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THE ECOLOGY OF *URTICA DIOICA*

BY CARSTEN OLSEN.

(*With Plate I.*)

I. INTRODUCTION.

The present paper is the result of an investigation that was carried out in the summer of 1917 with the object of ascertaining the factors that determine the occurrence of the common stinging nettle in the woods of Denmark.

Urtica dioica, which is widely distributed through Europe, North Africa, temperate Asia, as well as throughout temperate and sub-tropical America, occurs frequently in Denmark, particularly in those parts of the country where the soil is relatively good. Especially in the isle of Funen and in certain parts of east Jutland it appears in great abundance, whereas in west and mid-Jutland, which are occupied by heath, it is rare. Here it occurs, however, in places where better soil is met with, as in luxuriant growths near Bregning in the neighbourhood of Ringköbing, where a little patch of fertile soil is found as an oasis in the middle of the heath region of west Jutland.

II. MORPHOLOGY AND BIOLOGY OF *URTICA DIOICA*.

As is well known, *Urtica dioica* grows in large compact communities, most frequently without the intermingling of other species. This gregarious habit is due to the great power *Urtica dioica* has of spreading vegetatively by means of its underground runners (suboles). Most shoots begin with a shorter or longer horizontal rhizome, which lies a few centimetres deep in the soil, and bears opposite scale leaves. Every scale leaf consists of a rudimentary (serrated) lamina and two large stipules; the rhizomes, of which the youngest parts are reddish and like the aerial shoots are furnished with stinging hairs, can become more than 1 m. long, and branch. The roots arise from the rhizomes immediately above the base of the stipules, one root for every stipule, consequently four roots from every node. Solitary roots, however, also arise from the internodes. All the roots are strongly branched and bear very slender lateral roots of the second and third order. The largest and strongest roots arise from the region where the runner passes over into the base of the aerial stem. They mostly grow out in a horizontal or oblique direction and never penetrate deeply; they scarcely ever extend to a greater depth than 20 cms. The older roots are yellow on account of a cork layer which covers the surface. The aerial shoots are developed from the apical buds of the rhizomes, which sooner or later grow out into erect aerial stems, that may reach a height of 2·25 m. and bear opposite, ovate or ovate-cordate foliage leaves furnished with stipules. Late in the autumn there often takes place an abundant formation of vegetative lateral shoots on the stems.

The aerial parts keep fresh until late in the autumn, but finally wither when continued frost occurs. From the apical buds of the rhizomes, which winter in the soil, the new shoots grow out in the next period of growth.

Urtica dioica varies somewhat with respect to the form of the leaf and the size and number of the leaf serrations. Some plants have broad ovate-cordate leaves, others ovate to ovate-elliptical or almost lanceolate leaves; some have large-toothed, others finely-toothed laminae. Laciniate laminae also occur. This is doubtless a question of distinct elementary species (races) differing in specific heritable characters. Also the height of plants varies, which, as will be shown in the sequel, is due in part to the food content of the soil, but possibly may also result from hereditary differences. Variations in hairiness and leaf-size may probably also be due to small heritable differences; in regard to these, however, fluctuating variation plays a part, since all races of *Urtica dioica* in full light produce smaller and more hairy leaves, whereby the whole plant acquires a greyish appearance; likewise the stems are shorter. In the shade, on the other hand, *Urtica dioica* is taller and produces large, slightly hairy leaves.

III. Factors in the Distribution of *Urtica dioica*.

(*a*) *Light and Humidity. Nitrification in the Soil.*

As already stated, *Urtica dioica* grows in large close communities, which are met with both on peaty soil, particularly in alder and ash bogs in woods, and on damp mineral soils in woods, on places where sewage is discharged and round about inhabited places both on sand and clay. The *Urtica dioica* community rarely passes smoothly over into other plant communities, but is often separated from these by sharp boundaries. This is frequently conditioned by light intensity; thus, *Urtica dioica* is often found under the alder (*Alnus glutinosa*). If the alder wood is surrounded by beech wood, *Urtica* confines itself to the alder wood, in the shade of which it thrives well; but it does not enter the beech wood, the strong shade of which it cannot endure.

Urtica dioica is thus in a large measure dependent on light; it thrives well in full light as it does in not too strong shade; it attains, however, its most luxuriant and vigorous development in half-shade. In order to determine more precisely what light intensity is the most favourable, light quantities were determined, some with Wynne's actinometer, most of them with rhodamine paper (**1**). Contemporaneously with the measurements made in *Urtica dioica* localities, measurements were made in open daylight, and the light intensity in the nettle habitat is expressed in percentages of this.

From the measurements taken, of which some are found in a following table (page 7), it appears that the nettle can thrive quite well in as low a light value as 5 to 10 per cent. of that of open daylight; but the best value lies between 10 and 20 per cent. Thus, *Urtica dioica* is not confined to a narrowly limited light intensity, but can grow under most light trees; under shade trees, the beech for example, it cannot thrive.

Besides light, a change in the ground and consequent changes in humidity impose limits upon the extension of the nettle, since it requires a rather considerable water content in the soil. On the other hand it does not endure localities where water stands through the winter. In other cases neither light intensity nor humidity can be the cause of the nettle community being delimited as it is.

In such places the delimitation can be due either to the plant being a new immigrant that has not yet had time to colonise the ground that it is capable of conquering, or, if the association is old, to the soil relations setting limits to the extension of the plant. In localities where the latter must be presumed to be the case, samples of earth were taken for analysis, both from the *Urtica* community and from outside it, often a few metres distant from the boundary, where most frequently *Deschampsia caespitosa* was the dominant plant; and a comparison of the results of the analyses was made.

In addition, soil samples were taken from well-developed nettle communities and from localities outside the immediate neighbourhood, where *Urtica dioica* was not found, but which were of such a kind that one might have expected to find it there. Soil samples were taken from the soil layer in which the roots of the plants were found. Investigations were undertaken in the woods of Sealand, Funen and Laaland-Falster.

In several places in the literature (**14**, **9**) it is stated that *Urtica dioica* belongs among the so-called nitrate plants, that is, plants which, to thrive well, require nitrogen supplied in the form of nitrate, and which, moreover, may be presumed to require much nitrate-nitrogen, since nitrates are greedily taken up from the soil, and that which is not immediately assimilated is accumulated as a reserve material in the tissues, where it can be shown in sections of the plants in question, for example, with diphenylamine-sulphuric acid, which gives a blue colour with nitrates. Hence it is obvious to commence investigation with studies on this question. It may here be pointed out, that plants which contain nitrates in the tissues must necessarily have taken these as such from the soil, since it is proved that plants cannot transform other nitrogen compounds, for example, ammonium salts, into nitrates, because when they are cultivated in ammonium-containing, nitrate-free nutrient solution, they do not contain nitrates in the tissues (**4**, **15**).

Urtica dioica plants from the localities examined always contained nitrates, since a strong blue coloration was always produced in sections placed in diphenylamine-sulphuric acid. Nitrates are found particularly in the aerial stems, in the rhizomes and roots, but in smaller quantity in the leaves. The plants which most frequently grow along with *Urtica dioica*, for example, *Mercurialis perennis*, *Stachys sylvaticus* and *Chrysosplenium alternifolium*, also proved to be rich in nitrates. On the other hand, plants which grow outside the limit of the nettle community, such as *Deschampsia caespitosa*, give no nitrate reaction or only a slight one.

In order to investigate more closely the occurrence of the *Urtica dioica* community in relation to the nitrate content of the soil, estimations were made of the nitrates (in aqueous extract) of the soil samples taken. Since nitrates are easily soluble in water and therefore easily leached out of the soil by heavy rain, the quantity of nitrate in the same soil is very variable at different times, and estimations of the nitrate content in soil samples as collected can therefore not be used.

The content of nitrates in the soil, as is well known, is due to a biological process, namely nitrification, which proceeds through the activity of nitrite- and nitrate-bacteria, since the nitrite-bacteria oxidise the ammonia, produced by the breaking down of plants, to nitrites, which by the activity of the nitrate-bacteria are oxidised to nitrates. Thus, these are formed constantly in the soil, and it is therefore of interest to investigate how much of them is formed in a certain period of time, whereby an expression may be obtained for the nitrifying power of the soil.

Analyses were therefore undertaken in the following way. The soil sample was sifted in the fresh condition through a sieve with 2 mm. meshes. In one portion of the soil sample the nitrate content was estimated at once; the other part was allowed to settle loosely in an earthenware jar, which was covered with a glass plate and kept at a temperature of about 18° C. The jars were weighed from time to time, and the quantity of water evaporated made up with distilled water. After 25 days an estimation of the nitrate content of this portion was made. To employ the difference between the two nitrate values as an expression of the nitrifying power of the soil, which might seem natural, will however give a wrong idea of the nitrifying power of the soil. A soil sample taken from a strongly nitrifying soil after the weather has been dry for a long time may contain a very large quantity of nitrate, and this quantity can only increase a little in the course of 25 days, since an abundant accumulation of nitrates, which are not consumed in the soil samples as they are in nature by plants, retard the further course of the process. (See locality No. 17 in the following description of localities.) Therefore the nitrate quantities that were found after the lapse of 25 days were used exclusively as an expression of the nitrifying power of the soil, while the nitrate quantities found in the soil samples taken are given in the sequel for the sake of completeness.

The nitrate estimations were made colorimetrically by means of the phenol-sulphonic acid method (**20**), in which by addition of phenol-sulphonic acid to the quantity of nitrate to be estimated, nitrophenoldisulphonic acid is formed, the amount of which after neutralisation with aqueous ammonia can be determined colorimetrically. The method of analysis is briefly as follows:

200 c.c. of the fresh sifted soil are added to 400 c.c. distilled water and frequently stirred for one hour, after which the liquid is filtered through a folded filter, and 200 c.c. of the filtrate is used for the estimation. To this are added 20 c.c. saturated baryta water, and the mixture warmed to boiling, whereupon the precipitated humus substances are filtered from the extract. The filtrate is evaporated to dryness on the water-bath, 2 c.c. phenol-sulphonic acid added[1]. With the help of a spatula the latter is brought into contact with the whole of the residue after the evaporation. After the lapse of ten minutes 20 c.c. of distilled water are added and then 30 c.c. of 5 per cent. aqueous ammonia. The whole is transferred to a measuring flask and made up with water to 200 c.c. After standing until the next day so that the barium sulphate which separated out has time to settle, 100 c.c. are removed with a pipette, and the sample compared with standard solutions in a colorimeter.

The standard solutions consisted of a solution containing 0·1 mg. NO_3 per c.c. (163·05 mg. KNO_3 in 1 litre of water). Different quantities of this solution were taken, e.g. 200, 100, 60, 40, 20, 10, 4 and 2 c.c., which were each added to 200 c.c. of a nitrate-free soil (*Vaccinium myrtillus* moorland soil was used). The subsequent treatment was exactly as described above. This method, namely, adding the standard solutions to soil, proved to be necessary in order to obtain absolute uniformity, since the amount of nitrate is influenced a little by the presence of baryta and the coagulation of the soil colloids. The standard solutions will keep for several months if they are kept in the dark in well-stoppered flasks.

After the researches recorded above had been brought to a close it was found that the treatment with baryta-water in certain cases occasions loss of nitrate in the analysis, partly because on the addition of phenol-sulphonic acid nitric oxide may be lost in consequence of the impetuous reaction setting in between the sulphuric acid and the carbonate of barium formed, and partly because the sulphate of barium formed on the addition of sulphuric acid will carry down part of the phenoldisulphonic acid formed so that the results will be too low. The resulting error is, however, practically neutralised on account of the standard solutions having also been treated with baryta-water, as mentioned above.

The procedure described above may, however, be advantageously replaced by the following: To 200 c.c. of fresh sifted soil are added 700 c.c. of distilled water and a small dose (about ·5 g.) of sulphate of calcium (free from nitrate). The whole is left to stand for one hour with frequent stirring, and then filtered through a folded filter. The addition of calcium sulphate will effect a prompter clarification of the filtrate and a more rapid filtering, and the filtrate will become less coloured than it is without this addition. 200 c.c. of the filtrate are evaporated in a porcelain cup on the water-bath, after addition of a slight dose (about ·25 g.) of calcium oxide (CaO) to about 10 c.c. and subsequently it is passed through a small filter into another cup. The CaO filtered off will retain all the coloured substances in the extract so that the filtrate becomes quite colourless (when BaOH is used, some colouring matter always remains). The cup is rinsed over the funnel and the filter carefully washed with hot water. The colourless filtrate thus obtained is evaporated to dryness on the water-bath, and the residue treated with 2 c.c. of phenol-sulphonic acid, as described above.

As will be seen from the following, the amount of nitrate—like that of the remaining nutrient substances in the soil—is given, not per unit weight of soil, but per unit volume of soil, which is generally done in researches on peaty soils, though not with mineral soils; but in the present paper, where both peaty

[1] The phenol-sulphonic acid is prepared by dissolving 9 grams of pure phenol in 60 c.c. of concentrated sulphuric acid.

soils and mineral soils are dealt with, it is necessary for the sake of comparison to present the amounts of nutrient substances in the same units.

It was decided to give the quantities of nutrient substances per unit volume of soil, since it must be of importance for the plants how much nutrient material is found in a certain volume of soil, namely the volume of soil to which the roots have access. If the quantities of food material are given per unit weight of soil, the relation between the quantities of nutrient substances in different soils—particularly between those in peaty and mineral soils—will be quite different from what it is where the quantities of nutrient substances are given per unit volume, since the specific gravity of the soils differs exceedingly, although the plants are surely quite indifferent to this. Peaty soil is only half as dense as mineral soil, so that by giving its content of nutrient substances per unit weight, one will get a much higher value in comparison with mineral soils than if one gives it per unit volume.

The volume of soil used for analysis was measured by filling up a tall measuring cylinder little by little with the fresh sifted soil, the bottom of the cylinder being frequently tapped against a soft support; this method always gives approximately the same result with the same soil.

At the same time that the soil was measured out for nitrate determination, samples of soil were weighed out for determination of the water content. The values of the percentage of water given below, which is lost by drying to constant weight at 18°, are expressed as percentages of the weight of the fresh soil.

Since it may be assumed beforehand that the reaction of the soil is a determining factor for the course of nitrification, a determination of this was made by measuring the hydrogen-ion concentration in aqueous extracts of the soils.

To 50 g. of soil, 150 c.c. water were added; this was kept with frequent shaking for about 24 hours, after which the coarsest particles were allowed to settle, and the liquid decanted and used for the measurement. (For hydrogen-ion measurements in the soil, see list of literature cited, **6**). This was carried out electrometrically by means of the electrode described by S. P. L. Sörensen (**17**), which was used with a modification introduced by Hasselbalch (**9**), by which the carbonic acid present does not escape during the measurement.

For understanding the following it should be pointed out that the hydrogen-ion concentration of a liquid is expressed as the number of grams of hydrogen found as ion per litre of liquid, and that the hydrogen-ion concentration is always expressed as a negative power of 10. The usual practice is to give only the exponent which is called the hydrogen-ion exponent, and is denoted by p_H., in which expression 10^- is implied. The hydrogen-ion concentration of absolutely pure water has a p_H value 7·1, and since absolutely pure water has equal quantities of hydrogen and hydroxyl ions, its reaction is neutral. If the hydrogen-ion exponent is greater than 7·1, the reaction is alkaline; if it is less than 7·1 the reaction is acid, and the less the value of p_H. the greater the degree of acidity. In the following table the p_H. value for each soil sample is given.

In the following tabular summary the localities examined are described singly, with a statement of the composition of the flora and also the quantities of nitrate and water found in the soil samples collected; finally, the hydrogen-ion concentration (p_H. values) in the soil samples is given. The first 13 localities described are situated on mineral soils, the remainder on peat soils.

Description of locality	Light in % of full light	NO_3 in mg. found in 1 litre fresh soil: Immediately	After 25 days	% of water	p_H.
1. *Urtica dioica* community mixed with *Mercurialis perennis* under Oak (Köge). Urtica 140 cm. high. Soil sandy moraine mixed with mould	23	13·75	55·03	11·21	5·8
2. *Deschampsia caespitosa-Ajuga reptans* community under Oak, 10 m. from the limit of (1). Soil firmer and more clayey than in (1)	24	0·91	3·67	13·90	5·8
3. *Deschampsia caespitosa-Carex sylvatica* community under Oak, near locality (1). Soil sandy moraine, poor in mould	35	1·37	1·37	12·72	5·3
4. *Deschampsia caespitosa-Carex sylvatica* community under Oak, 30 m. from the limit of (1). Soil stiff moraine	35	3·11	21·30	11·66	6·4
5. *Urtica dioica* community about 140 cm. high, under Oak in Grib Wood. Urtica has here grown up through a heap of brushwood. Soil very sandy moraine ...	18	1·08	98·19	18·35	6·0
6. *Deschampsia caespitosa* community mixed with *Oxalis acetosella* and *Stellaria holostea*, 10 m. from the limit of (5). No brushwood covering. Soil as (5)	18	0·00	21·35	16·10	4·9
7. *Urtica dioica* association (160 cm. high) under Oak Köge). Soil very stiff moraine	6	8·05	56·32	15·08	6·2
After a long period of rain		1·51	103·25	26·26	6·1
8. *Urtica dioica* community (80 cm. high) under strongly cut Beech (Köge). Soil friable sandy moraine mixed with mould	6	10·49	40·98	21·98	5·8
9. *Asperula odorata-Oxalis acetosella* community 1·5 m. from the limit of (8). Soil as described under (8)	6	2·17	20·83	20·20	5·4
10. *Urtica dioica* community (160 cm. high) under Common Alder (*Alnus glutinosa*) (Köge). Soil stiff stoneless clay rich in humus	8	66·34	79·38	18·66	6·9
11. *Urtica dioica* community (200 cm. high) under Oak (Isle of Falster). Soil sandy moraine mixed with mould	20	8·90	225·87	12·00	6·3
12. *Urtica dioica* community (100 cm. high) mixed with *Mercurialis perennis* under Oak (Funen). Soil sandy mould mixed moraine	—	16·71	50·04	15·62	5·9
13. *Deschampsia caespitosa-Carex sylvatica* community under Oak (Lolland). Soil stiff moraine	20	0·00	22·82	22·22	6·3
14. *Urtica dioica* community (140 cm. high) mixed with *Oxalis acetosella* and *Chrysosplenium alternifolium* at the edge of an old drained high-moor planted with Birch and White Alder (*Alnus incana*). Grib-Wood. Soil loamy brown-coloured peat without organic structure	10	9·46	66·19	61·06	4·9
15. *Molinia coerulea-Deschampsia flexuosa* community middle of moor, about 30 m. from the limit of (14). White Alder planted here has disappeared. Peat less altered and lighter brown than in (14), and with distinct organic structure	20	0·00	24·79	67·94	3·6

Description of locality	Light in % of full light	NO_3 in mg. found in 1 litre fresh soil: Immediately	After 25 days	% of water	p_H
16. *Urtica dioica* community under Red Alder in the middle of a drained bog. Very loamy, dark brown peat without organic structure	6	45·11	90·98	61·40	7·1
17. *Carex elongata* community, same moor, about 4 m. from edge of (16). A few seedlings of *Urtica dioica* present. Soil as (16)	6	93·84	93·21	54·00	6·6
18. *Urtica dioica* community (225 cm. high), small drained bog without trees, but surrounded by Beech wood, which at certain times of day casts a shade on the bog, in Jaegersborg Deer-park near Copenhagen. Soil very loamy, dark-brown peat. Much used by deer, whose excrement is found in large quantity on the bog	—	15·20	107·79	70·14	6·2
19. *Mercurialis perennis* community under Ash in a drained bog (Sorö). *Urtica dioica* at border of bog on the mineral soil, but not penetrating into bog. Soil dark brown, very loamy peat	35	9·13	37·19	51·54	7·3
20. *Deschampsia caespitosa* community mixed with *Festuca rubra*, *Geum rivale*, *Anthoxanthum odoratum* and scattered *Urtica dioica* in a drained treeless bog (Sorö). Soil dark brown, very loamy peat ...	100	5·52	76·78	51·71	6·2

In the following two tables is presented the result of a closer floristic analysis of the localities. This was done by preparing statistics concerning the frequencies of the vascular plants and mosses present according to Raunkiaer's formation-statistical method. The numbers in the tables give the frequencies of the different species; this is done by enumerating in how many per cent. of the sample areas taken (1/10 sq. metre) each species occurs. Twenty-five sample areas were taken in every locality round the places from which the soil samples were taken.

Floristic Analysis of Localities 1—10.

Locality no.	1	2	3	4	5	6	7	8	9	10
Urtica dioica	*100*	—	—	—	*100*	—	*100*	*100*	—	*100*
Mercurialis perennis	*80*	—	—	—	—	—	—	—	—	—
Ajuga reptans	—	*72*	—	—	—	—	—	—	—	—
Deschampsia caespitosa ...	—	*92*	*100*	*72*	—	*100*	—	—	—	—
Carex silvatica	—	36	*72*	8	—	—	—	—	—	—
Poa pratensis	—	—	—	*76*	—	—	—	—	—	—
Oxalis acetosella	4	48	—	60	40	*100*	—	—	*80*	—
Stellaria holostea	—	4	—	—	—	*72*	—	—	—	—
Asperula odorata	—	32	8	—	—	52	—	—	*100*	—
Deschampsia flexuosa... ...	—	—	—	—	—	4	—	—	—	—
Melica uniflora	—	—	—	44	—	—	—	—	—	—
Calamagrostis lanceolata ...	—	—	8	—	—	—	—	—	—	—
Agrostis alba	—	—	—	—	—	4	—	—	—	—
Ficaria verna	—	—	—	—	—	—	20	—	—	—
Anemone nemorosa	—	28	—	—	8	12	28	—	—	—
Viola canina	—	—	4	—	—	8	—	—	—	—
Hypericum maculatum ...	—	4	—	—	—	—	—	—	—	—
Rubus idaeus	4	16	48	—	—	8	—	—	—	—
Primula elatior	—	—	—	8	—	—	—	—	—	—
Veronica chamaedrys ...	—	—	—	16	—	—	—	—	—	—
Nepeta glechoma	—	—	—	—	12	—	—	—	—	—
Mnium undulatum	4	—	—	—	—	—	—	—	—	—
Catharinea undulata	4	8	—	—	—	—	—	—	—	—
Hypnum purum	—	—	—	—	—	8	—	—	—	—

Floristic Analysis of Localities 11—20.

Locality no.	11	12	13	14	15	16	17	18	19	20
Urtica dioica	*100*	*100*	—	*100*	—	*100*	12	*100*	—	—
Mercurialis perennis	—	*100*	—	—	—	24	—	—	*100*	—
Deschampsia caespitosa ...	—	—	*68*	12	—	4	40	—	—	*72*
Carex silvatica	—	—	*72*	—	—	—	—	—	—	—
Oxalis acetosella	—	—	44	*80*	24	—	—	—	—	—
Chrysosplenium alternifolium	—	—	—	*80*	—	*100*	40	—	—	—
Molinia coerulea	—	—	—	—	*96*	—	—	—	—	—
Deschampsia flexuosa ...	—	—	—	—	*100*	—	—	—	—	—
Carex elongata	—	—	—	8	—	—	*100*	—	—	—
Festuca rubra	—	—	—	—	—	—	—	—	—	*100*
Geum rivale	—	—	32	—	—	—	—	—	—	*100*
Galium palustre	—	—	8	—	—	—	44	—	—	*100*
Anthoxanthum odoratum ...	—	—	—	—	—	—	—	—	—	*72*
Athyrium filix femina ...	—	—	—	—	—	12	8	—	—	—
Equisetum arvense	—	—	—	—	—	—	—	—	—	20
Juncus effusus	—	—	8	—	—	—	—	—	—	—
Poa pratensis	—	—	52	—	—	—	—	—	—	8
Holcus lanatus	—	—	4	—	4	—	—	—	—	4
Stellaria holostea	—	—	16	44	60	—	—	—	—	—
Ranunculus repens	—	—	36	—	—	36	60	—	—	64
Anemone nemorosa	—	—	24	—	—	—	—	—	20	—
Viola palustris	—	—	—	—	—	—	—	—	—	4
Hypericum hirsutum	—	—	4	—	—	—	—	—	—	—
Fragaria vesca	—	—	16	—	—	—	—	—	—	—
Rubus idaeus	—	—	—	12	20	—	—	—	—	—
Rubus caesius	—	—	40	—	—	—	—	—	—	—
Filipendula ulmaria	—	—	8	—	—	—	—	—	—	64
Lathyrus pratensis	—	—	—	—	—	—	—	—	—	8
Primula elatior	—	—	56	—	—	—	—	—	—	—
Lysimachia vulgaris	—	—	—	—	—	—	8	—	—	—
,, nummularia ...	—	—	20	—	—	—	—	—	—	—
Myosotis scorpioides	—	—	—	—	—	32	36	—	—	—
Veronica chamaedrys	—	—	—	—	—	—	—	—	—	24
,, scutellata var. villosa	—	—	—	—	—	—	—	—	—	16
Ajuga reptans	—	—	24	—	—	—	—	—	—	8
Brunella vulgaris	—	—	12	—	—	—	—	—	—	8
Asperula odorata	—	—	8	—	—	—	—	—	—	—
Valeriana dioica	—	—	—	—	—	—	—	—	—	4
Cirsium palustre	—	—	4	—	—	—	—	—	—	44
Hieracium pilosella	—	—	—	—	—	—	—	—	—	4
Mnium undulatum	—	—	12	—	—	8	—	—	—	4
,, cuspidatum	—	—	—	—	—	—	—	—	—	44
Climacium dendroides ...	—	—	—	—	—	—	—	—	—	24
Polytrichum attenuatum ...	—	—	—	—	—	—	—	—	—	8
Hylocomium parietinum ...	—	—	—	—	52	—	—	—	—	—
,, squarrosum ...	—	—	—	—	24	—	—	—	—	—
,, triquetrum ...	—	—	—	—	—	—	—	—	—	16
Hypnum purum	—	—	—	—	16	—	—	—	—	—
,, Stockesii	—	—	8	—	—	—	—	—	20	—

If the localities investigated are arranged according to the development of *Urtica dioica*, beginning with the localities where it thrives best (as judged by its height), and concluding with the localities where it is not found, the following table is obtained, in which is given for each locality the quantity of nitrate found in the soil samples after the lapse of 25 days, expressed in mg. per litre of soil.

Locality	Development of *U. dioica*	NO_3	Locality	Development of *U. dioica*	NO_3
18	225 cm. high	107·79	20	Scattered *U. dioica*	76·78
11	200 ,,	225·87	17	A few seedlings of *U. dioica*	93·21
16	160 ,,	90·98	19	Absent	37·19
7	160 ,,	79·78	15	,,	24·79
10	160 ,,	79·38	13	,,	22·82
5	140 ,,	98·19	9	,,	20·83
14	140 ,,	66·19	6	,,	21·35
1	140 ,,	55·03	4	,,	21·30
12	100 ,,	50·04	3	,,	1·37
8	80 ,,	40·98	2	,,	3·67

This table appears to make it highly probable that the nettle is dependent on the nitrifying power of the soil. Where *Urtica dioica* thrives best and becomes 2 m. high or more, an intense nitrification takes place in the soil (localities 11 and 18); where the height is somewhat less, a somewhat weaker nitrification, and where the plants are low (80 cm.), namely in locality 8, a very weak nitrification occurs, since only 40·98 mg. NO_3 per litre of soil were found in the soil sample at the end of 25 days. Where the nitrification in the soil is still smaller, the nettle is absent, and *Deschampsia caespitosa* is generally the dominant plant.

Only the analyses of the soil from localities 17 and 20 suggest that some soil factor other than nitrification may play a part in determining the development of *Urtica dioica,* in that these two localities exhibit a fairly intense nitrification, although the nettle is scattered and low growing (in locality 17 only seedlings are found). The particular circumstances which must be assumed to be the reason for the poor growth of *Urtica* in these localities, will be treated later.

(*b*) *Conditions for Nitrification.*

It will be evident from the foregoing observations that where *Urtica dioica* is not found in the localities investigated, the reason for this is, in most cases, an absence of, or too weak, nitrification. It will therefore be of interest to investigate which factors condition an active nitrification. A first condition for nitrification is naturally, that there should be found in the soil sufficient nitrogen-containing material which can be nitrified. Since it is ammonia that is nitrified, a formation of ammonia must take place in the nitrifying soils for which the material is furnished by the decaying plants and humus substances. Indeed it is seen from the foregoing tabular summary that the liveliest nitrification in most cases is met with in organic soils, namely in peat soils, though also in mineral soils rich in humus a lively nitrification may take place (e.g. locality 11).

Among other factors which have an influence on the course of nitrification, the following are stated in the literature cited to be the most important: (1) the stratification relations of the soil and the degree of aeration conditioned thereby; (2) the water-content of the soil; (3) its degree of acidity.

To the first of these factors is generally ascribed great significance; and the working up of the soil of arable land is considered to act particularly favourably in producing an active nitrification, because the working up brings about a looser stratification and, in consequence of this, better aeration.

In well worked arable land there is generally going on an active nitrification, and this has been known as long as nitrification has been recognised, while on the contrary it was not supposed that this proceeded in natural soils, e.g. woodland soils, because these were thought to be worse aerated than arable soil. This doctrine still figures in most text-books, e.g. that of Jost (**10**), who on account of the absence of, or weak, nitrification of uncultivated soils, considers ammonia to be the most important source of nitrogen of wild plants.

However, Boussingault in a single instance (**2**), and Grebe (**7**) with later Weis (**18**) and Hesselman (**9**) have already shown that an active nitrification can also proceed in natural soil, and this conclusion the analytical results presented in the present paper confirm. That nitrification can proceed in natural soil, Weis (**13**) explained thus: that such a soil, e.g. woodland soil, is far from always having to be regarded as badly aerated, since a working and consequent looser layering of the soil can be produced in a natural way, namely by the activity of earth-worms, moles and other burrowing animals. But even if the soil is not loosely layered, it yet appears possible for an active nitrification to proceed. In this connection reference may be made to locality No. 7 in which, as will be seen from the data given, a very lively nitrification proceeds, although the soil is a compactly layered, stiff and wet clay. Indeed, it also appears from the most recent researches undertaken by Gainey and Metzler (**5**), that the layering relations of the soil have not so great a significance for aeration as is generally supposed. These authors have instituted experiments on nitrification with soil strongly pressed together, and found that pressing the soil together did not result in any diminution of the activity of the nitrification, so that even in very closely layered soil the aeration will be sufficient for an active nitrification to be able to proceed.

The belief in the great significance of compact or loose texture in its effect on nitrification was based on observations on the course of nitrification in ammonium-containing nutrient liquids, in which an active aeration is necessary to provoke an active nitrification; but in liquids aeration proceeds more slowly and with more difficulty than in the most compactly layered soil, so that we cannot argue from the course of nitrification in such experiments to the conditions existing in the soil.

With regard to the water content of the soil, the significance of this for the course of nitrification must be said to be very great and certainly one of the most important factors. Koch (**11**) has shown that nitrification proceeds actively within rather narrow limits of the water content of the soil, since for a certain soil a water content of 16 per cent. was the optimum for the rate of the process, which was strongly retarded when the water content was either

10 per cent. or 26 per cent. These numbers can, however, only be accepted for sandy soils, since the numbers for clay soils, on account of the greater water-holding power of the latter, must be considerably higher, and they must be still higher for peat soils, of which the water-holding capacity is still higher than that of clay soils. Gainey and Metzler (**5**) state that the optimum water content for nitrification is one that amounts to 2/3 of the capacity.

The analyses recorded here also show the great significance of the water content for the rate of nitrification. The analyses relating to locality No. 7 are significant in this respect, since the first soil sample, which was taken after a long spell of dry weather, showed a water content of 15·08 per cent. and a rise in nitrate content from 8·05 mg. to 56·32 mg. per litre of soil, whilst a soil sample taken later from the same place after a long spell of rain and with a water content of 26·26 per cent., showed an increase in nitrate content from 1·51 mg. to 103·25 mg. per litre of soil. Thus, the greater water content in the latter soil sample has conditioned a much more intense nitrification. If localities Nos. 1 and 2 are compared with one another, it will be seen that there proceeds in locality No. 1 a much more intense nitrification than in locality No. 2. The hydrogen-ion concentration in the soil is the same in the two localities, but the physical condition of the soil is quite different, since the *Urtica dioica* community in locality No. 1 is found on sandy soil, the *Deschampsia caespitosa* community in locality No. 2 on the contrary on clay soil, and the limit between these two associations lies exactly where the sandy soil and clay soil meet. From the analysis it is seen that the absolute water content was somewhat greater in clay soil than in sandy soil; but on account of the greater capacity of the clay soil, the water content, from a physiological standpoint, is certainly greater in sandy soil, which would probably have become apparent if the water content had been expressed in per cent. of the capacity (that the capacity has not been determined is due to the fact that a satisfactory method is not so far to be had). It is then without doubt a rather low water content in the soil in locality No. 2 that is the cause of the feeble nitrification here, since clay soils in comparison with sandy soils must contain a considerably greater quantity of water to allow of an intense nitrification. The clay soils in which a powerful nitrification was going on (soil samples from localities Nos. 7 and 10) had indeed a considerably greater water content, namely 26·26 per cent. and 18·66 per cent. respectively, while the feebly nitrifying clay soil from locality No. 2 contained only 13·90 per cent. of water. Similarly, the weakly nitrifying clay soil from locality No. 4 had a very small water content, namely 11·66 per cent.

It appears therefore from these considerations that the greater or less water content of the soil has a very important influence on nitrification, since a relatively high water content is necessary for it to proceed actively. While *Urtica dioica* can only grow on relatively damp soils, this is not necessarily conditioned by a direct need of this plant for a high water-content in the soil;

but its dependence on the degree of humidity of the soil may be indirect, being dependent on the nitrification in the soil, which again depends on the degree of humidity.

Besides the stratification and degree of humidity of the soil, the acidity (hydrogen-ion concentration) of the soil is also stated in the literature to have great influence on the rate of nitrification, since nitrification is stated by most authors to proceed only in alkaline or neutral, and not in acid soils. That nitrification can proceed even extraordinarily actively in acid soil, appears with great clearness from the analytical results recorded above, since all the soil samples investigated had an acid reaction, with the exception of the soil sample from locality No. 16, which had a neutral reaction ($p_{H^{\cdot}} = 7{\cdot}1$), and the soil sample taken from locality No. 19, which exhibited a slightly alkaline reaction ($p_{H^{\cdot}} = 7{\cdot}3$).

It appears further from the investigations that a weak nitrification can proceed even in the most acid soils, since the soil sample from locality No. 15 belongs among the most acid Danish soil types, for the hydrogen-ion concentration in this soil was as high ($p_{H^{\cdot}} = 3{\cdot}6$) as in soil samples from untouched Sphagnum-bogs and from moor- and heath-soils[1]. That nitrification can proceed in acid soil has, moreover, already been shown by Grebe (**7**) and Christensen (**3**), and most recently by Hesselman (**9**) and Weis and Bondorff (**19**). Even if nitrification can proceed in acid soil, the hydrogen-ion concentration of the soil has, however, as the researches recorded in this paper show, a great influence on the activity of nitrification, since this is greatly reduced when the hydrogen-ion concentration is high.

Particular interest attaches to the soil samples from localities Nos. 5 and 6. As seen from the description of localities, these are taken from among oaks in Grib Wood in a very high-lying soil. The woodland soil among the oaks is covered with a flora of which the most frequent species are *Deschampsia caespitosa*, *Oxalis acetosella* and *Stellaria holostea*, and as is seen from the analysis of soil from locality No. 6, only a feeble nitrification takes place in the soil.

The soil at occasional places in this oak community is covered with piles of brushwood about ·5 m. high, that have obviously remained for some time in the wood. Where these heaps of brushwood occur, *Urtica dioica* has appeared and has grown up through the heap, whilst no *Urtica dioica* is found outside the heaps of brushwood, a circumstance which is also observed in other places. The soil samples from locality No. 5, which is taken from under such a heap of brushwood, shows that in the soil under the heap there proceeds a considerably stronger nitrification than outside the pile of brushwood (locality No. 6). It is seen further from the analyses that the water content is greater and the hydrogen-ion concentration lower in the soil under the heap of brushwood than in the soil outside it. This is confirmed for several other heaps of

[1] According to the author's researches these types of soil are not nitrifying.

brushwood in the same oak community. Thus, there can scarcely be any doubt that the covering with the pile of brushwood promotes nitrification in the soil. The introduction of the pile of brushwood has increased the water content of the soil, since the evaporation from the surface of the soil is reduced, and on this account nitrification is favoured. That the hydrogen-ion concentration is lowered, can perhaps be explained by the changes in micro-organic life caused by the altered humidity, since the hydrogen-ion concentration of the soil, at any rate in soils that are poor in calcium carbonate, is doubtless to a certain extent, dependent on the activity and products of metabolism of micro-organisms. Probably the heap of brushwood also acts directly in favouring nitrification, in that as it gradually decays away, it supplies the soil with nitrifiable nitrogen compounds.

(c) *The easily soluble Mineral Constituents of the Soil.*

After having dealt with the relation of *Urtica dioica* to the nitrogen of the soil, there remain to be considered the requirements of the species for the other plant nutrients. From the foregoing analyses it will appear that it is not in all cases a lack of, or too feeble, nitrification that is to be presumed as the reason for the absence of *Urtica dioica* from a locality that should otherwise be favourable for this plant. Of particular interest is locality No. 17, where there proceeds an active nitrification in the soil, without *Urtica dioica* being found there. It must be supposed that at least one of the remaining nutrient substances must be present here in too small quantity for the plant to be able to thrive.

In order to investigate the remaining plant nutrient substances, from the localities already dealt with ten were selected for complete analysis, namely localities 1, 2, 6, 7, 14, 16, 17, 18, 19 and 20. The soil samples taken were treated with distilled water saturated with carbonic acid, and in the obtained extract the quantities of the separate substances were determined. This method was employed instead of the more generally used hydrochloric acid extraction method, which gives much more of the various substances than is available for the plants. It is only of importance to know the materials which can be dissolved in water containing carbonic acid, since it is not likely that plant roots excrete acids other than carbonic acid. The water around the roots of plants can undoubtedly be quite saturated with carbonic acid, so that to employ water saturated with carbonic acid for extracting is justified. Four litres of water to one litre of soil were used. For the details of the analytical methods, reference is made to Mitscherlich's papers (**12**, **13**), whose descriptions have been exactly followed.

The results of the analyses are seen from the following table (p. 15):

The substances which are essentially of interest, apart from nitrogen already considered, are potassium and phosphoric acid, since these two substances are often present in the soil in very small quantities. The remaining substances will in most cases be present in adequate quantity, and from the table it does not appear that some of these substances are present in smaller quantity in the places where *Urtica dioica* is not found than in those where it is, from which one may suppose that these substances as a rule will be present in adequate quantity for *Urtica dioica* in every soil.

Milligrams from one litre of fresh soil

Soil sample from locality No.	1	2	6	7	14	16	17	18	19	20
Ca	63·4	67·9	35·8	222·4	66·4	219·4	262·7	483·3	423·7	407·4
Mg	17·0	18·3	13·1	16·9	9·2	13·0	11·9	31·0	60·0	10·5
Na	Not determined		35·4	45·7	74·7	Not determined		40·0	64·9	52·9
K	110·0	45·3	11·7	14·3	11·3	4·5	7·0	62·8	15·9	7·7
PO_4	9·4	2·0	2·9	2·6	4·9	2·6	0·7	50·7	2·2	5·8
SO_4	56·2	54·4	41·2	50·0	49·4	78·7	90·4	113·6	51·0	59·3
SiO_3	Not determined		56·9	112·6	15·2	Not determined		32·9	25·7	25·3

As regards potassium, it will be seen from the table that the absence of this substance does not exclude *Urtica dioica* from any place, since the smallest quantity found was obtained from locality No. 16, where there is a well-developed nettle community. On the other hand phosphoric acid behaves otherwise, in which respect the analyses of the soil samples from localities Nos. 16 and 17 are particularly instructive. The fact that *Urtica dioica* is wanting from locality No. 17, which is only 4 m. from locality 16, where a well-developed *Urtica* community is observed, is undoubtedly due to the very small quantity of phosphoric acid which was found here (0·7 mg. compared with 2·6 mg. in locality No. 16) since the other conditions for the good growth of *Urtica*, as already established, namely suitable light and humidity relations together with an active nitrification proceeding in the soil, are present in both localities. It will further be seen from the above table that the most vigorous of all the *Urtica dioica* communities (locality No. 18) investigated, occurs on a soil which contains a very large amount of phosphoric acid (50·7 mg.).

The smallest quantity of phosphoric acid, namely 2·6 mg., which was found in an *Urtica dioica* locality, comes from locality No. 7. Where the quantity of phosphoric acid is smaller than this value, no nettle is found in the localities investigated, as in localities Nos. 2, 17 and 19. In locality No. 2 *Urtica dioica* is absent, yet primarily on account of the feeble nitrification which proceeds here. In locality No. 19 nitrification does not proceed very actively, though more actively than in locality No. 2; here apparently both the small quantity of phosphoric acid and the weaker nitrification are the causes of the absence of the nettle.

In locality No. 20 it appears, on the other hand, that the quantity of phosphoric acid must be sufficient for the needs of *Urtica dioica*, and here there proceeds indeed an active nitrification. That *Urtica dioica*, which is found scattered over the bog, does not form closed communities here, is due without doubt to the fact that this bog, in opposition to all the other localities investigated, is exposed to full illumination (light per cent. 100), which gives the grasses a strong advantage in competition with the nettle. Possibly, however, *Urtica dioica* is invading this bog and will in time perhaps form closed communities.

IV. Sand Culture Experiments with *Urtica dioica*.

In order to determine how far sand culture experiments would confirm the conclusion drawn from the researches on the soil, namely that *Urtica dioica* requires a relatively high quantity of nitrogen, and that this is needed in the form of nitrate, the following research was made in the summer of 1918.

In four vessels each holding about 3 litres of washed sand, cuttings (rhizomes) of *Urtica dioica* were placed, 12 grams in each vessel. Each vessel received the following manuring:

KCl	1	gram
$CaH(PO_4)$	1	,,
$CaSO_4$	1	,,
$MgSO_4$	0·5	,,
$FeCl_3$	0·02	,,

The water content was maintained at 14 per cent. The experiments were started on the 12th of April, 1918, and there were given thereafter to the four jars, respectively, 50, 15, 5 and 1 mg. NO_3 per litre of soil a week. The experiment was brought to a close on 4th August, 1918. The plants in the vessels behaved so that they made the growth and height shown in the following table (see also Fig. 2):

Vessel No.	1	2	3	4
Mg. of NO_3 per litre of sand each week	50	15	5	1
Height of plants in cms. at close of the experiment	140	72	25	18
Wet weight of plants in gms. at close of the experiment	318·6	129·0	42·2	18·1
Dry-weight of plants in gms. at close of the experiment	75·0	30·4	9·5	4·2

The experiments consequently confirm the conclusions drawn from the researches on the soil, namely that a relatively great quantity of nitrogen is necessary for *Urtica dioica* to be able to attain a good development; for only in vessel No. 1, where the plants received 50 mg. NO_3 per litre of sand a week, the nettle attained a tolerably vigorous growth. That the growth however was not quite so strong as in the natural localities investigated, where a similar quantity of nitrogen is present in the habitat, is due without doubt to the circumstance that the small quantity of rhizome, namely 12 grams, which was put in every vessel, did not contain any reserve material of significance.

It might be supposed that if the research was continued over two growth periods, the plants in all the vessels would have attained a somewhat greater height and weight at the conclusion of the second growth period.

That *Urtica dioica* needs a large quantity of nitrogen, follows also from analyses which were made of its leaves and shoot apices. These contain about 3·4 per cent. of nitrogen, calculated on the dry weight.

In order to examine how the nettle behaves when ammonium is given as the source of nitrogen, the following research was instituted. On 28th April, 1918, plants of *Urtica dioica* which were at the beginning of the second growth period were placed in two flower-pots. The pots, which each held 3 litres of washed sand, received the same manuring as in the experiment described above. In addition, one of the pots received 150 mg. NO_3 (as $NaNO_3$) = 33·87 mg. N per week; the other 43·5 mg. NH_4 (as NH_4Cl) = 33·87 mg. N per week. The experiment was brought to a conclusion on 4th August, 1918. The growth of the plants, as appears from Fig. 3, was very different: whilst the plant that received nitrate thrived particularly well, the plant which received ammonium thrived much worse, since ammonium apparently acted as a poison on it; for the growth is strongly inhibited, and a part of the leaves developed brown spots and finally withered.

Also ammonium nitrate, which was given in another experiment, proved to be toxic, even when it was given in small quantities (4 mg. NH_4NO_3) per litre of sand a week.

Thus, the experiments showed that *Urtica dioica* requires a relatively high amount of nitrogen, which must be supplied in the form of nitrate, whilst ammonium appears to act as a poison on the plant.

These experiments, as well as the investigations on the soil, were carried out in the Chemical Department of the Carlsberg Laboratory, to the Director of which, Prof. S. P. L. Sørensen, I offer my best thanks for his kindness in placing the laboratory at my disposal for my researches, and for the valuable help which he and laboratory assistants, Mr Jessen-Hansen and Mr Sven Palitzsch have given me in the chemical analyses. Finally, I am greatly obliged to Prof. Walter Stiles for having taken the great trouble of translating this paper from Danish into English.

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EXPLANATION OF PLATE I

FIG. 1. *Urtica dioica* association (225 cm. high) in Jaegersborg Deer-park (Locality No. 18). Photographed 7 October, 1917.

FIG. 2. *Urtica dioica.* Variation of quantity of nitrate. The vessels, which each contained 3 litres of sand, received respectively from left to right 150, 45, 15, and 3 mg. NO_3 a week. Photographed 4 August, 1918.

FIG. 3. Young plants of *Urtica dioica* in the second growth period. The plant on the right received 150 mg. NO_3 (as $NaNO_3$) = 33·87 mg. a week. The plant on the left received 43·5 mg. NH_4 (as NH_4Cl) = 33·87 mg. N a week. The plant on the left was originally the stronger. Photographed 4 August, 1918.

FIG. 1

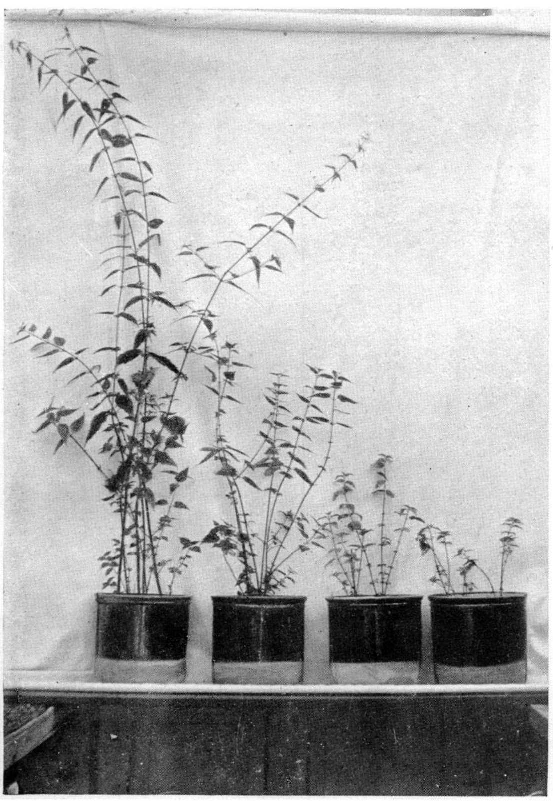

FIG. 2

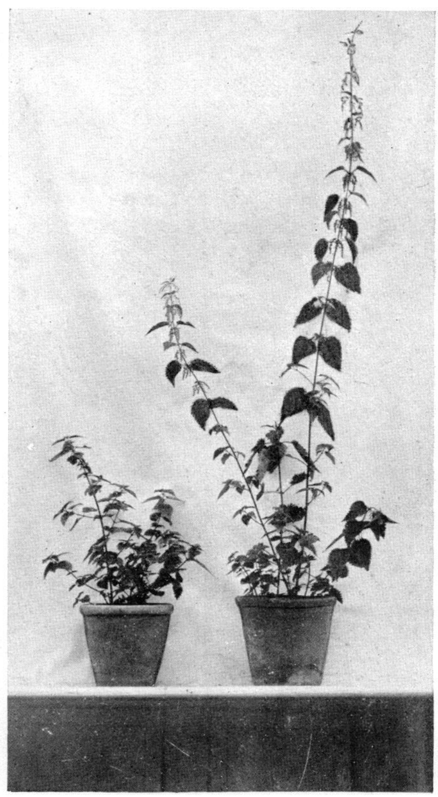

FIG. 3

OLSEN—ECOLOGY OF *URTICA DIOICA*.