Natural Regeneration of Tilia cordata in Relation to Forest-Structure in the Forest of Bialowieza, Poland

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NATURAL REGENERATION OF *TILIA CORDATA* IN RELATION TO FOREST-STRUCTURE IN THE FOREST OF BIAŁOWIEŻA, POLAND

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CONTENTS

The history of the forest of Białowieża is briefly reviewed. The National Park was created in 1923 in the central and apparently least exploited part of the forest. The composition of the forest varies in relation to the nature of the soils. Almost half of the wooded area of the park is occupied by forest composed of *Carpinus betulus*, *Tilia cordata*, *Quercus robur*, *Acer platanoides*, *Ulmus glabra* and *Picea abies* (Querceto-Carpinetum). The structure of this association is illustrated by maps and transects of selected plots. An almost continuous canopy is formed by *Carpinus betulus* with tall emergent trees of *Tilia cordata*, *Quercus robur* and *Picea abies*. *Tilia cordata* regenerates freely and there are numerous groups of seedlings, saplings and young trees which are sometimes in gaps but often beneath the main canopy. The origin of the groups is analysed and evidence is presented that those of *T. cordata* are probably always less than 50 years old. This is in contrast to analyses made by Paczoski (1928*a*, *b*, 1930) shortly after the park was established, when trees of *T. cordata* with trunk diameters less than 0.3–0.4 m were absent. There is now a discontinuity in the distribution of diameter classes in the population. The influence of this change on the structure of the forest is discussed.

INTRODUCTION

The great forest of Białowieża, or in Polish, Puszcza Białowieska, is situated partly in Poland and partly in the Byelorussian republic in longitude 24° E and in latitude 52° 40′ N. There is such an extensive literature on so many ecological aspects of the forest that it seems almost impertinent to publish results obtained during a relatively short visit. However, not only are many of the older publications in Polish and not readily accessible to English-speaking ecologists, but also there are, in fact, only one or two papers concerned with the structure and dynamics of the woodlands themselves (Paczoski 1928*a*, *b*, 1930; Faliński 1966). The particular aim of the present study was to investigate the regeneration of *Tilia cordata* in a forest where not only is the tree an important component of the canopy over quite large areas, but it also regenerates freely from seedlings.

2. HISTORY

The forest of Białowieża has generally been regarded as primary in the sense that large parts which are wooded today appear to have had an almost continuous history of tree-cover since prehistoric times. It is uncertain when the region was first settled but there are, even within the central area, grave-mounds dating from the early historic period (Borowik-Dąbrowska & Dąbrowski 1973).

The documentary history of the forest until the end of the eighteenth century has been analysed in detail by Hedemann (1939). There is evidence of sporadic settlement from the west by the end of the fourteenth century, which was regulated under German law, but from as early as the fifteenth century, parts of the forest benefited from protection as a reserve for hunting and were exploited for precious furs. Aurochs (*Bos taurus primigenius*), elk (*Alces alces*) and beaver (*Castor fiber*) were of special value and in 1557 these animals and roe deer (*Capreolus capreolus*) were given statutory protection but the local inhabitants were allowed to kill wolf (*Canis lupus*), fox (*Vulpes vulpes*), lynx (*Lynx lynx*) and smaller game. By comparison, timber seems to have been of secondary importance, probably because there was so much in Lithuania which was more readily accessible from the Baltic ports, although as early as the sixteenth century there is scattered documentary evidence which shows that oak was the most valuable timber, burning of wood for potash was established and the stripping of bark, including that of *Tilia cordata*, had to be licenced.

By the sixteenth century, in spite of increasing settlement, Białowieża remained part of the great forests which lay between the rivers Niemen and Dnieper. The earliest decrees of 1585 and 1592 which delimited the forest are now lost but the boundaries defined in later decrees of 1670 and 1703 do not differ greatly from those of today. There is similarly documentary evidence in the form of contracts and registrations of allotments which shows there has been little change in the density of settlement from the sixteenth century to the present day. Indeed, overall there has been a reduction in rights and exploitation has been increasingly controlled. Many rights, which had been claimed, were abolished in 1779–80 and burning of wood for potash, which had become widespread during the eighteenth century, was stopped at the end of the century. However, at the third partition of Poland in 1795, Białowieża passed into Russian hands and exploitation in the next three years (1795–8) was greater than during three centuries of Polish rule.

Throughout the nineteenth century the forest was under Russian administration but it remained a hunting reserve of the Czars. It was during this period that the whole forest was divided by ditched tracks into plots each of one square verst, which is a little over one square kilometre. In 1923, shortly after Poland regained its independence, the area of about 4600 hectares between the Narewka and Hwozna in the central part of the forest was declared a national park and all silvicultural treatment ceased from that time.

3. The general structure and composition of the forest

The composition of the forest shows considerable variation from one area to another. This can to a large extent be related, though secondarily, to silviculture. The area of the National Park was chosen to contain a wide and, so far as possible, representative selection of woodland types and, being in the central part of the forest, it was an area which appeared least influenced by human activity. In particular, *Tilia cordata* is much more plentiful in this central area and its scarcity in many peripheral parts of the forest was attributed by Paczoski (1930) to human influence. He argued that except for the absence of *T. cordata* and a corresponding increase of *Quercus robur*, the deciduous forests in the central and peripheral parts were similar in structure and the composition of their field-layers was the same. Moreover, *T. cordata* tended to be present in larger and less intensively exploited areas of deciduous forest and absent from smaller patches, indicating that its chance of survival was related to the size and perhaps diversity of an area of forest.

The general structure and composition of the various types of woodland have been described by Paczoski (1930) and more recently classified phytosociologically by Matuszkiewicz (1952). The distribution of the main associations within the national park has also been mapped (Matuszkiewicz & Matuszkiewicz 1954).

The southern half of the National Park is mainly oak–hornbeam forest (Querceto-Carpinetum), which all together occupies about 1900 ha, representing 44 % of the wooded area of the park. *T. cordata* is plentiful throughout much of the forest and there are extensive areas where it comprises 20–30 % of the canopy and limited areas where it attains 50 %. Its abundance varies markedly from one compartment to another and often changes abruptly along their edges, so that this variation seems likely to be caused by past silvicultural treatments. The northern part of the park is a mosaic of this association and others composed largely of *Quercus robur*, *Betula* spp., *Populus tremula*, *Pinus sylvestris* and *Picea abies* and classified as Pineto-Quercetum, Querceto-Piceetum and Pineto-Vaccinietum myrtilli. These occupy the more acid and nutrient-poor soils which have developed on coarser-textured parent materials. Although *T. cordata* occurs with quite high frequencies in these associations it is generally represented by seedlings and saplings only.

All the plots, in which the regeneration of *T. cordata* was studied, were within areas of Querceto-Carpinetum and only this association will be described in more detail. The association occurs throughout Poland, where it is mainly lowland and occupies moderately fertile and moist but free-draining loams and sandy-loams, usually derived from loess or glacial drifts (Szafer 1966). *Fagus sylvatica*, which is present in this association elsewhere in Poland, is absent from Białowieża, while *Quercus petraea* has a very restricted distribution.

The structure of the association in the forest of Białowieża is quite characteristic and is illustrated in transects of the plots (figures 2 and 4). There is an almost continuous canopy formed of trees which have slender trunks and relatively narrow crowns reaching to a height of 20–25 m above the ground. *Carpinus betulus* is usually the most important species in this canopy but *Acer platanoides*, *Tilia cordata* and *Ulmus glabra* are also present in varying quantities. Scattered more widely and sometimes also in groups are very much taller individuals of *Quercus robur*, *Tilia cordata* and *Picea abies*. The two deciduous species have a form reminiscent of the large trees in tropical rain-forest, with massive unbranched cylindrical trunks passing through the lower canopy and carrying broad emergent crowns up to 30–35 m above the ground, while the trees of *Picea abies* with their narrow spire-like crowns are even taller and may exceed 40 m.

Beneath the main canopy there is often no layer of shrubs, or there are occasional but scattered individuals of *Corylus avellana* and, much more rarely, *Euonymus europaeus*. There is, however, a very wide variation in the density of slender saplings belonging to all the species present in the lower canopy. This structure is analysed in detail for the individual plots.

The structure and composition of the field-layer appears to be partly dependent on the degree of shading by the canopy but also varies in relation to soil moisture. Even in the deepest shade, herbaceous plants and bryophytes form a low, though sometimes discontinuous, cover but in the better lit areas the herbaceous vegetation becomes dense and there are large patches of *Urtica dioica* up to 0.6–1.0 m tall. On the basis of the variation in composition of the field-layer, three sub-associations are recognized by Matuszkiewicz & Matuszkiewicz (1954) and their distribution is correlated with the moistness of the soil. The Querceto-Carpinetum stachyetosum, which is characterized by the presence of *Carex remota*, *Circaea lutetiana* and *Glechoma hederacea*, and by the high frequency of *Festuca gigantea*, *Impatiens noli-tangere*, *Stachys sylvatica* and *Stellaria nemorum*, occupies the dampest sites where the water-table rises to within 0.4–0.7 m of the surface and there is a well-developed gley horizon. The Querceto-Carpinetum-typicum which is characterized by reduced frequencies of the last four species and corresponding increases of *Carex pilosa*, *Anemone hepatica* and *Galium odoratum*, occurs in sites where the water-table is deeper and there is an indistinct gley horizon. Finally, the Querceto-Carpinetum caricetosum pilosae, which is characterized by the highest frequency of *Carex pilosa*, occupies the most freely drained sites with a deep moist soil but no evidence of gleying.

In general, the soils are a metre or more deep and consist of pale grey sandy-loams. There is no accumulation of leaves on the surface by late summer and only the top few centimetres of the profile contain sufficient humus to give them a dark colour. Mechanical analyses given by Matuszkiewicz & Matuszkiewicz (1954) show an increase in the proportion of clay and silt-size particles (< 0.02 mm) with depth from 7 to 13 % near the surface, to 9–25 % at 0.3 m and 35 % at 0.9–1.0 m. There is a corresponding decrease in the fine sand fraction (0.02–0.2 mm) from 56 to 66 % near the surface to 36–46 % at 0.9–1.0 m, while the proportion of coarse sand (0.2–2.0 mm) does not change significantly with depth (23–32 %).

4. PRODUCTION OF FERTILE FRUIT BY *TILIA CORDATA* IN BIAŁOWIEŻA

In common with many forest trees, the amount of fertile fruit produced by trees of *T. cordata* varies widely from year to year. This is partly but not entirely in response to climatic conditions because individual trees in any one locality may fruit heavily in different years. The direct influence of climate is most marked towards the northern limit of the distribution of the species. In northern England small quantities of fertile fruit are produced only in the warmest summers and the same is true in Finland and Sweden (Hertz 1926). Fruiting is both prolific and much more frequent in central Europe but even in eastern Poland relatively small quantities are formed in some years (Falińska 1971).

Trees of *T. cordata* normally begin to flower when they are more than 25 years old (Büsgen 1929) but inflorescences are initiated and develop only on the exposed branches and never on those which are deeply shaded. The fruits also appear to require to be unshaded to develop and ripen, even though July and August are normally warm and sunny months in Białowieźa with mean air temperatures of 19–20 °C. Examination of isolated trees and small groups of trees in 1973 in the Park Pałacowy, which had flowered even on their lower branches, showed a production of fertile seeds expressed in terms of the number of leaves (each inflorescence forms in the axil of a leaf) of 180/100 on the south and fully exposed sides of the trees, compared with only 8/100 on the north sides which were also shaded by neighbouring but quite separate trees. Golosov (1938) has found that in Russia the best-quality seed of *T. cordata* is produced on the upper part of the crown.

In the forest itself, the production of fertile fruit is probably almost confined to the emergent crowns of the old trees and, in so far as it is possible to see from the ground, they bore a very large crop of fruits in 1973. In contrast, there was only a very sparse crop on the tops of trees whose crowns reach only to the lower canopy.

Even in August, quite high densities of seedlings, still with their cotyledons, were present usually on bare ground and often in shade but always in the neighbourhood of large emergent trees, so that there seems little doubt that these old trees are an important, if not the main source of fruit.

5. Analysis of the structure of the oak–hornbeam forest

Probably the most striking feature of the forest within the National Park is the very large number of slender saplings and young trees with straight unbranched stems and narrow crowns which crowd between the trunks of the larger trees. Although these young trees are of many different sizes, it is immediately apparent that they tend to be in groups of more or less uniform girth and often each group is composed of only one or more rarely two species.

For the most part the forest floor is deeply shaded, but at intervals there are brilliantly lit patches of herbs beneath openings in the canopy resulting from the fall of a tree.

A preliminary examination of various areas of forest in compartments 340, 343, 369, 370, 371, 373 and 399 showed that this structure is generally characteristic of the association of oak, lime and hornbeam in Białowieża and is most conspicuously developed in areas where there are occasional very large trees. The ease with which the separate groups of saplings may be recognized and their tendency to consist of a single species allows the proportion of groups of each of the main species to be estimated. Surveys in compartments 369, 399 and 340 showed that about 19 out of 20 groups were either of *Carpinus betulus* or of *Tilia cordata* but the proportions of groups of these two species varied widely between different sites. About one group in 20 was of *Ulmus glabra* and there was a very low frequency of groups of *Picea abies*. In contrast, saplings of *Acer platanoides* tend to occur singly while neither groups nor isolated saplings of *Quercus robur* were encountered.

On the basis of this preliminary reconnaisance, two plots were selected for detailed investigation and the results serve to illustrate the grouped structure. Although the choice was made

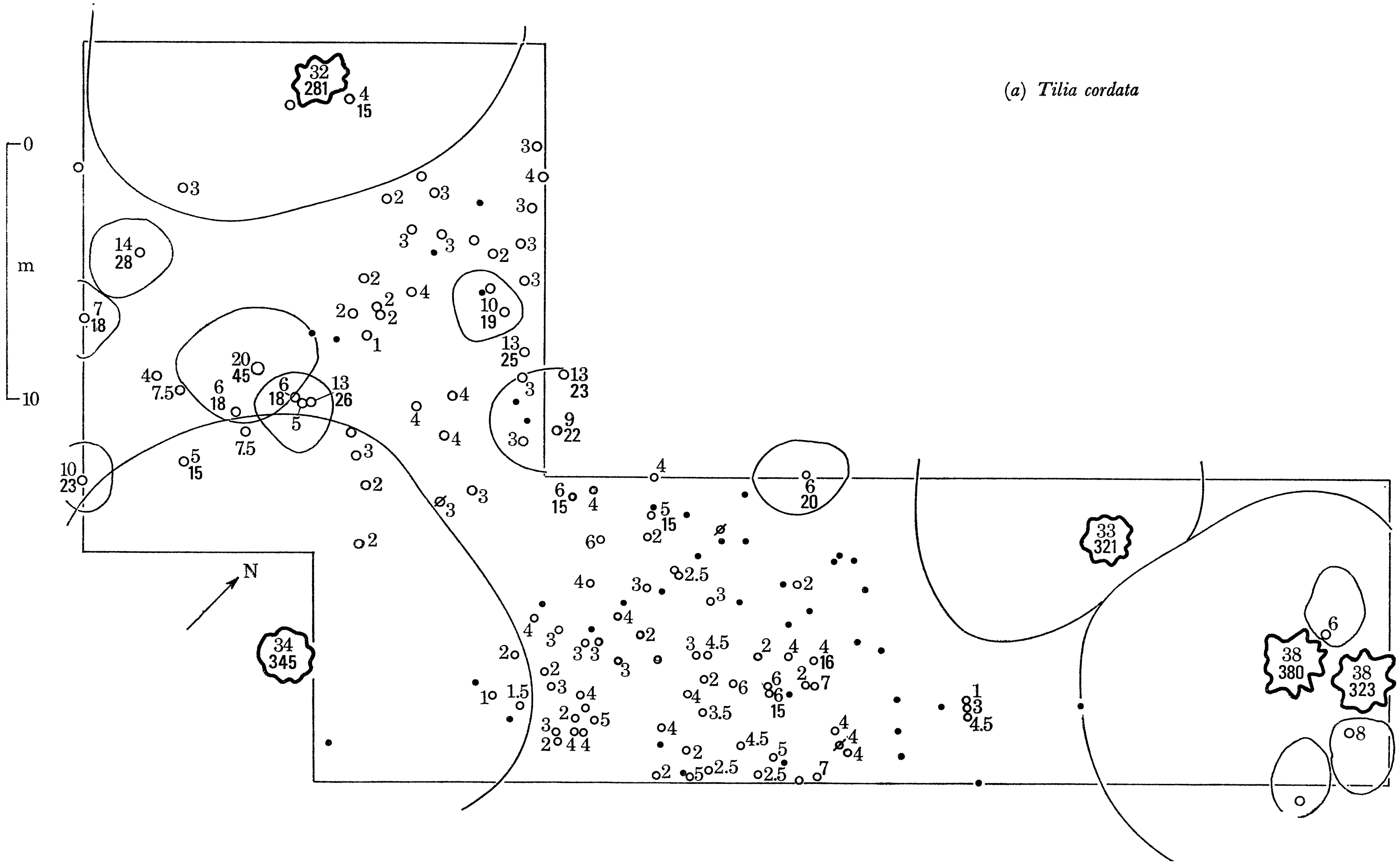

(*a*) *Tilia cordata*

FIGURE 1. Plan of trees, saplings and established seedlings of (*a*) *Tilia cordata*; (*b*) *Carpinus betulus*; (*c*) *Acer platanoides*; (*d*) *Ulmus glabra*; (*e*) *Quercus robur* and *Corylus avellana* (broken line and crosses); (*f*) *Picea abies* in plot 1. The ordinary numbers indicate the height (m) and bold numbers the girth (cm). Dead saplings are indicated by a diagonal line across the circle; seedlings by a solid circle (or cross); stumps by a double line.

(*b*) *Carpinus betulus*

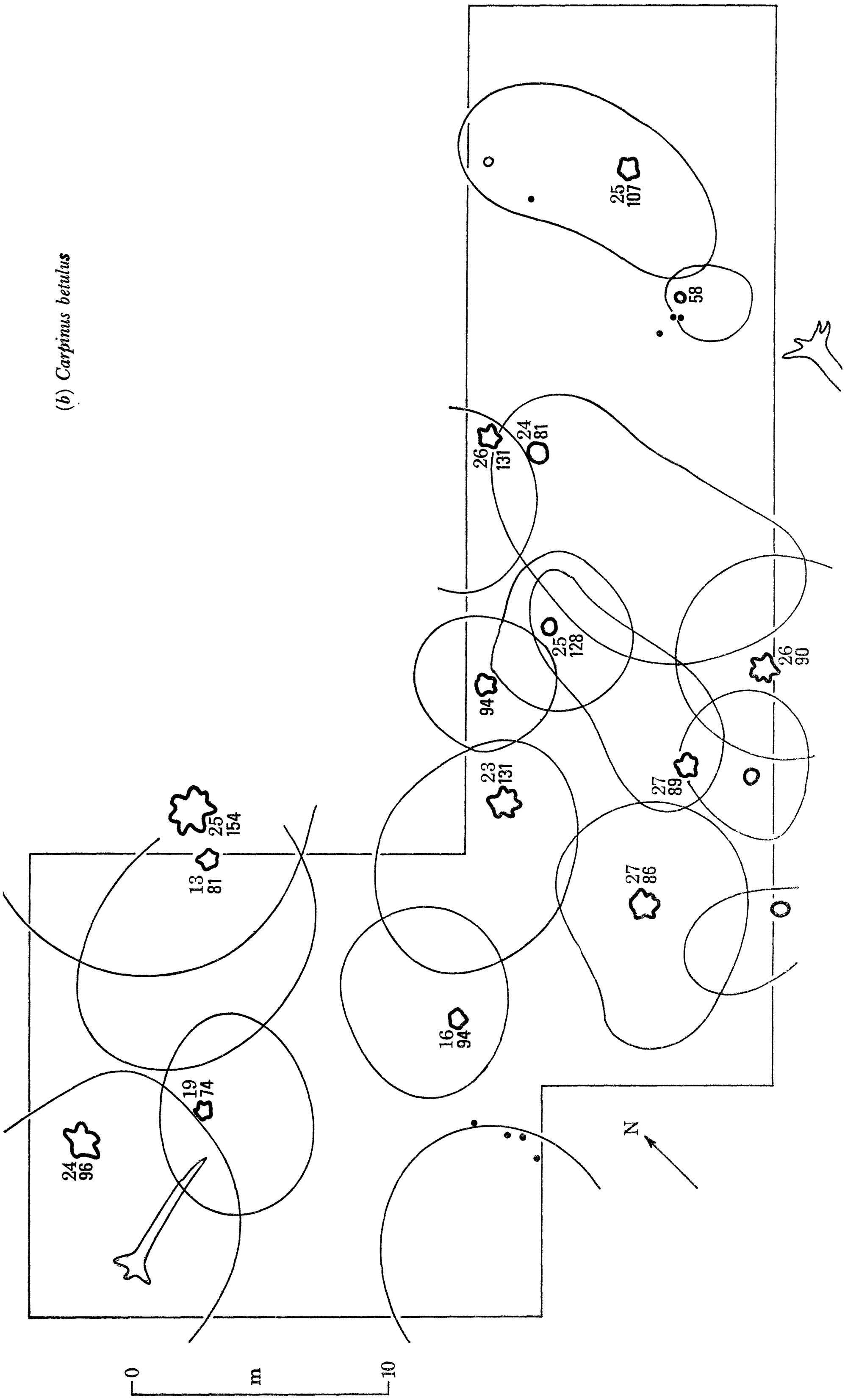


FIGURE 1(*b*). For description see p. 156.

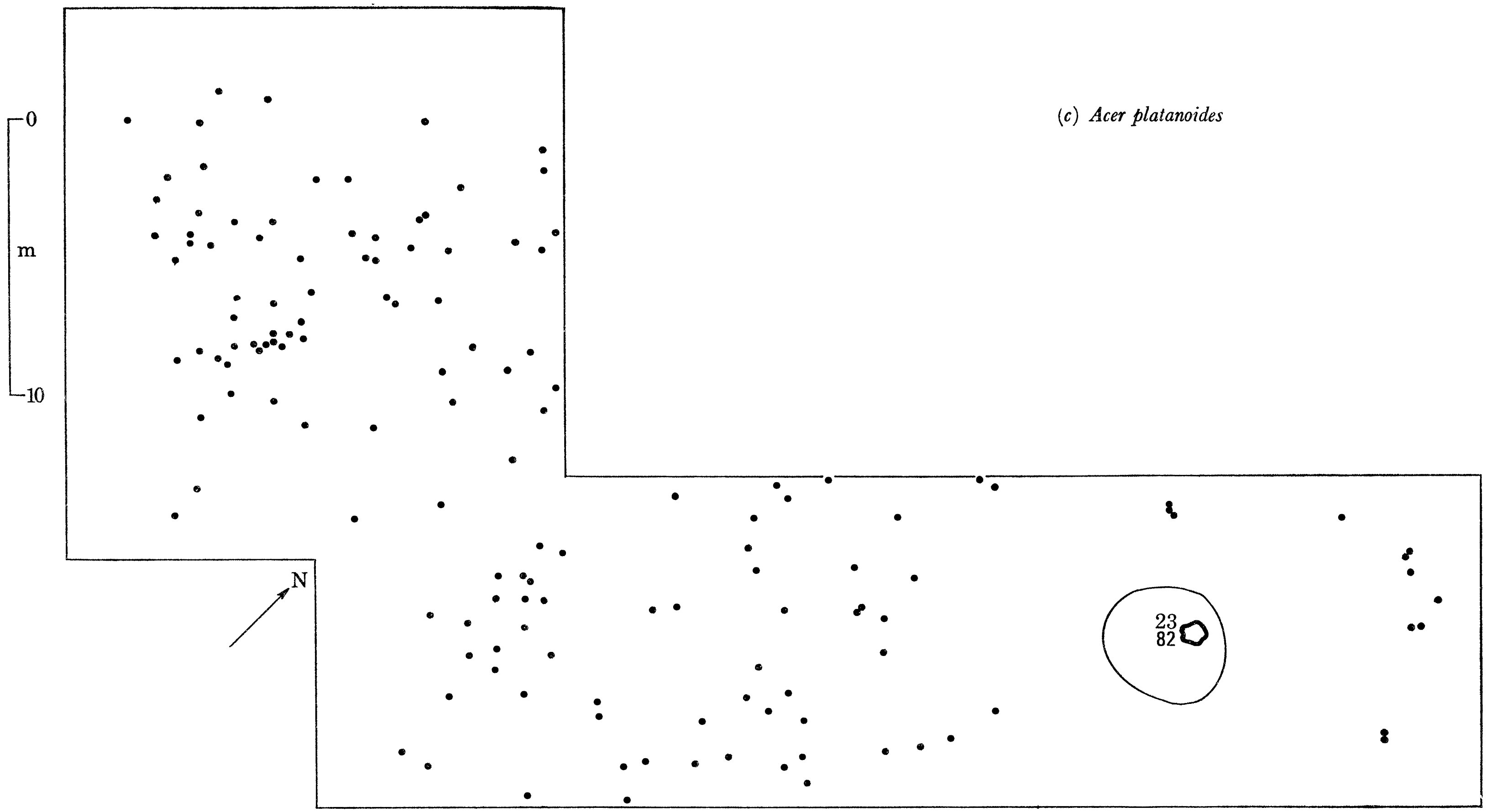

(c) *Acer platanoides*

FIGURE 1(c). For description see p. 156.

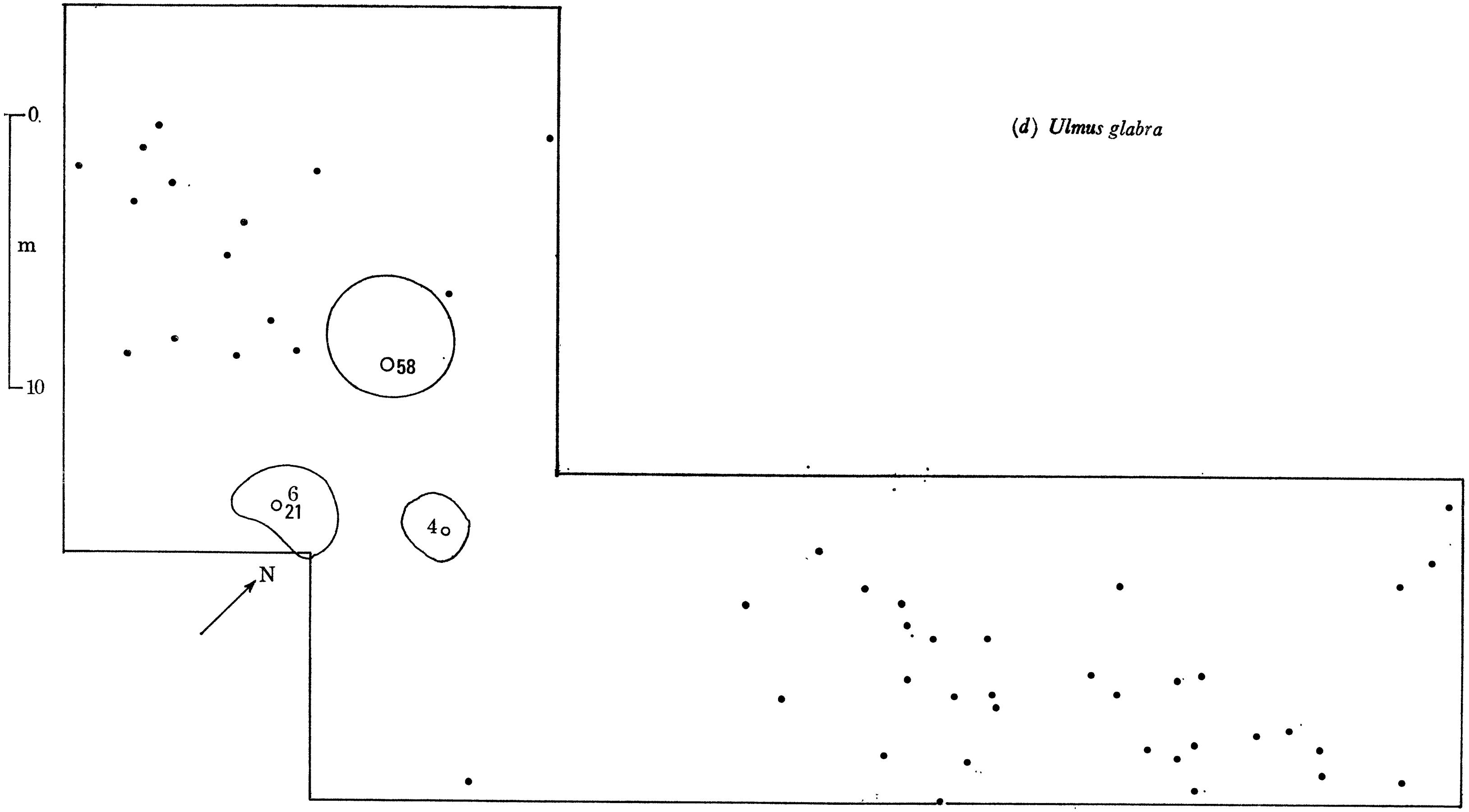
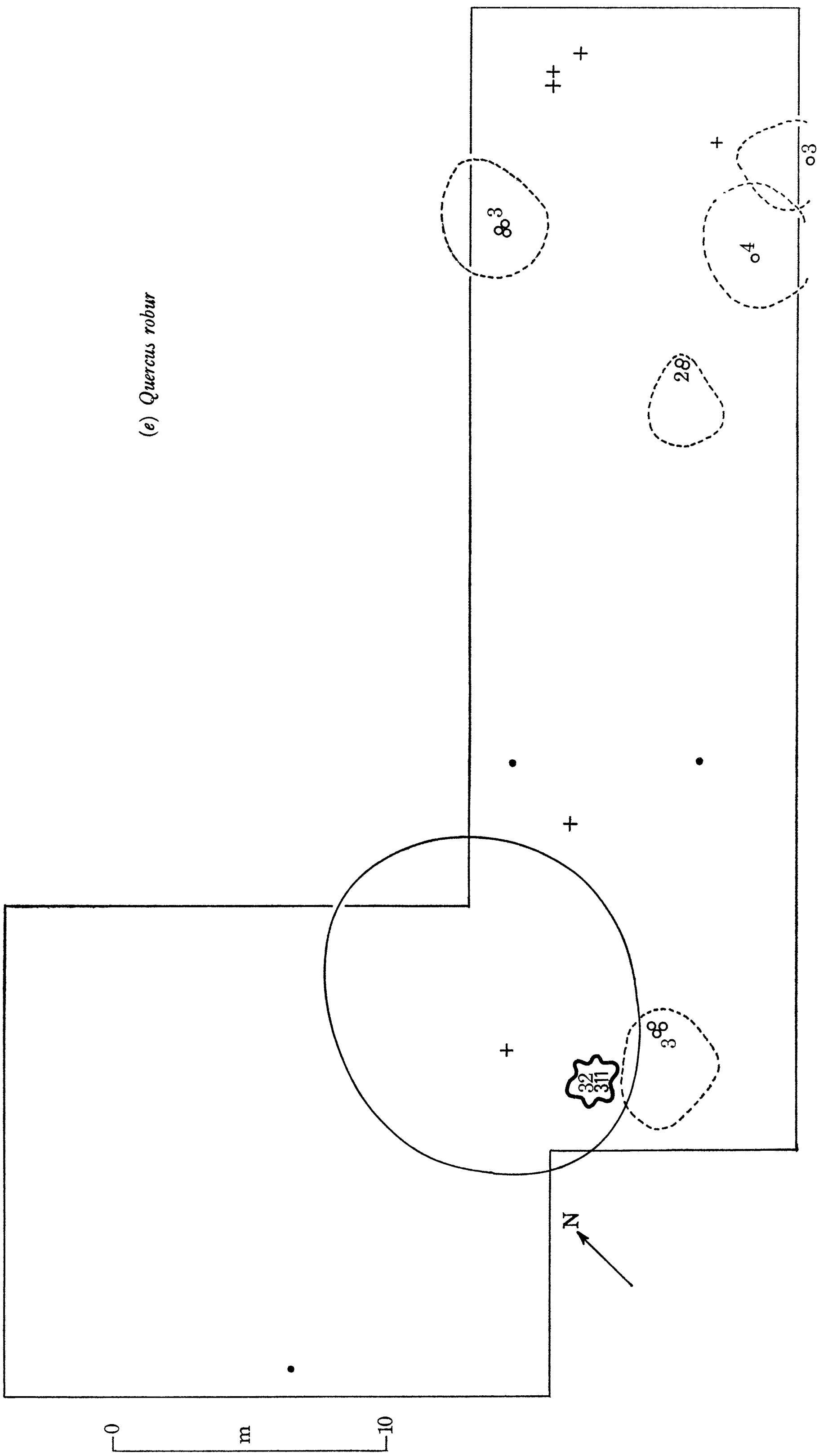


FIGURE 1(*d*). For description see p. 156.



(e) *Quercus robur*

FIGURE 1 (*e*). For description see p. 156.

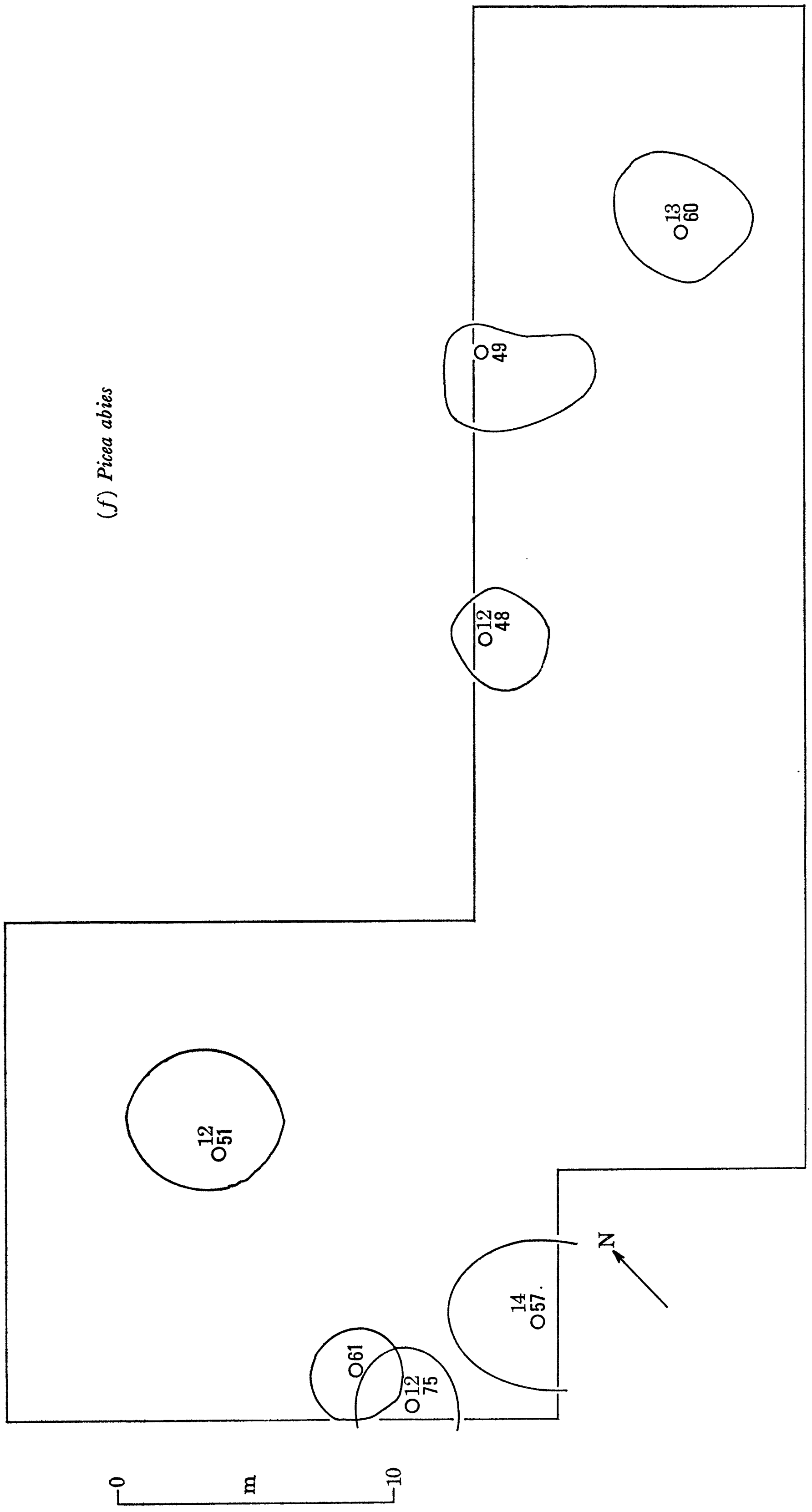


FIGURE 1(*f*). For description see p. 156.

subjectively in order to include large emergent trees, so far as can be judged the plots were not in any other way exceptional. Indeed, almost any site examined showed a similar structure and the difficulty was not to find representative sites but to select from the very numerous examples.

In each plot a rectangular grid was marked out and each square metre was examined in turn and the positions of the bases of all trees and their seedlings were plotted certainly to within 1 dm of their true position. The girth at 1.4 m above the ground was measured for all trees taller than 2 m, and the height of each tree was estimated by comparison with a limited number of trees whose heights were measured either by a marked pole or by Abney level.

Transects were also made at both sites to record the vertical structure but these were laid at right angles to the long axis of the plots to increase the area examined. The basal position, girths and heights of the trees and of their lowest branches were measured. The main branches are not shown conventionally but are fairly accurately represented because from their form conditions during the growth of the tree can be deduced.

5.1. *Plot* 1

This plot is a short distance north of the centre of compartment 399 in an area where large emergent trees of *Tilia cordata* and *Quercus robur* are spaced at a mean base-to-base distance of about 25 m but appear themselves to be grouped.

The plot includes the north edge of a large gap which was caused by the fall of a tree of *Carpinus betulus* and allows direct access of solar radiation to a limited area of the ground for several hours each day during the summer. Over almost all of the rest of the plot, the ground is shaded and the few sunflecks are small and transient. Although the heights of the trees are given on the plan (figure 1), the vertical structure is more readily appreciated from the transect (figure 2). The main canopy is formed largely of *Carpinus betulus* but it is overtopped by the very large trees of *Tilia cordata* and *Quercus robur*. Beneath this canopy are two adjacent but distinct groups of young trees of *T. cordata*. When the distributions of the individual species are plotted separately a remarkable feature which is by no means obvious in the field can be recognized. The two main groups of *T. cordata* are almost entirely restricted to the area outside the canopies of the large emergent trees of *T. cordata* (figure 1). The few stems close to the trunks of two of these large trees are in fact basal suckers. Moreover, the distribution of seedlings of *Tilia* (ranging from less than a year to about 4–5 years old) shows the same exclusion from beneath the canopies, not only of the oldest trees but also of the older group. At this stage the younger group is therefore composite consisting of two distinct age and size classes though the areas of the groups do not exactly coincide. Both the established groups show evidence of self-thinning. The mean density is 44 trees/100 m^2 in the younger group and 12 trees/100 m^2 in the older; both contain a number of dead and dying trees and some have become so weak that they no longer stand vertically but are curved over bringing their canopy into deep shade. Transverse sections through a few of the recently dead trees of the younger group show very narrow annual rings less than 0.5 mm wide and not becoming significantly narrower in the years preceding the trees' death. Cores from the most vigorous trees show that they are the same age (about 17 years) as the suppressed trees but, in contrast to them, have a few narrow rings in the centre and then their radial increment increases to an average of 2.6 mm/year from 1964 to 1973. This does not indicate that conditions were more favourable when the group originated but rather that they have improved subsequently at least for the most vigorous members.

FIGURE 2. Vertical section of
Tilia cordata in plot 1. T
robur; H, *Corylus avellan*

of trees along a strip of width 2 m passing through the two main groups of saplings of
T, *Tilia cordata*; C, *Carpinus betulus*; A, *Acer platanoides*; U, *Ulmus glabra*; Q, *Quercus*
a; P, *Picea abies*.


5
m
0
A
C
C
C
T
T
T
0
m
5

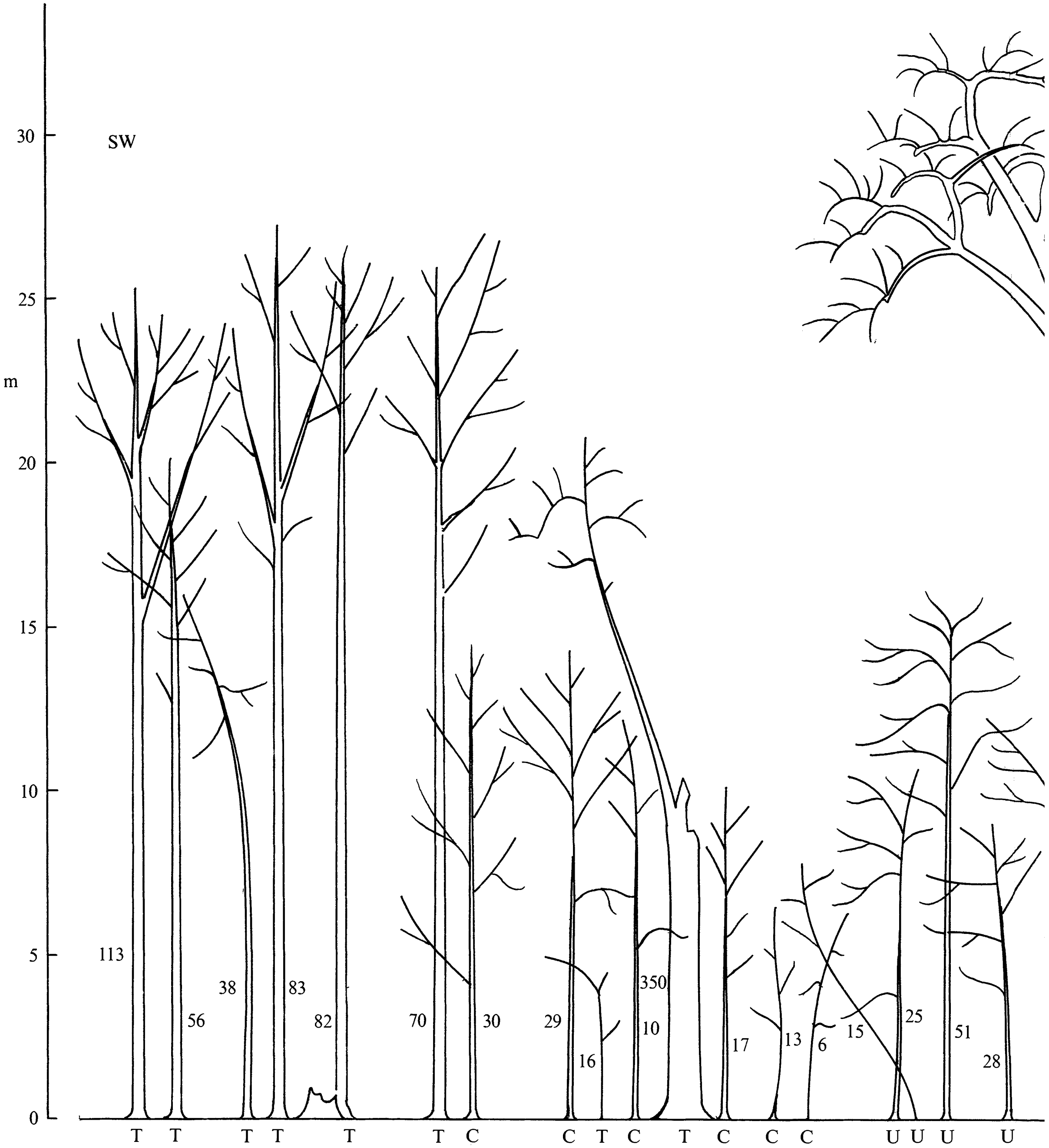
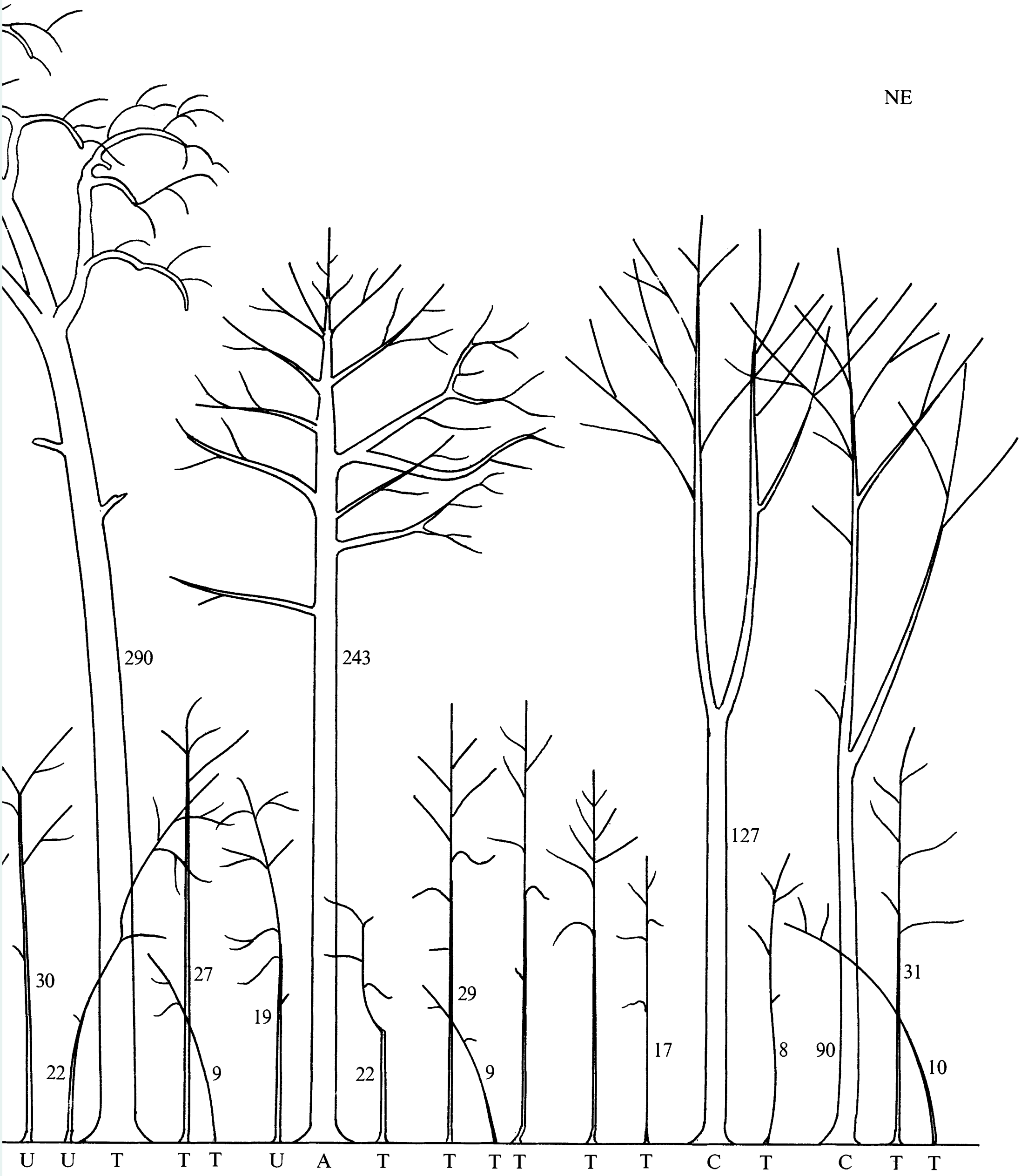


FIGURE 4. Vertical section of trees along a strip of
the group of *Ulmus glabra*. Symbols as in figur



width 2 m passing across plot 2 and through
re 2. Numbers are girth (cm) at 1.4 m.

Although the groups of *T. cordata* are absent from the area beneath the canopies of the emergent trees of the same species, they are almost completely beneath the canopy of what appears to be two overlapping older groups of *Carpinus betulus*. One of the older trees of *C. betulus* bears brackets of *Ganoderma applanata* and is dying. Another has fallen but the gap is already filled by the canopy of the tallest member of the older group of *T. cordata*. Clearly this gap formed long after the establishment of the group of *T. cordata* beneath, but it has allowed a sudden acceleration of growth of those trees which chanced to be immediately beneath.

Within the older group of *T. cordata* are two trees of *Ulmus glabra*, probably of similar age, but seedlings of *U. glabra* are in two clearly defined groups, one coincident with the younger group of *T. cordata* and the other to one side of the older group.

Both *Acer platanoides* and *Quercus robur* show distributions which seem to be characteristic of the species throughout much of the area of the forest examined. Single trees of both species are present in the plot and seedlings of *Acer platanoides* are scattered unevenly over most of the plot without forming clearly defined groups. They are absent only from areas where *Urtica dioica* grows densely. Analysis shows their distribution does not significantly depart from random. In spite of the relatively high density of seedlings there are no saplings. Very few seedlings of *Q. robur* are present and there are no saplings.

Finally, although there are large trees of *Picea abies* close to the plot, those of moderate size within the plot are dying, there are no seedlings and the few saplings are within the groups of *T. cordata* and are dead.

The composition of the herbaceous vegetation of the plot is shown in the first column of table 1. These plants almost completely cover some parts of the plot but there are extensive bare patches where both the herbaceous vegetation and the surface soil have been stripped off and pushed into ridges by the rootling of wild pigs (*Sus scrofa*). Some of the rhizomatous species, notably *Stellaria holostea*, which are gathered up into the ridges of debris, re-establish themselves but *Aegopodium podagraria* is destroyed, possibly because its rhizomes are consumed. Only tree seedlings with well-established tap-roots sometimes survive. However, apart from their absence from these recently bared patches, the distribution of tree-seedlings does not appear to be clearly related to the distribution of particular herbaceous species with the clear exception of *Urtica dioica*. This species forms two patches in the plot, and where it grows densely, seedlings of all trees except *Ulmus glabra* are absent.

The vertical structure is shown in the transect (figure 2), which has been so alined to pass through the centre of both groups of *Tilia cordata*.

5.2. *Plot* 2

The second plot is a short distance south of the centre of compartment 369 and was selected to include a group of *Tilia cordata* of larger girth than those in the first plot. The general structure of the forest in the two plots is similar.

In the second plot the large emergent trees of *T. cordata* are quite clearly in a group and one has recently collapsed. A small group of large trees of *Acer platanoides* is also present and the lower canopy is formed of a mixture of mature trees of *Carpinus betulus* and the group of *T. cordata* for which the plot was chosen.

When the distributions of the species are plotted separately (figure 3) the grouped structure is clearly shown. The group of large emergent trees of *T. cordata* is at the east end and the group of younger trees at the west end. These trees, which are larger than those in the groups in the first

TABLE 1. HERBACEOUS SPECIES AND BRYOPHYTES PRESENT WITHIN THE PLOTS

(Seedlings of trees are omitted. The first number of each pair is the index of cover and abundance of Braun-Blanquet and the second is his index of sociability. The symbol p records the presence of rhizomes of *Anemone nemorosa* in the plot.)

	plot 1	plot 2	plot 3
Carex digitata	—	—	1, 1
C. pilosa	3, 1	1, 1	—
C. remota	1, 1	—	—
C. sylvatica	1, 1	—	+, 1
Dactylis polygama	+, 1	1, 1	—
Deschampsia caespitosa	+, 1	—	—
Festuca gigantea	1, 1	2, 1	—
Milium effusum	+, 1	1, 2	3, 1
Lilium martagon	—	+, 1	—
Maianthemum bifolium	1, 1	+, 1	1, 1
Polygonatum multiflorum	1, 1	1, 1	1, 1
Actaea spicata	+, 1	1, 1	1, 1
Aegopodium podagraria	5, 3	4, 5	2, 3
Ajuga reptans	+, 1	1, 1	1, 1
Alliaria petiolata	—	+, 1	—
Anemone hepatica	1, 1	1, 2	1, 2
A. nemorosa	3, 3	p	p
Asarum europaeum	3, 1	2, 1	—
Chrysosplenium alternifolium	4, 2	2, 2	3, 2
Circaea lutetiana	2, 1	+, 1	—
Daphne mezereum	—	+, 1	+, 1
Dentaria bulbifera	+, 1	+, 1	+, 1
Fragaria vesca	—	—	1, 1
Galium odoratum	2, 1	2, 1	1, 1
Geum urbanum	+, 1	+, 1	+, 1
Geranium robertianum	+, 1	+, 1	1, 1
Glechoma hederacea	3, 1	—	3, 2
Impatiens noli-tangere	2, 1	—	1, 1
Isopyrum thalictroides	+, 1	1, 1	—
Lamiastrum galeobdolon	4, 3	4, 5	3, 2
Lapsana communis	—	+, 1	+, 1
Lathyrus vernus	1, 1	1, 1	—
Mercurialis perennis	—	1, 1	—
Oxalis acetosella	4, 3	3, 2	2, 2
Pulmonaria obscura	—	1, 2	1, 1
Ranunculus lanuginosus	1, 1	1, 1	1, 1
Rubus idaeus	—	+, 1	—
R. saxatilis	—	+, 1	—
Sanicula europaea	1, 1	1, 1	+, 1
Scrophularia nodosa	—	+, 1	—
Stachys sylvatica	1, 1	1, 1	1, 1
Stellaria holostea	4, 2	3, 3	3, 4
S. nemorum	1, 1	—	2, 3
Uritica dioica	5, 3	4, 2	5, 4
Vicia sepium	—	+, 1	—
V. sylvatica	—	+, 1	—
Viola mirabilis	—	1, 1	—
V. reichenbachiana	1, 1	1, 1	1, 1
Athyrium filix-femina	1, 1	—	1, 1
Dryopteris carthusiana	+, 1	1, 1	1, 1
D. filix-mas	1, 1	—	1, 1
Gymnocarpium dryopteris	1, 1	1, 1	2, 1
Equisetum pratense	1, 2	—	1, 2
Atrichum undulatum	—	3, 1	—
Brachythecium rutabulum	2, 1	—	—
Eurhynchium striatum	1, 1	4, 4	2, 2
E. swartzii	1, 1	—	—
Mnium affine	1, 1	3, 2	2, 2
M. undulatum	—	+, 3	2, 1
Rhodobryum roseum	—	1, 3	—

plot, are also at a lower density of about 7 trees/100 m². The established seedlings form a separate group which is largely outside the canopy of the older trees of the same species but in deep shade. One old tree of *Carpinus betulus* and a recently fallen trunk of similar girth are within the plot; these are part of a group whose members are now dying. A few trees of *C. betulus* are present within the group of *T. cordata* and are of much the same size, so that they are probably the same age. A well-defined group of saplings of *C. betulus* is also present and several groups of established seedlings. In the middle of the plot there is a very compact group of *Ulmus glabra* of which two members are dead. Seedlings of this species are much more plentiful at one end of the plot than at the other.

The distribution of *Acer platanoides* in this plot is in marked contrast to its distribution in plot 1. Groups of larger trees of this species are an unusual feature in the areas of forest examined. The seedlings also are restricted to a well-defined group in the plot. Apart from some suckers of *Populus tremula*, no other species of tree is present.

The vertical structure of part of this plot is shown in the transect (figure 4) which is alined across the plot and through the group of *Ulmus glabra*. From southwest to northeast the transect passes through a group of tall *T. cordata*, a group of *Carpinus betulus* which is beneath a gap caused by the collapse of most of the crown of a large tree of *T. cordata*, a group of *Ulmus glabra* and finally a large group of *T. cordata*, about 10–12 m high, beneath the canopies of members of the group of large *Acer platanoides* and a group of large *Carpinus betulus*.

Much of the ground at the east end of the plot has been bared by *Sus scrofa* but the herbaceous vegetation forms an almost complete cover over the remainder of the plot and its composition is given in the second column of table 1. Scattered shoots of *Urtica dioica* occur in the centre of the plot and beneath the group of *Ulmus glabra*.

5.3. *Plot* 3

The third plot is a short distance to the west of the main track in compartment 340 and was selected as an example of a recently formed gap in which *Tilia cordata* is a main colonist. Although seedlings or saplings of *T. cordata* are frequently present in such gaps, their density is very variable, and while in some they are almost absent, in others they are among the most frequent species.

This gap was formed by the collapse of an old tree of *Carpinus betulus* but it is immediately adjacent to an older gap formed by the fall of a large tree of *Picea abies*, which has already been filled with a dense group of saplings of *Tilia cordata* now about 12–15 m high (figure 5). On the southwest side of the new gap is another group of *T. cordata* whose tallest members are 20 m high. It would seem that this second group were completely shaded by the canopy of the surrounding trees of *Carpinus betulus* until one of them fell.

Most of the seedlings of *Tilia cordata* in the new gap are a few years old and 10–25 cm tall. Their mean density over the whole area is 230 trees/100 m² but locally the density is as high as 7/m². They grow mixed with seedlings of *Fraxinus excelsior* and *Carpinus betulus*, which are at similar densities over the whole central part of the glade, but they are a little taller than the former and much taller than the latter. Seedlings of all three species are almost absent from the dense patch of *Urtica dioica* but this does contain scattered seelings of *Ulmus glabra*. Although a large tree of *Quercus robur* is within 100 m of the gap only six seedlings of this species are present within it.

Herbaceous vegetation covers all the glade except for a hollow which is clearly a lair of

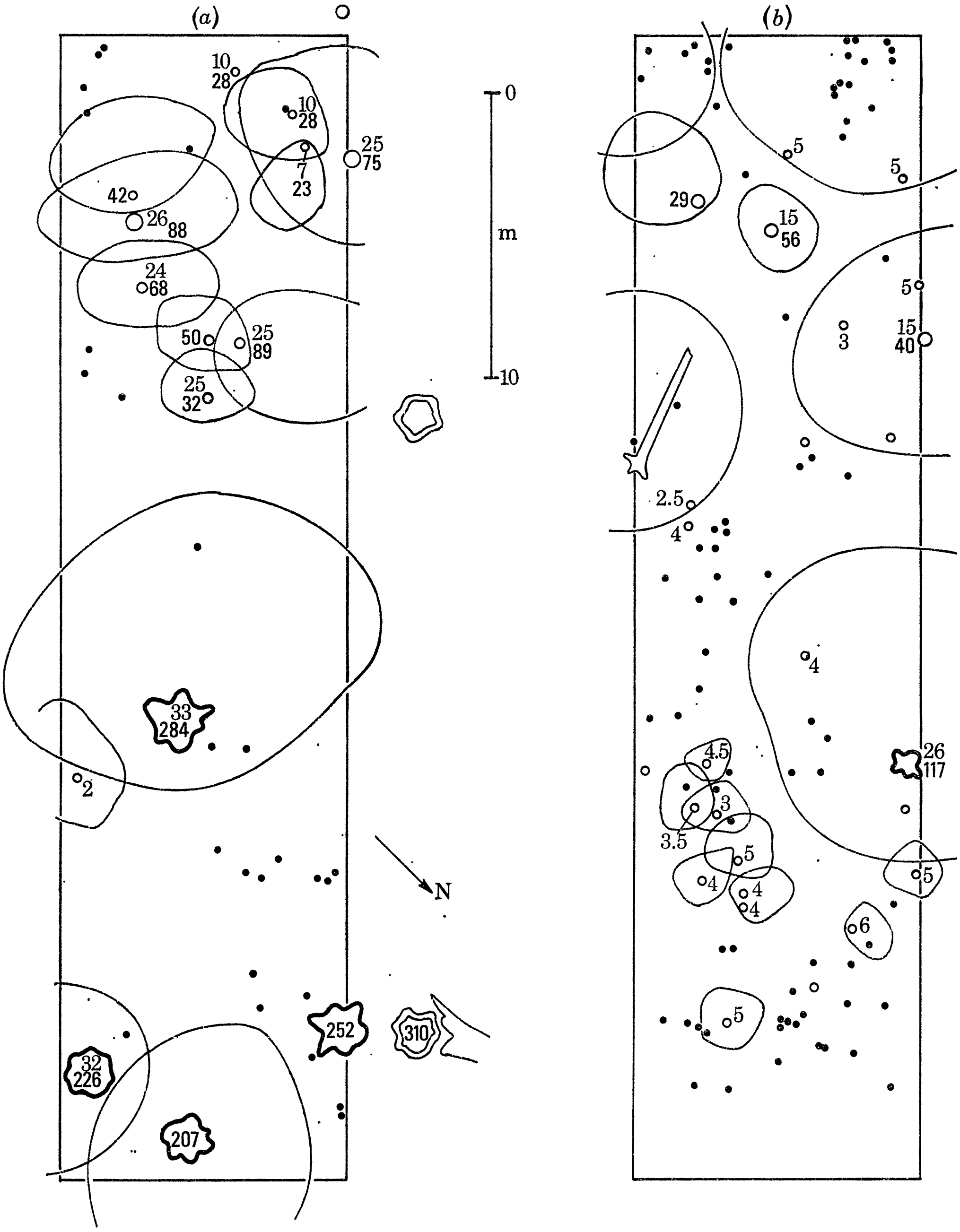


FIGURE 3. Plan of trees, saplings and established seedlings in plot 2. Symbols are as in figure 1. (*a*) *Tilia cordata*; (*b*) *Carpinus betulus*; (*c*) *Acer platanoides*; (*d*) *Ulmus glabra*. Ordinary numbers indicate height (m); bold numbers indicate girth (cm).

Sus scrofa. The composition of this vegetation is given in table 1 and the only conspicuous features associated with the glade are the dense patch of *Urtica dioica* and the numerous flowering plants of *Milium effusum*.

No transect was made of this plot but figure 6 is a transect of another recently formed gap in compartment 371, in which the overall density of seedlings of trees was much less but the growth of *Urtica dioica* more vigorous. Again the occurrence of seedlings of *Ulmus glabra* within the patch of *Urtica dioica* and the greater density of seedlings of *Tilia cordata* outside the patch extending under the surrounding trees of *Carpinus betulus* are conspicuous features.

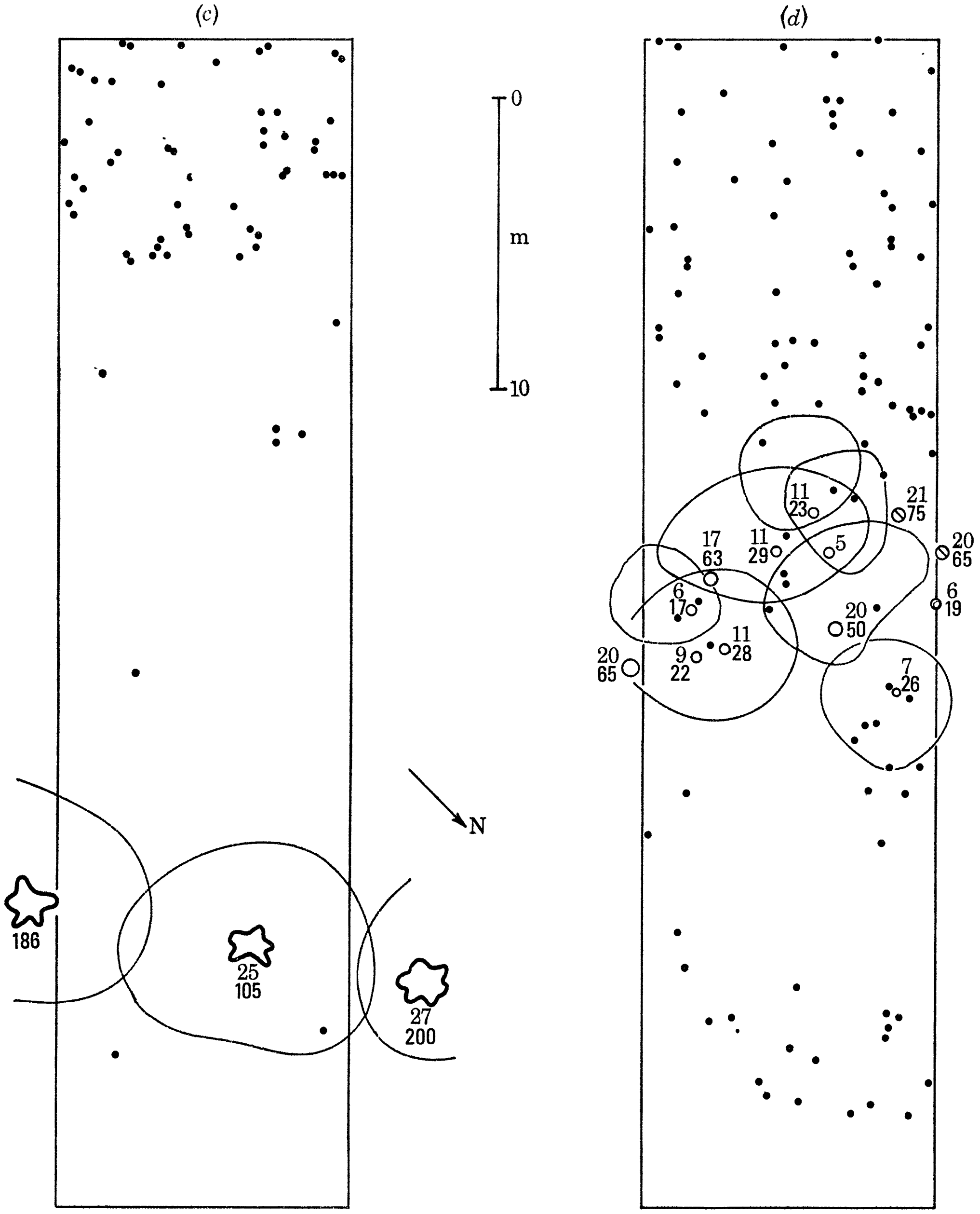


Figure 3 (*c*, *d*). For description see opposite.

6. Frequency distribution of girth in adjacent plots and the relation between density and girth

In the forest immediately surrounding the mapped plots 2 and 3, a series of adjacent plots were marked out so that each contained a more or less distinct group of saplings or young trees of *Tilia cordata*. The girths at 1.4 m above the ground of all trees in each plot were measured and are plotted as histograms in figure 7, where the shaded parts represent those trees which are dead or almost so. This demonstrates very clearly that each group is composed of a more or less homogeneous population with the members distributed asymmetrically about the mean

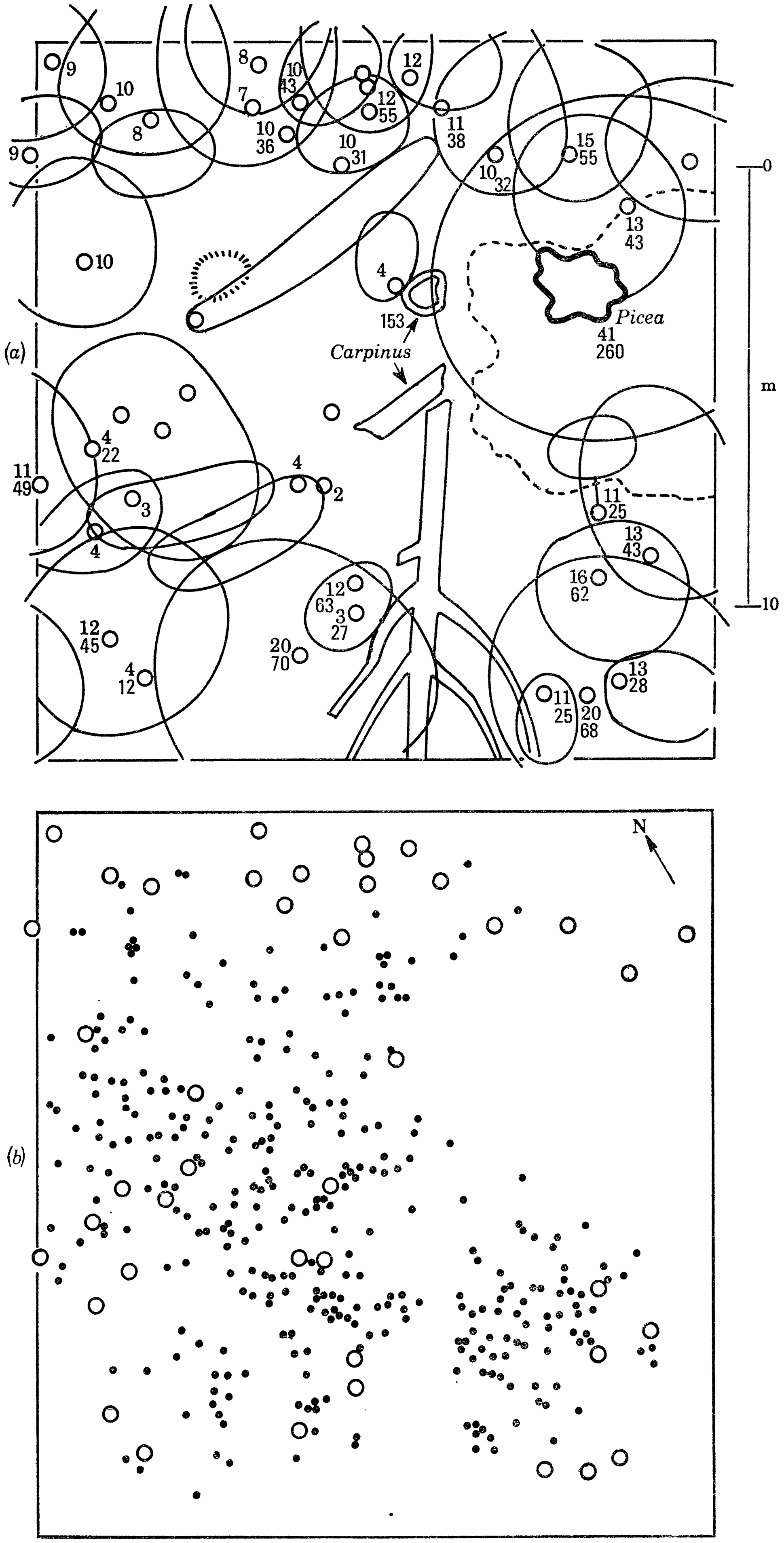


FIGURE 5. Plan of trees and saplings (*a*) and established seedlings of *Tilia cordata* (*b*) in plot 3. Symbols as in figure 1; the broken line indicates the boundary of the dense patch of *Urtica dioica*; the hatched line the site of a lair of *Sus scrofa*. Ordinary numbers indicate the height (m) and bold numbers the girth (cm). Plot dimensions 16 m × 17 m.

when young, but becoming increasingly symmetrically distributed as they grow older. As would be expected, dying and dead trees have a smaller mean diameter and are distributed among the smaller classes within each separate group, reflecting the process of self-thinning. As the mean diameter increases, so the density of the trees within each group decreases. This is illustrated in figure 8, where the mean density of trees in each group and its logarithm are

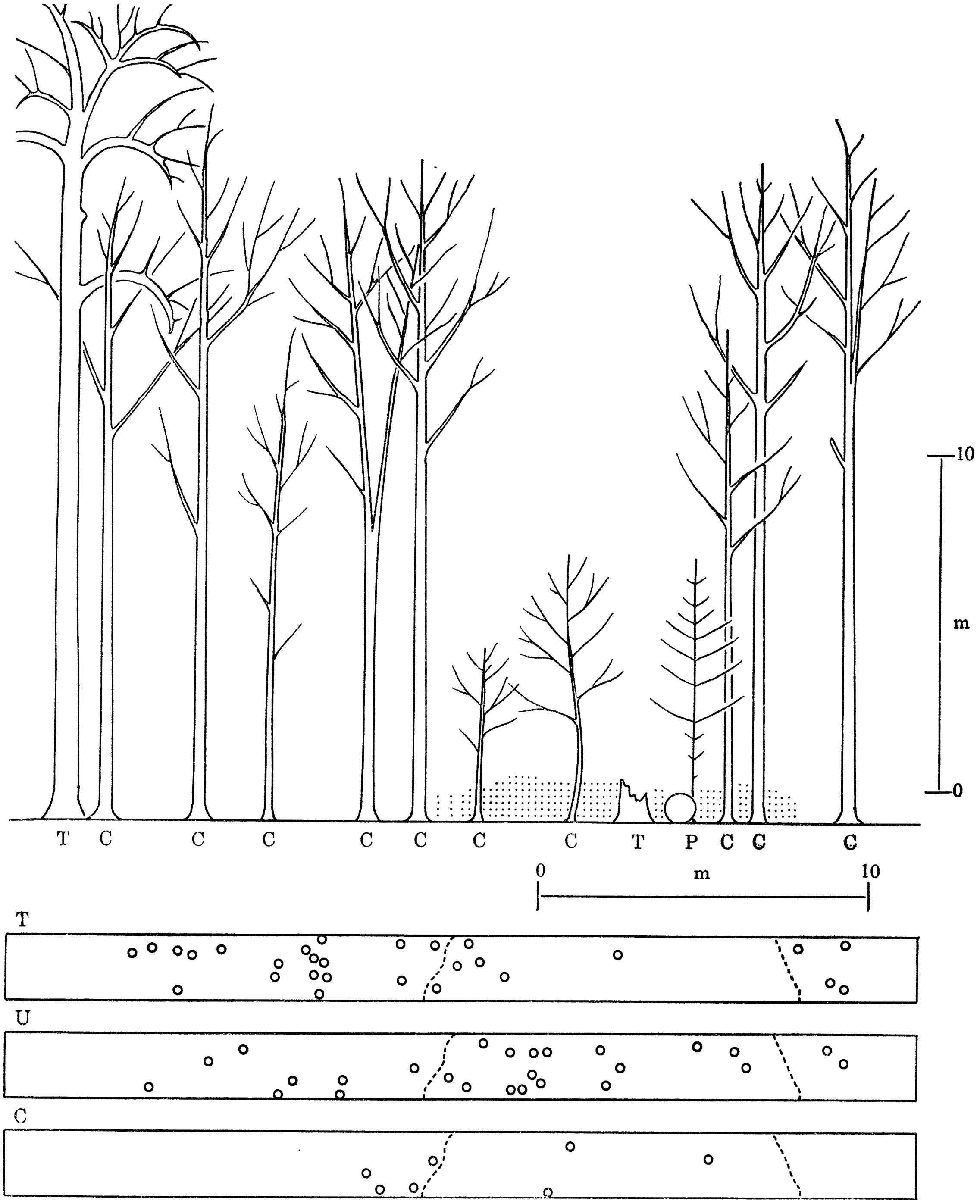


Figure 6. Vertical section of trees along a strip 28 m long and 2 m wide passing across a recently formed gap in compartment 371, and plans of the distribution of established seedlings. The patch of *Urtica dioica* is indicated. Symbols as in figure 2. T, *Tilia cordata*; C, *Carpinus betulus*; P, *Picea abies*; U, *Ulmus glabra*.

plotted against the mean girth of its members. Even with the limited information available, it is clear that the logarithm of density is not directly proportional to mean girth, at least beyond the stage when the trees exceed 0.2 m circumference, so that although mortality is approximately constant when the trees are small, it decreases as they grow larger. This change coincides with the acceleration of growth following the formation of a gap in the upper canopy, so that it reflects a real change in conditions. Unfortunately information is not available to allow the

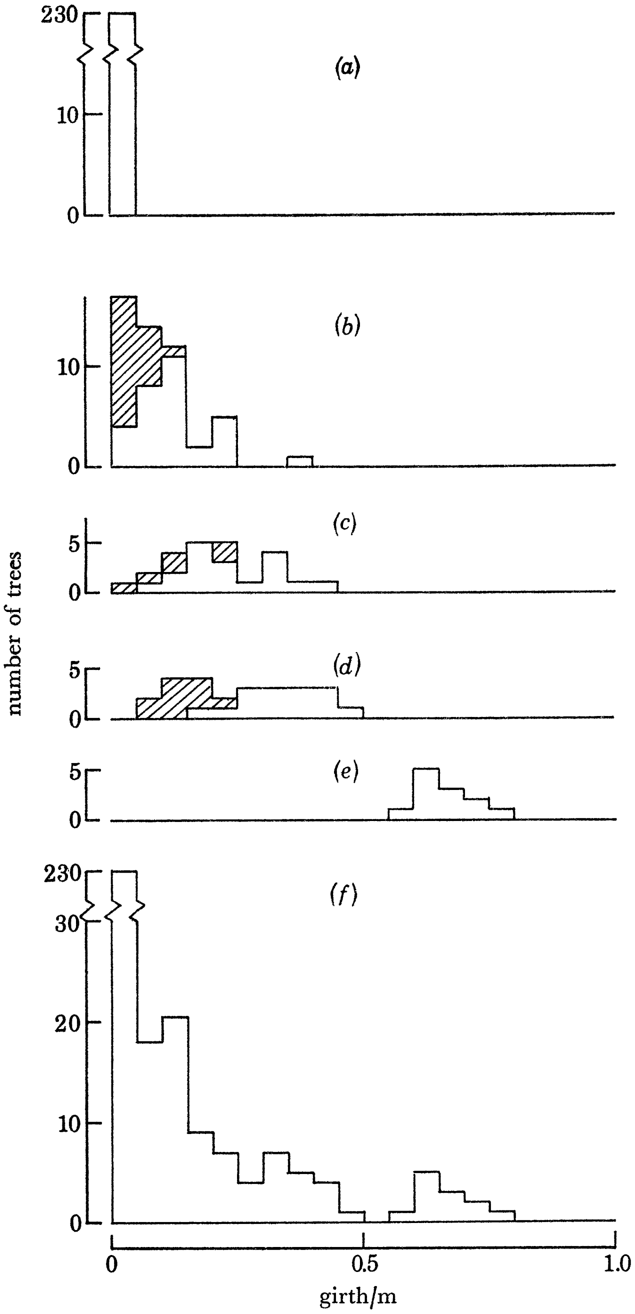


FIGURE 7. Frequency of trees of *Tilia cordata* in successive girth-classes in five groups in adjacent plots in compartment 340. Shaded parts represent dying or recently dead trees. Girth measured at 1.4 m above the ground or at the mid-point of trees less than 2 m tall.

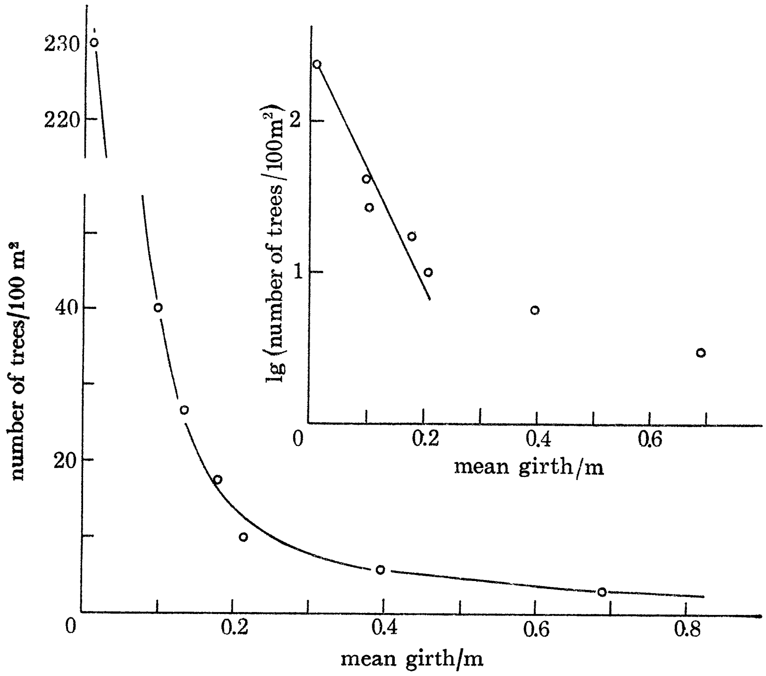


Figure 8. The number and the logarithm of the number of trees of *Tilia cordata* per unit area plotted against their mean girth in the groups in figure 7 and in the three plots.

relation between mortality and age to be established but clearly, as growth-rate has increased, the decline in mortality would be less marked. About 15–20 % of the trees in each group showed severe damage to the bark, extending to a height above the ground which suggests it has been caused by deer (*Capreolus capreolus* and *Cervus elaphus*). This damage sometimes extends to the vascular cambium so that the wood itself has become distorted; this may reduce the growth of the tree so that it has a greater probability of dying during self-thinning.

If the data for the separate plots are combined, the frequency distribution of girth in the whole population shows the form which is characteristic for uneven-age forest (figure 7*f*). Similar frequency distributions were obtained by measuring the girth of all trees of *Tilia cordata* in plots of larger area and these included a few of the tall emergent trees (figure 9). There is a clear discontinuity and trees of *T. cordata* with girth greater than about 1 m and smaller than 2 m are not only absent from these sample areas, but also none was encountered anywhere in the various parts of the forest examined.

The ages of a number of dead trees were established by counting the annual rings but cores were not taken from living trees. However, estimates of the age based on increments of the most vigorous trees over the past few years would indicate that trees with a girth of 80–90 cm could well be 50 years old and date from 1923 when the park was established. It is generally believed that the large emergent trees are about 300 years old (Karpiński 1949) but many of them are now hollow, or have their centres rotten. The mean radial increment of the collapsed tree in plot 2 was about 0.5 mm/year during the last 30 years of its life and from the form of growth of these large emergent trees it is clear that they grew up in shade and therefore may have suffered a long period of suppression with correspondingly narrow rings.

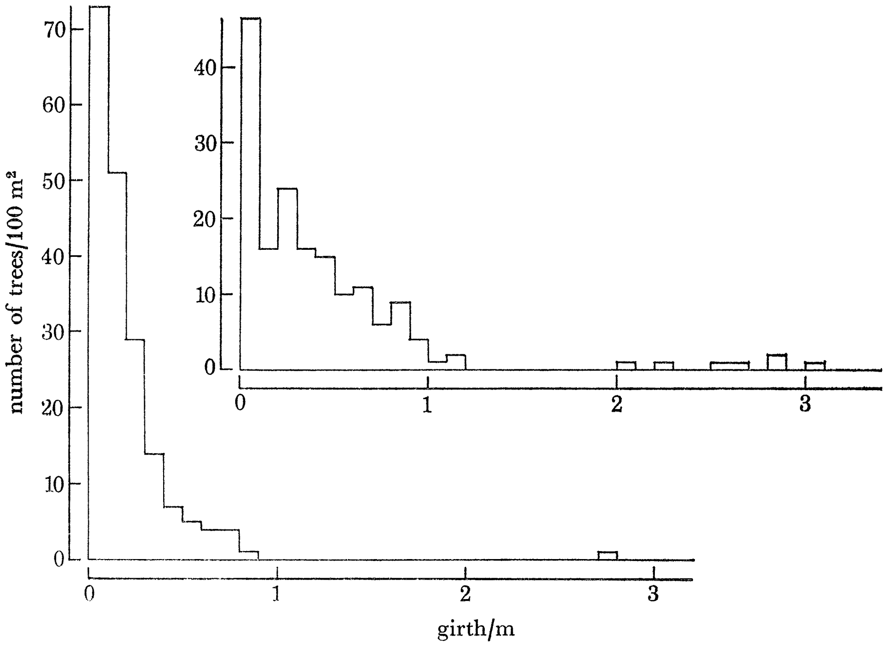


FIGURE 9. Frequency of trees of *Tilia cordata* in successive girth-classes in plots, each of 0.25 ha, adjacent to plot 1 and plot 2.

7. DISCUSSION

The maps and transects demonstrate very clearly that in these very small sample plots the forest consists of a complex mosaic of groups of trees, in which each group is probably more or less uniform in age and usually composed of a single species. Often the groups overlap with adjacent groups which are sometimes of the same species and sometimes not. It is believed that the plots illustrate a structure which is general for much of the area dominated by oak, hornbeam and lime.

It would seem that this grouped structure must result from the establishment of seedlings in restricted areas and their failure either to reach or to become established in other areas. That this is actually so is also clearly demonstrated in the maps when the species are plotted separately but is by no means always immediately obvious in the field. Even in the limited area of the mapped plots, there are examples of the grouped distribution of seedlings of *Tilia cordata*, *Carpinus betulus*, *Acer platanoides*, *Ulmus glabra* and *Fraxinus excelsior*. Grouped regeneration of trees has frequently been described from various types of forest in Europe, but especially from forests dominated by *Fagus sylvatica*, *Abies alba*, or *Picea abies* (Fröhlich 1930; Markgraf & Dengler 1931; Mauve 1931; Tregubov 1941), and in North America, including forest containing *Tilia americana* and *Acer saccharum* (Bray 1956). In Europe it is particularly characteristic of forest under selection treatment, and because the life of the large trees is cut short there is correspondingly a high density of regeneration groups. In forest which has never been subjected to silvicultural treatment, regeneration of groups occurs very much more sparsely because of the much longer life of the mature trees and, in fact, regeneration seems to be almost absent except for occasional heavily shaded saplings (Fröhlich 1954, p. 80). The simplest explanation for grouped regeneration is that when a single tree collapses naturally or is felled, relaxation of root-competition and increased irradiance below the gap in the canopy allows the establishment of a large number of small seedlings in the space formerly occupied by a single tree. These well-recognized events are illustrated by the third mapped plot, where very high densities of seedlings have become established following the fall of a tree, but the other two plots show that groups of seedlings are present even when there is no recently formed gap. Moreover, many groups of young saplings are present beneath a higher canopy and are not associated with a stump or any evidence that they originated beneath an opening in the canopy. At least one example is illustrated of a group of established seedlings beneath a group of saplings which are themselves still covered by an upper canopy. Sometimes the establishment of a group seems to result from an increase in irradiance from an adjacent gap but this is certainly not always so.

Many of the groups of seedlings and saplings of *Tilia cordata* which have become established elsewhere than in a gap are under the canopy of trees of *Carpinus betulus* which are themselves in groups. In all three plots there are examples where old trees of *C. betulus* have fallen and groups of *Tilia cordata*, which were already established, have then been able to take advantage of the gap. This structural relationship with groups of *T. cordata* already present beneath groups of *Carpinus betulus* is in fact a widespread feature of the forest surrounding the plots and suggests that as self-thinning of *C. betulus* occurs, conditions are produced which allow the establishment of *Tilia cordata*, *Ulmus glabra* and possibly *Acer platanoides* often well in advance of a gap forming in the canopy. It is, of course, characteristic of self-thinning that it is the shorter trees which die because they are beneath the main canopy, so that the deaths do not result in the formation of gaps in the canopy.

In plots 1 and 2, established seedlings of *Tilia cordata* between 1 and 5 years old are present in shaded sites and observations outside the plots confirm that this is generally so. Irradiance was measured in several of these sites and compared with measurements in the centre of plot 3 and in very deep shade at a site where seedlings of all species of tree were absent. Measurements were made with simple radiometers (Monteith & Szeicz 1962) placed at 5 cm above the ground with their receiving surface horizontal. Irradiance in the wave band 400–730 nm was obtained as the difference between values measured without a filter (transmission 400–2000 nm) and with a Kodak Wratten 88A filter (transmission 730–2000 nm) with allowance for the transmission factor of the filter. All measurements were made on clear sunny days in August, which were either cloudless or with very sparse clouds, and the values given refer to the total energy (400–730 nm) received in the 8 h period which is more or less symmetrical about true noon. Visible irradiance in the shaded sites at noon was usually about 20–30 W m^{-2}, with no allowance for sunflecks, while values at 4 h before or after noon rarely exceeded 3–7 W m^{-2} and were sometimes not significantly different from zero. The irradiance during this 8 h period therefore represents more than 90 % of the daily total, as would be expected in a woodland where almost all the energy reaching the ground is received when the sun is closest to the zenith. Values in June at the same sites may be estimated from standard meteorological data (Black 1960) and would be about 1.3 times the values in August.

The measurements show that the most shaded sites in which established seedlings of *Tilia cordata* occur are receiving about 250 kJ m^{-2} d^{-1} and sites below a canopy of *Carpinus betulus* at the stage when self-thinning of groups is almost complete, receive about twice to three times this value. A very deeply shaded site beneath an extensive and apparently even-aged stand of *T. cordata*, which probably originated about 1923 as a result of previous felling, gave values of less than 200 kJ m^{-2} d^{-1}. No seedlings of *T. cordata* were present in this or similar sites and the herbaceous vegetation consisted of scattered patches of *Oxalis acetosella* and *Asarum europaeum*. Measurements at the centre of plot 3 show that the irradiance is about 400–500 kJ m^{-2} d^{-1} but the values are extremely variable depending on the length of the period when particular sites receive direct solar radiation. Measurements were also made within the dense patch of *Urtica dioica* and, except for a brief period in the early afternoon, the values were not significantly different from zero. Experimental studies in controlled environments show that seedlings of *T. cordata* from English populations show no sign of etiolation and achieve a net assimilation rate of about 5 g m^{-2} per week at an irradiance of 180 kJ m^{-2} d^{-1}. After 3 months they have two or three mature leaves and have grown at about the same rate as would seedlings in similar natural conditions.

Even from the limited evidence available it would seem that *T. cordata* can become established and continue to grow slowly in situations where the daily irradiance is of the order of 200–300 kJ m^{-2} in August (approximately 250–400 kJ m^{-2} in June), so that establishment is unlikely to be dependent only on gaps in the canopy. Clearly it would be valuable to confirm this conclusion with experimental studies in the natural forest. Nevertheless, gaps do also provide very favourable conditions except in those areas occupied by dense stands of *Urtica dioica*.

At least on the evidence from measurements of irradiance during August, the restriction of seedlings of *T. cordata*, or indeed of *Ulmus glabra* and *Carpinus betulus*, to limited areas cannot, it seems, be simply explained in terms of irradiance at the forest floor.

There is, however, another very important difference between the groups of seedlings which occur in gaps and those which occupy shaded areas beneath the canopy. In gaps, the area where the seedlings of the particular species present obtain their highest densities are generally more or less coincident and if groups which are eventually composed of a single species, arise in this way, they must result from subsequent competition, while beneath an unbroken canopy the clusters of each species are commonly not coincident and often mutually exclusive. This is very clearly shown in both plots 1 and 2. The causes of this uneven distribution of seedlings in the shaded areas are by no means easily recognized and can probably only be identified by observations extended over many years, combined with field experiments. An explanation in terms of the species requiring different conditions for establishment is complicated by the probability that the pattern partly results from the uneven dispersal of seeds or fruits over the forest floor, arising from the uneven distribution of seed-parents and the large variations between years in quantity of fruit produced by individual trees (Falińska 1971). Thus it is possible that an area which would be favourable for the establishment of seedlings of several species may, in fact, become occupied by only one because of its proximity to a parent tree which produced a large crop of fruit in a particular year.

The importance of this source of variation is in fact demonstrated by the establishment of seedlings in the gaps. High densities of seedings of *Tilia cordata*, such as in plot 3, occur only in gaps which have large emergent trees of this species nearby but this is not true of all such gaps, so that conditions for establishment are apparently not always favourable. Indeed the establishment of *Urtica dioica* in a gap provides a striking example of conditions which can exclude seedlings of particular species of tree. The vigorous growth of *Urtica dioica* in gaps is related to both the increased irradiance and the release of mineral nutrients. Analysis of samples of soil from the top 5 cm of the profile in a gap near plot 1 and from the surrounding undisturbed forest, shows a marked increase in soluble phosphate. In this gap numerous healthy seedlings of *U. dioica* were present on bare soil. Large patches of *U. dioica* were examined in several gaps and in every case seedlings of *Carpinus betulus* were absent and seedlings of *Tilia cordata* were very sparse in those areas where the nettles were most vigorous, but well established seedlings of *Ulmus glabra* were always present. Except when the sun shines directly on them, the irradiance under these dense stands of *Urtica dioica* is so low that it could not be measured, yet apparently *Ulmus glabra* can grow in these conditions. When seedlings of *U. glabra* of English origin are grown in controlled environments they appear to be, if anything, less tolerant of shade than *Tilia cordata* so that the explanation for this difference is not obvious. It would be interesting to investigate the relative susceptibility of seedlings of the different species of tree to fungal disease and predation by invertebrates, particularly molluscs, in these moist and shaded conditions.

The very patchy distribution of tree-seedlings beneath the unbroken canopy must similarly be related to the interaction of uneven dispersal of seeds and variation in conditions favourable for establishment. In this latter respect the influence of rootling by wild pigs (*Sus scrofa*) seems likely to be very important and would repay detailed investigation. That wild pigs can improve conditions for establishment of tree-seedlings by destroying herbaceous vegetation and stripping off litter to expose the mineral soil has long been recognized (Fröhlich 1930) but little account seems to have been taken of the influence of the uneveness of their activity. Wild pigs usually feed as solitary boars or as family groups consisting of a sow with one or two litters of piglets, so that relatively limited areas are worked over very thoroughly and then left undisturbed for a period of time. The herbaceous vegetation is destroyed and the rhizomes of *Stellaria holostea*, *Asarum europaeum*, *Lamiastrum galeobdolon* and *Aegopodium podagraria*, are torn up and some are eaten. The soil to a depth of about 5–10 cm is disturbed and pushed into ridges. Although tree seedlings present at the time are mostly destroyed, the destruction of the herbaceous vegetation seems to provide very favourable sites for establishment of seedlings the following year. In several sites, groups of seedlings of *Tilia cordata* and *Carpinus betulus* were seen to occupy areas which had obviously been dug over previously by wild pigs. Moreover, the patches which are disturbed in this way are of similar size to the areas occupied by groups of seedlings. To what extent the wild pigs destroy the surface roots of the trees and thus temporarily eliminate root-competition as in a trenched-plot, would repay investigation.

Another interesting feature which is shown in both plots 1 and 2 is the tendency for seedlings of *T. cordata*, *Ulmus glabra* and *Acer platanoides* to be absent from beneath the canopies of mature trees of the same species. To establish the reality of this relation would require a very much more extensive investigation but in both these plots, and on the basis of other observations, it does appear that conditions under the canopy of old trees of *Carpinus betulus* are particularly favourable for both the establishment of seedlings of *T. cordata* and the growth of groups of saplings. What is not clear is why seedlings of *T. cordata* should be absent fron the relatively lightly shaded and often bare ground surrounding the trunks of the large emergent trees.

These relations between the conditions beneath the canopy of the mature trees and the regeneration of particular species are fundamental to the understanding of the structure of the forest and the coexistence of several species of tree. Even the limited evidence obtained in this study suggests that the predominantly grouped structure is not simply dependent on regeneration in gaps and groups of established seedlings of all species with the exception of *Quercus robur* often occur in quite deep shade. Why the seedlings are still in groups which are often composed of a single species is by no means clear. The establishment of these groups occurs during self-thinning of much older groups and is possibly, but not certainly, dependent on either the relatively slight increase in irradiance, the combination of this with the disruption of the canopy of the herbaceous vegetation by wild pigs, or the reduction in root competition during self-thinning and again the accentuation of this caused by rootling of wild pigs. These processes all occur unevenly and their scale suggests that they could possibly be responsible for initiating the groups. Although observation of permanent plots over a period of years would provide further valuable information, and might demonstrate the dependence of establishment on particular events, probably observation alone can never separate the relative importance of the different factors and a full understanding would depend on the results of trenching experiments and experimental alteration of the arboreal and herbaceous canopies.

Whatever the explanation, the fact that the groups of seedlings which become established in the shaded areas tend to be composed of a single species is of fundamental importance in its contribution to maintaining the diversity of species within the forest.

In gaps, there appears to be a much greater tendency for groups of seedlings to contain several species and this is perhaps to be expected in that both root-competition and shading are simultaneously relaxed, so that conditions are generally favourable and there is no selection for slight differences between the sensitivities of species. Nevertheless it is clear that purely by chance a particular species can predominate in a gap. This results from the proximity of sources of seed and variability of seed production from year to year in relation to the time a gap forms and the particular conditions it offers. Groups of a single species can still be derived from an originally mixed population. For example, seedlings of *Tilia cordata* often extend further under the canopy surrounding a gap than other species, so that groups of this species alone may originate in positions which are offset from the centre. The exclusion of *Carpinus betulus* and often of *T. cordata* but the survival of *Ulmus glabra* in the dense patches of *Urtica dioica* which develop in many gaps is a particularly interesting example of how selection may occur. A more thorough investigation would probably reveal other relations of this type. Eventual dominance of a single species in a gap could also result simply from interspecific competition but the tendency for groups of saplings to consist of a single species suggests it occurs at a very early stage. This last process could be readily investigated in permanent plots but many of the problems related to the success or failure of one species rather than another in a particular site require experimental investigation.

The real importance of understanding the processes which maintain the structure and diversity of mixed forest is, of course, related to general questions about the structure and composition of virgin forest – that is, forest which is not only unexploited by man for timber but also unaffected by other changes caused by man, such as the destruction of predatory carnivores and the consequent increase in deer. Although the forest within the National Park in Białowieża was selected because it was regarded as one of the areas least affected by exploitation (Paczoski 1930), its present structure is clearly not in equilibrium and is very much influenced by processes initiated after the cessation of hunting and timber-extraction in 1923.

One of the particular features of the central part of the forest, including the National Park, is the abundance of *Tilia cordata*, and this was attributed by Paczoski (1928*b*, 1930) to the sensitivity of this species to exploitation. He pointed out that much of the forest away from the central area differed only in the scarcity or absence of *T. cordata* and a corresponding increase of *Quercus robur* and *Acer platanoides*, while the herbaceous vegetation was the same. But even within the central area there was a general failure of regeneration of *T. cordata*, so that within areas of oak–lime–hornbeam forest, in spite of the presence of numerous large trees of this species, there

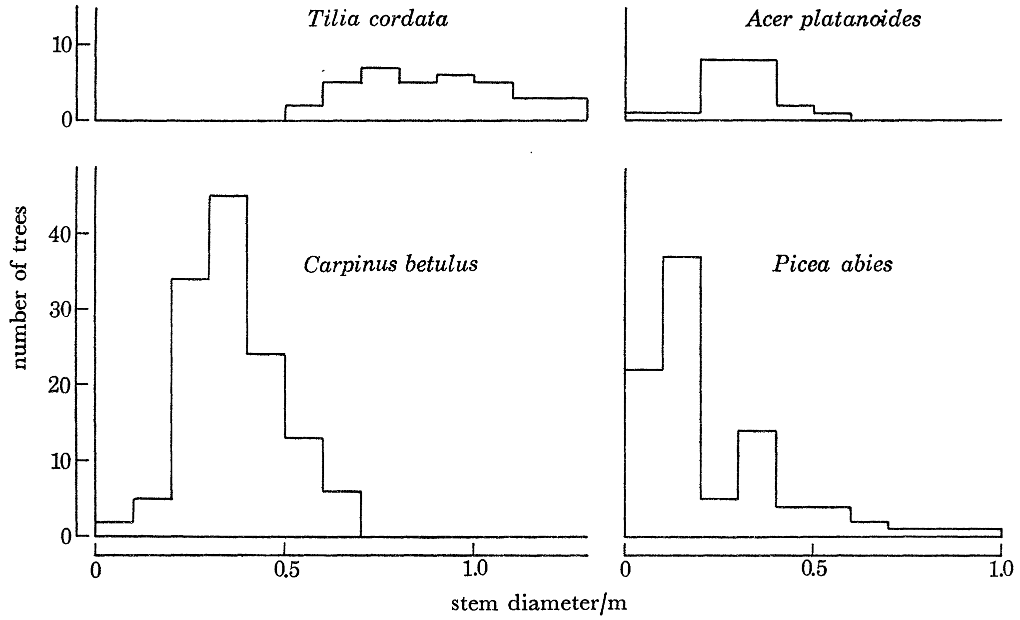


FIGURE 10. Frequency of trees in successive diameter-classes for the principal species in a plot of one hectare in Białowieża before 1928. Information for several plots is given by Paczoski (1928*a*, *b*) but these histograms are based on an example he regarded as typical.

was a complete absence of young trees with a stem diameter greater than about 0.05 m and less than 0.40 m. This is illustrated by tables showing the frequency of stems in successive diameter classes for the most important species in plots of one hectare within the area of the National Park (figure 10). *Carpinus betulus*, *Picea abies* and *Acer platanoides* all show continuous distributions over the whole range, down to the smallest classes (although only *Picea abies* shows a typical diminishing logarithmic relationship), but for *T. cordata* there are either no small trees or there is a gap from 0.05 to 0.40 m. The stems of diameter less than 0.05 m belonged to stunted individuals with shrub-like growth or to sprouts from stumps, and Paczoski (1928*b*) states that strong slender trees with trunks like poles were absent, so that there was no true regeneration. Paczoski (1930) also describes the re-establishment of forest on areas partly cleared in the early part of the century and, even though the very large trees of *T. cordata* were left, there was no persistence of seedlings and only sprouting from stumps.

The analyses presented in this paper show that the structure has now completely changed. Frequency distributions of stem diameter of *T. cordata* now show a typical logarithmic decline from seedlings to trees of about 0.8–0.9 m girth (0.25–0.28 m diameter). Then there is a discontinuity and the tail of the distribution consists of very low densities of large trees with girths generally over 2 m. The average incremental rate for young trees which are not suppressed is about 5 mm in diameter each year, so that trees of about 0.28 m diameter could well be 50–60 years old and are probably the very young trees recorded by Paczoski (1928*b*) which became established in 1923 or during World War I. Most of the trees in the populations described by Paczoski are of very much greater diameters and the smallest, which were 0.35–0.40 m, were likely to be those which were suppressed, so that it is improbable that they were less than 50–60 years old and they could well be much older. The gap in regeneration therefore extends from about 1923 to before 1870 when Białowieża was under Russian administration and used primarily for hunting. Possibly the failure of *T. cordata* to regenerate during this period can be attributed to the destruction of carnivores and the large numbers of deer and bison maintained for hunting, but this is simply conjecture. The analyses made by Paczoski show that whatever caused the failure of *T. cordata* to regenerate did not prevent regeneration of *Picea abies* throughout this period and regeneration of *Carpinus betulus* and *Acer platanoides* during most of it.

Since 1923 the freedom with which *Tilia cordata* has regenerated has given rise to very large numbers of groups, so that the proportion of young trees in the population is now very high, and in this respect the forest retains features derived from selective thinning (Föhlich 1954). If after self-thinning only one or two trees from each group survive to form large trees, they will nevertheless be at a very much higher density than the existing emergent trees and there would, therefore, be a marked change in the overall structure.

The shade tolerance of *T. cordata* when young, the great height of the mature trees and their longevity suggest that the species is potentially the dominant of this type of forest. *Carpinus betulus* forms a lower canopy and is shorter-lived so that it seems likely to be displaced at least temporarily from its predominant role in the present forest. The status of *Quercus robur* is very much more difficult to assess. At present it exists as large isolated trees; young trees and saplings are almost absent and seedlings occur sparsely in gaps. There has therefore been little change in 50 years as Paczoski (1930) comments on the low density of large oaks (0–5/ha) and the lack of young trees. Its behaviour in the oak–lime–hornbeam forest within the National Park is in contrast to its behaviour in this association ouside the Park and in the associations with *Pinus sylvestris* and *Picea abies* within the Park, where trees of all ages are present.

Overall it is difficult to avoid the conclusion that although the National Park of Białowieża contains some of the least-disturbed mixed forest in the European lowlands, its structure still retains characteristics originating from silvicultural treatment and its preservation for hunting. Nevertheless, the site provides unrivalled opportunities to investigate the interrelations between the potential dominants and the mechanisms by which the structure of deciduous forest is maintained.

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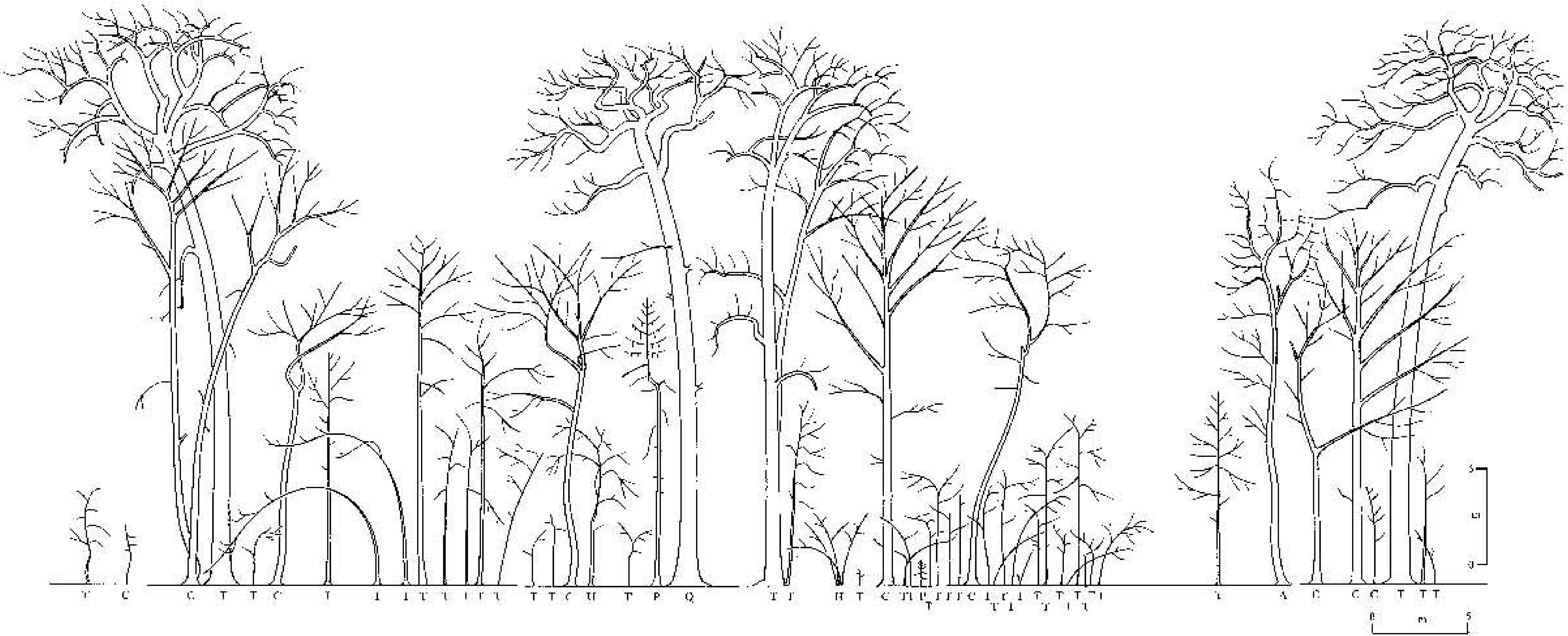

FIGURE 2. Vertical section of trees along a strip of width 2 m passing through the two main groups of saplings of *Tilia cordata* in plot 1. T, *Tilia cordata*; C, *Carpinus betulus*; A, *Acer platanoides*; U, *Ulmus glabra*; Q, *Quercus robur*; H, *Corylus avellana*; P, *Picea abies*.

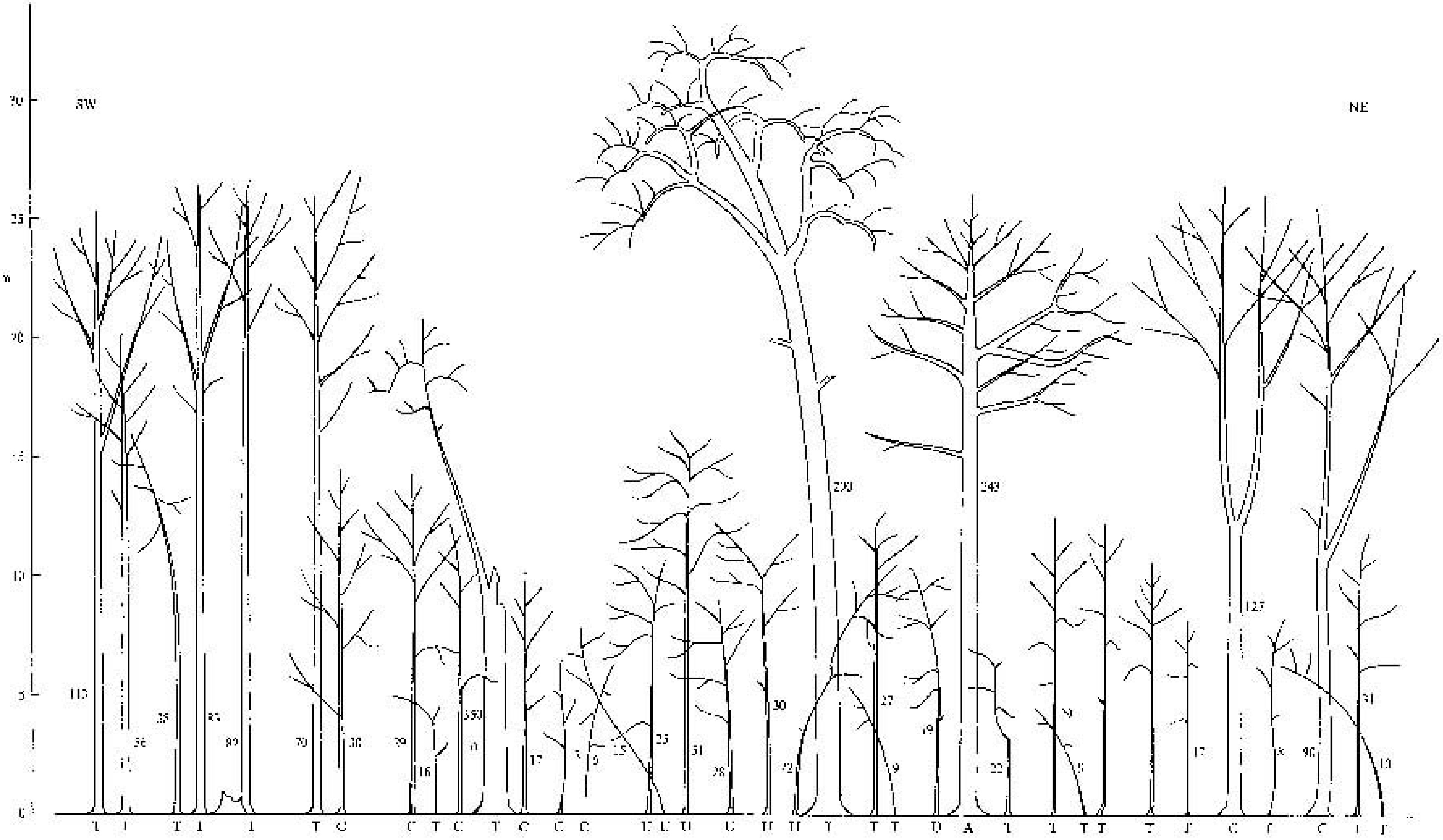

FIGURE 4. Vertical section of trees along a strip of width 2 m passing across plot 2 and through the group of *Ulmus glabra*. Symbols as in figure 2. Numbers are girth (cm) at 1.4 m.