Multivariate analysis of the elms of Northern France. I. Variation within France

R. H. RICHENS[1]) and J. N. R. JEFFERS[2])

(Received January I November 1975)

Introduction

The many problems surrounding the complex variation of the genus *Ulmus* L. in England have been discussed by RICHENS (1967) and JEFFERS and RICHENS (1970). It has become evident that further progress towards an understanding of the situation in England depends upon comparative studies between the elms of England and those of France, whence, almost certainly, many of the English elm stocks have been derived. This study is a first step towards providing such comparative material.

Material and Methods

The material used was a set of 655 samples. The major collections were made by the first author in Guernsey (1965), Jersey (1971), Picardy and Normandy (1972) and Brittany (1973); other collections were donated by J. R. RICHENS from the Sologne, T. M. RICHENS from Armagnac, Mrs. LE SUEUR from Jersey and Mrs. LE QUESNE from Alderney. Some small collections from other regions have also been included.

Since a comparison between the elm populations on either side of the English Channel was regarded as especially necessary, steps were taken to assemble a representative collection of samples from all the maritime departments of France from Nord to Loire-Atlantique. In addition to these, the department of Orne was also traversed. Material was obtained from all five of the larger Channel Islands. It is likely that all the types of elm of apprwiable frequency in northern France are covered by the various collections. For the rest of France, ony scattered material was available, and no conclusions are drawn on the situation at lower latitudes.

The method of collecting was as described by JEFFERS and RICHENS and the same foliar characters were measured as used in that paper, namely: absolute length of the longer side of the lamina (AL); breadth (TB), length (TL) and depth (TB) of the primary teeth at the shoulder of the leaf; relative breadth of the lamina (RB), the ratio maximum absolute lamina breadth (AB)AL; relative petiole legnth (RP), the ratio absolute petiole length (AP)AL; relative asymmetry (RA), the ratio absolute distance between the lower points of the lamina on each side (AA)AL; and the number of secondary teeth (TN).

The three measurements of thooth size were illustrated by RICHENS (1958). In contrast to earlier studies, only one instead of five typical subdistal leaves from dwarf shoots on stout branches was measured, though five leaves from each tree were collected.

It will be convenient to introduce a new notation to designate the measurements for individual leaves or the modal leaf measurements of groups. The range of each character is divided into three segments, a central mid-range segment, roughly one fifth of the range, and the segments on either side of this. If a measurement falls within the central segment, it is ignored; if the measurement is numerically above it, it is denoted by a capital letter and if below by a lower-case letter. The relevant letters for the range segments of each character are listed in *Table* 1. Tooth length, being strongly correlated with tooth breadth, is ignored for descriptive purposes.

Table 1. — Key to notation

AL	$l < 50$ mm	L	> 59 mm
TB	$b < 5.0$ mm	B	> 5.5 mm
TD	$d < 2.0$ mm	D	> 2.0 mm
RB	$w < 0.60$	W	> 0.69
RP	$p < 0.08$	P	> 0.11
RA	$a < 0.08$	A	> 0.11
TN	$n < 90$	N	> 109

For example, the leaf measurements of the sample from Doullens (Somme) were, in the order cited above, 61 mm, 3.0 mm, 1.0 mm, 0.55, 0.12, 0.09, 136. This leaf is designated LbdwPN. Since the relative asymmetry falls within the central segment of the range, it is omitted.

A similar notation is used to designate the mode of the leaf characters of groups. For these, the three range segments of each character are added separately, and whichever is greatest, taken as the modal value, preference being given to the mid-value when two values are equally frequent.

The method of multivariate analysis was as described by JEFFERS and RICHENS, i.e. principal-component analysis and clustering by means of a modification of the minimum spanning tree technique of GOWER and Ross (1969). As before, the ratios RB, RP and RA were converted back to the respective absolute values AB, AP and AA. An even severer distance restriction was imposed than previously. Clustering was inhibited unless members were within a distance of 1.00. The first-order clusters were themselves aggregated into second-order clusters and thence into higher-order clusters under this restriction till no more clusters could be formed. The distance restriction was then relaxed to 1.50 and a second cycle of clustering initiated till, again, no more clusters were formed. Cycles of clustering continued thus, with distance restrictions relaxed by 0.50 per cycle until the unit cluster was reached.

Clusters are designated by the notation already explained. A prefixed italic capital letter is used to designate the order of the cluster, thus *C*.LbdwPN designates the third-order cluster into which the Doullens sample already cited will be found to fall. Numerical subscripts are used to distinguish clusters with the same biometric designation.

Since second and higher-order clusters are liable to become too heterogeneous to be taxonomically useful, they were disqualified if they comprised *A* clusters whose modal biometric designations included both upper and lower values for any character. For example, the *A* clusters *A*.LbPa, *A*.bPa, *A*.bPan, *A*.bdPa qualify for aggregation under the B cluster *B*.bPa. However, the *A* clusters *A*.bWN and *A*.LbwP which aggregate under a potential B cluster, disqualify this cluster since W and w are both present.

[1]) Commonwealth Bureau of Plant Breeding and Genetics, Cambridge.

[2]) Institute of Terrestrial Ecology, Merlewood Research Station, Grange-over-Sands, Cumbria.

Results

The main results of the computations are set out in *Tables 2, 3 and 4*. *Table 2* presents the minimum, mean and maximum values and standard deviations of the eight foliar characters. *Table 3* provides the coefficients of correlation between the characters, while *Table 4* lists the first four principal components derived from these and used in the subsequent clustering.

Table 2. — Minimum, mean and maximum values and standard deviations of the foliar characters

Character	Minimum	Mean	Maximum	Standard Deviation
AL	29	59.7	138	13.3
TB	2.0	4.23	7.5	0.903
TL	2.5	4.41	7.5	0.904
TD	1.0	2.06	4.5	0.546
AB	20.4	38.7	68.0	9.40
AP	1.64	7.09	15.60	2.23
AA	0.67	5.24	16.56	2.78
TN	42	100.4	248	28.0

Table 3. — Coefficients of correlation

TB	0.622						
TL	0.600	0.936					
TD	0.494	0.718	0.787				
AB	0.865	0.737	0.697	0.653			
AP	0.272	0.196	0.125	0.035	0.278		
AA	0.582	0.415	0.342	0.308	0.642	0.494	
TN	0.682	0.262	0.283	0.294	0.646	0.272	0.559
	AL	TB	TL	TD	AB	AP	AA

Table 4. — First four principal components

		1	2	3	4
	Latent Root	4.63	1.46	0.82	0.38
	% Total variance	57.9	18.3	10.2	4.7
Latent vector elements	AL	0.9245	0.2650	0.3817	0.3482
	TB	0.9025	—0.6331	—0.3561	0.0572
	TL	0.8865	—0.7587	—0.2538	0.1326
	TD	0.7980	—0.7615	—0.0352	—0.2024
	AB	1.0000	0.0834	0.2168	0.0147
	AP	0.3846	1.0000	—1.0000	0.4665
	AA	0.7379	0.8166	—0.1530	—1.0000
	TN	0.6927	0.7737	0.7251	0.3093

The clusters built up as follows. In the first cycle (distance restriction of 1.00), the 655 samples fell into 216 *A* clusters and then into 114 *B* clusters, of which 2 were disqualified by the heterogeneity test. No further clustering occurred at a distance restriction of 1.00 so the second cycle at a distance restriction of 1.50 was entered. The 112 accepted *B* clusters, in their turn, fell into 33 *C* clusters, of which 14 were disqualified, and the residual 19 *C* clusters into 13 *D* clusters, of which 5 were disqualified. No further clustering occurred at the distance restriction of 1.50 so the third cycle at distance restriction of 2.00 was entered. The residual 8 *D* clusters fell into 4 *E* clusters, of which only one survived the heterogeneity test, and this survived one further clustering to the *F* level, after which the disqualified unit *G* cluster was attained.

We are thus left with an overall aggregation into 16 *A* clusters, 58 *B* clusters, 11 *C* clusters, 7 *D* clusters and 1 *F* cluster and these are set out, in ascending order of character designation in *Table 5*. This table also allocates the groups to the usual taxonomic taxa and lists the departments in which they were collected. These are set out in order from east to west for Nord to Manche, then the Channel Isles, then around Brittany to Loire-Atlantique; other departments then follow in alphabetic order.

The taxa to which the clusters in *Table 1* pertain are *U. minor* Mill. *(Um)*, *U. procera* Salisb. *(Up)*, *U. glabra* Huds. *(Ug)* and hybrids between *Um* and *Ug* (*Umg*.) The number of clusters of each taxon or combination of taxa are as follows: *Um*, 47; *Ug*, 3; *Umg*, 29; *Um, Umg*, 4; *Ug, Umg*, 5; *Up, Umg*, 1; *Um, Ug, Umg*, 1; *Um, Up, Umg*, 1; *Up, Ug, Umg*, 1. The greatest number of accepted clusters thus pertains to *Um*, followed by *Umg*. Only a few clusters are pure *Ug*. Several clusters range either from *Umg* to *Um* or from *Umg* to *Ug*. The very rare *Up* is dispersed among three heterogeneous clusters.

It is noticeable that the higher-order clusters tend to be assorted with cluster modes in the higher numerical ranges of the characters.

It is interesting to see to what extent the initial *A* clusters are localized. Of the 170 *A* clusters with more than one member, 39 comprise samples from only one or two adjoining departments. It is clear, however, particularly in cases where additional characters and diverse distribution indicate within-cluster heterogeneity, that the same *A* clusters may comprise populations that are quite distinct. Thus

Table 5. — Characterization and distribution of clusters.

B. lbdn(*Um*): Calv, Mche(2), IV, CN, Fin, Morb
B. lbdPan$_1$(*Um*): PC, So, Mche(5), Je, CN(2), Fin, Morb, Gers, LC(2), Lot
B. lbdPan$_2$(*Um*): Nd, Eu, Mche(4), IV, CN(2), Fin, Sthe
B. lbdPan$_3$(*Um*): So, CN, Fin, Morb, Gers, ML
C. lbdPa(*Um*): SMar, BR, Gers (2), Lret, Sthe
B. lbdWPA(*Um*): Calv
B. lban$_1$(*Um*): Calv, Mche(8), Je(2), Fin(4), Gers, LC(2), Lret(2)
B. lban$_2$(*Um*): Mche(2), Je, Gu, CN, Fin, LAtl
B. lban$_3$(*Um*): PC(2), Mche(2), CN, Fin, LC
F. lbPAn(*Um*): Mche
B. lbWPn$_1$(*Um*): SMar(2), Je, IV(2), Fin(4)
B. lbWPn$_2$(*Um*): Calv, Mche(2), Gu, Fin, Morb, LC
B. lbWPAn(*Um*): Mche, Gu, Fin
B. lan(*Um*): CN, Fin(3)
B. bdwPan(*Um*): Mche(3), Je, Ald, IV(2), CN, Fin(2), Morb
B. bdwPA(*Um*): Calv(3), Gers, Lret, Oi
B. bdN(*Um*): PC(3), So(3), Eu(3), Or, Mche(2), EL
B. bdPa(*Um*): PC, Calv(2), Mche(2), Je(2), EL, Sthe
B. bdPaN(*Um*): Gers
B. bdPn(*Um*): SMar, Eu, Or, Mche(2), Morb
B. bdP(*Um*): PC(2), SMar, Eu(4), Or, Calv(3), Mche(2), Je, Gu, IV(3), CN(2), Fin(2), Morb(6), LAtl(2)

Continued from Table 5

Continued from table 5

B. bdPN(*Um*): PC, SMar, Eu(2), IV, LAtl(2)
B. bdPAN(*Um*): SMar(2), Or, Calv(2), Mche, CN
B. bwan(*Um*): Or(2), IV, Fin, Gers
A. bwaN(*Um*): Eu, Je, LC
B. ba_1(*Um*): Nd, PC, So(2), Eu, Mche(2), Je(5), Gu, Ald, CN(2), BR, Gers (2)
B. ba_2(*Um*): So, SMar, Je(2), IV(3), CN, LAtl
B. b_1(*Um*): PC, So, Mche, Je(4), IV, Morb, Oi
A. b_2(*Um*): PC, Or, Mche, Gu(2)
A. b_3(*Um*): Calv, Je, Gu, IV
B. bPa(*Um*): PC, So, Eu, Or(2), Calv(2), Mche(3), Je, IV, CN(2), Fin(3), Fin(3), Morb(3), LAtl, HSne
B. bP(*Um*): Or, Calv, Mche, Morb
B. bPn_1(*Um*): PC, SMar, Mche(2), Gu, IV(4), CN(8), Fin(4), Morb(2), LAtl, Oi
B. bPn_2(*Um*): So, SMar(3), Or, Calv, Mche, IV, CN, Fin(2), Morb, LAtl, Sthe
A. bP(*Um*): Or, Calv, Mche, Morb
A. bPAn(*Um*): Calv, Mche, Gu, IV, CN, AlpM
A. bPA(*Um*): So, SMar, Mche
A. bPAN(*Um*): PC, So, SMar, Mche(2)
A. bWaN(*Um*): So, Je(2)
A. bWN(*Um*): AlpM(2)
A. bDpa(*Um*, *Umg*): PC, Or, Je, Sk, Gers
C. bDan(*Um*): PC(2), SMar, Eu(3), Or, Mche(2), Je(3), Gu(2), Ald, Herm, Sk, IV(2), CN(4), Fin(6), Morb, LAtl, BAlp, BR, EL
A. bDa(*Um*): Je(2), Gu, Morb, Gers
C. Dp(*Up*, *Ug*, *Umg*): PC, SMar, Calv, Mche, Je, Gu, Herm, Sk, IV, CN
C. DP(*Um*, *Umg*): PC, SMar, Mche(6), Je(2), Sk, IV(3), Morb, LAtl, AlpM(2), EL, SL
C. LbdwPN(*Um*): PC(6), So(5), Eu(3), Se, Gers
B. LbdwPAN(*Umg*): SMar
A. LbdaN(*Um*): Eu(2), Se
D. LbdWPAN (*Umg*): Or
A. LbwP(*Um*): Or(2), IV
B. LbwPAN(*Umg*): Eu
B. LbpN(*Ug*): Calv
A. LbaN(*Um*): PC, Mche
D. $LbPN_1$(*Um*, *Umg*): PC So, Eu, Or, Calv(2), Mche, Gers
B. $LbPN_2$(*Um*): PC(3), So(2), Eu, Or(3), Calv(2), Mche, IV, Oi, BAlp, Ch, Gers
C. LbPAN(*Um*, *Umg*): PC, So, Eu(6), Or(2), Calv(9), Mche(6), Je(2), Gu, Ald, IV, Fin, LAtl, AlpM(3), Aube, Lot, Oi, Sthe
B. LbWaN(*Umg*): PC
B. LbWAN(*Umg*): Calv
C. $LbDpaN_1$(*Ug*, *Umg*): So(2), Eu(2), Or, Calv, Mche, Gu, Ald(2), Fin, Gers, LC
C. $LbDpaN_2$(*Ug*): PC, Mche
B. LbDPN(*Umg*): HRh
B. LbDPAN(*Umg*): Calv
B. LbDWPAN(*Umg*): Morb
B. LaN(*Umg*): CN, Dord
B. L(*Umg*): Or, Mche
B. LDwpN(*Ug*): Je
C. $LDpaN_1$(*Ug*, *Umg*): Eu, Calv
B. $LDpaN_2$(*Ug*, *Umg*): Gu, Fin
C. $LDpN_1$(*Ug*, *Umg*): Eu, Calv
B. $LDpN_2$(*Umg*): PC(2), Or(3), Mche
B. $LDpN_3$(*Um*, *Ug*, *Umg*): So, Mche, CN, AlpM
B. LDN(*Umg*): Calv
B. $LDPN_1$(*Umg*): Calv(2), Mche(2), Je(6), Ald(2), Sk(2), Sthe(2)
B. $LDPN_2$(*Umg*): PC(2), Mche(2), Gu, Ald
C. $LDPAN_1$(*Umg*): Mche, Je(2), Gu(2), Ald(3)
A. $LDPAN_2$(*Umg*): Gu
A. $LDPAN_3$(*Umg*): Je
B. LDWpN(*Umg*): Eu, Mche, Vau
B. LDWpAn(*Umg*): Calv
B. LDWpAN(*Umg*): IV
B. LDW(*Umg*): PC, So(3), Eu, Calv, Mche, Je(8), Gu, IV(2)
B. LDWN(*Um*, *Up*, *Umg*): PC, So(3), Calv(2), Je, IV, CN, BR, Pyr0
B. LDWPAN(*Umg*): PC, So, Calv, Mche(2), Je(3), Gu, Ald(2), CN
D. LBP(*Umg*): Je(2)
B. LBWPAN(*Umg*): Je(2)
D. LBDpaN(*Ug*, *Umg*): Gu, IV
B. LBDAN(*Umg*): PC(2), So, Mche, Je, Ald
B. LBDPn(*Umg*): Calv, Mche, IV
D. LBDWpa(*Up*, *Umg*): PC, So, Eu, Je(2), Ald, IV
D. LBDWpAN(*Umg*): Or
D. LBDWN(*Umg*): Calv, Je(2), Ald, Herm
B. LDwpAN(*Ug*): Je

Abbreviations: Ald, Alderney; AlpM, Alpes-Maritimes; BAlp, Basses-Alpes; BR, Bouches-de-Rhône; Calv, Calvados; Ch, Chers; CN, Côtes-du-Nord; Dord, Dordogne; EL, Eure-et-Loir; Eu, Eure; Fin, Finistère; Gers; Gu, Guernsey; Herm; HRh, Haut-Rhin; HSne, Haute-Saône; IV, Ille-et-Villaine; Je, Jersey; LAtl, Loire-Atlantique; LC, Loire-et-Cher; Lot; Lret, Loiret; Mche, Manche; ML, Maine-et-Loire; Morb, Morbihan; Nd, Nord; Oi, Oise; Or, Orne, PyrO, Pyrénées-Orientales; Se, (Seine); Sk, Sark; SL, Saône-et-Loire; SMar, Seine-Maritime; So, Somme; SO, (Seine-et-Oise); Sthe, Sarthe: Vau, Vaucluse.

cluster B.LBDAN contains six members, three from Pas-de-Calais or Somme and three from Manche or the Channel Islands. Additional characters clearly indicate that these two groups correspond to two distinct populations which, as will be shown below, are *Umg* hybrids of independent origin in each of the two areas.

Additional characters, on the other hand, may sometimes indicate that a single population is represented by a quite extensive range of clusters. A case in point is provided by the small-leaved elms of Guernsey, all of which have a distinct stiff, pyramidal habit, and are likely to be monoclonal. The samples pertain to clusters $B.\mathrm{lban}_2$, $B.\mathrm{lbWPn}_2$, B.lbWPAn, B.bdP, $B.\mathrm{ba}_1$, $A.\mathrm{b}_2$ (twice), $A.\mathrm{b}_3$, $B.\mathrm{bPn}_1$, A.bPAn, C.bDan (twice), A.bDa, C.LbPAN. It is apparent that what may reasonably regarded as a single population can correspond to an assemblage of clusters of this order of magnitude.

Another point arises from the Guernsey assemblage. The cluster C.LbPAN is clearly an extreme form of the Guernsey population. Elsewhere, however, as in region IX (Roumois) below, this cluster is the principal form encountered. It is clear then that the same cluster may be of diverse significance in different populations, sometimes representing characteristics of or near the population mode and at other times, deviation from the mode in one or several respects.

These considerations indicate some of the reservations that are necessary in interpreting the significance of the clusters and their distribution, but, accepting these, and recognizing too that the number of samples is small for so extensive an area, the strikingly diverse patterns of geographical distribution of different clusters admit of considerable inference as to the taxonomic situation and of the history that lies behind it.

The distributions of some representative clusters are illustrated in *Fig. 1*. In *Fig. 1 a*, four small-leaved *Um* clusters are shown, B.lban, $B.\mathrm{lbdPan}_1$, $B.\mathrm{lbdPan}_2$ and B.bdw-Pan. It is immediately apparent that these clusters are concentrated in the Cotentin peninsula and along the north Breton coast. A smaller grouping occurs along the west Breton coast. Elms of this type are virtually absent inland in northern France and they were not found, except very sporadically, between Cotentin and Cap Gris Nez. Behind the latter, however, a small-leaved population was found, and another, further east, in Flanders. Though small-leaved elms were not found in inland locations in northern France, this does not hold further south. Most of the elms of the Sologne are of this type and they are frequent too, much further south, in Armagnac.

The cluster C.bDan, also *Um*, is quite differently distributed *(Fig. 1 b)*. It occurs throughout the Channel Islands but was totally lacking in Cotentin. It is widespread in northern Brittany. It reappears further east in Normandy, but more sporadically.

A third set, still *Um*, constituted by B.bdP, B.bPa, $B.\mathrm{bPn}_1$, $B.\mathrm{bPn}_2$, ist illustrated in *Fig. 1 c*. These elms have leaves of average size and long petioles. They are the characteristic elm of the south Breton coast and are also widespread in inland localities further east. They are not frequent in Cotentin.

Quite a different distribution is shown by the two clusters mapped in *Fig. 1 d*, $B.\mathrm{LbPN}_2$ and C.LbPAN, in which tooth breadth is low and tooth number high. Virtually absent from Brittany, elms of this type are especially abundant in Normandy, extending as far west as Cotentin. They are frequent too in Picardy. The last *Um* cluster whose distribution is illustrated is C.LbdwPN *(Fig. 1 e)*. This cluster represents a prominent elm of Picardy, the only area of north France in which it was found in any abundance.

Figure 1 f represents the distribution of clusters B.LDPN, B.LDW, B.LDWN and B.LDWPAN. Most of these elms are *Umg* hybrids, but it also includes *Up* from Jersey, which on account of its extreme rarity does not separate out into a cluster of its own. The *Umg* hybrids are found in four principal areas: Picardy, Cotentin and the neighbouring Channel Islands, central Normandy and, much less frequently, further south in Perche. These geographically distinct populations can also be differentiated by a combination of their biometric and other plant characters, and there is every reason to suppose that each hybrid focus has been the product of separate hybridization between *Um* and *Ug*.

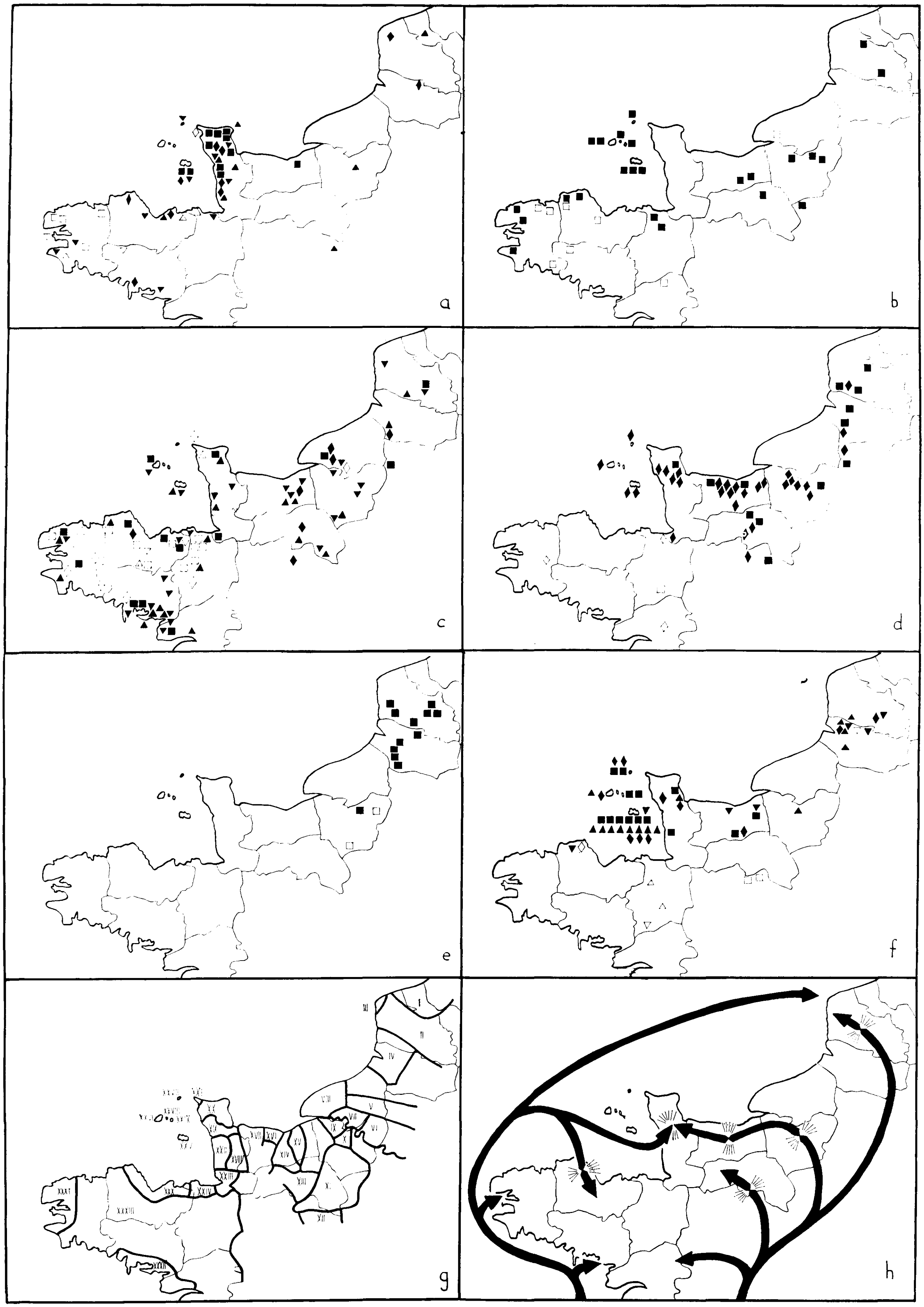
In order to provide some idea of the overall geographical distribution of the various elms studied, the area of the survey has been divided into regions, using three criteria: (1) type and frequency of elm, (2) natural region, (3) historical region, as defined by the dioceses and archdeaconries of the pre-Revolutionary period, these representing, as is well known, administrative units of Merovingian, Roman or even earlier times. These three criteria sometimes give different patterns; in many cases, however, they coincide and can be usefully combined. The areas used here are illustrated in *Fig. 1 g* and their elm floras are briefly characterized as follows.

I. Flanders. The small-leaved *Um* population of this area is represented by clusters $B.\mathrm{lbdPan}_2$ and $B.\mathrm{ba}_1$. Similar elms occur in Belgian Flanders, near the northern limit of high-frequency continuous distribution of *Um* (Huberty, 1904), also across the English Channel, in eastern Kent (Jeffers and Richens).

II. Artois. The elm populations of Artois are complex and there is considerable diversification within the region. Immediately east of the villages behind Cap Gris Nez is a zone of small-leaved elms resembling those of Flanders, represented by $B.\mathrm{lbdPan}_1$ and B.bdN. Around St. Omer, *Umg* hybrids are found, exemplified by C.Dp. In the rest of western Artois the dominant elm is *Um* with long, narrow leaves, mostly C.LbdwPN. In north-east Artois, the same narrow-leaved elm occurs but in company with a distinctive *Umg* hybrid which for convenience will be termed Hybrid I. It is represented by such clusters as D.LDAN and B.LDPN. The tree has a characteristic open,

Figure 1. — Solid marks, elm at high frequency; hollow marks, elm at low frequency.

a. Square, $B.\mathrm{lban}_1$; diamond, $B.\mathrm{lbPan}_1$; vertical triangle, $B.\mathrm{lbPan}_2$; inverted triangle B.bdwPan.
b. Square, C.bDan.
c. Square, $B.\mathrm{bPn}_1$; diamond, $B.\mathrm{bPn}_2$; vertical triangle, B.bPa; inverted triangle, B.bdP.
d. Square, $B.\mathrm{LbPN}_2$; diamond, C.LbPAN.
e. Square, C.LbdwPN.
f. Square, $B.\mathrm{LDPN}_1$; diamond, B.LDWPAN; vertical triangle, B.LDW; inverted triangle, B.LDWN.
g. Elm floristic regions.
h. Putative immigration routes; flash points represent *Umg* hybridization foci.


a
b
c
d
e
f
g
h

scraggy habit and the leaves frequently exhibit early, senescent, black and yellow discoloration. Towards the south-east, hybrid I is also frequent but in company, this time, with elms of biometrically average character, such as *A*.b_2.

III. Cap Gris Nez. The country immediately behind the headland is windswept and trees of any kind, including elm, are infrequent.

IV. Ponthieu. Three types of elm are widespread in Ponthieu. Two of these, the *Um* form with long, narrow leaves and the *Umg* Hybrid I are similar to the same forms described above for Artois. In addition, a third elm with long petioles and numerous teeth, represented by *A*.bPAN and *B*.$LbPN_2$ is present. *Ug*, e.g. C.$LbDpaN_1$, is of scattered occurrence. Hybrid I decreases in frequency towards north-west Ponthieu.

V. Bray. The C.LbdwPN long, narrow-leaved *Um* elms so characteristic of Artois and Ponthieu were not encountered in Bray and the *Umg* Hybrid I extended no further south than the northern edge. The characteristic elms were either biometrically average types, e.g. *B*.b_1 or the long-petiolate form with numerous teeth described from Ponthieu, represented here by *B*.$LbPN_2$ and C.LbPAN.

VI. Vexin. Elms are relatively infrequent in the Vexin and very heterogeneous. *Um, Ug* and *Umg* all occur but no clear picture of distinctive local types was obtained.

VII. North of the Seine. Similar remarks apply as above. Elms are not generally frequent and what was found was a confused medley of *Um* and *Umg* forms.

VIII. Caux. Like the two preceding regions, Caux is an area in which elm is relatively infrequent. All the specimens collected were *Um* but highly heterogeneous, declining in frequency from east to west.

IX. Roumois. In contrast to the areas north of the Seine, where elms are comparatively sparse, the regions immediately south of the Seine abound in elm. In Roumois, two types of elm were collected, towards the north, a small-toothed, long-petiolate *Um* type exemplified by *B*.bdPn and *B*.bdP, and towards the south, an asymmetric, large-leaved type, mostly C.LbPAN.

X. Plain of le Neubourg. The elms collected in the northern part of the plain pertained mainly, as in the adjoining Roumois, to C.LbPAN. Further south, the situation was more complicated, *Um* was represented by long-petoliate forms such as *B*.bdP and *D*.$LbPN_1$. *Ug*, e.g. C.$LbDpaN_1$, occurs, also a distinctive *Umg* hybrid, hybrid II, pertaining to C.LbPAN (though not in the same subordinate *B* clusters as the *Um* elm of this region) and *B*.LbwPAN.

XI. Perche. This extensive inland area, as used here, covers not only Perche in the strict sense but other adjoining thickly wooded areas, in particular Ouche to the north. In general, it is a region in which elm is comparatively infrequent. Towards the north, biometrically average *Um* elms exemplified by *B*.bdP, *B*.bPa and *B*.bP were most frequent, intermixed with a deep-toothed form represented by C.bDan and C.DP. The situation in the south is more complex with a highly heterogeneous admixture of *Um, Ug* and *Umg*.

XII. Sarthe Basin. A small number of *Um* samples was collected from this region, but these were too heterogeneous for any generalization as to the characteristic elms of this region.

XIII. Upper Orne Basin. This region covers Houlme and the country around Sées. *Um* is frequent and fairly uniform in appearance. It was possible, however, to distinguish three types: (1) smal-toothed elms represented by *B*.bdN and *B*.bdPn; (2) low-asymmetric elms exemplified by *B*.bwan and *A*.bDpa; and high-asymmetric elms pertaining to C.LbPAN.

XIV. Hiémois. Elms are frequent in this region and comprise both *Um* and *Umg*. The former are mainly long-petiolate types exemplified by *B*.bdP and *B*.bPa. The *Umg* hybrids are highly diverse; the most frequent cluster was *B*.$LDpN_2$ but eleven others were represented.

XV. Auge. *Um* and *Umg* occur with high frequency and *Ug* (*B*.LbpN) is also present. *Um* is mostly long petiolate, exemplified by *B*.bdPa and C.LbPAN. The *Umg* elms were heterogeneous.

XVI. Plain of Caen. The elms of this region are similar to those in Auge. The *Um* type is largely C.LbPAN. The *Umg* hybrids were heterogeneous.

XVII. Bessin. The elms collected here were a homogeneous *Um* population, mostly *A*.bPAN.

XVIII. Val-de-Vire. Two types of *Um* were encountered. Elms with average-sized leaves were represented by *B*.bdP. Small-leaved *Um* elms as are frequent throughout the Cotentin peninsula also appeared in quantity for the first time; they pertained to *B*.lbdn and *B*.$lbdPan_2$.

XIX. Bauptois. This region comprises most of the low-lying marshy land across the neck of the Cotentin peninsula. Most of the elms were of one of two types. The first is the small-leaved *Um* population already noted in Val-de-Vire, here most frequently *B*.$lban_1$, *B*.$lbdPan_1$ and *B*.$lbdPan_2$. In contrast, a new form of *Umg* (Hybrid III) with average to long-petiolate leaves appeared. This occurs elsewhere in the Cotentin peninsula and in the Channel Islands. It was represented by *D*.$LbPN_1$ and *D*.LDAN.

XX. Cotentin. The region more particularly carrying this description is the northern, more hilly part of the Cotentin peninsula. Elms are frequent throughout the area and include *Um, Ug* (C.$LbDpaN_2$) and *Umg*. As in Bauptois, the commonest *Um* elm is a small-leaved form, most frequently *B*.$lban_1$ and *B*.$lbdan_1$. Less frequently rather heterogeneous large-leaved *Um* forms were also encountered. Hybrid III, represented by *D*.LDAN, *B*.$LDPN_1$ and *B*.$LDPN_2$, occurs in the south of the area. Other *Umg* hybrids, of diverse type, are of scattered occurrence.

XXI. Cap de la Hague. Elms decrease in frequency in this exposed corner of the peninsula. The forms most frequently encountered were small-leaved elms similar to those found elsewhere on the peninsula, and also elms with average-sized leaves, such as *B*.bPa and *B*.bPn_2.

XXII. Coutances. The most frequent elm in this region is again the small-leaved form common in the Cotentin peninsula, e.g. *B*.$lbdPan_1$, *B*.$lban_1$ and *B*.$lban_3$. Various larger-leaved forms were also found, such as *B*.bdPa, *B*.bdN and *B*.bdPAN. Hybrid III is found in the north of the area, represented by *B*.$LDPN_2$ and C.$LDPAN_1$.

XXIII. Avranchin. Small-leaved elms predominate here also, but with a tendency to greater relative breadth than in the Cotentin peninsula, e.g. *B*.$lbWPn_2$. Some small-leaved elms with unusually high asymmetry occur north of Avranches, represented by *F*.lbPAn and *A*.bPAn.

XXIV. Dol. The *Um* elms of this small region have average-sized leaves, e.g. *B*.bPa, C.bDan and C.DP.

XXV. Jersey. Elms are abundant on this island, principally *Um* and *Umg*. *Ug* is occasional and one sample was markedly deviant (*B*.LDwAN). *Up* is also present but rare. Though samples of this species aggregate well into clusters in England (Jeffers and Richens), this did not occur in the present material owing to the paucity of specimens. The Jersey *Up* samples came into C.Dp and C.LDWN. The *Um* samples have leaves of average size, represented, in particular, by $B.ba_1$, $B.b_1$ and C.bDan. The *Umg* samples correspond to Hybrid III, most usually *D*.LDAN and $B.LDPN_1$. In the west of the island, another *Umg* population was found, all *B*.LDW.

XXVI. Guernsey. The situation in Guernsey is similar to but rather simpler than in Jersey. *Ug* (e.g. $C.LbDpaN_1$) occurs infrequently and *Um* and *Umg* abundantly. The *Umg* samples are Hybrid III, most frequently $C.LDPAN_1$. The *Um* samples are of special interest since they all have the stiff, pyramidal habit long associated with the Guernsey landscape (Quayle, 1815) and presumably constitute a single clone. They are distributed over 12 clusters, the most frequent, as indicated above, being $A.b_2$ and C.bDan.

XXVII. Alderney. The range of elms is similar to that in Jersey. *Um* is exemplified by $B.ba_1$ and C.bDan, and Hybrid III by *D*.LDAN and $C.LDPAN_1$. *Ug* (in particular $C.LbDpaN_1$) and *Up* (*D*.LBDWpa) are also present.

XXVIII. Herm. *Um* and *Umg* both occur, the latter Hybrid III (*D*.LBDWN). The *Um*, though bearing a general similarity to the *Um* populations in the larger Channel Islands, is mainly represented by clusters with deep teeth such as C.bDan and C.Dp.

XXIX. Sark. The general pattern of the Channel Island elm flora is repeated here. Both *Um* of the Jersey type, exemplified by C.bDan and the *Umg* Hybrid III ($B.LDPN_1$) are frequent. An intermediate type, represented here by C.Dp was also collected.

XXX. North Brittany. The most frequent elm in this coastal strip is a small-leaved *Um* type represented by *B*.lbdn and $B.lbdPan_1$. Intermixed with it are *Um* elms with average-sized leaves, such as $B.bPn_1$ and $B.bPn_2$, and similar forms with smaller teeth, represented by *B*.bdP and *B*.bdPAN. In the western part of the area, some *Umg* hybrids appear, pertaining to *B*.LaN, *D*.LDAN and *B*.LDWN.

XXXI. West Brittany. While elms diminish in frequency as one approaches northern promontories such as Cap de la Hague and Cap Gris Nez, the reverse occurs in the Breton peninsula behind the Pointe de Corsen and Pointe du Raz. The characteristic elm of the extreme west is small-leaved, mostly $B.lban_2$, *B*.lan or *B*.bdwPan. A rather larger-leaved elm occurs in the north of the area, represented by *B*.bwan and $B.bPn_1$.

XXXII. South Brittany. The predominant *Um* elms of this coastal strip are larger-leaved than in the preceding two regions, mostly *B*.bdP and $B.bPn_1$. Forms with low asymmetry (*B*.bPa) were encountered in the east of this area.

XXXIII. Interior Brittany. This extensive region is one in which elms occur with much lower frequency than in the coastal strips. It includes also the coastal areas in which elm occurs at reduced frequency. To a considerable extent, the elms of the interior correspond with those along the coasts behind which they occur. Thus in the west, small-leaved elms such as *B*.lban, and $B.lbdPan_2$ are found, as they are to a lesser extent, in the north-east. In the north generally, average-sized elms such as $B.bPn_1$, *B*.bPa and C.bDan are more usual, and in the south smaller-toothed forms such as *B*.bdPn and *B*.bdP. The situation is most complex along the eastern border of Brittany. A varied assemblage of *Umg* hybrids occurs north of Rennes. In south-east Brittany north of the Loire, a heterogeneous assortement of *Um* forms was found, perhaps representing a westward extension of elms from the middle Loire valley.

Historical Perspective

Pollen analysis has shown that the general course of post-Glacial tree establishment in northern France followed that typical of NW Europe (Nilsson, 1960, Elhaï, 1960, Planchais and Corillion, 1968, Ters *et al.*, 1971). Elm appeared in the Boreal and persisted in quantity till the Atlantic elm decline, after which it continued, with local interruptions, in reduced quantity. It is practically certain that the first immigrant elm was *Ug*, the only species entering into natural communities in NW Europe.

There is little to suggest that *Um* is native in northern France, and its presence here is almost certainly the result of human introduction, as in England. The present study reveals the striking dissimiliarity of the elm floras on the two sides of the English Channel. The only common element is the small-leaved elm population behind Cap Gris Nez and in Flanders, which resembles that of eastern Kent. It seems reasonable to suppose that the other elms of Artois reached their destination subsequent to the separation of England from the Continent, and nothing has been discovered telling against the supposition that this was equally the case with the small-leaved elms.

Some of the patterns of distribution described in this paper suggest certain historical events. In particular, distributions such as those of $B.lban_1$ or $B.lbdPan_1$ in *Fig. 1 a* are consonant with human introduction by sea into coastal areas. This has already been suggested by Richens (1967) for *Um* in England. Other patterns of distribution, such as that of C.LbPAN in *Fig. 1 d,* are here easily explained by immigration overland.

Place-name evidence documents the presence of elm in much of the area studied in earlier times (Dauzat and Rostaing, 1963). Celtic names based on *lem* do not occur though they do just outside the area, at Limours and Limeil (SO) and Lumeau (EL). Derivatives of Latin *ulmus* are however common and examples are set out under region in *Table 6,* together with date of first mention and details of the elms collected.

No reference has been found yet to the presence of elm in northern France by Roman writers though its presence further south is attested by Ausonius who dedicated a grove *nostro viridis qui frondet in agro ulmeus.* Medieval references to elm are frequent and a selection is listed in *Table 7,* set out under region, with date and source of citation, and details of elms collected.

Two of the elms mentioned in *Table 7,* the *ormeteau ferré* of Gisors and the court elm at Genêts were conference or justice elms, a customary use of elm that was formerly widespread in northern France. It also extended to the Channel Islands where an *orme du Conseil* is referred to in a Jersey court roll of 1707 (Messervy, 1923).

One difficulty in attempting to trace the history of elms is the confusion that was evidently widespread in early times concerning the identity of the large-leaved elms, which appear to have been often conflated with lime *(Tilia* spp.) under the general name *tilia.* The confusion is found in France, Ireland, Italy and Germany. The Breton term for elm in the Tréguier dialect is *tilh,* a borrowing from *tilia* which is evidenced as early as the 8th century when it appears in a macaronic Latin # — # Old Breton medical treatise (Stokes, 1897), though whether it means elm or lime in this context is not clear. A definite equation between Breton *tilh* and French *orme* is explicit in the Middle Breton *Catholicon* (Ernault, 1888).

The Irish term for elm is *lem* and lime is not native in Ireland. However the expression *crand leimh* in the 9th—10th century Irish life of St. Finian of Clonard (Stokes, 1890) is translated as *arbor quedam tylia nomine* in the

Table 6. — Place names based on *Ulmus*

I.	Flanders	Lomme (Nd)	11th century	
IV.	Ponthieu	Aumâtre (So)	12th century	*C*.LbdwPN, *B*.LbpN$_2$
V.	Bray	Osmoy-St. Valery (SMar)	11th century	
X.	Plain of le Neubourg	Ormes (Eu)	10th century	*B*.bdP, *D*.LbPN
XI.	Perche	St. Fulgent-des-Ormes (Or)	14th century	*A*.b$_2$
		L'Hôme-Chamondot (Or)	13th century	*A*.LbwP
XII.	Sarthe basin	St. Pierre-des-Ormes (Sthe)	11th century	*B*.LbPN$_2$
XIV.	Hiémois	Omméel (Or)	11th century	*B*.LbPN$_2$, *B*.L
		Ommoy (Or)	12th century	*B*.bwan, *B*.LDpN$_2$, *C*.LbDpaN$_1$
XVIII.	Val-de-Vire	le Hommet d'Arthenay (Mche)	14th century	*B*.lbdPan$_2$
XXIV.	Dol	les Ormes (IV)	14th century	

Anglo-norman Latin life (de Smedt and de Backer, 1888). Again, the term *tilia* appears denoting elm. The confusion was accentuated in the sixteenth century by botanists attempting to elucidate Theophrastus' distinction between female and male forms of φιλυρα which they rendered respectively in Latin as *Tilia foemina* and *Tilia mas,* the former figured unequivocally by L'Obel (1576) as *Tilia* sp. and the latter, galled by *Tetraneura ulmi* L. just as unequivocally as *Ulmus* sp. In Duhamel du Monceau's (1755) description of French elms he makes Gerarde's *Ulmus folio latissimo scabro,* which is *Ug,* equivalent to what he calls *orme-teille.* It is not clear exactly what Duhamel du Monceau understood by *orme-teille;* for later authors it was *Umg.* At all events, a lingering confusion between elm and lime is evident. It is therefore possible, and in fact likely, that some of the numerous place names in northern France based on Latin *tilia* denote the presence of large-leaved elms (*Ug* or *Umg*) and not lime, but only detailed local studies could elucidate this point.

The Breton names for elm afford some help in dealing with the history of elm in Brittany. The Celtic root for elm, *lem,* whence Welsh *llwyf,* occurs neither in Cornish nor Breton, and the Cornish and Breton names are also unrelated. The different dialects of Brittany have diverse words: *evlac'h* in the dialects of Léon and Cornouailles, *tilh* in that Tréguier, and *onn* and *oulm* in that of Vannes. The simplest explanation is to suppose that the immigrant Bretons from Cornwall and Devon were unfamiliar with elm and had to borrow or devise new terms when they encountered it. *Tilh,* as already observed, is ultimately derived from Latin *tilia;* it may already have denoted elm when it was borrowed, or if not, certainly did so later. *onn* usually denoted ash *(Fraxinus excelsior* L.) and *oulm* is a borrowing from French dialect *oulme.* Both *evlac'h,* whose derivation is obscure, and *tilh* are recorded with the meaning elm in Middle Breton so its presence in Brittany in the Middle Ages is certain. *oulm* is a relatively late borrowing.

Evidence relating to the range of variation of elm in earlier times is scanty and its interpretation beset with pitfalls. It is clear however that large-leaved elms, some of which were *Umg,* were recognized from the sixteenth century onwards.

The term *ypereau (ypreau),* signifying elm, is recorded by Cotgrave (1611) and is particularized in the anonymous book *La theorie et la pratique du jardinage* (1709) as a large-leaved elm. The word is recorded from Béthune (PC) in 1432 and remained in general use in the departments of Pas-de-Calais and Somme with the same meaning till the nineteenth century (Wartburg, 1928—61). It presumably corresponds to Hybrid I of this paper. This is similar both in leaf measurements and branching habit to what is called the Dutch elm in England, and there is a good *prima facie* case for supposing that the Dutch elm of England is the French *ypereau* and was derived ultimately from Artois.

Table 7. — Medieval references to elm

II.	Artois	Béthune (PC)	15th century	*yppereau* cited	(Wartburg, 1928—61)	*C*.LbdwPN
		St. Omer (PC)	15th century	*holmeaulx* for timber	(Deschamps de Pas, 1854)	*C*.Dp
VI.	Vexin	Gisors (Eu)	12th century	royal conference under the *ormeteau ferré*	(Guillaume le Breton)	*B*.bdPN
XI.	Perche	Breteuil (Eu)	14th century	*lourme de Bordigny* cited	(Delisle, 1851)	*C*.LbdwPN
XIV.	Biémois	Bures-s-Dives (Calv)	14th century	*ormyaux* cited	(Delisle, 1851)	*B*.bdP
		le-Mesnil-Touffray (Calv)	14th century	elms sold	(Delisle, 1851)	
		Robehomme (Calv)	14th century	elm cited	(Delisle, 1851)	*B*.LbPN$_2$
		Troarn (Calv)	14th century	*hulmellum de Troarno* cited	(Delisle, 1851)	*A*.b$_3$, *C*.LbWAN
XVI.	Plain of Caen	Caen (Calv)	14th century	elm for artillery	(Napoléon III and Favé, 1846—63)	
XVII.	Bessin	Littry (Calv)	14th century	*oulmam* felled	(Delisle, 1851)	
XXIII.	Avranchin	Genêts (Mche)	14th century	legal proceeding *sub ulmo*	(Delisle, 1851)	*B*.lbWPn$_2$
XXXIII.	Interior Brittany	Rennes (IV)	15th century	elm for timber	(Leguay, 1968)	

A distinction was current in northern France and Belgium between *orme maigre* and *orme gras*, corresponding to the Flemish distinction between *magere olm* and *vette olm* (POEDERLÉ, 1772; HUBERTY, 1904). The first term corresponds to small-leaved *Um*, and the latter to *Umg* and perhaps also to some of the large-leaved forms of *Um*. *orme gras* is recorded in 1595 at St. Omer (PC) under its Picard equivalent *gras ommeau* (DESCHAMPS DE PAS, 1882—87).

A parallel distinction was made between *orme à petites feuilles* and *orme à grandes feuilles* (HUBERTY, 1904), corresponding again to *Um* as against *Umg*. A plantation *dormes a grande fueille* is recorded at MESNIL- DURAND (CALV.) in 1654 (BOURRIENNE, 1898), and earlier on elm *met breeder bladeren* found in western Flanders is distinguished from the common sort, with smaller leaves, by l'OBEL (1581). Yet a further distinction is that between *orme mâle* and *orme femelle*, which again seems to indicate the distinction between *Um* and *Umg*. These terms were current in Flanders (HUBERTY, 1904), and Jersey and Guernsey (LE MAISTRE, 1966) up to the present century. In *La theorie et la pratique du jardinage, orme fémelle* is mentioned and identified with *orme à larges feüilles*.

Lastly, there is the distinction between *orme rouge (roode olm)* and *orme blanc*, current till recently in Flanders (HUBERTY, 1904) and Jersey (LE MAISTRE, 1966). This also appears to be the same distinction as before between *Um* and *Umg*. It is noted by POEDERLÉ (1772).

The cumulative conclusion to be drawn from these terms is that *Um* and *Umg* were sufficiently diverse and frequent in northern France to attract a number of differentiating names and that this divergence has existed at least from the end of the Middle Ages.

Discussion

The number of samples of north French elms collected was not high enough to allow of more than very provisional conclusions, and the interpretation of the clustering similarly required extreme caution. Nonetheless, it is possible, in combination with other evidence, to suggest a putative evolutionary history. *Ug* spread northward over France as the climate ameliorated at the end of the last Glaciation and, after the Atlantic elm decline, is likely to have persisted in scattered stands in shady declivities over a wide area in the north of the country. *Um* is native along rivers in the south of France.

The passage of *Um* to the extreme north is likely to have been by human introduction and two routes are supposed (1) by sea, and (2) overland, but the number and whereabouts of the Glacial refugia of this taxon are unknown.

OLDFIELD (1964) has provided evidence that there were none to the north-west of the Pyrenees. The present differences between *Um* elms in the Rhône and Garonne basins suggest that they may have immigrated from different sources. Of the 21 clusters represented from southern France, 11 were from the south-west only, 5 from the south-east only and 5 from both south-west and south-east. All the southern clusters were collected from the north except *B*.bdPaN from Gers and *A*.bWN from Alpes-Maritimes. Of the 13 larger clusters whose distributions are shown in *Fig. 1*, 7 had not been collected in the south, 3 also occur in the south-west, 3 occur in both south-west and south-east, and 1 only (*C*.bDan) in the south-east. It can be surmised from these comparisons that the Garonne basin has been the route via which many elms have passed to the north. Whether elms have also passed up the Rhone-Sâone corridor and over the Plateau of Langres to the Seine basin remains an open question on the present evidence. *Um* from the Garonne basin could have been transported by boat to the Breton coastal strips, Cotentin and Artois and perhaps also to the coastal elm districts in England. Clusters to which this explanation might apply include *B*.lbdPan$_1$, *B*.lbdPan$_2$, *B*.lban$_1$, and *B*.bdwPan.

The overland route would presumably have been from the Garonne basin, through the Poitiers gate to the Loire basin. Since such inland regions of northern France as interior Brittany, Perche, and the Caux-Vexin zone carry only sparse elm populations, it seems likely that the final stages of migration north would have been along the south bank of the Seine into Normandy and again into Cotentin, e.g. *C*.LbPAN, or along the Oise valley into Picardy, e.g. *C*.bdwPN. These speculations are illustrated in *Fig. 1 h*. Having arrived in the north, the various *Um* populations would have come into contact with relict *Ug* and hybrid *Umg* populations would have been formed, as in Picardy and the various sites above described above in Normandy and Brittany. *Um* was almost certainly taken to northern France in pre-Roman times and the hybrid populations had become established by the end of the Middle Ages.

Acknowledgment

Acknowledgment of collectors who have supplemented the principal material used in this paper is made in the text. Prof. J.-L. FLEURIOT gave assistance on questions of Breton philology.

Summary

A collection of 655 samples of elms, mainly from northern France, was subjected to principal-component analysis of eight biometrical foliar characters. Principal components were clustered under severe distance restrictions and under a cluster-range restriction. The samples fell into 216 *A* clusters. Subsequent clustering under the cluster-range restriction led to a grouping of the 655 samples into 93 clusters: 16 *A* clusters, 58 *B* clusters, 11 *C* clusters, 7 *D* clusters and 1 *F* cluster. Of these, 47 are *Ulmus minor*, 3 *U. glabra*, 29 *U. minor* × *U. glabra* and the rest mixed. On the basis of the geographical distribution of the clusters, the north of France is divided into 33 floristic regions. By combining the results of the biometrical analysis with historical evidence, it is postulated that *U. minor* was transported northward by man in pre-Roman times (1) by sea and (2) overland, and that in the north it hybridized with relict *U. glabra* to form a series of distinct hybrid populations.

Key words: *Ulmus minor* MILL., *Ulmus glabra* HUDS., Geographical distribution, Comparative studies in England and France, Hybrid populations.

Zusammenfassung

Aus der Untersuchung von 655 Blatt-Proben, die in den Ulmen-Vorkommen zu beiden Seiten des Ärmelkanals, das heißt hauptsächlich in den nordfranzösischen Küstendepartements und auf den 5 großen Kanalinseln eingesammelt worden waren, ergaben sich fünf blattmorphologische Gruppen, die den Arten *Ulmus minor* MILL. und *U. glabra* HUDS. zugeordnet werden konnten sowie solche, die als Hybriden zwischen den beiden Arten anzusehen sind. Desgleichen ergaben die Untersuchungen Anhaltspunkte über mögliche Wanderwege im Rahmen der natürlichen Verbreitung und derjenigen durch den Menschen. Im gleichen Zusammenhang wird die Entstehung des Gattungsnamens, dessen Entwicklung und diejenige der Volksnamen diskutiert.

Literature

ANONYMUS: La theorie et la pratique du jardinage (1709). — AUSONIUS: Ephemeris. — BOURRIENNE, V.: Le journal de Luc Duchemin, Seigneur de la Haulle. Bull. Soc. Antiq. Normandie 20, 469—582 (1898). — Cotgrave, R.: A dictionarie of the French and English tongues (1611). — Dauzat, A. and Rostaing, C.: Dictionnaire étymologique des noms de lieux en France (1963). — Delisle, L.: Études sur la condition de la classe agricole et l'état de l'agriculture en Normandie au moyen âge (1851). — Deschamps de Pas, M.: Essai sur l'art des constructions à Saint-Omer. Mém. Soc. Antiq. Morinie, 9 (2), 159—251 (1854). — Deshamps de Pas, L.: La porte Sainte-Croix. Bull. Hist. Soc. Antiq. Morinie, 7, 23—29 (1882—87). — Duhamel du Monceau, H. L.: Traité des arbres et arbustes qui se cultivent en France en plaine terre (1755). — Elhaï, H.: La Tourbière de Gathémo (Manche-Normandie). Pollen et Spores 2, 263—74 (1960). — Ernault, E.: Dictionnaire étymologique de breton moyen (1888). — Gower, J. C. and Ross, G. J. S.: Minimum spanning trees and single linkage cluster analysis. Appl. Statistics 18, 54—64 (1969). — Guillaume le Breton: Philippidos libri XII. — Huberty, J.: Étude forestière et botanique sur les ormes. Bull. Soc. Centr. For. Belg., 11, 480—527 (1904). — Jeffers, J. N. R. and Richens, R. H.: Multivariate analysis of the English elm population. Silvae Genetica 19, 31—38 (1970). — Leguay, J.-P.:La ville de Rennes au XVme siècle à travers les comptes des miseurs (1968). — Le Maistre, F.: Dictionnaire jérsiais-francais (1966). — l'Obel, M. de: Plantarum seu stirpium historia (1576). — l'Obel, M. de: Kruydtboeck (1581). — Messervy, A.: Précis historique sur le fief des Arbres. Bull. Soc. Jersiaise 10, 47—56 (1923). — Napoléon III and Favé, I.: Études sur le passé et l'avenir de l'artillerie (1846—63). — Nilsson, T.: Recherches pollen-analytiques dans la vallée de la Somme. Pollen et Spores 2, 235—62 (1960). — Oldfield, F.: Late-Quaternary deposits at Le Moura, Biarritz, South-West France New Phyt. 63, 374—409 (1964). Planchais, N. and Corillion, R.: Recherches sur l'évolution récente de la flore et de la végétation de Belle-Ile-en-Mer, (Morbihan) d'après l'analyse pollenique de la tourbière submergée de Ster-Vras. Bull. Soc. Bot. France 15, 441—58 (1968). — Poederlé: Manuel de l'arboriste et du forestier belgiques (1772). — Quayle, T.: General view of the agriculture and present state of the islands on the coast of Normandy (1815). — Richens, R. H.: Studies on *Ulmus*. II. The village elms of Cambridgeshire. Forestry 31, 132—146 (1958). — Richens, R. H.: Studies on *Ulmus*. VII. Essex elms. Forestry 40, 185—206 (1967). — Smedt, C, de and Backer, J. de: Acta sanctorum Hiberniae ex codice Salmanticensi (1888). — Stokes, W.: Lives of saints from the Book of Lismore (1890). — Stokes, W.: A celtic leechbook. Z. celt. Phil. 1, 17—25 (1897). — Ters, M. *et al.*: Sur le remblaiement holocène dans l'estuaire de la Seine, au Havre (Seine Maritime), France. Quaternaria 14, 151—74 (1971). — Theophrastus: Enquiry into plants. — Wartburg, W. v.: Französisches etymologisches Wörterbuch (1928—61).

Geographic Variation and Early Growth in South-eastern Semi-arid Australia of Pinus halepensis Mill. and the P. brutia Ten. Species Complex

By Christel Palmberg

Division of Forest Research, CSIRO
P.O. Box 4008, Canberra A.C.T. 2600
Australia

(Received August / October 1975)

Introduction

A century of investigation has clearly indicated that species from the vicinity of the Mediterranean or California are the most successful conifers in the relatively dry winter-rainfall areas in the southern parts of Australia (Hall 1951). In these regions most coniferous plantations consist of exotic species of the genus *Pinus*.

In addition to *Pinus radiata* D. Don, the most widely planted introduced species, *Pinus pinaster* Ait. and *P. nigra* Arn. have been successfully grown in Australia. To the same sub-section of the genus as the two last-mentioned species (sub-section Sylvestres Loud.) belongs the species complex of *Pinus halepensis* Mill./*P. brutia* Ten. (Critchfield and Little 1969). Species in this group are exceptionally resistant to adverse climatic conditions. (For description of species see e.g. Allegri 1973, Beissner and Fitschen 1930, Debazak and Tomassone 1965, Mirov 1955 and 1967, Mirov *et al.* 1966, Nahal 1962 and Safarov 1970. For description of the species as exotics in Australia see Brown and Hall 1968 and Hall *et al.* 1972).

In 1967 the Forest Research Institute[1]) of the Forestry and Timber Bureau acquired seed for an arboretum in the semi-arid region of south-eastern Australia in which a number of species and provenances might be screened to determine their value as plantation, shelterbelt, soil stabilisation and amenity species. The seed received included material from throughout the natural range of *Pinus halepensis* and *P. brutia*, as well as samples of the closely-related species of *P. eldarica* Medw., *P. pithyusa* Steven and *P. pithyusa* Steven var. *stankewiczii* (Suk.) Fom. Little information is available on the composition of the seedlots except for their geographic location *(Tables 1* and *2)*.

Material and Methods

A total of 42 provenances of *Pinus halepensis*, 18 provenances of *P. brutia*, 2 provenances of *P. eldarica* and 2 provenances of *P. pithyusa* were raised in polythene tubes at the Forest Research Institute, Canberra.

As there are no obvious potentially important gaps in the set of sample the provenances can be considered to represent the natural distribution of the species fairly well, athough the number of provenances from any specific area does not necessarily reflect the extent and importance of the species in that area *(Figure 1)*.

Field trials were established in June 1968 20 km west of Jerilderie, New South Wales (35° 22' S, 145° 44' E, elevation approx. 100 metres above sea level) on a site representative of the semi-arid region of south-eastern Australia.

Average annual rainfall at Jerilderie (1887—1975) is 390 mm *(Table 3)*. The dry season, during which the actual evapotranspiration falls below the potential evapotrans-

[1]) Now the Division of Forest Research, CSIRO.