cover in the lime-tree forest proved to be stones, trunks and tree branches on the ground. This is due to the fact that the moss excluding factor really is given by the lime-tree itself, namely its abundant dead foliage which pre-

Percentage of soil components



Depth in cm.	Water	Humus	$CaCO_3$	Coarse sand	Fine sand	Silt	Clay
	30.9	20.3	0.13	81.4	7.4	5.7	5.5
12							
	12.8	14.2	0.32	86.3	8.5	2.6	2.6
30							
			0.69	97.3	1.5	0.4	0.8
65							
	2.5		1.04	97.3	1.9	0.2	0.6
110	6.2		2.32	96.8	1.8	0.7	0.7
130							

Fig. 7. Soil profile of the *Mercurialis* society (12th July 1937).

vents the mosses from conquering the ground simply by covering it.

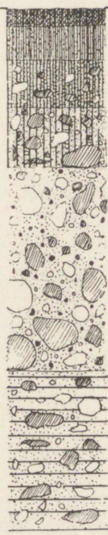
The lime-tree forest with its complicated stratified vegetation has developed from the vegetation analysed in chapter 2. This is obvious if we consider only the fact that the backbone of the islet, now covered with the lime-tree forest and surrounded to-day by an extended swamp forest, about

2000 years ago was a relatively narrow open ridge washed in the west as well as in the east by the waves of the sea.

What changes in soil structure and composition and in the local climate have taken place during this development? To analyse the actual habitat conditions and to compare them with the data communicated on p. 38 to 44 means to answer this question.

T h e s o i l. The soil conditions were investigated sepa-

Percentage of soil components in sieved (2 mm mesh) soil.



Depth in cm.	Water	Humus	$CaCO_3$	Coarse sand	Fine sand	Silt	Clay
4	71.9	54.3	0.00				
12	68.4	58.9	0.00				
	4.5	2.9	0.02	94.1	4.9	0.4	0.6
24							
		1.4	0.03	97.8	1.0	0.7	0.5
40							
	1.08		7.21	97.8	1.1	0.5	0.6
90							
	8.0		13.29	16.0	24.2	26.3	33.5
130							

Fig. 8. Soil profile of the *Asperula* society (12th August 1937).

rately for the *Mercurialis* society and the *Asperula* society. Fig. 7 represents the soil profile under forest ground vegetation dominated by *Mercurialis perennis*. The surface soil or horizon A_1 has a perfect crumb structure and consists of a dark brown subneutral humus mixed with coarse sand and is about 12 cm. in depth. Under this lies horizon A_2 (18 cm.) which is lighter brown, contains less humus and fifty per cent of gravel. This horizon contains some stones. The subsoil, or horizon

B (its depth is about 90 cm.), is a yellowish brown to yellow coarse sand mixed with a large amount (73 p. c.) of gravel and contains a great number of stones (granite, gneis, limestone, etc.). Under this lies a horizon which consists of grayish-blue clay mixed with sand and gravel. Fig. 8 gives the soil profile beneath the vegetation dominated by *Asperula odorata.* The dark brown surface soil A_1 consists of a humus mat and roots and is mixed with coarse sand; it is without gravel and stones, about 4 cm. in depth. This is followed by 8 cm. of dark brown coarse sand richly containing humus and less abundantly roots. Both, A_1 and A_2 have a distinct crumb structure. A_3 is leached, its colour is grayish. B_1 is reddish-brown coarse sand containing about 40 pc. gravel and is very stony. Under it is horizon B_2 of a similar character but much lighter in colour and more stony.

Horizon C is composed of a mixture of coarse sand, fine sand, silt and clay. It is a bluish-gray loam.

Although both soil profiles (fig. 7 and fig. 8) coincide in many essential features, there are evident differences between them. To appreciate the value of these differences a certain amount of data concerning the water content, $CaCO_3$ percentage, the pH of the soils and the percentage of soil fractions are certainly indispensable.

Water content in p. c. of dry soil.

A. The *Mercurialis perennis* society.

13. July 1937:	15.8;	13.1;	14.1;	33.8;		Average:
	25.1;	50.1;	37.7;	17.6;		25.9
8. August 1937:	21.3;	40.6;	27.7;	44.0;	58.4;	Average:
	26.8;	23.7;	39.5;	37.7;	57.2.	37.7

B. The *Asperula odorata* society.

13. July 1937:	20.5;	23.2;	26.0;	28.0;		Average:
	51.2;	19.8;	27.6;	31.3;		32.0
	48.3;	45.1;	31.4.			
8. August 1937:	41.6;	17.0;	18.6;	42.2;		Average:
	46.8;	31.0;	31.5;	29.1;	31.2.	32.1

As seen from these data, the variations in water content are large enough even between samples collected on the same day.

There is no evidence for a distinct difference in water content in the soils occupied by the *Mercurialis* and *Asperula* societies at least in summer.

A characteristic feature is the extremely low percentage (2.8; 4.3; 4.5; 1.1; 2.1; 4.6; 1.4; 1.3; 2.5; 5.1; 1.5; 1.9; 2.6) of water in the uppermost horizons of subsoil from the depth of about 20—25 cm. to a depth of 80—90 cm. This is true fcr both soils, those inhabited by *Asperula* as well as those inhabited by *Mercurialis*. During two months at least this important part of the subsoil is absolutely dry for every plant. It is noticeable that this horizon does not contain the roots of herbaceous species; it contains, however, the roots of trees. At a depth of about a metre the water percentage rises suddenly reaching 6—8 or more per cent and a little deeper the water table is often reached.

Organic matter.

The organic matter of the sieved forest soil is called humus here, as usual. It contains besides the true humus fraction the residues of plants (and animals) which are more or less humified but which in part can even be recognized microscopically as belonging to one or another definite organism. There are different methods in use to determine the organic matter of the soil. In this investigation the organic matter of soil samples was removed by burning. The author is aware of the different arguments which might be advanced against this proceeding. However this is surely the simplest method of estimating to a certain extent the amount of the complicated and not yet clearly defined substance we call "humus".

The humus content.

In places dominated by *Mercurialis perennis* (depth of the sample about 5 cm. below the surface): 18.7; 14,4; 20,3; 12,2; 17,0; 8,4; 9,5; 11.0; 24.4; 12.2; 36.2; 28.5; 14.5; 12.4; 34.6; 24.2; 53.2; 22.1.

Average: 20.8.

In places dominated by *Asperula odorata* (depth of the sample about 5 cm. below the soil surface).
9.8; 11.1; 16.2; 22.0; 29.2; 12.9; 19.5; 21.7; 24.5; 28.3; 24.5; 9.8; 11.2; 17.9; 14.1; 42.1; 23.5; 16.6; 19.4; 34.5; 14.0; 42.2; 54.3; 13.3.
Average: 22.2.

Both the average as well as the lowest and the highest percentage of humus in both places are essentially the same. It follows that there is no evidence that the humus content of the soil is the factor that determines the distribution of the *Mercurialis perennis* and *Asperula odorata* societies on the forest floor.

When compared with the immature soil described on p. 38, the development from the ålvar-vegetation to the forest vegetation is bound up with a d e c r e a s e in the humus content of the uppermost layer, the average found for ålvar soil (39 p. c.) being about double the average for the forest soil (21.6 p. c.). This decrease of humus percentage is however balanced by the almost double depth of the humus layer in the forest when compared with the ålvar-soil.

The pH of the soil.

The pH of the soil was determined by using soil samples dried in the air at ordinary room temperature. For the preparation of soil suspensions 50 cc. of distilled water were added to 20 g. of fine soil. After 24 hours of standing the pH of the mixture was determined by using the electrometric method.

The results thus obtained are summarized in the following table:

A_1 horizon under *Mercurialis* society:			A_1 horizon under *Asperula* society:		
6.33;	6.14;	5.48;	6.04;	5.59;	6.33;
5.34;	6.46;	6.96;	5.11;	6.42;	6.29;
6.04;	6.17;	6.60;	6.72;	6.84;	6.06;
6.24;	6.74;	4.72;	5.08;	6.04;	5.52;
5.80;	6.70;	6.26;	4.82;	6.24;	6.05;
Average: 6.13.			Average: 5.94.		

The humus of the *Asperula odorata* society turned out to be markedly more acid than that of the *Mercurialis* society. In both habitats the subsoil is neutral or slightly alkaline, the alkalinity growing with depth.

The percentage of carbonates in the soil.

For the determination of the carbonate content (essentially calcium carbonate) Bernard's calcimeter was used. For the uppermost horizon of the soil (A_1) the following percentage was found:

In places dominated by *Mercurialis perennis:* 0.13; 0.08; 0.32; 0.05; 0.13; 0.02; 0.07; 0.12; 0.03; 0.02.
Average: 0.10 p. c.

In places dominated by *Asperula odorata:* 0.05; 0.06; 0.00; 0.01; 0.07; 0.14; 0.05; 0.06; 0.02; 0.04.
Average: 0.05 p. c.

It follows that the humus layer (A_1) in the *Mercurialis perennis* society contains about twice as much carbonate as the more acid humus of the *Asperula* society. In some places the uppermost horizon below the *Asperula* society is wholly decalcified.

The subsoil of the forest is very rich in carbonate, the percentage varying here from about 0.1 to 25.0 p. c.

As regards the buffering of the humus horizon, there is no evidence for any difference present in the soil of the *Asperula* society and that of the *Mercurialis* society. Both are relatively well buffered against acids and alkalis.

Humus horizon (15 cc. soil + 50 cc. of distilled water)	pH	Buffering					
		Against alkali (N/10 KOH) pH			Against acid (N/10 HCl pH		
		1cc. KOH	2cc. KOH	3cc. KOH	1cc. HCl	2cc. HCl	3cc. HCl
Mercurialis soc.	6.1	0.9	1.6	2.2	0.7	1.1	1.3
„	6.4	0.5	1.0	1.3	0.4	0.9	1.2
„	5.5	0.5	1.1	2.1	0.5	0.8	1.2
„	7.0	0.4	0.7	1.0	0.4	0.8	1.2
Asperula soc.	5.9	0.6	1.1	1.9	0.7	1.3	1.7
„	6.6	0.5	1.1	1.6	0.4	1.1	1.4
„	6.4	0.3	0.5	0.9	0.3	0.5	0.9
„	6.0	0.7	1.4	1.7	0.4	0.8	1.2

Soil fractions of the uppermost soil horizon.

In places dominated by *Mercurialis perennis*:

Nr.	Coarse sand	Fine sand	Silt	Clay
1	87.9	4.6	2.5	5.0
2	88.0	3.8	2.9	5.3
3	81.4	7.4	5.7	5.5
4	88.3	4.9	3.6	3.2
5	90.1	3.4	3.0	3.5
6	87.1	3.6	3.3	6.0
7	88.8	4.4	2.1	4.7
8	89.5	4.0	3.1	3.4
9	91.1	3.6	2.9	2.4
10	89.6	3.2	3.0	4.2
11	85.0	3.9	3.4	7.7
12	88.1	3.7	3.2	5.0
13	90.2	3.4	2.0	4.4
14	92.1	3.5	1.5	2.9
15	92.5	4.5	1.0	2.0
16	92.8	2.8	1.8	3.6
17	81.9	5.7	4.1	8.4
18	90.2	4.4	1.7	3.7
19	92.3	4.8	1.1	1.8
Average	88.8	4.2	2.7	4.3

In places dominated by *Asperula odorata*:

Nr.	Coarse sand	Fine sand	Silt	Clay
1	86.8	3.6	3.4	6.2
2	91.0	3.1	2.2	3.7
3	93.3	3.1	1.5	2.1
4	92.8	3.2	1.7	2.3
5	87.0	4.1	2.8	6.1
6	92.4	3.5	1.9	2.2
7	89.9	3.9	2.2	4.0
8	88.5	5.0	2.1	4.4
9	94.7	2.0	1.2	2.1
10	91.9	4.2	0.9	3.0
11	88.2	4.3	2.4	5.1
12	93.6	3.0	0.9	2.5
13	90.6	3.6	1.4	4.4
14	91.0	4.5	1.8	2.7
15	94.1	2.8	0.8	2.3
16	87.6	4.3	2.9	5.2
17	93.5	2.4	1.4	2.7
18	89.0	3.6	2.4	5.0
19	90.7	4.1	1.4	3.8
20	84.4	5.6	3.5	6.5
21	88.2	4.8	3.8	3.2
Average	90.4	3.8	2.0	3.8

Average percentage of soil fractions in ålvar soil and forest ground.

	Coarse sand	Fine sand	Silt	Clay
Ålvar soil	92.5	2.9	1.5	3.1
Forest soil under *Asperula*	90.4	3.8	2.0	3.8
Forest soil under *Mercurialis*	88.8	4.2	2.7	4.3

The percentage of soil fractions[1] has changed little during the evolution to forest soil. There seems to be a difference between the soil fit for *Asperula* and that fit for *Mercurialis*.

The properties of any soil depend much upon its water

[1] The average for ålvar-soil is founded on three analyses.

capacity and air capacity. As is known, the water capacity is the amount of water which a water-saturated soil is capable of retaining against gravity. The air capacity is the air content in water-saturated soil at the moment when the gravitational water has disappeared (Kopecky, 1914). These determinations were carried out by the Kopecky method changed in some details by Siegrist and the author.[1]

Water and air capacity of the soil

	in places dominated by *Mercurialis*:			in places dominated by *Asperula*:		
	Air capacity vol. p. c.	Water capacity vol. p. c.	Solid part of soil vol. p. c.	Air capacity vol. p. c.	Water capacity vol. p. c.	Solid part of soil vol. p. c.
	2.6	62.6	34.8	5.3	59.3	35.4
	7.4	55.7	36.9	0.4	64.4	35.2
	0.3	58.4	41.3	0.4	64.8	34.8
	6.0	60.2	33.8	0.2	63.4	36.4
	10.6	63.1	26.3	3.3	56.4	40.3
	1.6	58.7	39.7	6.3	66.1	27.6
	6.9	67.1	26.0	2.2	69.2	28.6
	4.1	60.1	35.8	0.1	59.8	40.1
	10.0	70.0	20.0	0.1	66.3	33.6
	5.9	65.7	28.4	2.1	67.1	30.8
	3.6	74.2	22.2	2.0	60.2	37.8
	6.0	67.0	27.0	1.1	62.5	36.4
Average	5.4	63.6	31.0	1.9	63.3	34.8

As seen from these data there is a large scale of fluctuation in air capacity and water capacity in both societies. To find out the causes of this variability the structure of the soils studied was observed carefully. The uppermost layer from which all the samples were taken is rich in humus, dark

[1] The steel measuring cylinders used were only 8 cm. high and of 250 cc. volume because of the nature of the soils studied (cf. fig. 4, 7 and 8). Each imperforate covercle was provided with an opening for the air to get out. This proved to be very useful as it permitted one to work with well adjusted covercles. Before weighing, the opening for air in the covercle was closed with a small rubber cork and the cylinder wiped dry. It was found that often 2 hours were not sufficient to free the sample from the gravitational water.

brown in coloration and has often a pronounced crumb structure. By sifting the soils of this horizon it is easy to obtain a dark brown fraction entirely composed of crumbs. By destroying the crumbs mechanically a structureless dark brown soil fraction, which shows white coarse grains of sand mixed together with humified particles of dark coloration, was formed. The steel cylinders used for the determination of air and water capacity were filled partly (Nr. 1 and 2) with soil crumbs, partly (nr 3 and 4) with the structureless fraction. Care was taken to fill up the cylinders tightly without however destroying the crumb structure if present. The following results were obtained.

Nr.	Texture of soil	Air capacity vol. p. c.	Water capacity vol. p. c	Solid parts of soil vol. p. c.
1.	with crumb structure	22.2	54.4	23.4
2.	„ „ „	23.4	53.4	23.3
3.	crumb structure destroyed	2.9	60.0	37.1
4.	„ „ „	3.3	59.5	37.2

The air capacity of soil with a highly developed crumb structure was found to be seven times greater than the air capacity of the same soil after the destruction of the crumbs. This result entirely explains the data communicated on p. 54. Evidently the proportion of crumbled fraction to that without crumb structure varies largely in the forest soil studied.

As seen from the data communicated, there is a pronounced difference in soil structure (and therefore in air capacity) under the *Mercurialis perennis* and *Asperula odorata* societies, the first having an air capacity about three times greater.

The humus in places dominated by *Asperula odorata* is on the average more acid (cf. p. 51) than in those dominated by *Mercurialis*. It is of a more or less different kind and to some extent matted.

In the forest the temperature in the different societies differs markedly (see p. 56 to p. 58).

Temperature in the *Ulmus* — *Acer* — *Tilia* society.

	8^h	10^h	12^h	14^h	16^h	18^h	20^h	22^h	24^h	2^h	4^h	6^h	8^h	
5. July	21.2	26.3	25.1	24.1	23.0	19.9	20.0	18.0	16.4	15.5	15.0	17.4	18.5	6. July
9. July	22.0	22.5	22.2	24.0	21.0	20.8	20.0	17.6	17.2	17.4	17.4	18.1	20.0	10. July
12. July	16.9	17.7	19.0	19.2	17.8	17.9	17.5	17.0	16.0	15.3	16.0	15.8	15.5	13. July
20. July	20.1	20.6	23.0	23.3	27.5	28.0	22.2	22.0	20.1	20.1	19.8	23.2	22.5	21. July
22. Aug.	20.2	21.1	22.2	23.8	23.5	23.5	21.0	19.8	20.1	18.0	18.3	18.5	20.1	23. Aug.
24. Aug.	20.5	23.0	23.1	25.3	25.0	23.2	22.0	20.8	20.0	19.5	19.0	19.0	20.0	25. Aug.
25. Aug.	20.5	21.1	21.3	24.0	25.1	22.5	21.0	19.6	21.0	20.4	20.1	20.1	21.0	26. Aug.
26. Aug.	21.0	21.2	21.0	22.5	22.2	21.8	21.1	19.9	19.0	18.9	17.5	19.6	20.0	27. Aug.
Average	20.3	21.7	22.1	23.3	23.1	22.2	20.6	19.3	18.7	18.1	17.9	19.0	19.7	

Temperature in the *Corylus avellana* society.

	8^h	10^h	12^h	14^h	16^h	18^h	20^h	22^h	24^h	2^h	4^h	6^h	8^h	
5. July	20.2	22.0	24.5	24.2	23.4	19.3	18.5	17.5	14.7	13.7	13.0	14.8	17.0	6. July
9. July	18.0	20.1	20.4	21.9	21.1	20.0	18.9	17.0	16.8	16.4	16.1	17.0	18.5	10. July
12. July	16.4	17.6	18.1	18.8	18.2	18.0	17.0	16.7	15.6	15.3	15.6	15.4	16.0	13. July
20. July	19.0	20.8	21.3	22.3	24.4	23.5	21.5	19.7	18.4	18.0	17.5	18.8	21.0	21. July
22. Aug.	20.1	22.1	24.9	25.2	25.0	23.8	21.8	19.8	19.0	17.7	17.9	17.9	20.0	23. Aug.
24. Aug.	20.8	24.0	26.1	25.5	25.7	23.7	21.3	20.1	19.0	18.6	18.3	18.0	20.8	25. Aug.
25. Aug.	20.8	22.0	23.2	23.3	24.0	22.8	20.8	19.2	20.0	19.6	19.0	19.0	20.8	26. Aug.
26. Aug.	20.8	22.3	23.5	23.1	23.2	22.0	19.0	18.7	17.7	18.0	17.6	17.9	19.0	27. Aug.
Average	19.5	21.4	22.7	23.0	23.1	21.6	19.8	18.6	17.6	17.2	16.9	17.3	19.1	

Temperature in the *Ulmus* — *Acer* — *Tilia* society.

	8^h	10^h	12^h	14^h	16^h	18^h	20^h	22^h	24^h	2^h	4^h	6^h	8^h	
3. July	17.2	18.3	19.0	21.0	19.3	18.0	18.0	15.3	15.6	15.3	16.0	18.1	21.0	4. July
8. July	22.1	25.3	23.0	23.5	22.2	21.3	20.6	17.6	17.0	17.0	17.0	18.7	22.0	9. July
13. July	15.5	15.8	17.3	18.0	17.5	17.0	17.2	16.8	16.8	16.3	16.1	17.5	19.3	14. July
22. July	22.8	22.8	25.0	22.0	17.9	21.7	20.8	20.2	18.0	19.0	19.0	18.7	20.1	23. July
Average	19.4	20.5	21.1	21.1	19.2	19.5	19.1	17.5	16.9	16.9	17.0	18.2	20.6	

Temperature in the *Lonicera xylosteum* — *Ribes alpinum* society.

	8^h	10^h	12^h	14^h	16^h	18^h	20^h	22^h	24^h	2^h	4^h	6^h	8^h	
3. July	16.2	18.0	19.5	23.0	20.0	20.2	15.8	14.4	14.5	14.6	14.3	15.1	18.0	4. July
8. July	16.8	19.6	20.8	24.0	22.0	20.7	19.0	16.8	16.0	16.0	16.1	17.0	18.2	9. July
13. July	16.0	16.0	18.0	18.6	16.5	16.0	16.3	15.2	15.1	15.4	15.8	16.5	18.1	14. July
22. July	20.5	22.4	23.0	21.9	18.2	19.4	19.2	18.8	17.5	16.4	16.7	16.7	18.0	23. July
Average	17.4	19.0	20.3	21.9	19.2	19.1	17.6	16.3	15.8	15.6	15.7	16.3	18.1	

Temperature in the *Ulmus* — *Acer* — *Tilia* society.

	8^h	10^h	12^h	14^h	16^h	18^h	20^h	22^h	24^h	2^h	4^h	6^h	8^h	
7. July	21.8	23.2	25.0	23.2	20.8	19.5	20.2	17.5	16.3	16.0	15.8	19.0	22.1	8. July
14. July	19.3	19.5	21.4	21.2	22.0	22.0	20.0	17.0	15.7	15.0	15.1	16.8	18.0	15. July
15. July	18.0	19.0	17.2	19.5	19.5	19.0	17.7	16.2	15.0	15.1	14.9	17.0	19.0	16. July
16. July	19.0	19.0	18.1	17.7	20.1	19.3	19.1	15.5	15.6	15.4	15.1	15.5	20.0	17. July
17. July	20.0	17.1	17.5	17.7	22.0	18.1	17.9	17.2	16.6	16.0	15.8	18.7	19.5	18. July
23. July	20.1	17.0	18.5	19.2	19.8	19.1	19.0	17.5	17.1	17.0	16.8	17.0	19.8	24. July
24. July	19.8	22.0	22.5	23.2	24.5	24.0	21.8	20.1	19.0	18.1	18.2	19.0	20.1	25. July
Average	19.7	19.5	20.0	20.2	21.2	20.1	19.4	17.3	16.5	16.1	15.9	17.6	19.8	

Temperature in the *Asperula odorata* and *Mercurialis perennis* societies.

	8^h	10^h	12^h	14^h	16^h	18^h	20^h	22^h	24^h	2^h	4^h	6^h	8^h	
7. July	18.0	19.5	21.0	21.0	20.3	19.7	18.3	16.6	15.7	14.2	13.7	14.3	17.3	8. July
14. July	18.0	19.1	20.3	21.1	21.3	20.0	18.6	17.0	15.8	15.0	15.0	16.0	17.9	15. July
15. July	17.9	18.7	17.8	18.0	19.1	18.2	17.0	16.0	15.0	14.7	14.3	15.2	17.8	16. July
16. July	17.8	18.5	18.3	17.1	19.0	18.6	17.7	16.0	15.0	14.8	14.7	14.8	17.0	17. July
17. July	17.0	17.7	18.4	17.4	18.9	18.0	17.0	16.0	15.5	14.8	13.0	14.4	17.0	18. July
23. July	18.0	17.4	18.0	18.0	18.2	18.0	17.6	16.8	16.0	16.3	16.0	16.4	18.0	24. July
24. July	18.0	19.9	21.0	21.0	21.0	19.4	17.9	16.4	16.0	15.3	15.0	15.5	—	25. July
Average	17.8	18.7	19.2	19.1	19.7	18.8	17.7	16.4	15.6	15.0	14.5	15.2	17.5	

Temperature in the *Corylus avellana* society.

	8^h	10^h	12^h	14^h	16^h	18^h	20^h	22^h	24^h	2^h	4^h	6^h	8^h	
6. Aug.	19.2	19.8	20.7	19.1	20.0	19.7	18.7	18.0	17.4	17.7	18.0	18.0	19.0	7. Aug.
7. Aug.	19.0	19.8	20.5	21.1	21.0	20.0	18.4	17.0	16.8	17.0	16.7	17.0	18.5	8. Aug.
18. Aug.	18.9	20.0	21.8	21.8	22.0	20.4	19.0	17.7	16.5	16.0	16.4	16.8	19.8	19. Aug.
19. Aug.	19.8	21.3	24.2	24.0	25.1	23.0	20.6	20.0	19.0	19.0	18.4	18.8	20.2	20. Aug.
20. Aug.	20.2	21.0	22.2	22.2	24.2	21.1	20.0	19.7	19.7	18.3	18.4	17.7	19.8	21. Aug.
21. Aug.	19.8	21.1	22.2	23.8	25.1	22.2	20.8	19.0	18.1	17.5	16.9	17.0	20.1	22. Aug.
Average	19.5	20.5	21.9	22.0	22.9	21.1	19.6	18.6	17.9	17.6	17.5	17.6	19.6	.

Temperature in the *Rhytidiadelphus — Eurhynchium* society.

	8^h	10^h	12^h	14^h	16^h	18^h	20^h	22^h	24^h	2^h	4^h	6^h	8^h	
6. Aug.	18.9	19.2	20.1	19.0	19.8	19.2	18.0	17.4	17.0	17.0	17.1	17.5	18.9	7. Aug.
7. Aug.	18.9	18.8	19.5	20.8	20.1	19.0	17.7	16.3	16.0	15.8	15.4	15.8	—	8. Aug.
18. Aug.	18.1	19.7	21.5	24.0	21.0	20.0	18.0	17.0	16.2	16.1	16.0	16.1	19.2	19. Aug.
19. Aug.	19.2	21.0	24.0	26.5	24.0	22.1	20.0	19.3	19.0	18.5	18.0	18.4	19.8	20. Aug.
20. Aug.	19.8	21.0	22.2	26.0	21.8	20.6	19.0	18.9	18.8	17.9	17.8	17.0	19.2	21. Aug.
21. Aug.	19.2	21.1	22.6	25.1	24.0	22.0	20.0	18.6	17.8	17.0	16.1	16.0	19.0	22. Aug.
Average	19.0	20.1	21.7	23.6	21.8	20.5	18.8	17.9	17.5	17.1	16.7	16.8	19.2	.

The temperature was measured by thermographs. Since the author had at his disposal only two thermographs, while the number of habitats to analyse was five, the only possibility was to compare the temperature of these habitats from time to time. The results so obtained are communicated on p. 56 to p. 58. All measurements were made in the rather dry summer of 1937.

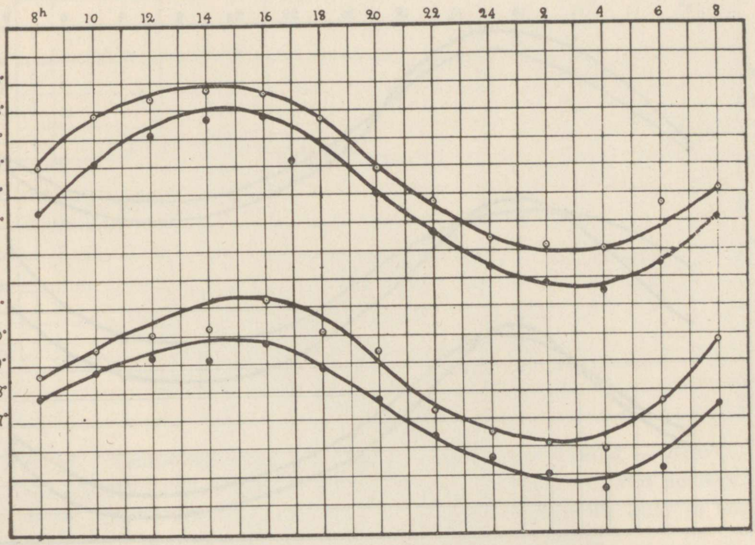


Fig. 9. The range of temperature in July (average of four days). Above: in the *Ulmus* — *Acer* — *Tilia* society (white dots) and the *Corylus avellana* society (black dots). Below: in the *Ulmus* — *Acer* — *Tilia* society (white dots) and the *Mercurialis* and *Asperula* societies (black dots).

In the first part of the summer (June and July) the curves obtained for the different superimposed communities were of the character shown in fig. 9. The temperatures measured in all the protected communities (*Corylus avellana* society, *Lonicera* — *Ribes* society, *Mercurialis* society, *Asperula* society) were 1—2 degrees below the temperatures measured at the same time in the exposed *Ulmus* — *Acer* — *Tilia* society. It is noteworthy that even during the nights the temperature in the inner parts of the forest was constantly lower than that in the tops of the crowns.

In the second part of the summer (August) the character of the curves changed visibly (fig. 10). During the whole of the daytime or at least during the warmest hours of the day the temperature inside the wind sheltered forest (from the *Corylus avellana* society to the moss society) was found to be

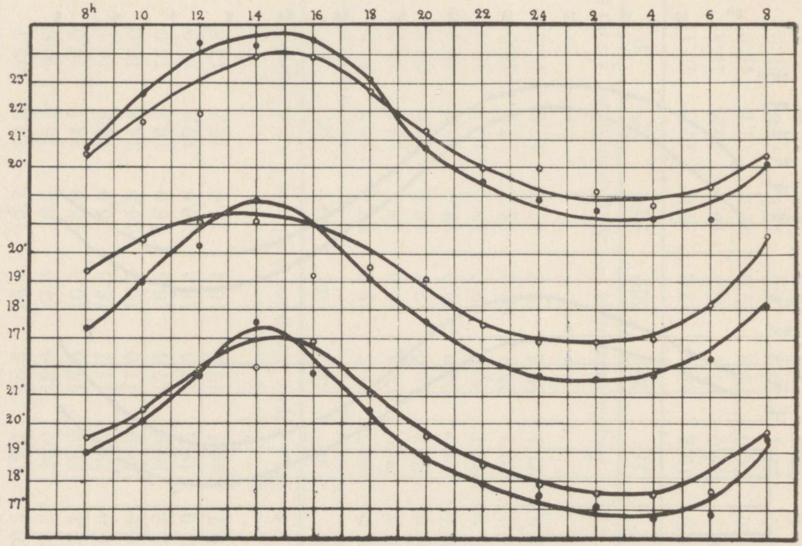


Fig. 10. The range of temperature in August (average of four days). Above: the *Ulmus — Acer — Tilia* society (white dots) and the *Corylus avellana* society (black dots). Middle: the *Ulmus — Acer — Tilia* society (white dots) and the *Lonicera — Ribes* society (black dots). Below: the *Corylus avellana* society (white dots) and the *Rhytidiadelphus — Eurhynchium* society (black dots).

distinctly higher than that in the tree crowns of the *Ulmus — Acer — Tilia* society. Yet there was no change in the character of the curves for the night. As in the first part of the summer, the temperature at night in the protected societies remained still lower than that at thirty metres above the ground in the tree crowns.

What is the cause of this singular behaviour of the temperature curves (fig. 10)? The explanation is given by certain observations which will be communicated later.

There are some characteristic differences in the appearance of the daily curve of the *Ulmus — Acer — Tilia* society and those of the subjacent communities from the *Corylus avellana* society to the *Rhytidiadelphus — Eurhynchium* society

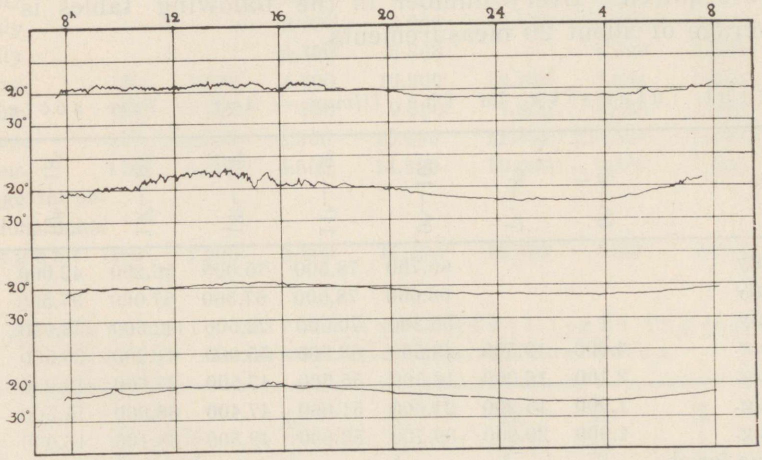


Fig. 11. Temperature curves. (1) 9th July in the *Ulmus — Acer — Tilia* society; (2) 6th July in the *Ulmus — Acer — Tilia* society; (3) 9th July in the *Corylus avellana* society and (4) 6th July in the *Rhytidiadelphus — Eurhynchium* society.

The curve for the tree society is finely denticulated due to the repeated occurrence of small and brusque changes in the temperature. On the average every 5 min. has a small maximum and a minimum. Without doubt these are caused by the wind. Here and there the curve has some deeper minima: those are caused by some passing cloud. The curves for the protected societies are without these denticules. Here and there occurs some maximum caused by sun rays which have reached the thermograph directly.[1] In the second part of the summer the number of these maxima increased visibly.

[1] It is to be noted that the thermographs were freely exposed to the habitat factors, without any cover. Only on some rare rainy days were they protected from the rain by waterproof cloth.

In the development and life of the superimposed forest societies light is of eminent importance.

The measurements of light intensity were carried out by the Lange photo-element. There is in a forest an utterly imperceptible transition from sunny spots to deep shade. To obtain reliable results a great number of single observations are required. Every number in the following tables is an average of about 20 measurements.

Light intensity in the *Ulmus* — *Acer* — *Tilia* society.

Time	5^h—6^h	7^h—8^h	9^h—10^h	11^h—12^h	13^h—14^h	15^h—16^h	17^h—18^h	19^h—20^h
14. July			60.700	78.500	75.000	56.200	42.000	
18. July			63.000	78.000	67.500	57.000	37.500	
20. July			55.200	70.500	72.500	62.500	36.000	
14. Aug.	4.000	19.500	48.500	63.500	55.000	41.200	20.500	3.000
15. Aug.	2.100	16.000	13.500	55.500	47.500	27.600	13.000	1.000
19. Aug.	1.900	15.200	21.600	51.000	47.400	38.000	15.500	2.800
20. Aug.	1.900	20.000	39.700	53.000	49.500	38.100	16.000	2.200
Average for observations made in August	2.500	17.700	30.800	55.800	49.800	36.200	16.200	2.200

Light intensity (direct and diffuse light together) in the *Corylus avellana* society.

Time	5^h—6^h	7^h—8^h	9^h—10^h	11^h—12^h	13^h—14^h	15^h—16^h	17^h—18^h	19^h—20^h
14. July			4.000	14.400	9.900	5.600	2.900	
18. July			8.600	13.000	13.600	—	4.900	
20. July			7.200	9.300	—	9.100	2.700	
14. Aug.	230	1.800	8.400	10.900	8.600	10.800	2.600	150
15. Aug.	150	1.600	700	8.600	4.800	2.500	9.900	80
19. Aug.	180	1.500	2.400	12.200	7.300	8.500	2.200	140
20. Aug.	200	2.000	7.600	9.400	7.900	9.800	1.200	180
Average for observations made in August	190	1.700	4.800	10.300	7.100	7.900	4.000	140

Light intensity (direct and diffuse light together) in the *Lonicera xylosteum* — *Ribes alpinum* society.

Time	5^h—6^h	7^h—8^h	9^h—10^h	11^h—12^h	13^h—14^h	15^h—16^h	17^h—18^h	19^h—20^h
14. July			4.800	6.300	12.300	6.600	1.500	
18. July			2.700	3.900	3.800	5.800	—	
20. July			3.300	5.800	—	4.200	3.700	
14. Aug.	190	1.600	4.300	10.900	12.200	3.600	1.300	150
15. Aug.	130	900	800	9.500	7.800	2.000	1.000	80
19. Aug.	140	1.200	2.300	10.800	11.300	3.800	2.300	170
20. Aug.	170	1.300	4.500	14.300	10.600	6.700	1.400	160
Average for observations made in August	160	1.200	3.000	11.400	10.500	4.000	1.500	140

Light intensity (direct and diffuse light together) in the *Mercurialis* and *Asperula* societies.

Time	5^h—6^h	7^h—8^h	9^h—10^h	11^h—12^h	13^h—14^h	15^h—16^h	17^h—18^h	19^h—20^h
14. July			4.900	3.500	5.900	4.600	1.400	
18. July			3.300	12.800	10.600	5.900	3.100	
20. July			5.800	8.700	—	6.200	3.400	
14. Aug.	80	1.700	4.300	14.900	12.100	5.700	1.900	130
15. Aug.	80	900	400	6.200	8.000	1.800	600	50
19. Aug.	70	1.000	1.400	8.600	8.400	4.900	2.600	200
20. Aug.	90	2.400	5.300	10.300	9.100	5.700	2.200	130
Average for observations made in August	80	1.500	2.800	10.000	9.400	4.500	1.800	130

The average light intensity in the *Corylus avellana* society is about five times less than in the *Ulmus* — *Acer* — *Tilia* society. In the morning and evening this difference is even much greater, the light intensity in the *Corylus avellana* society being only $^1/_{10}$ to $^1/_{16}$ of the light in the open. It is very probable that this shortening of the day is the principal

Light intensity (direct and diffuse light together) in the *Rhytidiadelphus* — *Eurhynchium* society.

Time	5^h—6^h	7^h—8^h	9^h—10^h	11^h—12^h	13^h—14^h	15^h—16^h	17^h—18^h	19^h—20^h
14. July			1.000	1.300	2.000	1.800		
18. July			—	3.400	2.800	2.900		
20. July			1.700	2.900	—	4.100	600	
14. Aug.	50	700	1.200	5.200	2.600	4.600	400	80
15. Aug.	40	460	200	3.100	1.500	1.200	630	50
19. Aug.	50	450	1.300	3.400	2.700	1.400	740	130
20. Aug.	60	750	2.600	5.200	6.200	2.800	650	130
Average for observations made in August	50	590	1.300	4.200	3.200	2.500	600	100

Average of light intensity (direct and diffuse light together) in forest societies in the middle of August (1937).

	5h—6h	7h—8h	9h—10h	11h—12h	13h—14h	15h—16h	17h—18h	19h—20h
Ulmus — *Acer* — *Tilia* society .	2.500	17.700	30.800	55.800	49.800	36.200	16.200	2.200
Corylus society .	190	1.700	4.800	10.300	7.100	7.900	4.000	140
Lonicera — *Ribes* society . .	160	1.200	3.000	11.400	10.500	4.000	1.500	140
Mercurialis and *Asperula* soc. .	80	1.500	2.800	10.000	9.400	4.500	1.800	130
Rhytidiadelphus — *Eurhynchium* society . . .	50	590	1.300	4.200	3.200	2.500	600	100
Ulmus — *Acer* — *Tilia* society .	1	1	1	1	1	1	1	1
Corylus society .	1/13	1/10	1/6	1/5	1/7	1/5	1/4	1/16
Lonicera — *Ribes* society . . .	1/16	1/15	1/10	1/5	1/5	1/9	1/11	1/16
Mercurialis and *Asperula* soc. .	1/32	1/12	1/11	1/5	1/5	1/8	1/9	1/17
Rhytidiadelphus — *Eurhynchium* society . . .	1/50	1/30	1/24	1/13	1/15	1/15	1/27	1/22

reason for the reduced vitality of hazels growing under the forest trees. Indeed there are many other unfavourable factors as for instance the root competition with the species of the *Ulmus — Acer — Tilia* society, etc.

The light intensity scarcely differs in the low-growing *Lonicera — Ribes* society and in the *Asperula* and *Mercurialis* societies. Here too in summer, the light intensity attains one-fifth of that in the *Ulmus — Acer — Tilia* society but only for a short period of about three hours daily.

The lowest light intensity rules in the habitat of the *Rhytidiadelphus — Eurhynchium* society. Here even during the most favourable time of the day the average light intensity does not exceed $^1/_{10}$ of the light in the top of the trees.

These observations concerning the general light conditions in the forest are completed in the following pages by some data on the distribution of diffuse light in the forest.

In the protected societies (from the *Corylus avellana* society to the *Rhytidiadelphus — Eurhynchium* society) the ordinary light is the diffuse light. As seen from the data of the tables on p. 62, 65 and 67 there is a gap between the light conditions in the *Ulmus — Acer — Tilia* society and the *Corylus*

Intensity of diffuse light in the *Corylus avellana* society.

Time	5^h—6^h	7^h—8^h	9^h—10^h	11^h—12^h	13^h—14^h	15^h—16^h	17^h—18^h	19^h—20^h
14. July			670	720	820	670	470	
18. July			960	1.290	920	730	660	
20. July			1.600	1.220	1.370	960	610	
Average			1.080	1.080	1.040	790	580	
14. Aug.	230	580	2.420	2.550	1.860	1.460	650	150
15. Aug.	150	1.300	700	2.330	1.600	2.030	1.140	80
19. Aug.	180	850	2.400	2.690	2.320	2.220	780	140
20. Aug.	190	1.480	2.250	2.090	2.280	2.040	710	180
Average	190	1.050	1.940	2.410	2.010	1.940	820	140

Intensity of diffuse light in the *Lonicera xylosteum — Ribes alpinum* society.

Time	5^h—6^h	7^h—8^h	9^h—10^h	11^h—12^h	13^h—14^h	15^h—16^h	17^h—18^h	19^h—20^h
14. July			630	590	570	500	500	
18. July			790	1.150	1.040	720	680	
20. July			1.000	960	920	900	540	
Average			810	900	840	710	570	
14. Aug.	190	490	1.830	2.980	1.540	1.150	620	160
15. Aug.	130	770	770	2.250	1.810	1.680	1.000	80
19. Aug.	140	730	2.360	2.350	2.100	1.560	730	170
20. Aug.	170	860	2.200	2.780	1.920	1.300	720	160
Average	160	710	1.790	2.590	1.840	1.420	770	140

Intensity of diffuse light in the *Mercurialis* and *Asperula* societies.

Time	5^h—6^h	7^h—8^h	9^h—10^h	11^h—12^h	13^h—14^h	15^h—16^h	17^h—18^h	19^h—20^h
14. July			620	520	560	480	350	
18. July			500	600	550	580	460	
20. July			670	720	630	490	440	
Average			600	610	580	520	420	
14. Aug.	80	340	890	2.120	1.180	800	440	100
15. Aug.	80	540	390	1.490	1.980	1.250	490	50
19. Aug.	70	500	1.400	1.810	1.500	1.070	530	200
20. Aug.	90	630	1.000	1.690	1.120	990	500	130
Average	80	500	920	1.780	1.440	1.030	490	120

avellana society, the light intensity in the second being only $^1/_{50}$ to $^1/_{70}$ of that in the first. The differences between the societies of the forest undergrowth are much more limited. Even the ratio between the *Corylus avellana* society and the *Rhytidiadelphus — Eurhynchium* society is only as two or three to one.

Intensity of diffuse light in the *Rhytidiadelphus — Eurhynchium* society.

Time	5h—6h	7h—8h	9h—10h	11h—12h	13h—14h	15h—16h	17h—18h	19h—20h
14. July			280	290	330	290	220	
18. July			260	420	410	380	310	
20. July			440	600	600	560	370	
Average			330	440	450	410	300	
14. Aug.	50	220	530	1.070	770	580	350	80
15. Aug.	40	400	240	1.580	1.060	720	630	50
19. Aug.	50	400	1.350	2.370	1.980	930	490	240
20. Aug.	60	620	1.250	1.390	970	880	500	130
Average	50	410	840	1.600	1.200	780	490	120

Average of light intensity (diffuse light only except in the *Ulmus — Acer — Tilia* soc.) in the forest societies in the middle of July (1937).

	9h—10h	11h—12h	13h—14h	15h—16h	17h—18h
Corylus avellana society	1.080	1.080	1.040	790	580
Lonicera — Ribes society	810	900	840	710	570
Mercurialis and *Asperula* soc. . .	600	610	580	520	420
Rhytidiadelphus — Eurhynchium soc.	330	440	450	410	300
Ulmus — Acer — Tilia society . . .	1	1	1	1	1
Corylus avellana society	1/55	1/74	1/69	1/74	1/66
Lonicera — Ribes society	1/74	1/84	1/83	1/82	1/68
Mercurialis and *Asperula* societies .	1/100	1/124	1/124	1/113	1/92
Rhytidiadelphus — Eurhynchium soc.	1/180	1/172	1/159	1/143	1/128

Average of light intensity (diffuse light only except in the *Ulmus — Acer — Tilia* soc.) in the forest societies in the middle of August (1937).

	5^h—6^h	7^h—8^h	9^h—10^h	11^h—12^h	13^h—14^h	15^h—16^h	17^h—18^h	19^h—20^h
Corylus avellana society	190	1050	1940	2410	2010	1940	820	140
Lonicera — Ribes society	160	710	1790	2590	1840	1420	770	140
Mercurialis and *Asperula* societies .	80	500	920	1780	1440	1030	490	120
Rhytidiadelphus — Eurhynchium soc.	50	410	840	1600	1200	780	490	120
Ulmus — Acer — Tilia society . . .	1	1	1	1	1	1	1	1
Corylus avellana society	1/13	1/17	1/16	1/23	1/25	1/19	1/20	1/16
Lonicera — Ribes society	1/15	1/25	1/17	1/21	1/27	1/25	1/21	1/16
Mercurialis and *Asperula* societies .	1/31	1/35	1/33	1/31	1/35	1/35	1/33	1/19
Rhytidiadelphus — Eurhynchium soc.	1/50	1/43	1/37	1/35	1/41	1/46	1/33	1/18

The light intensity in the open naturally decreased in August being about $^2/_3$ of that in July. In the forest on the contrary an increase of light intensity was noted in all subjacent societies beginning with the *Corylus avellana* society (cf. the tables on p. 62 to 68). The rise of light intensity increased two to three times, the relative even three to five times.

The cause of this fact is the same as the cause of the rise of temperature curves in August (cf. p. 59 and 60). Little by little the crowns of the trees forming the protecting society — the *Ulmus — Acer — Tilia* society — got lighter and lighter because of the fall of the leaves owing to the drought. This process started at the end of July and increased daily. At the end of August only about half of the foliage was present, the soil being covered with a deep brown cover of dead leaves.

The air humidity in the forest was determined by

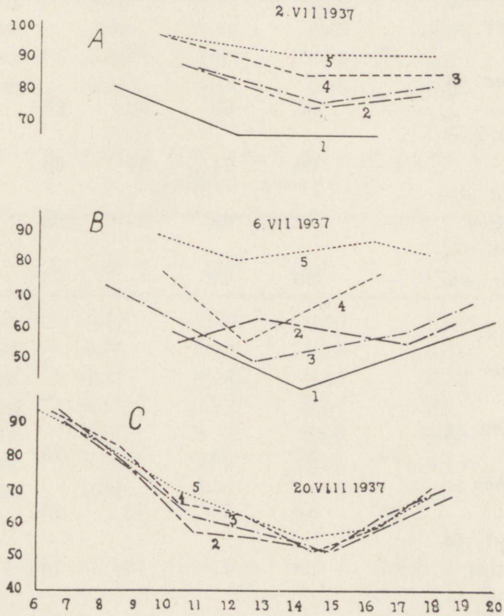


Fig. 12. The daily range of relative air humidity (given in percentages) in the *Ulmus — Acer — Tilia* (1), *Corylus avellana* (2), *Lonicera — Ribes* (3), *Asperula odorata* (4) and *Rhytidiadelphus — Eurhynchium* (5) societies.

the Assmann psychrometer. The observations were made in July (5, 6, 14, 18, 19 and 20) and August (6, 13, 15, 19 and 20). The results obtained were arranged in the following table. Some examples are also to be found in fig. 12.

The low percentage of relative humidity found in the habitat of ålvar-vegetation (p. 42) is never realised in the forest or occurs here only exceptionally (40 to 45 p. c. was regisered only twice in a series of about 250 determinations).

Average relative air humidity in p. c. (observations made in July and August 1937).

July (hours):	7—8	9—10	11—12	13—14	15—16	17—18	19—20
Ulmus — Acer — Tilia society . . .	78	—	—	59	—	—	68
Corylus avellana society	—	65	63	62	63	61	65
Lonicera — Ribes society	—	68	71	51	65	65	—
Mercurialis and *Asperula* societies .	—	78	68	57	65	71	—
Rhytidiadelphus — Eurhynchium soc.	—	86	77	—	73	77	—
August.							
Ulmus — Acer — Tilia society . .	—	—	—	—	—	—	—
Corylus avellana society	94	82	74	72	73	72	82
Lonicera — Ribes society	95	86	77	73	73	73	85
Mercurialis and *Asperula* societies .	97	88	79	78	74	77	86
Rhytidiadelphus — Eurhynchium soc.	92	87	81	78	79	82	92

In July there is ordinarily a pronounced stratification of air humidity, the highest stratum *(Corylus avellana* society) being the driest and the lowest stratum (*Rhytidiadelphus — Eurhynchium* society) the most humid. In August as the drought advanced the difference between the superimposed habitats became more and more effaced.

On p. 43 some measurements of the evaporation rate in the ålvar vegetation are given. In the following these data are completed with those made in the forest.

Evaporation rate (in cm.^{3} per hour) in the *Ulmus — Acer — Tilia* society 30 m. above the ground.

	10^h	14^h	18^h	Average for day	Average for night
20. July	0.34	0.46	0.52	0.44	0.09
22. Aug.	0.66	0.94	0.46	0.65	0.22
23. Aug.	0.74	0.70	0.41	0.63	0.06
24. Aug.	0.36	0.45	0.29	0.37	0.16
25. Aug.	0.50	0.52	0.47	0.42	0.22
26. Aug.	0.65	1.02	0.54	0.74	0.14
Average	0.54	0.68	0.45	0.54	0.15

Evaporation rate (in cm.^{3} per hour) in the *Corylus avellana* society.

	10^h	14^h	18^h	Average for day	Average for night
20. July	0.07	0.10	0.10	0.09	0.02
22. Aug.	0.05	0.13	0.11	0.11	0.03
23. Aug.	0.11	0.14	0.10	0.12	0.02
24. Aug.	0.10	0.14	0.10	0.11	0.02
25. Aug.	0.05	0.11	0.08	0.08	0.02
26. Aug.	0.10	0.12	0.09	0.10	0.02
Average	0.08	0.12	0.10	0.10	0.02

Evaporation rate (in cm.^{3} per hour) in the *Ulmus — Acer — Tilia* society.

	10^h	14^h	18^h	Average for day	Average for night
15. July	0.45	0.42	0.53	0.46	0.08
17. July	0.59	0.26	0.21	0.33	0.11
18. July	0.39	0.42	0.34	0.39	0.15
19. July	0.19	0.95	0.27	0.42	0.12
Average	0.40	0.51	0.34	0.40	0.11

The climatical conditions of the *Ulmus — Acer — Tilia* society differ fundamentally from those of the subjacent communities. This is particularly evident in the light intensity, Evaporation rate (in cm.^{3} per hour) in the *Mercurialis* and *Asperula* societies.

	10^h	14^h	18^h	Average for day	night
15. July	0.05	0.02	0.02	0.03	0.01
17. July	0.02	0.04	0.04	0.04	0.01
18. July	0.06	0.10	0.06	0.07	0.02
19. July	0.05	0.07	0.05	0.06	0.02
Average	0.04	0.06	0.04	0.05	0.01

Evaporation rate (in cm.^{3} per hour) in the *Corylus avellana* society and the *Rhytidiadelphus* — *Eurhynchium* society.

	9^h	11^h	13^h	15^h	17^h	19^h	Average for day	night
Corylus society:								
29. July	0.05	0.09	0.04	0.05	0.00	0.02	0.05	0.01
30. July	0.04	0.07	0.07	0.05	0.02	0.01	0.04	0.01
6. Aug.	0.07	0.05	0.07	0.08	0.06	0.05	0.06	0.02
18. Aug.	0.11	0.10	0.10	0.11	0.08	0.06	0.09	0.01
19. Aug.	0.06	0.07	0.10	0.09	0.07	0.05	0.08	0.01
20. Aug.	0.06	0.07	0.10	0.12	0.09	0.05	0.08	0.03
21. Aug.	0.05	0.08	0.09	0.13	0.10	0.06	0.08	0.02
Average	0.06	0.08	0.08	0.09	0.06	0.04	0.07	0.02
Rhytidiadelphus — *Eurhynchium* society:								
29. July	0.05	0.08	0.04	0.08	0.00	0.00	0.04	0.00
30. July	0.06	0.09	0.04	0.01	0.04	0.01	0.04	0.00
6. Aug.	0.02	0.01	0.02	0.08	0.05	0.01	0.04	0.01
18. Aug.	0.10	0.12	0.14	0.09	0.10	0.05	0.11	0.01
19. Aug.	0.03	0.10	0.07	0.09	0.09	0.03	0.08	0.01
20. Aug.	0.05	0.08	0.11	0.13	0.11	0.05	0.09	0.03
21. Aug.	0.04	0.08	0.08	0.17	0.10	0.11	0.10	0.02
Average	0.05	0.08	0.07	0.09	0.07	0.04	0.07	0.01

wind conditions (not yet exactly measured) and in the evaporation rate. Roughly speaking the evaporation rate in the tops of the trees is about five times higher than that in the *Corylus* *avellana* society. Therefore it is by no means surprising that the foliage, e. g. of lime-trees, in the crowns show many xeromorphic features if compared with the foliage on the hazel level.

From the *Corylus* society to the *Rhytidiadelphus* — *Eurhynchium* society the differences in the evaporation rate are much smaller than those between the first and the *Ulmus* — *Acer* — *Tilia* society. Nevertheless the evaporation in the *Mercurialis* and *Asperula* societies in July was only half of that in the *Corylus avellana* society. It is interesting to note that no difference was found in the evaporation rate in the *Corylus avellana* society and *Rhytidiadelphus* — *Eurhynchium* society in the dryest part of the summer (1937) — August.

4. The influence of drought upon the forest vegetation.

The summer of 1937 happened to be very dry. During July and August there was rain only in the last week of July,

Name of species	Depth (in cm.) to which the roots penetrate		Maximum length of roots in cm.
	bulk of roots	longest roots	
Tilia cordata	5—10	>100	300—500
Acer platanoides	5—7	>100	>1000
Corylus avellana	3—7	30	>1000
Lonicera xylosteum	6—8	30	150
Daphne mezereum	3—7	25	72
Mercurialis perennis	3—5	8	
Asperula odorata	1—3	5	
Hepatica triloba	3—7	15	
Dentaria bulbifera	3—5	12	
Oxalis acetosella	2—4	8	
Majanthemum bifolium . . .	2—5	10	
Carex digitata	1—5	15	
Milium effusum	1—4	8	
Orobus vernus	3—9	25	
Luzula pilosa	2—5	10	

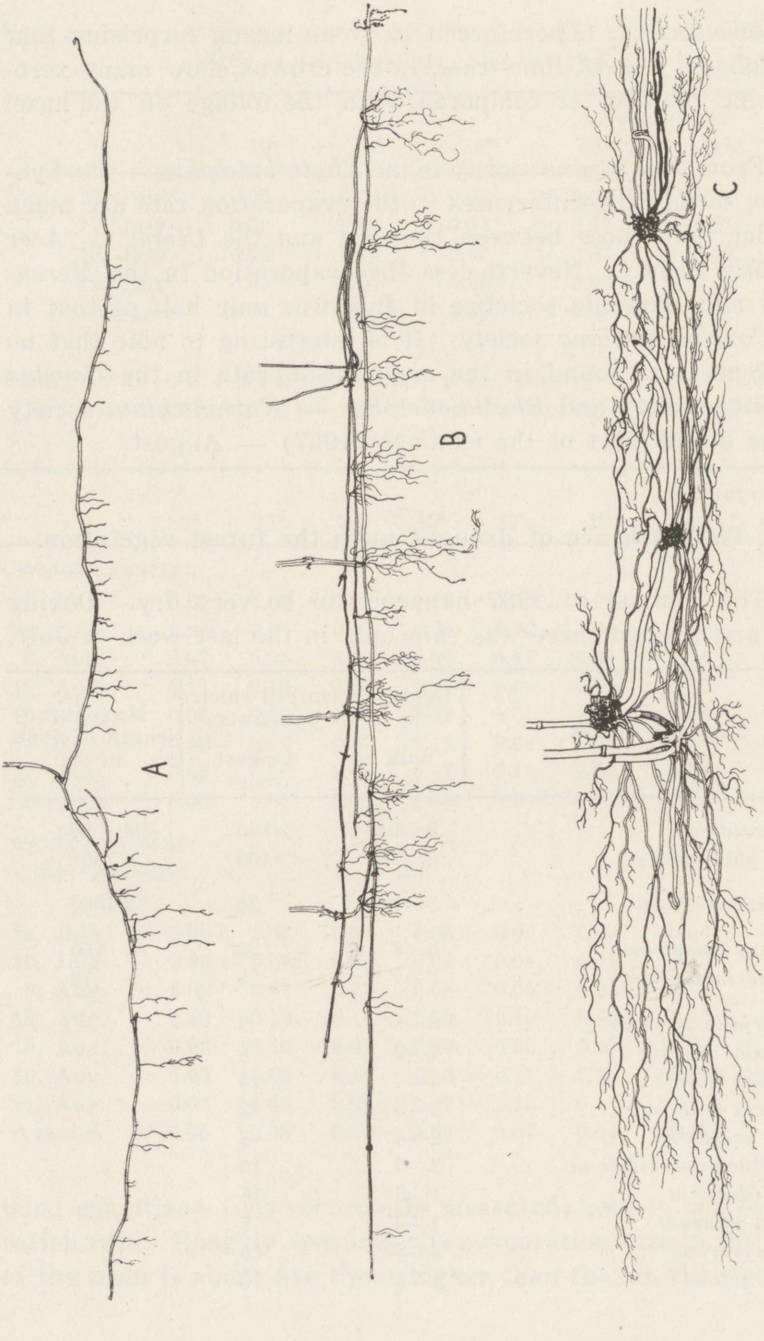


Fig. 13. A — *Vicia sepium* L., B — *Asperula odorata* L., C — *Mercurialis perennis* L. $^3/_7$ of the normal size.

on the 15th, 16th, and the 27th August. Except the heavy rain on the 27th August the forest soil often remained practically dry even after rain, or, if there was more precipitation, only the uppermost soil horizon containing humus got it.

Considering this and the peculiarities of soil structure communicated on p. 50 and later, it is not at all surprising that the prevailing majority of the species of societies here treated are shallow-rooted. Some data concerning this point are summarized in the table on p. 73.

Tilia cordata. The principal roots of this tree often show to some degree the character of buttresses, the relation of diameters being for instance about 3 to 1. The buttresses are ordinarily buried in the soil and therefore observable only after digging. These anchoring roots obliquely force their way through the stony soil to a depth of about 1 m. There are some absorbing roots attaining 3 to 5 m. in length and placed entirely in the uppermost layer rich in humus. These roots penetrate only to a depth of about 15 cm. Other absorbing roots are much smaller; they densely cover the principal roots especially in the humus layer of the soil.

Acer platanoides. The general character of the roots is the same as in the foregoing case so far as the anchoring roots are concerned, only the buttressing seems to be absent in the maple. The absorbing roots are extremely long, often exceeding 10 metres. These roots are more or less densely covered with small rootlets and occur in the uppermost humus layer.

Corylus avellana. The roots of the hazel cover a space which exceeds by many times the projection of the crown on the soil. The adscendent tap root is wanting here as in *Tilia* and *Acer*. All the roots are very superficially located (ordinarily 3 to 7 cm. below the ground, partly deeper — 30 cm., and exceptionally even more). The root system resembles the superterrestrial parts of the shrubby tree in so far as the radially placed roots are relatively very slender and often exceed 10 m. in length. They utilise for water and nourishment the uppermost soil horizon.

Lonicera xylosteum and

Daphne mezereum. Both species have very superficially located roots, a tap root being absent as in previous cases. The ordinary depth is about 3—7 cm., *Lonicera* penetrating a little deeper than *Daphne*.

The herbaceous plants (fig. 13 to 16) have roots inhabiting the same soil horizon as the absorbing roots of trees and shrubs.

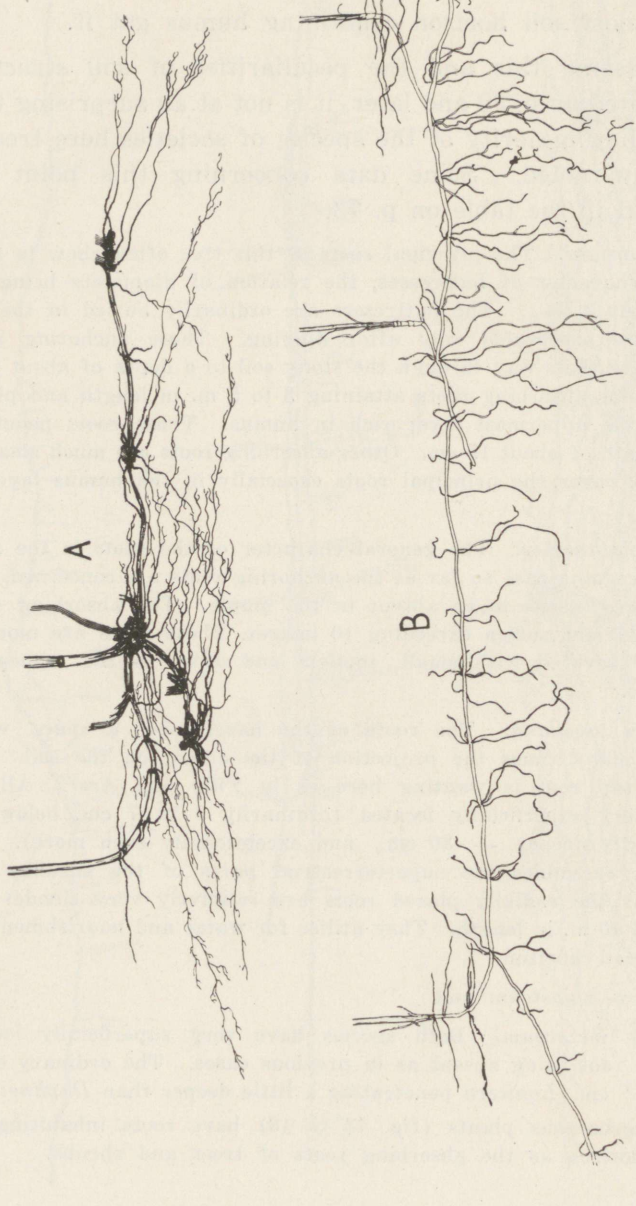


Fig. 14. A — *Milium effusum* L., B — *Majanthemum bifolium* F. W. Schm. $^3/_7$ of the normal size.

Thus the water and nourishment absorbing roots of the four superimposed communities, inhabit the same uppermost soil horizon. Without doubt the competition here is hard, especially in times with an insufficient water supply.

The water content of the leaves changes from spring to fall for every summergreen mainland plant. Moreover there

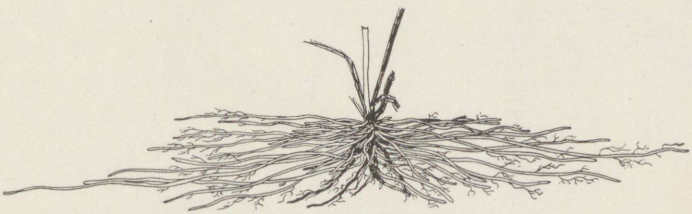


Fig. 15. *Ranunculus cassubicus* L. $^{3}/_{7}$ of the normal size.

are daily fluctuations in the water content. The observations carried out on the 9th of August on a sunny and dry day gave the following results:

Water content of leaves in p. c. of dry substance.

	6^h	10^h	14^h	18^h
Hepatica triloba	344	347	340	349
Mercurialis perennis	465	465	436	453
Asperula odorata	457	460	432	433

In some species (e. g. *Hepatica triloba*) these fluctuations are relatively small. This means that the water lost by transpiration is easily replaced. In other species (e. g. *Asperula odorata)* the equilibrium is reached only during the night. Therefore in observations continued for some months the material for every single observation has to be collected at a definite time of day (e. g. at 9 o'clock in the morning).

The samples for these determinations were collected in tightly closing aluminium boxes and dried in the laboratory in a thermostat at a temperature of 102^0 C.

Water content of leaves in p. c. of the dry weight.

	7. July	22. July	6. Aug.	22. Aug.
Carex digitata	282	236	255	215
Hepatica triloba	361	358	357	292
Orobus vernus	397	337	373	187
Milium effusum	395	336	322	—
Mercurialis perennis . . .	455	392	440	369
Asperula odorata	609	463	495	242
Oxalis acetosella	680	622	698	616

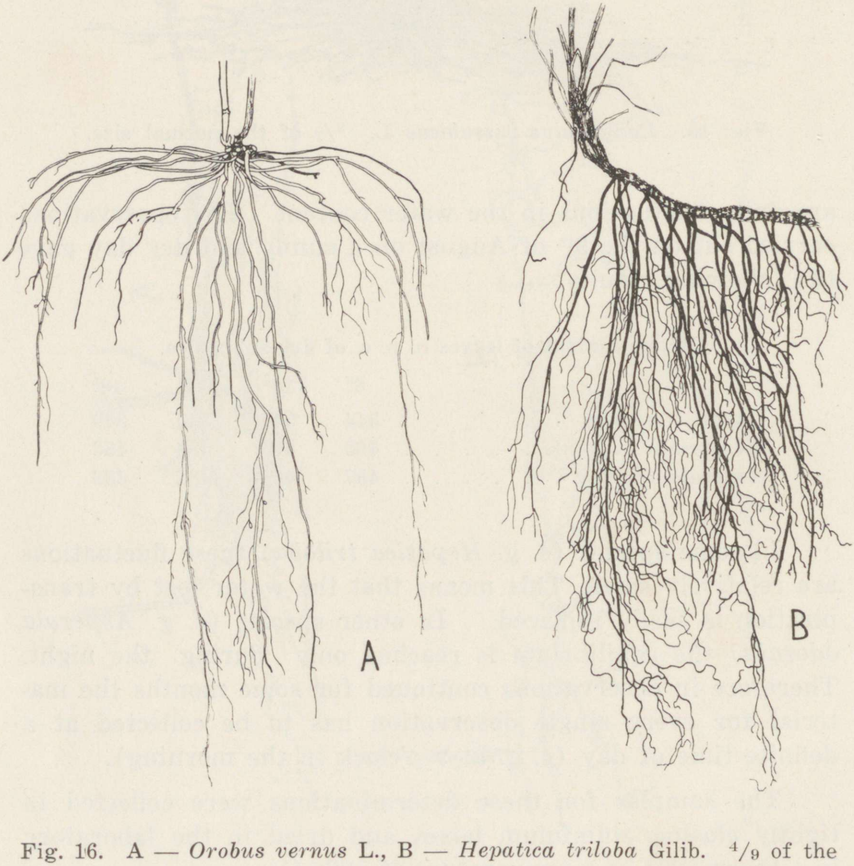


Fig. 16. A — *Orobus vernus* L., B — *Hepatica triloba* Gilib. $^4/_9$ of the normal size.

Fig. 17. The lime-tree forest on July 1937.

Fig. 18. The lime-tree forest during the drought. The soil is covered with dead foliage. The picture was taken on 20th August 1937.

Fig. 19. The *Mercurialis perennis* society in the lime-tree forest before the drought in July.

Fig. 20. The *Mercurialis perennis* society during the drought. In the foreground the foliage of *Daphne mezereum* has lost its turgor.

As stated on p. 73 both July and August 1937 were very dry. The last week of July had some rainy days. This water supply caused the rise of water content ascertained on the 6th August. Later on the water content diminished rapidly being two weeks later 12 *(Oxalis)* to 51 *(Asperula)* p. c. less than on the 6th August. As seen from these data, the behaviour of different species varies profoundly. The decrease of water content goes more or less parallel with the degree of morphological xeromorphism. The evergreen *Hepatica* and the grass type *(Carex, Milium)* lose much less water than the pronouncedly mesomorphic species such as *Mercurialis, Asperula* and *Orobus*. An interesting exception to this principle is *Oxalis acetosella* with its apparently unprotected thin leaflets containing abundant oxalate.

The behaviour of superimposed forest societies during the drought differs profoundly.

In the *Ulmus—Acer—Tilia* society the drought first caused incurving of the leaves of the lime-tree wherefore the grayish coloured underside of the leaves came forward more than usual. Little by little the coloration turned yellow and in the middle of August half the foliage of the lime-tree was already yellow and for the most part fallen. Coloured foliage appeared soon also on the rowan tree, birch and elm. This premature formation of autumnal foliage was entirely caused by the drought, the nightly temperatures being at this time very high (17^{0} to 20^{0} C).

During the drought the stomata are closed [1] for weeks both night and day as was proved by the M o l i s c h infiltration method using alcohol and xylol. This is a period of starvation, not only because the stomata are closed but in consequence of the loss of a great amount of the assimilating surface. It is of interest to note that during the whole dry period the leaves of all trees remained turgescent, the green ones as well as those with the autumn coloration.

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[1] For *Tilia cordata* and *Corylus avellana* it was proved that during the drought the guard cells of the stomata contained starch.

Essentially the same was observed for the hazel, except during the last week of August (the culmination of the drought) in which it was common enough to find leaves which

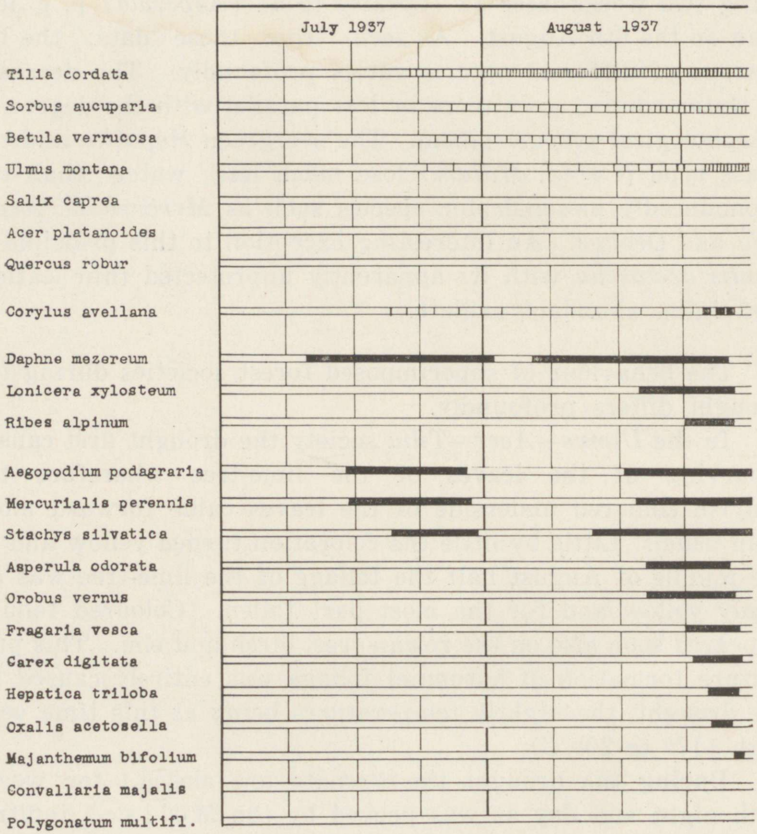

Fig. 21. Drought-resistance of different species. White indicates turgescent green foliage; streaked — turgescent yellow or red foliage together with green; black — temporarily withered green.

had lost their turgescence. The first yellow leaves appeared on *Corylus* in the last week of July. Their number was augmented considerably in the second half of August. In the last week of August about a fourth of the foliage was yellow.

The reaction in the *Lonicera* — *Ribes* society and the *Mercurialis* and *Asperula* societies was different in so far as the foliage remained on the plants during the whole period of the drought. Only when the drought was at its height did the leaves of *Daphne mezereum* and *Polygonatum multiflorum* become red or yellow and defoliation followed. The regular reaction to drought in these societies is the withering of the foliage. This loss of turgor is temporary and disappears after rain if this happens to supply the uppermost soil layer with sufficient water as occurred, e. g., at the end of July.

In the withered foliage the stomata are closed even during daytime.[1] This was proved for *Oxalis acetosella, Hepatica triloba, Veronica chamaedrys, Festuca gigantea, Dryopteris filix mas.* Partly open stomata (infiltration of xylol present) were found in *Mercurialis perennis, Asperula odorata, Orobus vernus, Majanthemum bifolium, Daphne mezereum, Aegopodium podagraria* and others.

The drought resistance of the species investigated is as

[1] For the following species it was proved that during the drought the guard cells of the stomata contained starch: *Fragaria vesca, Sanicula europaea, Luzula pilosa* (abund.), *Hepatica triloba* (abund.), *Convallaria majalis, Mercurialis perennis, Asperula odorata, Orobus vernus, Majanthemum bifolium.* No starch was found in the leaves of *Viola Riviniana, Vicia sepium, Carex digitata, Ranunculus cassubicus, Veronica chamaedrys.*

In some of the species mentioned the number of stomata present per sq. mm. was determined:

	Upper surface	Lower surface		Upper surface	Lower surface
Tilia cordata . . .	—	110	*Hepatica triloba* . .	9	48
Corylus avellana . .	—	74	*Oxalis acetosella* . .	—	49
Lonicera xylosteum .	—	148	*Asperula odorata* . .	—	68
Daphne mezereum .	—	64	*Orobus vernus* . . .	—	58
Polygonatum multifl.	—	68	*Fragaria vesca* . .	—	88
Majanthemum bifol. .	—	48	*Mercurialis perennis*	—	64
Carex digitata . . .	—	71			

different as their morphology. The following sequence of decreasing drought resistance was found (fig. 21):

Quercus robur *Acer platanoides* *Salix caprea*	>	*Tilia cordata* *Sorbus aucuparia* *Betula verrucosa* *Ulmus montana*	>	*Picea excelsa*
Ribcs alpinum	>	*Lonicera xylosteum*	>	*Daphne mezereum*

Polygonatum multiflorum *Convallaria majalis* *Majanthemum bifolium*	>	*Carex digitata* *Hepatica triloba* *Oxalis aceto-sella*	>	*Asperula odo-rata* *Orobus vernus* *Fragaria vesca*	>	*Aegopodium podagraria* *Mercurialis pe-rennis* *Stachys silva-tica*

For a phytogeographer visiting the Islet of Abruka the first question is why the rich deciduous forest covers the higher parts of the islet and why is it not a mixed wood with *Picea excelsa* dominating as is usual on the Estonian mainland and islands. This question is justified. It is still more justified by the fact that spruce occurs abundantly on the islet as a forest tree on low ground together with ash, birch and alder. In these places the reproduction of spruce is abundant as seedlings and young trees occur everywhere.

Except on sand-dunes and inland sand plains populated by pine, the spruce in Estonia is a dangerous competitor for every forest tree because of its ability to grow up even in deep shade in which the progeny of foliferous trees or pine would be killed. Since the woods in which the spruce occurs on the islet are contiguous to the lime-tree forest it is natural to suppose that spruce seeds should be repeatedly carried into the lime-tree forest by the wind. Nevertheless no spruce progeny was found in the lime-tree forest, if we except some isolated individuals found here and there after careful search.

On the contrary, the seedlings of the deciduous trees are frequent in the lime-tree forest as seen from the table preceding p. 47.

Fig. 22. A lime-tree "family" in the deciduous forest of Abruka.

Fig. 23. Vegetative propagation of the lime-tree in the forest of Abruka.

The maple *(Acer platanoides)* especially reproduces abundantly by seeds. The same is true of the ash and the rowan tree. Seedlings of the elm and the oak are not uncommon, though their number is exceeded greatly, for example, by those of the maple. It is really surprising that the dominating species — the lime-tree — was found only here and there as a seedling or young tree. Nevertheless the propagation of the lime-tree is efficient enough owing to the highly developed faculty of vegetative reproduction. This is proved by direct observation upon the distribution of the lime-trees in the forest. They occur in definite circled "families" — sometimes 20 and more trees in the "circle" close together — the offspring of some old, dead tree which formerly occupied the centre of the circle (fig. 22). The propagation is sometimes assured in the way shown on the fig. 23, that is by offspring from the trunk and the crown of fallen trees.

This vigorous vegetative propagation of the lime-tree is indeed sufficient to explain its permanence. The composition of this forest as a mixed wood is due to the fact that from time to time there is place enough for some maple, ash, or rowan tree to grow up.

The question remains why in the lime-tree forest is the spruce of no importance and why it ordinarily does not even occur at all. As stated, this is not due to a lack of seeds. It seems to be certain that the conditions of life in the lime-tree forest are not suitable for the spruce. Of scattered individuals in the lime-tree forest five spruce were investigated closely. The results were as follows:

Species	Nr.	Height	Diameter of crown	Diameter of trunk	Age
Picea excelsa	1	4.2 m.	2.5 m.	9.6 cm.	66
„ „	2	5.3 m.	3.0 m.	9.5 cm.	56
„ „	3	4.7 m.	2.6 m.	9.5 cm.	60
„ „	4	5.3 m.	2.3 m.	10.1 cm.	55
„ „	5	3.8 m.	2.5 m.	9.0 cm.	52

Trees whose age was found to be 52 to 66 years are only about 4 to 5 m. high. Their trunks measured about 10 cm. in diameter. That they have grown very slowly is shown also by the narrow annual rings which could be counted only by using a lens.

We have analysed the life conditions in the superimposed societies of a deciduous forest of Northern Europe. Every one of these societies has its definite floristic composition and is characterized by its habitat. The influence of the *Ulmus-Acer — Tilia* society as a habitat-creating community upon the subjacent societies is beyond doubt. The climatical differences existing between the habitat of these and the habitat of the ålvar vegetation are due to the protecting influence of the tree society. Whether there is a counteraction from the side of the subjacent communities which might influence the tree community is not clear. It seems that the subjacent communities could be destroyed without perceptibly influencing the life of the protecting community and that this community could exist very well if the soil were covered only with dead leaves instead of the moss, herb and shrub societies. It is possible that this state would even be advantageous to the tree society.

Some light could probably be thrown on these questions by careful studies of the animal societies of the forest.

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