STUDIES ON *ULMUS*

I. THE RANGE OF VARIATION OF EAST ANGLIAN ELMS

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The English elms have been taxonomically recalcitrant for over three hundred years. The present paper is an attempt to see how far a biometric analysis based on a systematic sampling survey can be used to provide an objective description of the range of variation encountered in the genus and to elucidate some of the taxonomic and other problems that it presents.

Sampling Technique

The area surveyed was major square 52 of the Ordnance Survey national grid; the corners of this 100 km. square are located respectively in the vicinity of Stamford, Wymondham, Amersham and Maldon (cf. Fig. 1). This area is one of crucial importance as far as the systematics of *Ulmus* is concerned. The sampling units within the major square were the hundred 10 km. squares composing it. A site in each minor square was selected beforehand for subsequent visiting. The sites chosen were ancient parish boundary hedges with trees and within convenient access from a road. Such sites can be located on the first edition of the 6 inch to a mile Ordnance Survey maps. These mark both trees and parish boundaries. Many of these sheets were issued before the taking effect of the Divided Parishes Acts of 1876 and 1882, and these can usually be taken as giving a reliable indication of the course of the medieval boundaries. The later sheets must be used with more caution lest recent boundaries of no historic standing should be selected.

Boundaries are utilized because these are extremely permanent features of the countryside and are only alterable by Act of Parliament. It seems reasonable to suppose that the trees growing in them will usually represent the descendants of trees growing on the same site at a considerably earlier period. This supposition is supported by the fact that, in some cases, boundary trees mentioned in Anglosaxon charters are still represented today by the same species marking the same point in the boundary (cf. Stonor, 1951).

Collection is deferred till 1 June and continued till 30 September. Sampling earlier in the year is inadvisable since the leaves are apt to be immature. Each preselected locality is visited and the relevant hedge examined for elms. Ten leaves are then collected from a representative tree, or, if more than one evidently dissimilar elm is present, ten leaves from each sort. The leaves are picked from dwarf shoots growing from major branches, taking care to avoid suckers, lammas shoots, and trees heavily attacked by insect pests. The leaves chosen are the subdistal members of the dwarf shoots.

Biometric Technique

Each leaf is measured for five quantitative characters : lamina breadth/lamina length; the number of teeth; petiole length/lamina length; the degree of basal asymmetry; and the tendency towards obverse configuration. Lamina length is measured on the longer side of the leaf. Breadth is taken as maximum breadth. Minor teeth are counted, not the major teeth on which they are superposed. Basal asymmetry is calculated from the ratio : length between the transverse axes marking the lowest point on each side of the leaf/lamina length. The tendency towards obverse configuration, which may conveniently be termed obversity, is calculated from the ratio : length between the transverse axes marking (1) the point of maximum breadth on the shorter side of the leaf and (2) the point where the longer side runs into the petiole/lamina length.

In addition, it is noted whether the upper surface of the leaf is scabrous or smooth. Although gradations exist in this characteristic, a convenient method of measuring scabrosity was not found. Scabrous leaves will be denoted hereafter by an asterisk *, smooth leaves by a dagger †.

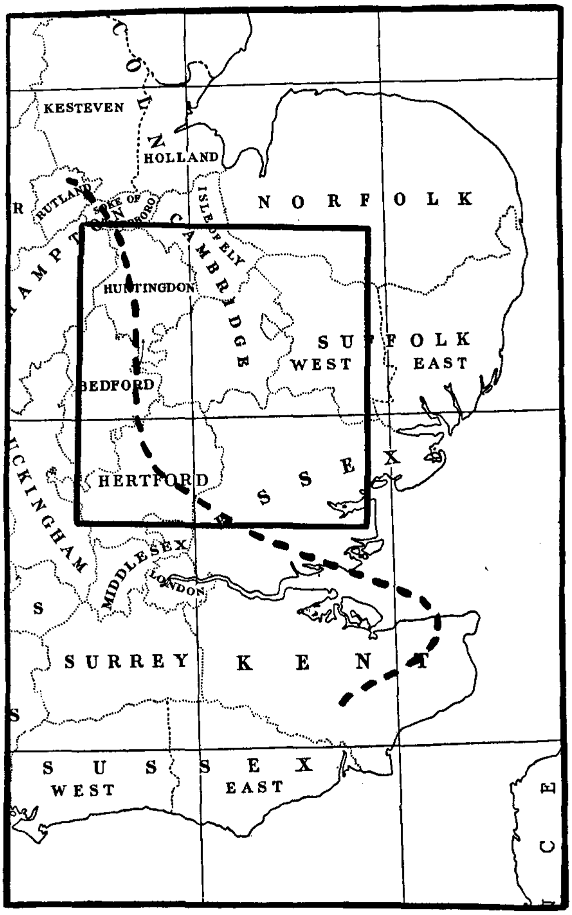


Fig. 1. Area of survey. The solid line represents major square 52 of the Ordnance Survey. The broken line represents the eastern boundary of *U. procera*.

From these primary measurements, means for each character per tree are calculated, together with their standard deviations. Then, for each pair of fairly similar trees, the t test for significance of difference between means ($P = 0{\cdot}05$) is made for each character. A record is made of all pairs of sample trees which do not differ significantly in any of the five characters studied.

RESULTS

Specimen samples from each minor square in which elms were encountered are illustrated in Fig. 2. Where two samples were obtained from one minor square, they are referred to as samples *a* and *b*, respectively; in Fig. 2, the *a* samples are on the left, in Table 1, the *a* samples are above the *b*. The measurements pertaining to each sample are given in Table 1. To simplify the presentation of the data, each character is expressed in terms of a scale of 10 units (0-9), the order of the characteristics being (1) relative

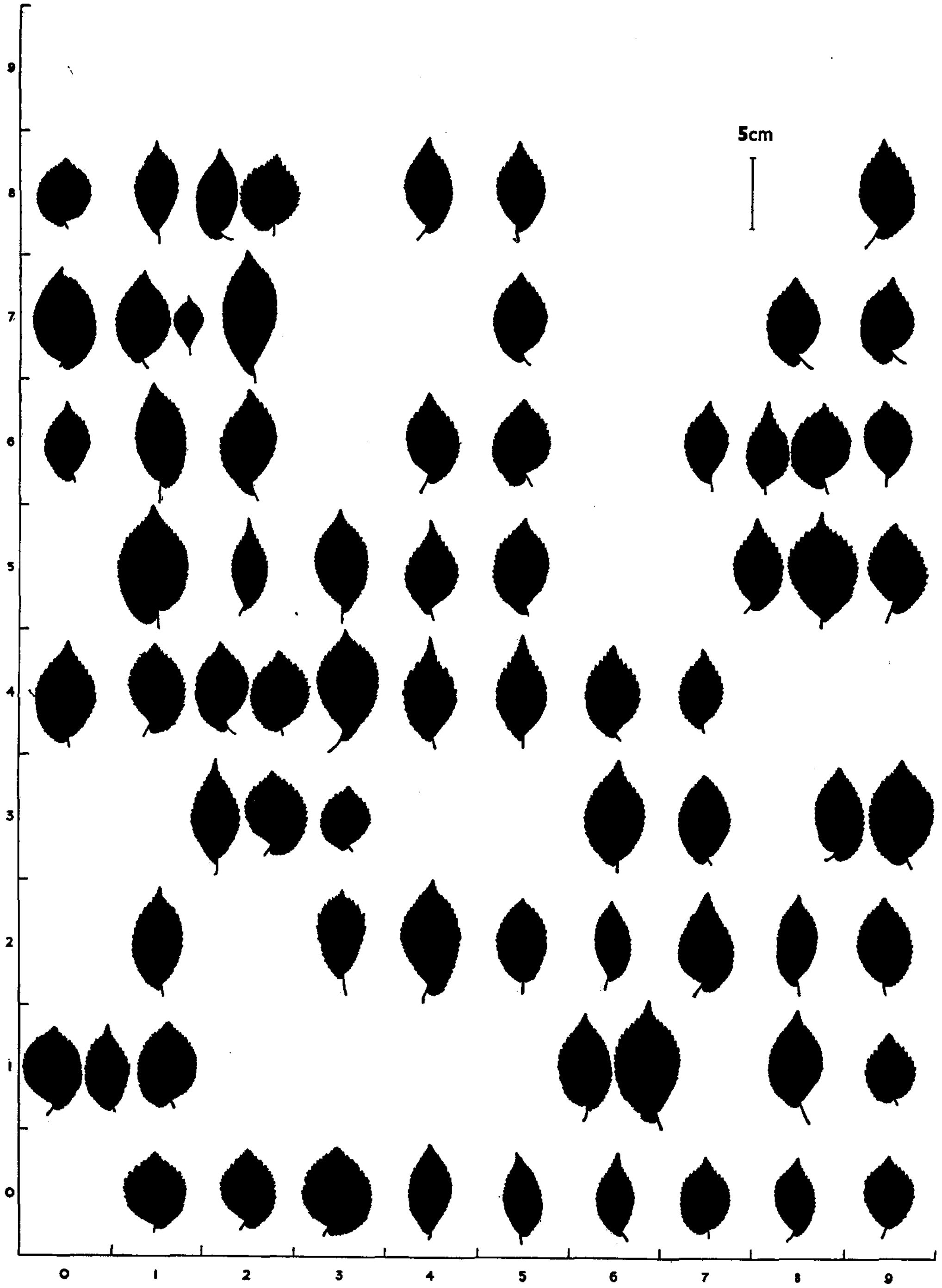


Fig. 2. Specimen leaves from major square 52. The figures are the grid reference coordinates of the minor squares.

TABLE 1.

Mean values for (1) *relative breadth,* (2) *tooth number,* (3) *relative petiole length,* (4) *basal asymmetry, and* (5) *obversity, of elm leaf samples collected from major square* 52. *A range scale of* 0-9 *is used for each character. The marginal figures are the grid reference coordinates of the minor squares.*

9										
8	72443*	15536†	18535† 82552*		26634†	33644†				44853†
7	57121*	44433† 33807†	16326†			53555†			45963†	44973†
6	41334†	27726*	44568†		33666†	63754†		35616†	27331* 64665†	44525†
5		49551†	06434*	27535*	36323†	45545†			34434† 59232*	65565†
4	56422*	73555*	63453† 71434*	44747†	35651†	36431†	46431*	36432†		
3			14623† 83557*	81544*			33423†	44533*		44444* 54443*
2		22323†		43929†	25646†	43704†	13617†	44641†	25557†	52834†
1	63534* 34524†	63436*					34715† 48346†		35922†	72620†
0		82325*	72436*	93344*	25325†	10514†	23522†	53631†	33545†	62915†
	0	1	2	3	4	5	6	7	8	9

breadth, (2) number of teeth, (3) relative petiole length, (4) basal asymmetry, and (5) obversity. The absolute range for each of these characters is as follows :

Relative breadth	·40– ·90
Number of teeth	50–150
Relative petiole length	·00– ·20
Basal asymmetry	·00– ·20
Obversity	·40– ·60

Thus, sample 08 in the top left-hand corner of Table 1, expressed as 72443*, relates to the following set of mean absolute values; relative breadth, ·79, tooth number, 74; petiole length, ·08; asymmetry, ·09; and obversity, ·47.

In Fig. 3, the results are presented graphically. The two most discriminant characteristics, relative breadth and number of teeth, are used as coordinates, suitably deformed for convenience of illustration, and the three other characteristics are represented as sectors in the circles or triangles pertaining to each sample. Circles are used for smooth-leaved samples, triangles for scabrous material. Sector 8-12 o'clock represents relative petiole length, sector 12-4 basal asymmetry, and sector 4-8, obversity. Each sector is blacked in clockwise to show where the value of each characteristic lies relative to the total range.

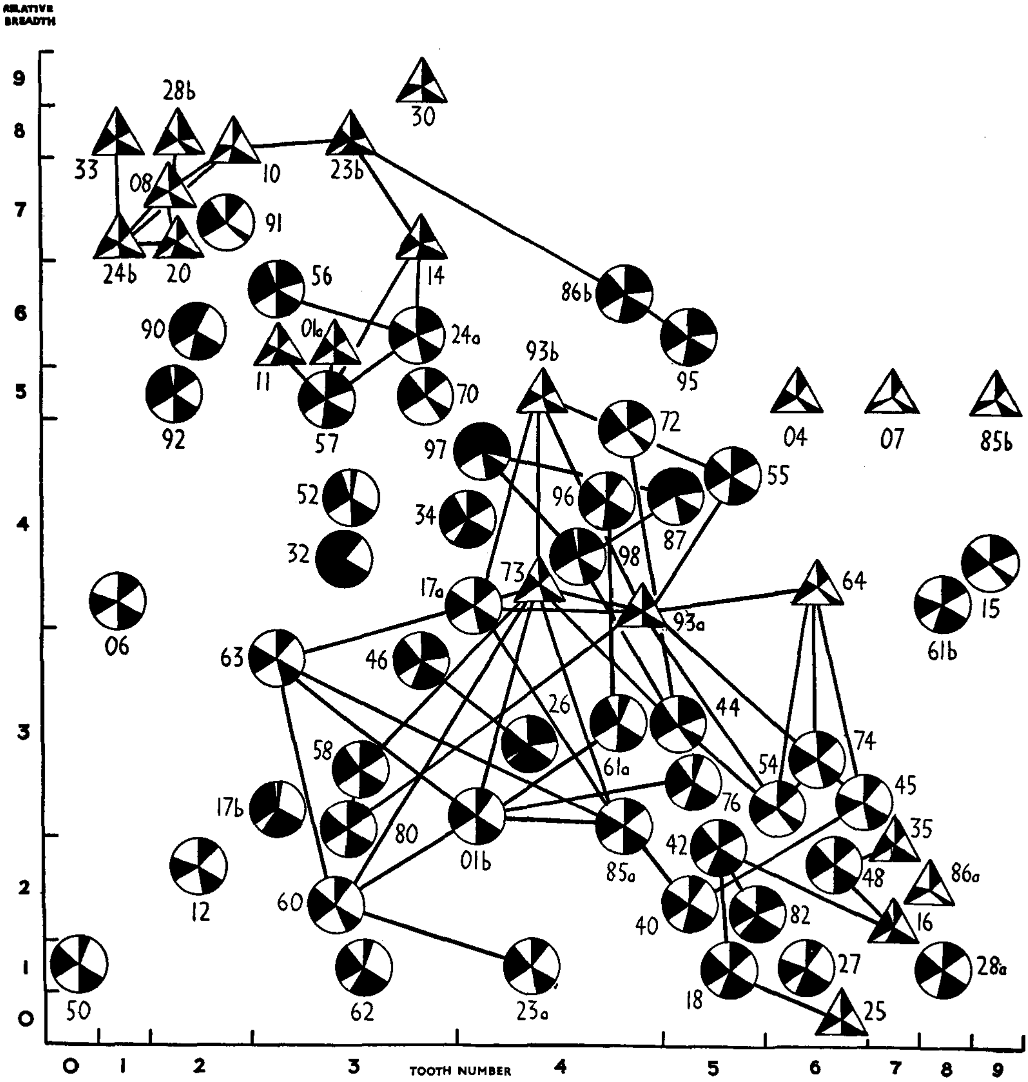


Fig. 3. Graphical representation of the affinities of the samples collected in major square 52. The coordinates indicate relative breadth and tooth number; a range scale of 0-9 is used. The widths of the shaded sectors represent three minor quantitative characters. Circles indicate smooth leaves; triangles, scabrous leaves. The bars connect samples which the *t* test fails to separate.

All samples which cannot be separated by the *t* test in any of the 5 characters are joined by a connecting bar. As a general rule, differences between the absolute means were significant if they exceeded the following values :

Relative breadth	·07
Number of teeth	10–15
Relative petiole length	·02
Basal asymmetry	·02
Obversity	·03

Tooth number is not normally distributed and the number of teeth required for a significant difference rises with the absolute number of teeth. Since, however, comparisons are only made between closely similar samples, scale transformation is probably unnecessary.

Preliminary tests showed that comparisons between 10 leaves from each sample gave little increase in discrimination above comparisons between five leaves per sample, provided that the initial sampling procedure was rigorously followed. The data presented are therefore based on 5-leaf samples.

TABLE 2.

Taxonomic analysis of the elm samples collected from major square 52.

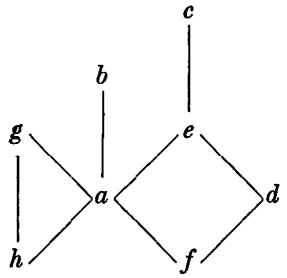
Group	*Subgroup*	*Samples*	*Range*	*Taxonomic relations*
I			13311, 46976*†	
	a	01*b*, 17*a*, 23*a*, 58, 60, 63, 73, 80, 85*a*, 93*a*	13422, 44645*†	*U. diversifolia* *U.* ?aff. *carpinifolia* sens. str.
	b	61*a*, 76, 96	34515, 45726†	*U.* ?aff. *diversifolia*
	c	87, 97, 98	44853, 45973†	*U.* ?aff. *coritana* var. *media*
	d	54, 64, 74	36431, 46432*†	
	e	44, 72	34641, 45651†	
	f	40, 45	25323, 36325†	
	g	93*b*	54443*	*U. glabra-carpinifolia*
	h	55	45545†	*U.* ?aff. *diversifolia* *U.* ?aff. *carpinifolia* sens. str.
II			51432, 85767*†	
	a	01*a*, 08, 11, 14, 20, 23*b*, 24*a*, 24*b*, 28*b*, 33, 56, 57	51432, 84757*†	*U. procera* *U.* ?aff. *coritana* *U.* ?*procera-carpinifolia*
	b	86*b*, 95	64565, 65665*	*U. coritana* var. *media*
III		16, 18, 25, 35, 42, 48, 82	05424, 27757*†	*U. carpinifolia* sens. str.
IV		26, 46	33566, 44668†	*U.* ?aff. *carpinifolia* sens. str.
V			42600, 73935†	
	a	70, 92	52631, 53834†	*U. coritana* var. *rotundifolia*
	b	52, 90	42704, 63915†	
	c	91	72620†	
VI		07, 85*b*	57121, 59232*	*U. glabra*
VII			48341, 49556†	
	a	15	49551†	*U. glabra-carpinifolia*
	b	61*b*	48346†	*U. glabra-carpinifolia* *U.* ?aff. *carpinifolia* sens. str.
VIII			10514, 13617†	
	a	50	10514†	
	b	62	13617†	*U.* ?aff. *coritana* var. *angustifolia*
IX		81	35922†	
X		32	43929†	
XI		06	41334†	*U. plotii-carpinifolia*

An examination of Fig. 3 indicates that the elms collected fall into a number of groups and subgroups. These are listed in Table 2, together with the minimum and maximum values for the five characteristics studied in each assemblage; a note is added on the probable relation of each assemblage to the elm species and varieties recognised by Tutin (1952). A hyphen is used to indicate intermediate characteristics, not necessarily hybridity.

AXONOMIC ANALYSIS

It will be assumed that the groups and subgroups listed in Table 2 are genetically diverse entities. Without transplantation experiments it is impossible to rule out the possibility that some of the differences observed are environmental rather than genetic, but it seems improbable that environmental effects are a major source of variation because (*a*) within a single tree or clonal stand, variation in the characteristics investigated was usually very small, (*b*) no correlation was detected between any particular type of variation and habitat, and (*c*) striking differences were frequently noted between adjacent clones in a single hedgerow.

Coming now to the groups recognised, it is evident that group I is a highly variable assemblage showing smooth intergradations between the extremes. The subgroups are interconnected thus :



I*a* is a large assemblage characterised by a low tooth number and low obversity; it includes both smooth and scabrous leaved types. It is closely connected to I*g*, a scabrous-leaved type with notably broad leaves, to the smooth-leaved subgroup I*b* with rather long petioles but low asymmetry, and to I*h*, characterised by its high tooth number.

A very homogeneous assemblage is constituted by I*d*, with both smooth and scabrous leaved representatives; the tooth number is high, the obversity low. I*a* and I*d* form a ring with I*e* and I*f*. I*e* resembles I*d* in its low obversity, while I*f* has rather narrow leaves with shortish petioles.

I*c* stands rather apart from the others. It has broad leaves with very long petioles and highly asymmetrical bases.

It is clear that I as a whole, excluding perhaps the scabrous members, comes within *U. carpinifolia* Gled. as interpreted, for instance, by Rehder (1940). In the rest of this paper, *U. carpinifolia* will denote this broad conception of the species; *U. carpinifolia* Gled. emend. Melville (1946) will be referred to as *U. carpinifolia* sens. str. The scabrous-leaved types are intermediate between *U. carpinifolia* and *U. glabra* Huds. Attempts, however, to equate the subgroups with Melville's microspecies are difficult. The type description of *U. diversifolia* Melville (1939) applies to some members of I*a*, though the coexistence of asymmetrical and symmetrical leaves on dwarf shoots from the same tree was never observed. I*b* and I*h* also come fairly near to *U. diversifolia.* It should be pointed out, however, that the straight-sided leaf margin making a right-angle turn into the petiole, regarded by Melville (1946) as diagnostic of *U. carpinifolia* sens. str., occurs in some members of I*a* and in I*h*. I*c* has a remote affinity to *U. coritana* var. *media* Melville

(1949), but the leaves are narrower, and the petioles longer, than in the type description of this variety. I*d*, I*e*, and I*f* do not correspond closely with the type descriptions of any of Melville's segregates.

The second largest group, II, is quite sharply differentiated from I. The principal subgroup, II*a*, has ovate to orbicular leaves with a low tooth number. The leaves are usually scabrous but exceptions occur. Two samples with a higher tooth number are relegated to II*b*; these forms have smooth leaves.

The scabrous members of II*a* correspond exactly with *U. procera* Salisb. The smooth-leaved members of this subgroup are more of a problem. Their relationship with *U. procera* is obviously close. On the other hand, they might be regarded as extreme forms of *U. carpinifolia*; they bear some resemblance to the microspecies *U. coritana* but do not correspond at all closely with either var. *rotundifolia* Melville, which has fewer teeth and more symmetrical leaves, or with var. *media*, which has longer petioles and more highly asymmetrical leaves. Another possibility is to regard these forms as intermediate between *U. procera* and *U. carpinifolia*. II*b* can probably be classed as a member of *U. carpinifolia*, since the high tooth number as well as the smooth leaf surface differentiate it fairly sharply from *U. procera*. It corresponds quite closely with *U. coritana* var. *media*.

III includes a set of narrow-leaved elms with high tooth numbers. They differ from I*f* in having longer petioles. Forms with smooth and with scabrous leaves both occur. The group, in spite of its scabrous tendency, can probably be classified under *U. carpinifolia*. The allocation to a microspecies is less certain. The nearest is *U. carpinifolia* sens. str., but only some members of III show the straight leaf and right angle turn into the petiole characteristic of this segregate.

IV differs from I*a* in the longer petiole, greater asymmetry and higher obversity. It clearly comes under *U. carpinifolia*, but does not correspond well with any of the microspecies. Sample 26 has the characteristic leaf shape of *U. carpinifolia* sens. str. but in other respects recedes considerably from the type description of this segregate.

Five samples, 52, .70, 90, 91 and 92, though all significantly different from each other and from II, the nearest group, resemble each other in being smooth and broad-leaved elms with relatively few teeth, markedly long petioles and low asymmetry. They are associated into group V. The two samples of V*a* differ from V*b* in their rather shorter petioles and more pronounced basal asymmetry. Sample 91, the sole representative of V*c*, has broader leaves than either of the other subgroups and very low obversity. The group as a whole comes within *U. carpinifolia*, but is far more sharply separated from the other members of this species than any of the segregates hitherto considered. As will be seen below, this group has a distinctive geographical distribution. V*a* is fairly close to *U. coritana* var. *rotundifolia* though having a rather longer petiole. The other two subgroups do not correspond closely with any of the previously described segregates.

The two scabrous-leaved samples 07 and 85*b*, though differing significantly in tooth number, agree in having broad leaves with very shortpetioles, low asymmetry and low obversity. They are typical representatives of *U. glabra*, and are consigned here to group VI.

Three samples were collected which were intermediate between VI and the smooth-leaved elms of I. Sample 04 has broad scabrous leaves with an intermediate tooth number, the petiole being significantly longer than in VI. It approaches close to sample 64 of I*d*, but the leaves are slightly more symmetrical. Samples 15 and 61*b* resemble VI in their high tooth number, but in other respects, including the smooth leaf surface, come fairly close to I*d*. These last two samples differ considerably from each other, 15 having longer petioles and much lower obversity than 61*b*; they are therefore relegated to separate subgroups, VII*a* and VII*b*, respectively, of a single group. This group and 04 are clearly intermediate between *U. carpinifolia* and *U. glabra*; 61*b* has the characteristic leaf shape of *U. carpinifolia* sens. str.

Of the remaining samples, two, 50 and 62, agree in being very narrow-leaved types with low asymmetry. In other respects they are remote from one another, 50 having much fewer teeth. Both these samples differ from I*a* in their low asymmetry and fairly high obversity. These samples are therefore relegated to separate subgroups VIII*a* and VIII*b* of a single group. Both appear to pertain to *U. carpinifolia*, and 62 approaches *U. coritana* var. *angustifolia* Melville, though it is less asymmetrical than the type. Sample 50 is remote from any of the described microspecies.

Another isolated type is the smooth-leaved sample 81. It comes nearest to I*d* and I*e* but differs in the very long petiole and rather low asymmetry. It is relegated to a separate group IX. It obviously pertains to *U. carpinifolia*, but corresponds to none of the described microspecies.

A much more extreme type, and, in fact, one of the most distinctive elms collected in the whole area, is sample 32. Its outstanding characteristics are its very long petiole and extreme obversity. In addition, the veins leave the midrib at a narrow angle and show a tendency to curve inwards at the apex. This elm, which was only encountered in the vicinity of Buntingford, appears not to have been previously recognised. It could possibly be accommodated under *U. carpinifolia*, but is very remote from the other smooth-leaved elms. It is classed here as the sole representative of group X.

It is convenient, at this point, to refer to those isolated samples which have not been referred here to any group, mainly because of the possibility that further collection will reveal intermediate types connecting them with the groups already recognised. Sample 04 has been discussed already; 12 is close to I*a* but has fewer teeth; 27 is fairly close to I*f* but is considerably narrower. Sample 30 would come into II*a* were it not for its shorter petiole, while it is only the high tooth number that separates 28*a* from III. Sample 34 approaches IV but has a longer petiole; like 26 in this group, it has the leaf shape characteristic of *U. carpinifolia* sens. str.

Elm 17*b* is a small-leaved type. Although so small, its tooth number is not proportionally low, and its other salient characteristics, long petiole, low asymmetry and high obversity, may be consequences of its reduced size. It is possible that such small-leaved types occur sporadically in each of the groups recognized. In the meanwhile, 17*b* will not be placed in a separate group.

An unusual combination of characters is found in 86*a*, in which the narrow scabrous leaves have a high tooth number, short petiole and low obversity. It is possible that this sample may eventually link up with I*d* so that, for the time being, it is not allocated a group of its own.

The last sample to require consideration is 06. This is a type with smooth, moderately broad leaves, few teeth and shortish petioles. Its nearest subgroup is I*a*, but it has the proliferating habit characteristic of *U. plotii* Druce. Typical *U. plotii*, however, which has rather longer petioles, was not collected in the area studied, and sample 06 is probably to be regarded as a form intermediate between *U. plotii* and *U. carpinifolia*. It is relegated here to group XI.

The bearing of these observations on the problem of specific discrimination in *Ulmus* is somewhat intricate. In general, the demarcation of species within a genus depends on the recognition of discontinuities in the range of variation shown by the group as a whole. It is customary, in sexually-reproducing organisms, to distinguish between species proper and hybrids, the latter being usually few in numbers compared with the putative parent species. The genus *Ulmus*, however, is atypical in that, while *U. glabra* regularly reproduces by seed, *U. carpinifolia* and *U. procera* normally reproduce vegetatively,though seed is produced in the former species in very favourable seasons (cf. Henry, 1910). Such vegetative propagation tends to increase and conserve variability (cf. Muller, 1951), and heterozygous types, if well-adapted to their environment, may well equal or even exceed in abundance the relatively homozygous parent types. The frequency distinction, therefore, that normally subsists between species and their hybrids is liable to disappear.

Within *Ulmus*, no fundamental sterility barriers appear to exist between the English species, and hybrids are readily produced (cf. Doorenbos, 1938). The chromosome number of all the English species, is the same, as far as is known, although it is possible that triploid or tetraploid clones may occur, as they do in *U. turkestanica* Reg. (cf. Krijthe, 1939). The subdivision of the genus into species must therefore rest entirely on the discovery of discontinuities, and the data here reported support, on the whole, subdivision of the English elms into the sexually-reproducing species *U. glabra* (VI), and the two vegetatively reproducing species *U. procera* (II) and *U. carpinifolia* (I, III and IV). There are, however, forms intermediate between these species and some of these may well be hybrids, for example VII, intermediate between *U. glabra* and *U. carpinifolia*, but it would be rash to presume too far on this point without further evidence as to the range of variation of each species when not in proximity to the other. Thus, scabrosity in *U. carpinifolia*, as in 64, suggests introgression from *U. glabra*. But it has to be remembered that the juvenile leaves in *U. carpinifolia* are scabrous, and it would probably require only a slight physiological change for this character to persist to the adult condition.

The distinction between *U. procera* and *U. carpinifolia* is also blurred. The smooth-leaved elms in II*a* may well be hybrids, and 24*a* in this subgroup occurs in the region of overlap of these two species, but the full range of variation of *U. carpinifolia* is not yet known, and it is possible that the smooth-leaved members of II*a*, and even more likely, II*b*, are only extreme forms of *U. carpinifolia*.

Further subdivision of *U. carpinifolia* is obviously possible. Melville (1939, 1946, 1949) partitioned it into the three microspecies *U. carpinifolia* sens str., *U. diversifolia* and *U. coritana*, excluding for the moment *U. plotii* and *U. stricta*. The data presented here, however, suggest relationships which cut across and transcend Melville's groups. Thus the large group I includes *U. diversifolia*, forms with a somewhat remote relationship to *U. carpinifolia* sens. str. and *U. coritana* var. *media*, and forms receding considerably from any of these. Typical *U. carpinifolia* sens. str. is found in III, but samples with the characteristic leaf shape of this species appear also in I, IV and VII. *U. coritana* seems a rather artificial aggregate. *U. coritana* var. *angustifolia* is nearest to VIII ; it is very remote from var. *media*, in II, and var. *rotundifolia* in V. Thus the groups derived by the present analysis include, in some cases, several of Melville's microspecies; in other cases, one microspecies has to be partitioned into several distinct groups. A more concordant return would be obtained, however, if Melville's three varieties of *U. coritana* are treated as independent microspecies with an equivalent status to the other two.

It is true that the type descriptions of Melville's microspecies relate to highly characteristic and well-defined entities, but the analysis given here raises considerable doubt as to the status of these types as foci of the populations into which the genus can most naturally be divided. It is indeed probable that further work will reveal more intermediate types and intergroup connections than those here described; this would render the status of the microspecies even more uncertain. The conclusion would seem to follow that the application of Latin names to segregates of *U. carpinifolia* is of doubtful utility.

The data given here are not adequate to discuss the status of *U. plotii* or *U. stricta*, but the indications are that these species might turn out to be nothing but extreme variants of *U. carpinifolia*. Typical *U. plotii* is a very distinct elm with a characteristic habit, but it is probably only a single clone from among many other small-leaved elms that make up a much wider entity, widespread in north Northamptonshire and elsewhere in the northeast Midlands, and which may eventually be shown to intergrade continuously with typical *U. carpinifolia*.

The preceding discussion has been somewhat critical of the status of the microspecies and varieties of *Ulmus* already described. Yet it is clear, in the case of the vegetatively-reproducing elms at least, that taxonomic discrimination is possible between very minute categories, and between individual clones. It is true that many of the samples can be connected into a web in which numerous pairs of samples cannot be significantly separated, but this must not be allowed to obscure the fact that most of the samples do differ significantly from each other. The final picture that emerges is that of an aggregate of clones, perhaps several hundred in East Anglia, whose interrelations can be expressed in an *n*-dimensional network such as that in Fig. 3.

Since the present treatment is perhaps unsympathetic to classical taxonomic procedures, it is pertinent to enquire what is to replace it. It is possible that further work will provide a complete series of intermediates connecting even the major species *U. glabra*, *U. carpinifolia* and *U. procera*. Should then only a single species be recognised ? It is not necessary to go so far. Should morphological discontinuities be absent, it is still possible to utilise discontinuities of another sort.

Thus, it can be seen in Fig. 3 that I*c* (samples 87, 97 and 98) are only connected with the other members of I by a single bond to sample 44. That is, connectivity between I*c* and the rest of I is lower compared with connectivity within I*c* and within the rest of I. Such a zone of low connectivity can be regarded as a type of taxonomic discontinuity and used as a basis for discriminating between the two contiguous groups.

Should even this type of discontinuity fail, it would still be possible to fall back on relatively low frequency of individual types in the field as a basis for discrimination. Thus, even were multifarious connecting links discovered between *U. carpinifolia* and *U. procera*, the greater frequency of elms representing the typical species as compared with the intermediates, would probably, of itself, serve to justify the discrimination between these species.

The present evidence suggests that the three species *U. glabra*, *U. carpinifolia* and *U. procera* can be legitimately distinguished on the basis of one or other of the types of discontinuity discussed above. With regard to the subdivision of *U. carpinifolia*, it seems best to eschew altogether the classical taxonomic categories. As an alternative, subordinate systematic groups can be conveniently defined in terms of the range exhibited in a number of selected characters. In the present paper, five quantitative characters have been principally studied. If each of these is regarded as a dimension in a 5-dimensional anisotropic taxonomic space, then, by citing the lower and upper limit for each characteristic, we define a 5-dimensional parallelepiped, which can then be used as a taxonomic category. This, in fact, is what has been done in Table 2. The highly distinctive assemblage of elms referred to as I*c* can be denoted by *Ulmus* ' 44853, 45973 ' or even by *U. carpinifolia* ' 44853, 45973.' This suffices to exclude all the other elms collected in the area and seems to offer a better and more objective method of characterizing the East Anglian elm population than the taxonomic methods used hitherto.

GEOGRAPHICAL ANALYSIS

The first point requiring mention is the distribution of the zones in which elms were not collected, These include the fens, but exclude the " islands " such as Ely where elms are abundant. This explains why no samples were obtained in minor squares 92 to 97. The chalk scarp, which runs diagonally across the area, is also devoid of elm, but since the scarp is narrow, this feature has hardly affected the sampling. The Breckland (for example minor square 77) provided no elms, and elm is sparse on the limestone outcrop in the extreme north-east part of the area.

The most striking result of the survey in respect of the distribution of the various groups is the discovery that *U. procera*, in the older hedges, does not extend eastward of a line running approximately north-south from Peterborough to Waltham (cf. Fig. 1). This is especially noteworthy in view of the fact that *U. procera* is frequently planted in later hedges and grows well east of this line. It is of interest to note that this line, to anticipate the results of further work, bends round sharply south of our area, and runs eastward, parallel with the Thames, reaching the sea near Shoeburyness. It reappears in east Kent, near Herne Bay, and runs thence in a south-westerly direction, leaving a small area in south-east Kent where *U. carpinifolia* is once again the predominant elm.

U. glabra occurs only sporadically throughout the area, suggesting a relict distribution. It is fairly frequent on the oolitic limestone outcrop, for example, in minor square 07, but this formation only just comes into the area. It is possible, however, that the widespread scabrous-leaved types, here considered under *U. carpinifolia*, have resulted from introgression from this species.

U. plotii, or rather the related sample 06, was only encountered once. This is not surprising since this species is known to be characteristic of the country to the west of Stamford. It appears to reach its eastern limits around Kimbolton.

U. carpinifolia occurs throughout the whole area. It penetrates beyond the eastern boundary of *U. procera*, though with reduced frequency, but how far it extends westward has not yet been ascertained. It has been collected along parish boundary hedges as far west as Bletchley.

What is of more interest is the distribution of some of its constituent groups and subgroups. Thus I*d*, with leaves of medium breadth and high tooth number, is characteristic of the country between Royston and Clare, while the elms with very long petioles and highly asymmetrical leaves that constitute I*c* have only been collected around Thetford. As might be expected, some of the smooth-leaved representatives of II*a*, the subgroup which includes typical *U. procera*, are found where *U. carpinifolia* and *U. procera* overlap, for example, 24*a*. Samples 56 and 57, however, which also belong to this subgroup, were collected in hedges adjoining the fens.

III, the group of narrow-leaved elms with a high tooth number, is fairly widespread, but especially frequent in Huntingdonshire and the adjacent parts of Cambridgeshire, e.g. 16, 18, 25, 35 and 48. IV was only collected in Cambridgeshire.

With the broad-leaved elms in V, a totally different area is concerned. V*a* was only observed in the coastal region of Essex. Sample 90 of V*b* grows alongside the Blackwater estuary, while 52, which is the least typical representative of the group, was the only inland specimen. Sample 91 of V*c* also came from near the Blackwater estuary. V extends south beyond our area to the estuary of the Crouch, but is then replaced by *U. procera*. South of the Thames, it has not been found. *U. procera* occurs along the north Kentish coast as far east as Herne Bay, while in Thanet some very small-leaved elms, most nearly resembling some of the elms of the Lincolnshire limestone, appear. It is not known how far north of Colchester V extends, but the elms around Walton-on-the Naze and along the Norfolk coast are totally different. This group, then, which is very distinct from all other elms, seems to be quite narrowly localised along the Essex coast.

The other groups of *U. carpinifolia*, VIII, IX and X, are only known from single collections. It is possible that these, especially the very distinctive sample 32, are single extremely localised clones, but more intensive sampling would be necessary to confirm this.

It is not supposed that the sampling procedure utilised in this study is at all adequate for ascertaining the precise geographical limits of the various groups recognized. There is every reason to suppose that the overall pattern of distribution is extremely complex, rather in the nature of a jig-saw puzzle involving a large number of distinct clones.

The topocline concept has been applied to East Anglian elms (cf. Melville, 1949); the present evidence suggests that this concept is too coarse and involves far too great a simplification of the data to warrant its use. None of the five quantitative characteristics studied here show any simple relationship with geographical direction.

HISTORICAL ANALYSIS

It is pertinent to inquire what light the above data throw on the history of the genus and on the general question of the sequence of postglacial vegetation in this country.

Many lines of evidence suggest that the present distribution of the three major species, *U. glabra*, *U. carpinifolia* and *U. procera*, may be of considerable antiquity. The earliest account that differentiates satisfactorily between the British species is in the 1633 edition of Gerard's Herball, where their relative distribution appears to be more or less the same as now. Earlier than this there is little direct evidence, but it is possible to draw some inferences from the distribution of place names and surnames derived from elms, and from mention of elms in early documents, in particular charters.

In East Anglia, the surnames Elmes and Elmy occur in the seventeenth century Hearth Tax returns for Suffolk and in early wills pertaining to Essex, Huntingdonshire, Norfolk, Northamptonshire and Suffolk; the Latin rendering de Ulmis also occurs. Making due allowance for migration, there seems no reason to doubt that elms were sufficiently widespread in the Middle Ages to afford a basis for East Anglian surnames.

Place names take us back much further. There are three etymological roots to consider, the Anglosaxon *elm* and *wice* and Celtic *lem*. Parish names in our area thought to be based on *elm* include Elmdon and Elmswell; those based on *wice* include Witchford and Witcham (cf. Ekwall, 1947). Other parish names based on these roots occur in the adjacent regions. No examples based on *lem* have been detected in major square 52, but the River Lymn in Lincolnshire and Lympne (Rother), from which the Kentish parochial names Lympne and Lyminge originate, are believed by Ekwall (1928) to be derived from this root.

It is highly probable that all these etymological roots refer to elm in general, without restriction to particular species. The suggestion of Hoops (1903) that *elm* is *U. campestris* L. (i.e. *U. carpinifolia* or *U. procera*) and *wice*, *U. montana* Stokes (i.e. *U. glabra*), appears to be based on very tenuous grounds; the argument from modern English usage is particularly weak since this dates back no further than the eighteenth century. In Gerard's Herball, *U. carpinifolia* is called *wych*; earlier still in Turner's list of plant names (1548) and in the fifteenth century *Promptorium parvulorum*, *elm* and *wich* appear to be used indifferently for elms in general. Cognates of *elm* occur in High German and in the Scandinavian languages. *Wych* corresponds to the Low German *Wiecke* or *Wietzer*, also with the Slav *vyaz* and the Lithuanian *vinkšna* (cf. Pokorny, 1930). A whole series of etymological roots for the elm occur on the continent; in Germany, in addition to the two already cited, there is a root *ip*, corresponding to the Dutch *iep*, and a root *rust*, in addition to the borrowed *Ulme*. In the Slav languages, there is also a root *brest* and words based on the borrowed Teutonic root *elm*. It may well be that, at certain times and in certain places, these terms have been used differentially to discriminate between different types of elm, but there is little satisfactory evidence of any consistent discriminant usage. In England, the distribution of place names based on *elm* and on *wice* suggests different linguistic traditions in different regions rather than a reflection of regional differentiation in the elms themselves. Thus, parish names based on *elm* are conspicuous in Kent, Essex and Suffolk, but no names based on *wice* are reported (cf. Ekwall, 1947); in Cambridgeshire, Norfolk and Northamptonshire, the reverse situation occurs. It will therefore be assumed that place names involving (1) *elm* or *wice*, or (2) the Celtic *lem* indicate the presence of elms in post-Roman and pre-Roman times, respectively, without any restriction as to species.

The next step in our argument, namely, the postulation that the species or clones, frequent in the ancient parochial hedges in localities whose names indicate the presence of elms in earlier times, are the descendants, sexual or vegetative, of the earlier elms, is obviously more hazardous. The alternative, however, would require the extinction of one type of elm and its replacement by another, which is obviously a more elaborate and less likely hypothesis.

Other lines of evidence, too, provide grounds for supposing that the present elms have persisted *in situ*, at least since Roman times. The elm played an important role in Roman agriculture as a forage plant, in addition to its use as a timber and shade tree and as a support for vines. Cato gives instructions for planting elms around fields and along roads; the somewhat discrepant accounts of Pliny and Columella indicate clearly that the Romans distinguished between different types of elm in respect of fodder value and introduced clonal material from one region into another. The value of the elm as a source of fodder is reiterated in the Middle Ages by de Crescentiis, and the fact that it was so employed in England is stated in the writings of such early English agriculturalists as Fitzherbarde (1534) and Markham (1631). It is quite feasible that a number of Roman farming practices were perpetuated after the Anglosaxon invasions. Gray (1915) has shown, with reference to field systems, that this may be particularly the case in Kent and East Anglia. It seems reasonable, therefore, to suppose that elms were extensively distributed in eastern England in Roman times and have persisted since then without major distributional change.

There is no reason to suppose, however, that the Romans are responsible for the present pattern of distribution. Elm has been a conspicuous component in the British flora since mesolithic times (cf. Godwin, 1940). The earliest type was presumably *U. glabra*. This is not a frequent species in old hedges in East Anglia, and the present distribution suggests that it may be a relict species.

U. carpinifolia is abundant in East Anglia and occurs also in East Kent; it is probably the species that gave rise to the Celtic place names based on *lem* in Kent and also to the frequent East Anglian place names based on the Anglosaxon *elm* or *wice*. The fact that this species is seldom found in woods makes it rather doubtful whether it occurred in England before the opening up of the country by neolithic agriculturists, unless, possibly, it was present in some open communities no longer extant. The failure of the species to set seed except in exceptionally favourable seasons suggests that it has been introduced, directly or indirectly, from warmer regions to the south.

The present evidence, therefore, seems to suggest that *U. carpinifolia* was introduced by, or in the wake of, settlers arriving in England from the east and settling both in Kent and East Anglia, some time in the neolithic, Bronze or Iron ages. Intensive study of the distribution of the English clones composing *U. carpinifolia* and a comparison between these and those of the European seaboard might well throw further light on the source and date of this introduction.

U. procera presents a much more difficult problem. It only occurs along the western edge of our area, and, although it is generally recognised as a Midland species, no detailed knowledge has been obtained yet as to its distribution in the Midland counties. It is known to extend eastward along both sides of the Thames estuary, severing the East

Anglian and Kentish populations of *U. carpinifolia*. It is obviously premature, therefore, to speculate as to its early history, but it may prove useful to list the following facts, which will have to be taken into consideration when adequate distributional data have been obtained. In the first place, place names based on *elm* or *wice* are rare in the Midlands, and agricultural settlement appears to have been sparse till well after Roman times (cf. Darby, 1936). It therefore seems probable that elms were relatively infrequent in this region in early times as compared with East Anglia. However, the absence of *U. procera* from East Anglia and eastern Kent suggests that this species did not migrate into England from the east. *U. procera* does not appear to be known as an indigenous tree on the continent. *U. procera* var. *australis* (Henry) Rehder from southern Europe is very remote from the typical variety and should almost certainly be excluded from the species. *U. procera* occurs in Spain, and samples from Aranjuez and Mondoñedo in the Cambridge Herbarium are indistinguishable from English material. It seems probable that the Spanish trees were, as stated by Evelyn (1679), introduced into Spain from this country.

It would therefore appear that the origin of *U. procera* must be sought somewhere in the English Midlands. Possibly it arose as a single local clone and became widely spread on account of such desirable characters as straight bole and late defoliation. Its relation to *U. carpinifolia* is problematical. Transitional forms, notably II*b* and the glabrous members of II*a*, occur, and, of these, samples 86*b* and 95 of II*b* are from far beyond the eastern limit of *U. procera*. It may be, then, that *U. procera* arose from some such type of *U. carpinifolia*, the scabrous character deriving either from a persistence of the juvenile condition or from introgression from *U. glabra*. On the other hand, it is quite likely that some intermediates between *U. procera* and *U. carpinifolia* are later hybrids.

The data presented here are not adequate to discuss the history of *U. plotii*.

SUMMARY

A technique for analysing the taxonomic variation of East Anglian elms is described, based on systematic sampling of the boundary hedges of ancient parishes. Five quantitative and one qualitative leaf characters were determined for each sample, and the degree of affinity between samples was ascertained by a graphical method based on an application of the *t* test. As a result of this approach, eleven taxonomic groups could be distinguished within the genus, together with a number of subgroups. The three major species, *U. glabra*, *U. carpinifolia* and *U. procera*, were fairly satisfactorily distinguishable, but the groups here recognised both cut across and transcend the segregates of *U. carpinifolia* recognised in the new *Flora of the British Isles*. It seems probable that *U. carpinifolia* is composed of a large number of distinguishable clones, and it is doubtful whether any useful purpose is served by applying Latin names to assemblages of these. A method of characterising the clones and clonal groups numerically is described.

U. glabra occurs sparsely in the area studied; *U. carpinifolia* is widespread; while *U. procera* hardly occurs east of a line running from Peterborough to Waltham. Many of the recognised groups and subgroups of *U. carpinifolia* have characteristic geographical distributions.

The evidence suggests that *U. carpinifolia* was introduced from the east as a forage plant, sometime in the neolithic, Bronze or Iron ages. *U. procera* appears to have arisen somewhere in the Midlands, whence it is spreading eastward.

It is considered likely that an intensive study of the distribution and relationships of the individual clones of *U. carpinifolia* would throw an interesting light on the history of agricultural settlement in England.

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