Ausseralpine Vegetation : the structure of woodlands

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V.

The structure of woodlands

By E. J. SALISBURY, London

Mit einer Textabbildung und vier graphischen Darstellungen

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It is proposed to consider here the structure of the undisturbed plant community dominated by trees. Forests and woodlands have long been recognised as exhibiting a stratification of the aerial organs which reaches its extreme manifestation in the tropical rain forest in which a large number of stories can be distinguished. It is particularly such spatial relations as are exhibited by both the aerial and subterranean organs in the temperate woodland that will be dealt with in this article, together with some of the consequent implications.

Every field naturalist is familiar with the three tiers normally present in the temperate woodland respectively consisting of trees, shrubs and herbs. In addition the lianes of the tropics are represented by *Lonicera periclymenum* and *Clematis vitalba* whilst epiphytes, except for Bryophytes and Lichens, are rare; the only frequent epiphytic vascular plant in Britain being *Polypodium vulgare*. In reality however the stratification of the aerial organs is far more complex than at first sight appears. Various authors and in particular LOUDON (Arboretum et Fruticetum Britannicum) furnish abundant data regarding the height of well grown examples of native trees and shrubs. These data may be taken to represent the extreme heights to which the species attain in Britain since they are mostly taken from examples remarkable for their large size. These data are summarised for a number of species in table I. We are at once struck by the fact that the potential heights of the species enumerated form an almost continuous series from undershrubs such as *Vaccinium myrtillus* and *Calluna vulgaris* to *Fagus sylvatica* which may attain a height of over thirty six meters.

In the tropical belt the number of woody species is very large due perhaps in no small measure to the repeated influx of species whose immigration owed its impetus to the recurrent glaciations in the northern and southern hemispheres. In Britain however the number of woody species is comparatively small and a relatively large proportion are near their climatic limit, frequently with marked edaphic limitations so that the number of shrubs and trees involved in any one woodland community is

Table I

Average maximum heights of British Trees and Shrubs

Species	Average maximum	Recorded maximum	Species	Average maximum	Recorded maximum
	m	m		m	m
Fagus sylvatica	26	36.3	Corylus avellana	6.1	9.2
Quercus sessiliflora	25.5	40	Buxus sempervirens	6.1	9.2
Ulmus montana	24.6	37	Acer campestre	4.6	6.1
Fraxinus excelsior	24.6	40.6	Prunus padus	4.6	6.1
Quercus robur	24.3	37	Crataegus oxycantha	4.6	6.2
Pinus sylvestris	23.7	30.7	Crataegus monogyna	4.6	6.1
Castanea vesca	22.1	30	Euonymus europaeus	4.6	6.1
Populus tremula	19.7	40	Viburnum lantana	4.0	6.0
Betula alba	18.4	24.5	Viburnum opulus	2.7	3.7
Carpinus betulus	17.0	28	Ligustrum vulgare	2.5	3.0
Alnus glutinosa	15.5	27.7	Rhamnus cathartica	2.2	3.0
Taxus baccata	11.0	17	Rhamnus frangula	2.1	3.0
Pyrus communis	9.2	12.3	Prunus spinosa	2.0	3.0
Sorbus aucuparia	9.2	12.3	Rubus idaeus	1.2	1.5
Ilex aquifolium	9.2	12.3	Daphne mezereum	1.2	1.5
Arbutus unedo	8.0	10	Daphne laureola	1.0	1.3
Sorbus aria	7.6	12.3	Calluna vulgaris	0.9	1.2
Sambucus nigra	7.6	15.4	Vaccinium myrtillus	0.6	0.9
Salix cinerea	7.6	9.2			

comparatively small. Nevertheless the marked inequality in the frequency of the different species is so great that in British woodlands 80 % to 90 % of the tree layer often consists of one species and the same is true for the shrub layer also.

The chief influence determining dominance in woodlands is that light sooner or later becomes the limiting factor. Hence the species with the greatest potentiality for growth in height and the species which casts the greatest shade will, other things being favourable (e. g. shade tolerance of the seedling) predominate over those of lower stature and less dense canopy. The importance of height is indicated by the fact that of the first twelve potentially highest species cited in Table I, all but *Populus tremula* and *Ulmus montana* attain to the position of dominants in Britain under suitable climatic and edaphic conditions.

The evergreen habit is clearly important in this connection since where evergreen species form continuous canopy they inhibit the growth of possible competitors. Thus we find *Taxus baccata*, normally present as a sparse second tree story in the *Fagetum*, locally featuring as a dominant on steep slopes. Similarly the local dominance of *Buxus sempervirens* is only maintained where the continuity of its canopy prevents the advent of competitors.

Whilst, however, it is comparatively easy to appreciate the probable causes that have led to the dominance of particular species the extreme sparsity of others remains to be accounted for. *Populus tremula* despite its potential height forms a translucent canopy and in Britain only spreads by vegetative means, which latter not infrequently results in local dominance, in the *Quercetum roboris.*

It is not however our intention to discuss in detail the causes of dominance but merely to draw attention to the fact that the comparatively simple structure of the British woodland is due not so much to the absence of species exhibiting a gradation in height as to a failure of all but a few woody species to attain a sufficient frequency to affect materially the woodland structure.

Probably the nearest approach to the two storied tree layer in Britain is seen in the *Quercetum sessiliflorae* near its upper limit where *Sorbus aucuparia* and *Betula pubescens* may combine to form a second tier, or again in the *Fagetum sylvaticae* where a second tier may be formed by *Taxus baccata.*

In the shrub layer also we find comparatively few species (Notably *Corylus avellana, Carpinus betulus,* and occasionally *Sambucus nigra)* which ever attain sufficient frequency to form a definite layer of the vegetation.

The herbaceous vegetation exhibits the same feature. *Mercurialis perennis* in the *Fagetum sylvaticae, Pteridium aquilinum, Scilla nutans,* and *Anemone nemorosa* in the *Quercetum,* attain a frequency in comparison with which the accompanying species are often a negligeable quantity. Thus in the *Mercurialis* society over 90 % of the shoots present are not uncommonly *M. perennis* whilst in the *Quercetum roboris Anemone nemorosa* and *Scilla nutans* frequently constitute 85 % of the total herbaceous carpet.

This marked predominance of particular species in the respective stories results in the comparatively even height development of ground-flora, shrub-layer, and tree-layer over considerable areas and thus brings about a highly accentuated stratification of the aerial organs that is reflected in the climatic conditions of the woodland interior. We find for instance that there is not merely an abrupt change as we pass from above the tree tops into the tree canopy but similar relatively abrupt changes are encountered as we reach the shrub level and again when we come to the herbaceous carpet. The effect on the conditions of exposure are perhaps best seen by the change in the rate of evaporation as we pass from below upwards. At the inception of the "shade phase" when the tree canopy is fully formed and the ground flora is still unwithered the exposure is least in the shelter of the ground vegetation, it increases between this layer and the shrub-layer canopy at the level of which it may again fall though the degree of shelter is typically less than in the herbaceous-layer. On passing above the shrub canopy the rate of evaporation again increases and may then drop as the tree canopy is reached. The exposure could thus be presented as a curve which alternately rises and falls but exhibits a general upward trend. Data furnished by ADAMSON (LINN Soc.

Jour. Bot. Vol. xl, p. 354, 1912) for a windy day, shew this feature quite clearly. Thus the evaporation at the level of the ground flora was 142 cc. just above the ground flora 176 cc. In the shrub canopy it again fell to 149 cc. and above the shrubs rose to 182 cc. In dense woods the curve however is not infrequently a steady rise from below upwards. Moreover British woodlands rarely exhibit a continuous canopy formed by both tree and shrub layer (The *Fraxinetum* is an exception) whilst the chief shelter is frequently that afforded by the latter. Though in general the effect of forests is to reduce the rate of evaporation, as compared with that in the open, by about 50 % or more (cf. Forest influences U. S. Dept. Agric. Bull. No 7, 1893) it is apparent that the members of each successive tier are subject to more and more exposed conditions and that species of trees and shrubs other than the dominants, with differing potentialities for growth must either accomodate their stature to the general level or be able to withstand the additional exposure entailed by an intermediate position. This probably tends to maintain the sharply delimited tiers which, as we might expect, are in general accentuated in exposed situations whilst on sheltered valley slopes the stratification is often less pronounced.

The degree of development of the shrub and herbaceous layers is chiefly determined by the light intensity and hence we find that the densest and most varied shrub-layer is met with under the relatively translucent canopy of the *Fraxinetum excelsioris.* It is in marked contrast with this that in the interior of the *Fagetum sylvaticae* the shrub layer is poorly developed although at the well-illuminated wood margin the ‘chalk scrub’ presents a large variety of shrubs often forming continuous canopy.

The correlation of development of the ground flora with the degree of illumination is too well recognised to require emphasis, but we may note in this connection that it is important to distinguish between the shading effect of the tree and shrub layers on the pre-vernal constituents of the ground flora on the one hand, and on the other their effect on the species which develop later.

One of the most striking features of woodland architecture is the succession in time with respect to leaf development corresponding to the succession in space of the different layers. The writer has elsewhere shewn that the average date for the development of new assimilatory organs for those herbaceous plants which commonly occur in the interior of woodlands and which lose their leaves in winter, is February 19th. The average date for the various members of the shrub layer is March 21st, whilst the full tree canopy is not attained till about May 13th (cf. SALISBURY, E. J. Phenology and habitat with special reference to the phenology of woodlands Q. J. R. Met. Soc. Vol. XLVII, 1921). Moreover many of the shade species retain some or all of their foliage throughout the 'light phase' and thus the phenological relations of many members of the shade flora enable a large part of their assimilation to be carried on before the light intensity diminishes with the onset of the shade phase. From this point of view we can recognise four main types amongst the constituent species of the ground flora, viz: —

Type I **Pre-vernal Type**: Well illustrated by *Ficaria verna*, *Adoxa moschatellina*, *Arum maculatum*, *Anemone nemorosa*, *Allium ursinum* and *Scilla nutans*. In all these new foliage is formed each spring or sometimes even in the previous autumn and withers soon after the complete development of the canopy formed by the shrub and tree layers. Plants of this type, since they carry on their chief assimilation in the early spring, are dependent on the conditions of illumination during the light phase but can occur where the shade phase intensity is extremely low. Indeed these plants of the mesophytic community may be compared biologically with the geophytes of the xerophytic community; both wither at the onset of adverse conditions namely low illumination in the one case and drought in the other. The pre-vernal species are well represented in the *Quercetum roboris* where the light intensity in the light phase is quite commonly between 40 % und 60 % but during the shade phase often falls to under 1 %, cf. Fig. 1.

Type II **Summergreen Type**: In these the foliage persists throughout the greater part of the shade phase. Here we can recognise two sub-types according as the new foliage is formed early (sub-type *a)* or late (sub-type *b)* in the season. Representatives are furnished by *Mercurialis perennis* in which the new leaves begin to expand in January and *Pteridium aquilinum* in which the new fronds appear at the beginning of May. Both are dependent on a moderate illumination during the shade phase but *Mercurialis* less so than *Pteridium* owing to its earlier development. Summergreen types are well represented in both the *Fagetum sylvaticae* fig. 3, where the shade phase intensity is quite commonly over 4 % and in the *Quercetum sessiliflorae* fig. 2, where the average intensity is frequently about 7 %.

Quercetum roboris (Assimilatory periods of typical members)

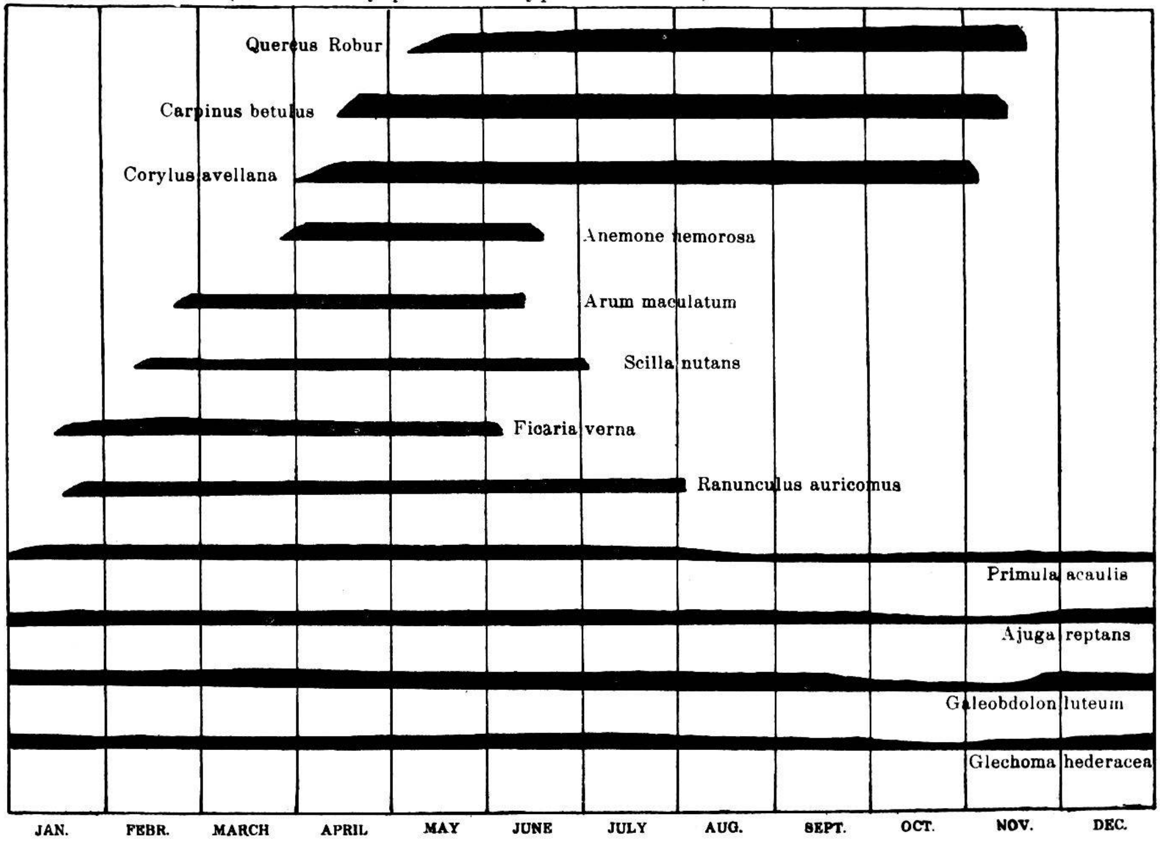

Fig. 1

Type III **Wintergreen Type:** In these new leaves are normally formed in the autumn and some or even most of the foliage may persist throughout the year. Examples are afforded by *Sanicula europaea, Potentilla sterilis, Luzula maxima, Viola sylvestris, Ajuga reptans, Galeobdolon luteum, Glechoma hederacea* and *Oxalis acetosella.* These species whilst naturally less tolerant than the pre-vernal types of extremely low intensities during the shade phase, are often found where the light phase intensity is low. Shaded situations of comparatively uniform intensity throughout the year sometimes exhibit non-flowering vegetation of this type as a continuous carpet.

Type IV **Evergreen Type**: In these species, represented by *Ruscus aculeatus*, *Iris foetidissima*, *Vinca minor*, *Helleborus foetidus*, *Hedera helix* (prostrate var.), the assimilatory organs persist throughout the year. Like the summergreen types they rarely occur where the shade phase intensity is very low.

Types I and II agree in the discontinuity of their assimilation periods. The inactive season, with respect to photosynthesis in Type I is the 'shade phase', whilst in Type II the resting period corresponds, either wholly (sub-type *b)* or in part (sub-type *a)* to the 'light phase'.

In Types III and IV, on the other hand, the period of assimilation is continuous, but in the former as contrasted with the latter, the individual leaves only persist for a comparatively short period. Thus whilst Types III and IV are both, strictly speaking, evergreen, in Type IV almost the full complement of foliage is maintained throughout the year whereas in Type III the assimilatory surface exhibits marked seasonal fluctuations.

In addition to these four types the ground flora includes many relatively unspecialised species which constitute the 'marginal flora' of which the majority retain their foliage throughout the shade phase and about 40 % are wintergreen (Phenology and Habitat Loc. cit. p. 257). Most of the marginal species are members of the 'Scrub' vegetation and are features also of the hedgerow (cf. SALISBURY, E. J. The Ecology of Scrub. Trans. Herts. Nat. Hist. Soc. Vol. XVII, pp. 53—64, 1918).

The ground flora species may shew successive tiers of aerial organs especially where these are to some extent complementary in time as well as in space, such for example as *Pteridium aquilinum* and *Holcus mollis* (cf. WOODHEAD, T. W. Ecology of Woodland plants in the neighbourhood of Huddersfield, p. 343. Jour. Linn. Soc. Vol. XXXVII, 1906). *Ficaria verna* and *Arum maculatum*, or *Mercurialis perennis*, with either *Adoxa moschatellina* or *Ficaria verna* (cf. SALISBURY, E. J. The Oak-Hornbeam woods of Hertfordshire, Pts. 1 & 2, p. 110. Jour. Ecology, Vol. IV, 1916). In the *Fraxinetum* owing to the light canopy of the dominant tree the shrub-layer may be so dense as almost to preclude the development of more than a scanty herbaceous vegetation whilst under conditions of low illumination combined with great humidity in winter and spring, often accompanied by relatively dry conditions in summer, the herbaceous vegetation may be almost replaced by a Bryophytic carpet.

Quercetum sessiliflorae **(Assimilatory periods of typical members)**

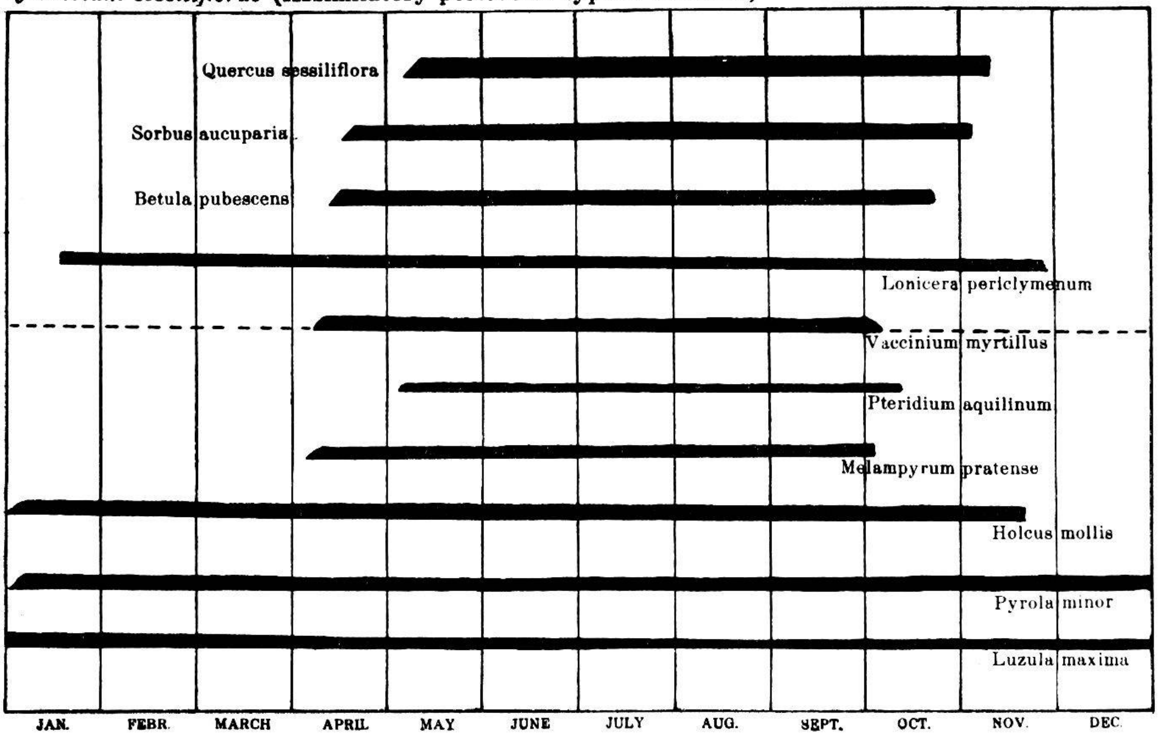

Fig. 2

It is rare to find two social species associated together unless they are of approximately the same potential height or are complementary in time. In the untouched woodland we recognise light intensity as the chief factor determining the incidence of species and therefore success in competition is largely dependent on a capacity for growth above the aerial organs of neighbouring plants.

Several physiological investigators have shewn that light favours germination even in the case of woodland plants. But if we assume that the light intensity is adequate for the germination of the seed beneath the herbaceous canopy it is evident that little if any assimilation can be carried on by the seedling until its leaves attain the general level of the herbaceous foliage or grow above it. The limit of this growth, before the seedling can manufacture its own carbohydrates, will be dependent on the food reserves in the seed and it is perhaps partly for this reason that so many plants which have relatively large seeds, or fruits, succeed in the woodland despite the handicap to dispersal which this imposes. Be this as it may there can be little doubt that the success of the rhizomatous plant, so prevalent in the woodland community, is partly due to the power which the rhizome confers of spreading into already occupied territory and producing shoots which have the entire resources of the parent plant at their disposal for growth, until they can assimilate for themselves. The invasion by vegetative means is thus much more efficient than invasion by seedlings and as we know many woodland species chiefly propagate in this way.

Associated with the normal woodland structure there is a well marked gradient in the atmospheric conditions quite apart from the exposure gradient already considered.

As we pass from the wood margin inwards or from the tree tops downwards the air becomes in general moister and the climatic conditions become more oceanic in type as compared with the more continental conditions exterior to the woodland. Thus the maximum summer temperatures are on the average about 3° C. to 4° C. less in the interior than outside, whilst the average winter minimum is about half a degree Centigrade higher. The shading effect prevents heating up of the soil in summer so that even at a depth of about 1.23 meters the mean temperature is nearly 2° C. less than in the open, but the extremes in the soil as in the air exhibit a smaller range and this effect is the more pronounced as the altitude increases (cf. Forest Conditions loc. cit.).

In view of these facts it is hardly surprising that half the Southern element in the British woodland flora belongs to the Atlantic type of distribution (cf. O. Stapf «The Southern Element in the British Flora» Bot. Jahrb. 1914).

Woodlands like other undisturbed plant communities exhibit a definite soil structure which must be taken into account in any consideration of the depth and distribution of the root system. The substratum presents four definite regions, viz: —

1. The surface litter
2. The surface soil rich in organic material
3. The subsurface, comparatively poor in organic material
4. The subsoil in which the proportion of organic material is also comparatively small.

Frequently these layers grade into one another, but the limits may be relatively sharp.

The density of the soil increases as we descend and the proportion of the total volume occupied by the soil atmosphere diminishes. This diminution of pore space in fine grain soils is very rapid as is shewn by the following data taken from two examples of *Quercetum roboris* growing on clay-with-flints.

Percentage Pore Space (Averages)

Depth	Loc. A	Loc. B
0—5 cms.	10.6 %	21.4 %
5—8 cms.	5.0 %	
8—13 cms.	4.0 %	8.1 %

These data represent the spring condition at average water content. The pore space will obviously vary being highest in summer when the water content is least and low in spring when the water content is high.

Another feature connected with the decrease in pore space accompanying increasing depth is the augmenting density of texture accompanied by a decreasing penetrability. Warming (Om Jordudlöbere. Med. Acad. Roy. d. Sci. a Danemark Ser. 8, T. II, No. 6) has drawn attention to the relation between depth of rhizomes and the degree of robustness in these organs. The following data regarding the depths of occurrence and thickness of various woodland rhizomes obtained by the writer from woods on calcareous and non-calcaeous loam bring out this point clearly and are evidently correlated with the decrease of penetrability accompanying increase in depth.

Fagetum sylvaticae **(Assimilatory periods of typical members)**

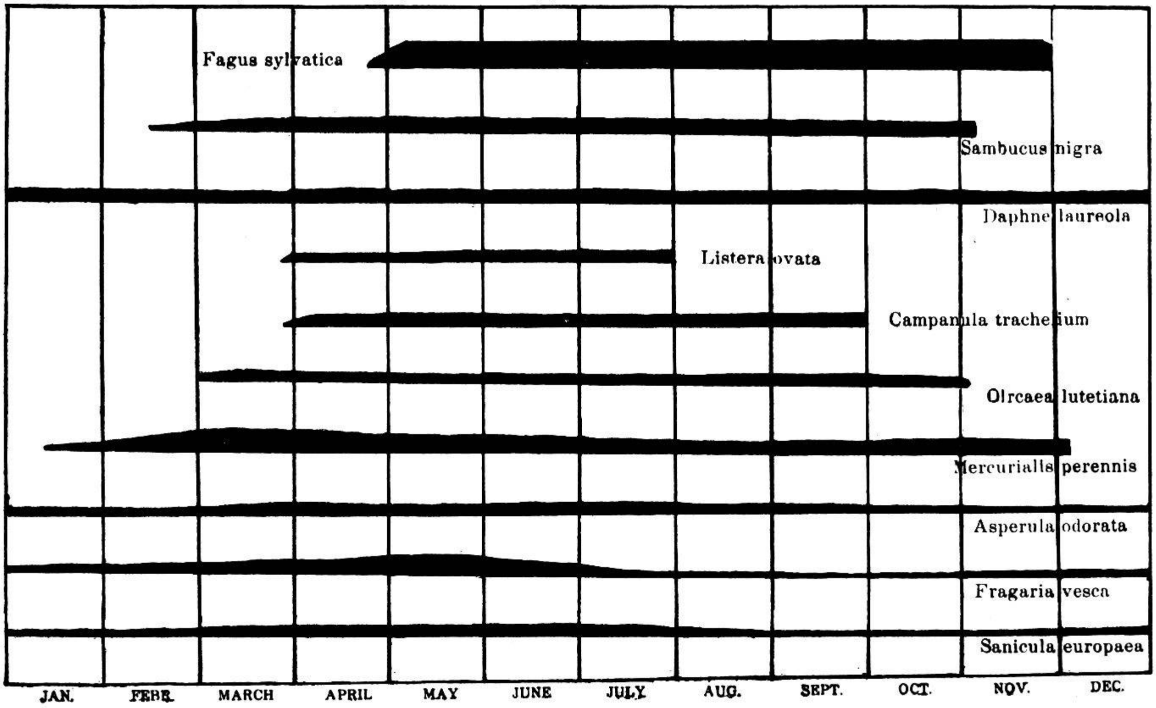

Fig. 3

	Average depth of rhizome	Diameter of rhizome
Adoxa moschatellina	0.5—2.5 cms.	1—1.5 cms.
Oxalis acetosella	1.0—3.0 cms.	1 mm.
Trientalis europaea	1—3 cms.	1.5 mm.
Asperula odoreta	2—4 cms.	1—1.5
Stachys sylvatica	4 cms.	3 mm.
Convallaria majalis	3—5 cms.	3.5 mm.
Anemone nemorosa	2—5 cms.	4—5 mm.
Mercurialis perennis	2—5 cms.	2—3 mm.
Dentaria bulbifera	6—8 cms.	5—6 mm.
Polygonatum multiflorum	10—15 cms.	14 mm.
Pteridium aquilinum	15—30 cms.	9—18 mm.

To determine the degree of penetrability a large block of soil was carefully removed intact and placed on its side. A vertical rod with one end pointed and the other heavily weighted was attached to an apparatus that enabled vertical movement to take place freely and to be recorded by a magnifying arm. The pointed end was then placed on the side of the soil block facing upwards and the reading taken. On release the rod penetrated the soil and the reading was again taken this was repeated several times for successive depths and the averages give a relative measure of the penetrability. The absolute values of course vary with the water content. The following figures obtained from the *Quercetum roboris* growing on clayey soil illustrate sufficiently the character of the gradient in this respect.

Depth	Range of Penetrability	Average
1.5 cms.	5.5—11	7.3
2 cms.	3—7.5	5.6
3 cms.	2—4.2	3
4 cms.	2.5—5.6	3.6
5.5 cms.	1—5	2.5
7 cms.	1.2—4.1	2.4

In a *Quercetum roboris* on loam the average penetrability at 1.5 cms. was 10 and at a depth of 10 cms. was still 3.8. The effect of the decrease in penetrability is to reduce the rate of growth as is shewn by a comparison of the annual increments of rhizomes in dense and loose soil respectively. Measurements of the underground organs of *Anemone nemorosa* in relation to soil texture shewed that the average depth of the rhizome in clay soil was 3 cms. and in loam 4—6 cms. and the respective rooting depths 8 and 15 cms. Yet despite the fact that in the heavier soil the rhizome occupied a higher level, the length of the annual increase in 30 examples from the clay soil ranged from 0.6 to 2.3 cms. with a mean value of 1.4 cms., whilst 22 examples from the wood on light loam shewed a range of from 1.0 to 3.0 cms. with an average of 1.72 cms: A mean increase in the loose-textured soil of over 22 %.

Again, *Agropyrum repens* in a stiff soil with a penetrability of 5 exhibited an average annual growth of 16.3 cms., whilst in light soil with a penetrability of 18 the average increment was 32.9 cms.

The higher pore space as the surface is approached is intimately associated with the organic content. This latter decreases with depth (cf. below) and its distribution and amount correspond fairly closely with the distribution of the root systems of the plant covering. This is shewn by a comparison of the organic content at varying depths beneath pasture and woodland occupying the same type of soil.

Curves and data shewing the character of this organic gradient have been furnished by the writer (Salisbury E. J. Stratification and Hydrogen-ion concentration of the soil in relation to Leaching and Plant Succession, with special reference to Woodlands. Jour. of Ecology, Vol. 9, pages 220 to 240, 1922) but the accompanying data which illustrate the same feature also shew the effect of this on the water content after heavy rainfall.

Quercetum sessiliflorae (Somerset): Light sandy soil

	Holcus mollis - Society			*Vaccinium myrtillus* - Society		
Depth cm.	Organic Content (H)	Water Content (W)	W/H	Organic Content (H)	Water Content (W)	W/H
0—5	39 %	52 %	1.33	61.7 %	70.9 %	1.13
5—15	11.44 %	25 %	2.18	16.6 %	31.5 %	1.8
25				9 %	18 %	2
45				5 %	12.3 %	2.46

Quercetum sessiliflorae (Shropshire): Loamy soil

	Pteridium - Holcus - Society			*Luzula maxima* - Society		
0—5	15.8 %	76.9 %	4.8	14.1 %	75.4 %	5.3
5—15	4.6 %	29.0 %	6.3	7.9 %	34.5 %	4.36

Quercetum sessiliflorae (Hertfordshire): Loamy Clay

	Mercurialis - Society			*Pteridium* - Society		
0—5	8.7 %	45.9 %	5.16	7.7 %	34.0 %	4.4
5—15	8.1 %	34.4 %	4.2	4.8 %	26.2 %	5.45

The rapid decrease of both the water and organic content at a slight depth is here well seen and also the marked effect of the different dominants in the same wood on these features. The figures also illustrate the steeper character of the gradient on the heavier types of soil as compared with the lighter. Great variability is shewn by the organic content of the surface, whilst the absolute range for the subsurface is considerably less and perhaps its coefficient of variation also.

In view of the much higher organic content of the surface, the maximum natural water content is here with rare exceptions much higher than the subsurface, but if we consider the ratio of maximum water content to the corrected loss on ignition (this is a modification of CRUMP's Water Coefficient Ratio, using the maximum in place of the minimum natural water content, cf. Jour. of Ecology, Vol. 1, p. 96, 1913) we find that this increases in most woodland soils as we descend. It is therefore probable that the proportion of available water is greater as the roots go deeper. We must however emphasise (cf. also below) that the oxygen content of the soil atmosphere diminishes both relatively and absolutely with increasing depth. It follows that added advantage with respect to respiration may involve a diminishing supply of water and *vice versa* so that the distribution of the root systems will *inter alia* depend on the maintenance of a proper balance between these two factors, cf. Fig. 5.

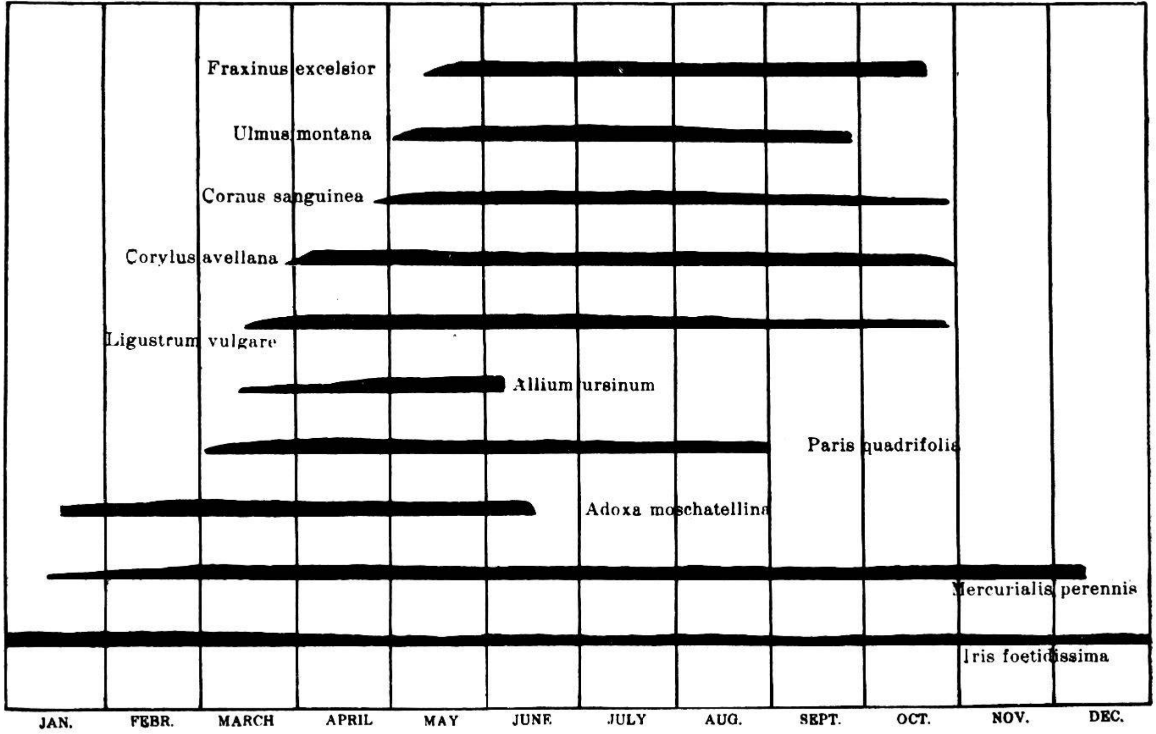
Fraxinetum excelsioris (Assimilatory periods of typical members)

Fig. 4

As to the actual values exhibited by the ratio of water content to loss on ignition we may note that in the *Vaccinium* Society it tends to be low (e. g. in one location examined 0.98 for the surface and 2.7 for the subsurface), whilst in Societies of *Allium ursinum* and *Colchicum autumnale* constituting 'flush' vegetation the values obtained for this ratio were 5.19 and 5.2 respectively. The water contents in these two cases were 52 % and 48 % as compared with 73 % for the *Vaccinium* Society referred to above. The data given for the *Luzula maxima* and the *Mercurialis* Societies shew an inversion of the usual sequence, the ratios for the subsurface being lower than for the sur-

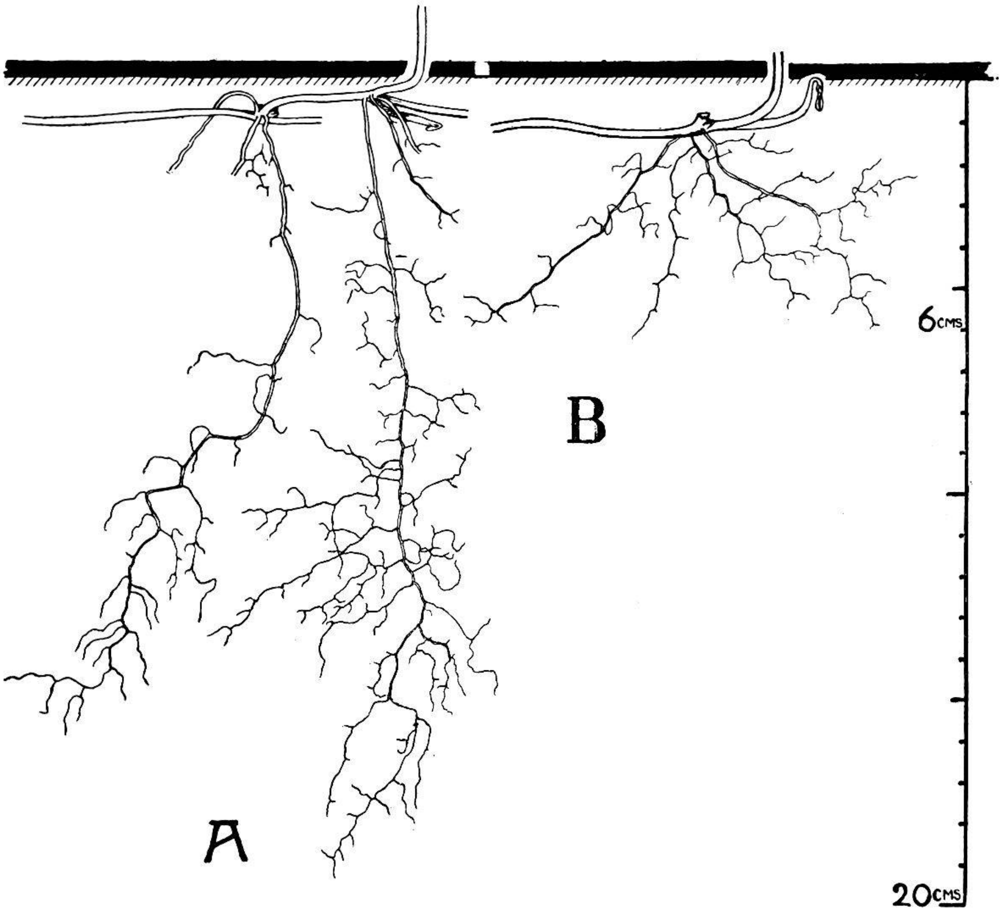

Fig. 5
Root systems of *Mercurialis perennis* grown on well-aerated calcareous soil (A) and on badly-aerated calcareous clay of high water-content (37°/o). In both cases the surface reaction was pH. 6.9, but in A the roots reach a level at which the reaction was pH. 7.6 whilst those of B, in the poorly-aerated soil, encounter a more acid reaction as they descend (pH. 6.6 at 10 cms.).

face. The highest ratio noted by the writer was obtained in a "flush" vegetation of *Mercurialis perennis* and *Eurynchium striatum* where the surface yielded a ratio of 6.9 and the subsurface 8.1, the maximum water contents being respectively 41.8 and 32.4 %.

An equally important effect of the high organic content of the litter and surface soil is the presence of a teeming micro-fauna and micro-flora with a consequently high output of CO_2. J. B. BOUSSINGAULT and E. LEWY (Mémoire sur la Composition de l'air confiné dans la terre végétale. Ann. Chim. Phys. 37. V, 1853) were the first to demonstrate the high CO_2 content of the soil atmosphere and to shew that its amount tends to increase with that of the organic fraction of the soil. E. EBERMAYER (Mitteilungen über den Kohlensäuregehalt der Waldluft und des Waldbodens im Vergleich zu einer nicht bewaldeten Fläche, Forsch. Geb. Agr. Phys. 1: 158, 1878) studied the soil atmosphere of a Beech wood and found that one meter below the surface this contained no less than 0.5 % CO_2. The humus layer contained 0.14 % whilst even 2 meters above the ground the proportion of CO_2 was double that in the open, viz: 0.05 %. The same author in a later paper (Unters. ü. d. Bedeutung des Humus als Bodenbestandteil und über den Einfluss des Waldes verschiedener Bodenarten und Bodendecken auf die Zusammensetzung der Bodenluft, Forsch. Geb. Agr. Phys. 13, 15, 1890) found that the CO_2 of the soil atmosphere of pine forests is nearly double that of beech forests. It remained for FODOR (Hygienische Unters. ü. die Luft i. Boden u. Wasser, Braunschweig 1881), and still more recently RUSSELL and APPLEYARD (The Atmosphere of the Soil, its composition and causes of variation. Jour. Agr. Sci. V. II, 1915) to shew that the CO_2 content of the soil atmosphere exhibits a spring and autumn maximum corresponding to spring and autumn maxima in the number of organisms.

The greater density of CO_2 as compared with air tends towards its accumulation at lower levels and hence the gradient of increasing CO_2 already noted above ground is continued downwards into the soil. This is well illustrated by the data given by L. ROMELL (Medd. Statens Skogsförsöksanstalt, pp. 124 to 359, 1922) which include previous observations and many new determinations. In a mossy Spruce wood this author found that the percentage volume of Carbon dioxide at a depth of 15 cms. ranged from 0.2—0.3 %; at 30 cms. from 0.2—0.4 %; at 45 cms. and 60 cms. the percentage volume was 0.4 %; whilst at a depth of 75 cms. the CO_2 content ranged from 0.3—0.5 %. A Fen soil investigated by ROMELL contained 0.2 % CO_2 at 15 cms. 1.0 % at 30 cms. and as much as 2.0 % at a depth of 45 cms. His data also shew quite clearly that the Oxygen deficit becomes greater with increasing depth, in one case amounting to 12 % at a depth of 60 cms.

We have noted that the pore space diminishes with depth and this is at, or near, its minimum in spring when the water content is high: Also that this is a period of maximum CO_2 production. Therefore the root systems of woodland plants as they extend downwards encounter both a diminished partial pressure of oxygen and an absolute diminution of its volume, especially at the period when growth is most active. The total effect on root respiration probably has a profound influence on the distribution of root systems, and it is significant that in woodlands these are in general shallow, especially where the organic content is high. The observations of CANNON and FREE (Ecological significance of soil aeration, Science N. S. 45, 1917) and those of NOYES, TROST and YODER (Bot. Gaz. p. 364, 1918) have not only demonstrated that high concentrations of CO_2 in the soil atmosphere are accompanied by a more shallow development of the root system but also that, as might be expected, different species react in differing degrees to high CO_2 concentrations.

The stratification of woodland soils in relation to the Hydrogen-ion concentration has already been treated by the writer in some detail (loc. cit. 1922). It is therefore unneccessary to quote data on this point and it will suffice to recall that in general the surface of a woodland soil is often appreciably, or even highly, acid and that the acidity decreases from above downwards. For a given soil type and under a uniform plant covering the acidity tends to increase *pari passu* with the organic content. The supply of mineral salts, especially of calcium, is usually least at the surface and increases with depth.

In the *Fraxinetum* and *Fagetum* on calcareous soils earthworms are present which exert an ameliorating effect on the acidity gradient, and by their cultivating action increase the pore space of lower levels. In most types of woodland, however, the reaction is too acid for earthworms to flourish (cf. SALISBURY, E. J. The Influence of Earthworms on soil reaction and the stratification of undisturbed soils. Linn. Soc. Jour. Bot. Vo. XLVI, 1924).

To summarise it is then apparent that the descending root encounters increasing resistance and increasing difficulties in respiration. On the other hand the conditions become more favourable for the supply of water and mineral salts. It is the balance between the favourable and unfavourable conditions which determines the level to which the root systems penetrate. It is also evident in the case of plants whose roots occupy different levels in the soil that these may be subject to very divergent conditions.

The root systems of woodland plants even including the tree layer are mostly shallow. In general for any one type of soil the higher the aerial organs the deeper the penetration of the root. The feeding roots of the tree layer usually penetrate to a depth of not more than about 1.5 meters: those of the shrubs to about 0.6 meters, and the roots of the herbaceous vegetation to from 2 to 45 cms. The relation of root depth to height of the aerial organs varies however with the soil texture and its water content. As WEAVER (The Ecological relations of roots. Pub. CARNEGIE Inst. 286, 1919) and HAASIS (Relation between soil type and root form. Ecology Vol. 2, page 292, 1921) have shewn the ratio of top to root tends to be high with soils of high water content and *vice versa.*

As to the relations between the root systems of the various species it is clear that their spatial distribution may enable a shallow rooted species, for example, to occupy the same area as a deep rooted species, but it must be further borne in mind that in addition to slightly different specific demands on the soil solution the period of maximum absorption for the different nutrient salts may vary with the species (cf. Bauer and Ramann. Jahrb. f. Wiss. Bot. V. 50, 1911), so that even if making the same demands on the soil solution they may be seasonally complementary.

So far we have considered woodland structure from the purely static standpoint but actually the community is undergoing a more or less marked change either in the nature of a definite succession to a climax, or the climax community itself may undergo a secular change. From a study of both maritime communities, where the change is rapid, and a study of woodlands, where the change is comparatively slow, the writer has suggested that the continual and inevitable leaching to which the soil is subjected and the changes consequent thereon, are the fundamental cause of the progressive change in the plant covering. That is to say the biotic change is initiated by an edaphic change though clearly, as the process proceeds, the two react upon one another to produce the ultimate resultant.

Broadly, these successional changes lead in the soil to a diminution in the concentration of mineral salts of which the most soluble (e. g. $CaCO_3$) decreases most rapidly and the less soluble at a slower rate, incidentally the latter though absolutely diminished are relatively more abundant as is sometimes very pronounced in highly calcareous soils, where too the effect of leaching is to replace the well aerated chalk or limestone soil by a poorly aerated clay residue. Further, leaching brings in its train an increasing organic content and increasing acidity all of which factors probably tend to promote the CO_2 content of the soil and consequently to diminish the facilities for respiration. Such changes which are most marked at the surface are reflected both in the aerial and subterranean architecture of the woodland.

It follows from what has been already said that for the ground flora at least the CO_2 of the atmosphere is rarely the limiting factor for assimilation. On the other hand, owing to the specialised character of the typical shade species in respect to this process by which assimilation attains its optimum in low intensities of light (cf. SALISBURY, E. J. The effects of coppicing as illustrated by the woods of Hertfordshire. Trans. Herts Nat. His. Soc. Vol. XVIII, pages 1 to 21, 1924 and literature there cited) when the shade is removed, as when a wood is felled or the undergrowth coppiced, the photophilous marginal species will alone be able to take full advantage of the high CO_2 output from the soil and these flourish at the expense of the specialised shade flora. Thus in exploited woods there is a constant natural change in the structure of the herbaceous vegetation consequent upon the artificial change imposed by man on the upper layers. In natural conditions the same ebb and flow takes place in relation to light gaps caused by the death of the dominant trees.

VI.

A cycle of the salton sea

By D. T. MACDOUGAL, Tucson (Arizona)

Mit einer Kartenskizze und einer Tafel

Eingegangen 14. Februar 1925

Twenty-one years ago (February 1904) a party, including Mr. GODFREY SYKES, Professor R. H. FORBES, now Chief Agricultural Engineer for the Compagnie Générale des Colonies (France), who since 1922 has been engaged in a study of the agricultural possibilities of the Niger in the region near Timbuktu, and myself, left Yuma in a specially constructed open boat for the purpose of learning something of the course of the Colorado River in the lower part of the delta and to determine the general character of the vegetation of the alluvial land and of the desert shores of the Gulf of California.

We eventually reached Bay San Felipe on the western shore of the Gulf and were rewarded by many things of interest to the botanist and the geographer.