and HATAKEYAMA, S.: Estimation of genetic parameters in forest trees without raising progenies. Silvae Genetica 12, 152–157, 1963. — SHRIKHANDE, V. J.: Some considerations in designing experiments on coconut trees. J. Ind. Soc. Agr. Stat. 9, 82–99, 1957. — SINGH, K. D.: Vollständige Varianzen und Kovarianzen in Pflanzenbeständen. III. Monte Carlo Versuche über den Einfluß der Konkurrenz zwischen Genotypen auf die Voraussage des Ausleseerfolgs. Zeitschr. f. Pflanzenzücht. 57, 189—253, 1967. — SMITH, H. F.: An empirical law describing soil heterogeneity in the yields of agricultural crops. J. Agric. Sci. 28, 1–23, 1938. — STERN, K.: Vollständige Varianzen und Kovarianzen in Pflanzenbeständen, I. Ein Modell für Konkurrenz zwischen Genotypen. Silvae Genetica 14, 87–91, 1965. — STERN, K.: Einige Beiträge genetischer Forschung zum Problem der Konkurrenz in Pflanzenbeständen (Im Druck), 1969. — WRIGHT, J. W., and FREELAND, F. D.: Plot size and experimental efficiency in forest genetic research. Michigan Agric. Exp. Stat., Techn. Bull. 280, 1960.

Multivariate Analysis of the English Elm Population

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

(Received for publication January 6, 1969)

In view of the known complexity of the variation of the elm in England and the embarrassment this has caused to those rash enough to attempt to describe it and delimit taxa, it was considered that this population would provide useful experimental material for multivariate analysis. Also, extensive biometrical data were already available, much of it having been used in the series of studies on local English populations of elm published by RICHENS (1959, 1961a, 1961b, 1965, 1967).

Material and Methods

The material used was a collection of 1131 samples, representing almost the whole of the range in variation of the genus in England. More material would probably have been advisable in two cases, namely, the elm population of Cornwall and that of the upper Witham Valley, Lincolnshire. From a geographical point of view, most English counties were represented but the part of England most adequately sampled was the south-east. Material was collected from almost every parish in Bedfordshire, Essex, Hertfordshire, Huntingdonshire, Holland (Lincolnshire), Isle of Ely, and from extensive areas in Kent and Suffolk. Since there may have been a slight divergence in sampling technique, the data on the elms of southern Cambridgeshire (RICHENS, 1958) were not used; all the types of elm in this area, however, are believed to be represented by samples from the adjoining counties. It is in these counties that the very variable species U. minor MILL., till recently usually referred to as U. *carpinifolia* GLED., and its hybrids with U. *glabra* HUDS. mostly occur. It is likely that none of the types of elm significantly contributing to the English landscape have been overlooked.

Each collection comes from a single tree from which five typical subdistal leaves from dwarf shoots on stout branches were collected. These were each measured for the following characters: absolute length of the longer side of the lamina (AL); relative breadth (RB), the ratio maximum absolute lamina breadth/absolute lamina length; relative petiole length (RP), the ratio absolute petiole length/absolute lamina length; relative asymmetry (RA), absolute distance between the lowest points of the lamina on each side/absolute lamina length; number of secondary teeth (TN); breadth of primary teeth at shoulder of leaf (TB); tooth length (TL); and tooth depth (TD). The last three measurements are illustrated by RICHENS (1958).

[1]) Merlewood Research Station, Grange-Over-Sands, Lancashire.
[2]) Commonwealth Bureau of Plant Breeding and Genetics, Cambridge.

It will be convenient to express measurements of these characters in two ways; firstly, the original recordings, in which case the character abbreviations will be given in Roman type as above, and secondly, as in the papers already published, converted to a scale 0–9 (occasionally transcended) based on range, in which case, the character abbreviations will be in italics. The range and size of the units of these scales are as follows: —

L	30—80 mm.	1 unit being 5 mm.
RB	0.40—0.90	1 unit being 0.05
RP	0.00—0.20	1 unit being 0.02
RA	0.00—0.20	1 unit being 0.02
TN	50—150	1 unit being 10
TB	3–8 mm.	1 unit being 0.5 mm.
TL	3–8 mm.	1 unit being 0.5 mm.
TD	0–5 mm.	1 unit being 0.5 mm.

The use of ratios as data for analysis was regarded as unsatisfactory by one of us (J.N.R.J.), and for this reason, RB, RP and RA were converted back to the respective linear measurements absolute breadth (AB), absolute petiole length (AP), and absolute asymmetry (AA) for purposes of computation.

Before dealing with the data for the whole of England, initial trials were made for the data concerning Bedfordshire (RICHENS, 1961b). Two methods of multivariate analysis were applied, principal-component analysis and canonical analysis. Both of these methods are described in detail by SEAL (1964). In the first case, means for each character were computed for each sample, and principal components were derived in three ways using:

1. linear measurements converted back from ratios, i. e. L, AB, AP, AA, TN, TB, TL, TD;
2. the data as recorded, i. e. L, RB, RP, RA, TN, TB, TL, TD; and
3. as 1. but transformed to logarithms.

Of the three approaches, none appeared to offer any advantage over the first and simplest, and this was, therefore, used in subsequent studies both of the separate counties and of the data for the whole country.

The Bedfordshire data (1.) above were also used for a canonical analysis. This method of analysis did not seem to provide as satisfactory a concordance with previously derived taxonomic conclusions as the principal-component analysis and was, therefore, not used subsequently. It was noted that the canonical variates seemed to be dominated by tooth size.

The principal-component analysis is based on the character means per sample, their standard deviations and the

coefficients of correlation between each character. In the case of Bedfordshire, most of the variation was accounted for by four principal components and this number of principal components was used in all subsequent work.

In order to extract meaningful taxonomic conclusions from this analysis, a clustering technique was employed to determine the discontinuities within the four-dimensional space described by the components. The method of cluster analysis used was a modification of the minimum spanning tree technique described by GOWER and ROSS (1969), in which clusters were defined by two individuals which were mutually nearest neighbours, together with all individuals which nominated any previous member of the cluster as its nearest neighbour. In the case of Bedfordshire, clusters of three orders, A, B and C emerged before the final comprehensive cluster, D. In most of the counties studied, three orders of clustering appeared, but for Essex and for the whole-country data, four orders of clusters, A, B, C, D, emerged before the final comprehensive cluster, E. The preliminary trials of the data for the separate counties showed that clustering without distance restriction was liable to cause very severe distortion in the higher-order clusters. The all-England clustering was, therefore, made with two severe distance restrictions:

1. All members of an A-cluster had to be within a distance of 1.000,
2. All members of a B-cluster had to be within a distance of 2.000.

Results

The main results of these computations for the whole of England are presented in the *Tables 1, 2, and 3*. *Table 1* presents the mean, minimum, and maximum values and standard deviations of each of the foliar characters measured. *Table 2* gives the coefficients of correlation between the characters. *Table 3* defines the first four principal components, and *Table 4* summarises the results of the clustering analysis and sets out the mode, minimum, maximum values for all characters except *TL* for each D and C cluster. Clusters are designated decimally. Thus, the sample of *U. glabra* from Appleby, Westmorland, is assigned to cluster A7.1.3.4 of B7.1.3, of C7.1 of D7. TB and TL are so closely correlated that there seemed little point in tabulating both. This table also shows the number of B-clusters in each C-cluster and the number of A-clusters disposed according to the generally recognised taxa *Ulmus procera* SALISB. *(Up)*, *U. minor* MILL. sensu lato *(Um)*, *U. glabra* HUDS. *(Ug)*, *U. minor* × *U. glabra (Umg)* and clusters comprising a mixture of these taxa, including also *U. minor* × *U. procera (Ump)* and *U. procera* × *U. glabra (Upg)*. The final column gives the number of original samples.

Table 1. — Mean, minimum and maximum values and standard deviations for the eight foliar characters studied.

Character	Minimum	Mean	Maximum	Standard Deviation
L	262.00 mm.	597.15 mm.	1166.00 mm.	113.08 mm.
L	T	5	17	
AB	173.00 mm.	384.76 mm.	676.00 mm.	77.90 mm.
AP	20.00 mm.	65.83 mm.	172.00 mm.	22.39 mm.
AA	4.00 mm.	51.74 mm.	132.00 mm.	20.90 mm.
TN	44.000	97.677	222.400	25.905
TN	T	4	17	
TB	2.500	4.875	8.200	0.880.889
TB	T	3	10	
TL	2.800	5.015	9.600	0.882
TL	T	4	12	
TD	1.100	2.360	4.800	0.532
TD	2	4	9	

Discussion

The first point requiring discussion is the degree of homogeneity of covariance. The coefficients of correlations between characters for the whole country are shown in *Table 2*. Similar coefficients of correlation were also calculated for all the counties well represented. In *Table 2*, twenty four of the correlations are significant at $P = 0.01$. The number of correlations significant at this level both for England as a whole and for Bedfordshire, Essex, Hertfordshire, Huntingdonshire, Kent and Suffolk is, however, much smaller. Those significant in all cases are L.B, L.TN, AB.AA, AB.TB, AB.TL, AD.TD, AA.TB, TB.TL, TB.TD and TL.TD, i. e. a total of only ten. The correlation TN.TL is significant and positive for all England, Essex and Suffolk, but significant and negative for Bedfordshire and Hertfordshire. Other cases of significant correlations reversed in signs occur for AP.TB, positive for Hertfordshire but negative for Kent, and TN.TB, positive for Essex and Suffolk but negative for Bedfordshire. These discrepancies suggest that there is considerable heterogeneity in the covariances of the various characters; some caution is, therefore, required in interpreting the results of the analysis.

Bearing in mind the possible heterogeneity of the covariances of the data from different counties, however, the components extracted from the various sets of data are remarkably consistent. In no case was there any suggestion that the fifth and subsequent components extracted from the correlation matrices were of any practical significance. For all England, the first four components accounted for 90.3 per cent of the total variability, and for all the sets of county data, the first four components accounted for between 86.7 and 93.6 per cent.

The interpretation of the components was also consistent, in that, for all counties, the four components extracted were describable as components of leaf size, tooth size and number, petiole length, and degree of asymmetry. In general, and for all England, the components were extracted in that order, i. e. leaf size accounted for the largest proportion of the variability, and the degree of asymmetry for the smallest, but there were minor changes in the order of importance of the components in some counties, and, for Ely and Suffolk, tooth size and leaf size were merged into a single component.

A further check on the sufficiency of the all-English data can be made by comparing the A-clusters in the all-England analysis with those for the same samples in the analysis for the individual counties. This has been done for five counties and *Table 5* shows:

1. the number of times in which the members of an A-cluster in one county in the all-English analysis occur in a single A-cluster for the corresponding county (complete concordance),
2. the number of times in which some only of the members of an A-cluster in one county in the all-English analysis are assembled in a single A-cluster for the corresponding county (partial concordance),
3. the number of times in which each member of an A-cluster in one county in the all-England analysis occurs in a different A-cluster for the corresponding county (discordance).

Table 2. — Coefficient of correlation between the foliar characters studied.

AB	+0.652*						
AP	+0.312*	—0.101*					
AA	+0.450*	+0.578*	+0.289*				
TN	+0.673*	+0.376*	+0.081*	+0.369*			
TB	+0.414*	+0.646*	—0.051*	+0.424*	+0.065		
TL	+0.446*	+0.544*	+0.023*	+0.368*	+0.143*	+0.936*	
TD	+0.217*	+0.618*	—0.201*	+0.295*	+0.008*	+0.759*	+0.759*
	L	AB	AP	AA	TN	TB	TL

* Significant for $P = 0.01$.

Table 3. — First Four Principal Components.

		1	2	3	4
Latent Root		3.895	1.705	1.019	0.602
% total variance		48.69	21.31	12.74	7.52
Latent vector elements	IL	0.8141	0.7743	—0.2182	—0.4622
	AB	0.9864	0.0772	—0.2773	0.4305
	AP	0.0440	0.7931	1.0000	—0.2784
	AA	0.7490	0.5332	0.3052	1.0000
	TN	0.4877	1.0000	—0.5426	—0.2821
	TB	1.0000	—0.5319	0.2016	—0.2084
	TL	0.9801	—0.4568	0.2387	—0.5020
	TD	0.8650	—0.7501	0.0088	0.0610

One-member A-clusters are excluded from this comparison.

It can be seen that the total number of cases of complete concordance is slightly higher than the combined totals for partial concordance plus discordance. In one county, Hertfordshire, however, discordance was considerably higher than the combined totals for complete and partial concordance. The discrepancy in clustering between the all-England and county analyses is partly a result of the slight differences in the extracted components, but underlines the need for caution in interpreting the results.

So far, we have been concerned purely with the internal consistency of the analysis. It is now time to describe and interpret the results in terms of the taxa generally recognised for the English elms, and to consider such additional information as geographical distribution, which was not used in the analysis.

It is generally agreed that the major division of the English elms is between *Ug*, native in the north of England and more sporadic in the south, and which occurs throughout northern Europe, on mountains in central Europe and reappears in north-east Asia, and the *Um* + *Up* complex. These last two species are probably native to southern Europe with vicariants in Asia. Their presence in England, where they seldom set seed, is easiest explained by human introduction at various times from late pre-Roman time onwards. *Um* and *Up* are usually easily distinguishable in

Table 4. — Clustering analysis.

Cluster D	Cluster C	Minimum, modal and maximum values for each character *L*	*RB*	*RP*	*RA*	*TN*	*TB*	*TD*	Number of B-clusters	Number of A-clusters *Up*	*Um*	*Ug*	*Umg*	mixed	Number of samples
1		3.5.10	2.7.9	2.4.8	1.5.9	0.3.9	2.4.10	4.5.10	22	71	8		4	15	384
	1	3.4.5	2.7.9	2.3.7	1.4.6	1.2.5	2.4.5	5.5.6	3	10	1			2	46
	2	3.5.9	3.7.9	2.5.8	3.5.8	2.3.7	2.4.5	4.5.6	6	15	2			7	110
	3	4.5.10	2.7.9	2.4.8	2.5.9	0.3.9	4.5.10	4.6.10	13	46	5		4	6	228
2		1.4.5	0.4.9	2.5.10	1.2,3.6	1.3.6	1.1,2.5	2.3.6	8	1	34			2	141
	1	1.4.5	1.2,3.6	2.5.10	1.2.4	0.3.6	1.1.5	2.3.4	4		20				75
	2	1.4.5	0.4,5.9	3.6.9	1.3.6	1.2.6	1.2.5	3.4.6	4	1	14			2	66
3		2.4.7	0.3.7	5.7.13	1.4.9	0.4.10	1.2.4	2.3.6	8		37			9	148
	1	3.4.7	0.3.7	5.6,7.11	2.5.7	2.3,4.7	1.2.3	2.3.4	3		19			3	71
	2	2.4.6	1.3.7	7.7,8.13	1.4.7	0.2.4	1.2.4	3.4.6	3		12			1	39
	3	3.6.7	1.2.5	5.8.13	2.4.9	3.4,6.10	1.2.3	2.3.5	2		6			5	38
4		4.6.10	1.4.7	6.8.11	3.6.8	0.4.9	3.4.9	3.4.7	5		12		3	4	54
	1	4.6.7	1.4.7	7.10.11	4.6.8	1.3,4.5	3.3,4.6	3.4.5	2		6				24
	2	5.7.10	1.4.7	6.8.11	3.6.7	0.4.9	3.6.9	3.5.7	3		6		3	4	30
5		3.5.13	0.3.8	2.6.12	0.3.7	0.4.13	0.3.8	3.4.8	22	7	43		13	26	313
	1	3.5.9	0.4.6	2.5.12	0.3.4	0.3.6	2.4.6	4.5.6	6		18			65	887
	2	3.5.10	1.4.8	2.6.9	1.3.6	0.1,2,3.6	4.5,6.8	4.5.7	5	7	10		1	3	68
	3	3.5.11	0.2.5	3.6.7	2.3.5	2.5.10	2.3.4	3.4.6	2		7		1	4	49
	4	4.7.10	1.3.7	2.6.8	2.4.7	2.6.13	0.3,4.5	3.4.6	7		6		9	13	99
	5	4.7.13	0.2.4	2.3.4	0.3,4.5	5.5,6,10	5.7.8	5.7.8	2		2		2		10
6		9.13.15	2.3.8	2.6.8	3.6.7	5.6.12	5.7.10	5.5,6,7.8							
	1	12.13.15	3.3.4	2.3,6.6	3.3,4.6	7.9.12	7.9.10	5.6,7,8					6		6
	2	9.11.14	2.6.8	4.7.8	3.6.7	5.6.8	5.7.7	5.5.7	2				7		10
7		8.11.17	1.3.7	1.4.7	1.4.7	5.9.17	2.3.8	3.5.7	9		1	14	20	1	75
	1	9.11.14	1.3.6	1.2.5	1.4.6	5.10.17	2.3.5	3.4.6	4		1	8	4		25
	2	8.9.17	1.3.7	1.4.7	2.4.7	5.8.16	4.5.8	3.5.7	5			6	16	1	50
7	19	total							80	79	135	14	53	57	1131

Table 5. — Number of A-clusters in the all-England analysis concordant or discordant with the A-clusters in the county analysis.

	Complete Concordance	Partial Concordance	Discordance	TOTAL
Bedfordshire	26	4	6	36
Hertfordshire	12	4	21	37
Huntingdonshire	11	1	11	23
Kent	9	5	3	17
Suffolk	14	6	4	24
Total	72	20	45	137

England. In southern France, they possibly intergrade. Hybrids between *Ug* and *Um* are well known. RICHENS (1965, 1967) has suggested that hybrids may also occur between *Up* and *Ug* and between *Um* and *Up*.

The all-England analysis establishes seven D-clusters of diverse size. D1, which includes most of the elms with leaves of medium size, teeth of medium size but above-average relative breadth, comprises the bulk of the *Up* samples, seventy-one A-clusters all told, but also some *Um* and *Umg*. Clusters D2, D3, D4 and D5 do not differ greatly from one another, though leaf size tends to be greater in D5, relative petiole length greatest in D3 and D4, relative asymmetry highest in D4, and tooth size smallest in D2 and D3. All four clusters correspond in the main to *Um*, but C5.2 is mainly *Up* and C4.2 and much D5 includes *Ump* A-clusters. D6, in which leaf size and tooth size are usually large but tooth number, though above average, does not rise to such high values as in D7, comprises only sixteen samples, all *Umg*. D7, differing from D6 in higher tooth number but smaller teeth, consists of roughly equal numbers of samples of *Ug* and *Umg*.

In very rough outline, then, the principal-component analysis reproduces some of the features of the classical taxonomy but the discrepancies in detail are numerous and serious.

It will be noted that, of the 338 A-clusters, 80 are *Up*, 135 *Um*, 14 *Ug* and 57 *Umg*. Of the remaining 52 A-clusters, 25 are mixtures of *Um* and *Umg*, 6 of *Um* and *Up* and 3 of *Um* and putative *Ump;* the remaining clusters are very heterogeneous.

The most serious problems of elm taxonomy concern infraspecific groupings, and here it was hoped that the principal-component analysis might have thrown new light. However, the very approximate correspondence between the higher-order clusters and the generally accepted taxa slightly reduce confidence in the help that the analysis might provide at the infraspecific level.

There was a possibility that the clusters would in some cases be separated by obvious discontinuities. A simple method of ascertaining whether such discontinuities exist is to see to what extent the various clusters can be distinguished on the basis of the one or more of the original measurements. When this was done, out of 79 A-clusters of *Up*, only 9 could be so distinguished within their relevant B-cluster; out of 141 A-clusters of *Um*, only 42 were so distinguishable; out of 14 A-clusters of *Ug*, 10 were distinguishable; and out of 52 A-clusters of *Umg*, 40 were distinguishable. This suggests almost continuous variation in *Up* and perhaps a little less in *Um*. *Ug* and *Umg* appear more discontinuous. Of B-clusters, none of *Up*, 4 of *Um*, 2 of *Ug* and 1 of *Umg* could be similarly separated within their relevant C-clusters. No C-cluster or D-cluster could be separated within its next higher group. The picture that emerges, therefore, suggests very wide but fairly continuous variation in *Up* and *Um*, of convergent variation involving *Up* and *Um* and of an almost complete range of hybrids linking *Um* and *Ug*.

Since it is known from previous studies that much of the variation in English elms is localised, a study was made of the number of A-clusters in two local populations, each conceivably monoclonal, one the BRAUGHING group in Hertfordshire (RICHENS, 1959) restricted to a small area in the north-east of the county and defined biometrically as:

L 2—5. *RB* 4—5. *RP* 8—13. *RA* 1—2. *TN* 1—3. *TB* 1—4. *TL* 2—5. *TD* 5—6 and the other, the much larger GODMANCHESTER group, covering much of Huntingdonshire (RICHENS, 1961 a) and defined biometrically as:

L 4—5. *RB* 1—3. *RP* 5—8. *RA* 2—4. *TN* 3—7. *TB* 0—3. *TL* 2—4. *TD* 3—5. The number of A-clusters in these two populations are shown in *Tables 6 and 7.*

In both cases, the wide scatter of what appear to be rather homogeneous, well-localised groups among so many clusters at each level is rather disconcerting. It is possible that this type of cluster analysis is unsuitable for so continuously variable a population or perhaps there is so much

Table 6.

Clusters composing the BRAUGHING group					
	Cluster				Number
	D	C	B	A	of samples
	3	3.2	3.2.2	3.2.2.2	1
				3.2.2.3	1
	5	5.1	5.1.3	5.1.3.1	1
				5.1.3.2	3
Total	2	2	2	4	6

Table 7. — Clusters composing the GODMANCHESTER group.

	Cluster			Number
D	C	B	A	of samples
2	2.1	2.1.2	2.1.2.2	1
			2.1.2.4	1
		2.1.3	2.1.3.3	1
			2.1.3.4	1
			2.1.5.5	1
		2.1.4	2.1.4.2	2
			2.1.4.3	2
			2.1.4.4	1
			2.1.4.5	1
	2.2	2.2.1	2.2.1.2	1
3	3.1	3.1.2	3.1.2.8	3
			3.1.2.9	2
			3.1.2.10	1
			3.1.2.11	2
		3.1.3	3.1.3.3	1
	3.2	3.2.1	3.2.1.3	2
	3.3	3.3.1	3.3.1.2	1
			3.3.1.3	1
		3.3.2	3.3.2.6	1
5	5.1	5.1.1	5.1.1.2	1
		5.1.3	5.1.3.4	1
		5.1.6	5.1.6.4	1
	5.3	5.3.1	5.3.1.2	4
		5.3.2	5.3.2.4	1
			5.3.2.9	3
	5.4	5.4.2	5.4.2.1	1
			5.4.2.2	2
Total:				
3	8	15	27	40

parallel clonal evolution within separate populations that virtually indistinguishable clonal variants have arisen polyphyletically. It is encouraging to note, however, that, out of 338 A-clusters, just under half are localised in the sense that they are confined to one county or to two adjoining counties.

In the case of *Up* and *Um*, the proportion is considerably lower than for *Ug* and *Umg*. It seems, therefore, that the analysis has certainly picked up appreciable traces of local variation. It remains uncertain, however, to what extent widely scattered A-clusters represent widespread biological entities and to what extent they are artefacts of the clustering technique.

Certain clusters, such as A5.4.7.3, illustrate to what extent samples remote, both geographically and taxonomically, can be brought together; it comprised:

Um From Cranfield, Bedfordshire;
Umg from Great Gaddesden, Hertfordshire; and
Ug from Lyminge, Kent.

Another heterogeneous cluster is A1.3.11.4; this associates:

Um from Alpheton, Coney Weston, Hartest and Rougham, all Suffolk;
Um from Coveney and Mepal, both Isle of Ely;
Up from Leigh and West Hanningfield, both Essex;
Umg from Borley and Ashen, both Essex; and
putative *Upg* from Bennington, Holland (Lincolnshire).

It seems unlikely, however, that the large number of widely distributed A-clusters should correspond, in many cases, with extensive parallel variation in the field. *Ug* is of special interest in this connection since it has the widest distribution of all the species. Although 14 localised *Ug* A-clusters occurred, others were very widespread, such as A7.2.5.9, comprising samples from: Ponteland, Northumberland; North Meols, Lancashire; and Benechurch, Essex. Such assemblages suggest the absence of any general clinal variation, but rather a number of widespread forms interspersed with local variants. This, indeed, appears to be the general pattern of infraspecific variation.

However, it also seems that the species themselves have converged, in some cases through hybridisation, in particular between *Um* and *Ug*, but in other cases through convergent variation, as with *Um* and *Up*. Some samples proved difficult to allocate with certainty to *Um* or *Up*, and the principal-component analysis reflects a similar difficulty. In the case of *Um* and *Ug*, hybridisation is well evidenced and many of the intermediates can be confidently taken as hybrids. However, the limits of variation of *Um*, under circumstances where introgression from *Ug* can be ruled out, are not known, and it is not possible to speak with assurance about the status of many of the intermediates that occur in England, where hybridisation can seldom be ruled out as a possibility.

It is clear, therefore, that it is not to be expected that the clusters at any level will correspond exactly to taxa, but there remains the possibility that confirmatory correspondence may be found between populations previously defined and sets of A-clusters or B-clusters not necessarily closely associated in the present analysis.

A brief synopsis of infraspecific groups previously used by him is given by RICHENS (1967) and they will serve as a basis for the comparisons that follow.

Ulmus glabra (Ug) is the only species certainly indigenous in England and extends over most of the country. It is represented by one markedly divergent sample in A5.1.6.1 from Bowes, Yorkshire, and constitutes the bulk of B7.1.1, B7.1.2, B7.1.3 and most of B7.2.5. This species shows relatively few signs of geographical variation. The wide distribution of A7.2.5.9 has been mentioned above. Another example is A7.1.2.2, from: Holcot, Bedfordshire; Crossthwaite, Cumberland; Castle Eden, Durham; and Wigtoft, Holland (Lincolnshire). There is some evidence, however, that interspersed amongst these wide-ranging forms there are local variants such as A7.1.3.1 and A7.1.3.2, confined to Bedfordshire, and A7.2.5.5, confined to Essex.

The species *Ulmus procera (Up)* is comparatively easy to deal with. It is, in general, easily distinguishable from the other species and the degree of infraspecific variation is less than in the others. It is possibly a single clone introduced in late pre-Roman times. In the present analysis, it is practically equivalent to D1 excepting B1.2.6, B1.3.10, B1.3.11, B1.3.12, and B1.3.13, plus B5.2.5. RICHENS defined seven infraspecific groups, BEDFORD, BIGGLESWADE, LUTON in Bedfordshire, RAYLEIGH and WANSTEAD in Essex and HITCHIN and ST. ALBANS in Hertfordshire. It has already been suggested that the groups BEDFORD, HITCHIN and WANSTEAD were equivalent. The present analysis supports this view, and indeed provides no grounds for maintaining the BIGGLESWADE, LUTON or ST. ALBANS populations as distinct groups. The *Up* samples from Essex with high tooth numbers, constituting the RAYLEIGH group, do, however, remain distinct and make up most of B1.2.5, B1.3.8 and B1.3.9. An affinity between these elms and those of northern Kent, previously suggested, was not confirmed. Some minor local variants noticed previously reappeared in the present analysis, for example, elms from Clifton, Shillington, and Tingreth, Bedfordshire, noted in passing as long-petiolate deviants from the BIGGLESWADE group, reappear together as a component of A1.2.4.4. An unexpected result was the discontinuous distribution of the B1.1.1, restricted mainly to Kent and Hertfordshire. No obvious reason for this presented itself.

It is *Ulmus minor (Um)* that poses the really acute problems. It principally corresponds in the present analysis to B1.3.10, B1.3.11, D2, D3, D4 and the greater part of D5. Previous work had led to the delimitation of a considerable number of local populations within this species. Of these, the first to be discussed will be the elms with small teeth, the leaves themselves usually being of small to medium size. The relevant groups are the DEAN group of Bedfordshire, the CHELMSFORD, CLACTON and DENGIE groups of Essex, the GIDDING and GODMANCHESTER groups of Huntingdonshire and the *Um* elms of eastern Kent. It is clear that all these forms are fairly closely related. The question is whether there are sufficient grounds for keeping some of them, at least, apart. It had already been suggested that the DEAN population is only the southern outlier of the GODMANCHESTER population of Huntingdonshire with which it is continuous, and the present analysis confirms this supposition. The analysis moreover seems to indicate that the distinction between the GODMANCHESTER and GIDDING groups of Huntingdonshire is not worth retaining, nor the distinction between the CHELMSFORD, CLACTON and DENGIE groups of Essex. We are left then to determine the relationships between the three geographically distinct *Um* populations of Huntingdonshire (including northern Bedfordshire), Essex and Kent. *Table 8* records the distribution of all the 85 A-clusters including samples in the groups under immediate discussion, and it will be noted that of the 31 A-clusters occurring in Kent, and the 41 A-clusters occurring in Essex, rather under half do not occur in the other counties.

Table 8. — Distribution of A-clusters of small-toothed elms in Huntingdonshire, Essex and Kent.

	Huntingdonshire (Hunts.)	Essex	Kent	Hunts. + Essex	Hunts. + Kent	Essex + Kent	Hunts. + Essex + Kent	Total
Hunts.	25			12	6		2	45
Essex		17		12		10	2	41
Kent			13		6	10	2	31

In the case of Huntingdonshire, of the 45 A-clusters just over half do not occur in the other counties. Only 2 A-clusters occur in all three areas and only 6 are common to Huntingdonshire and Kent. These observations are compatible with maintaining distinctions between the elms of the three areas; the Essex and Kent populations are probably more closely akin than either is to the Huntingdonshire population. Additional support for this view is provided by the observations reported by RICHENS (1967) that a strain of the gall mite *Eriophyes ulmicola* NAL. causes heavy infection of the small-toothed *Um* elms of Kent and Essex but is unknown in Huntingdonshire.

Two deviant groups of small-toothed Essex elms, the MANUDEN group, with very small leaves, and the EPPING group, with unusually long petioles, reappear to some extent in the clustering analysis, but in the latter group, every stage of intergradation between it and the more typical small-toothed Essex elms appears to occur.

The small-toothed EASTWICK group of elms in Hertfordshire, mainly located along the Essex border, occurs in A-clusters together with the small-toothed Essex elms just considered, and is probably best regarded as part of the same complex.

Two groups have to be considered in relation to the GODMANCHESTER group of Huntingdonshire. The first is the HADDENHAM group of the Fenland. This frequently occurs in the same A-clusters as GODMANCHESTER elms and can be regarded as an extension of this group towards the north and east. The ST. NEOTS group of Huntingdonshire differs from the GODMANCHESTER group in its higher values for relative petiole length and relative asymmetry. It largely retains its identity in the present analysis.

There are two remaining small-toothed populations to be considered, one from the coastal region of Hampshire and the other from the Upper Witham valley, Lancashire. The Hampshire specimen, from Lymington, appears to come within the same general circle of affinity as the Essex and Kent small-toothed elms; it occurred in cluster A2.1.4.6, together with samples from these two counties. A similar but more remote affinity probably applies to the Witham valley population, first recognised by MELVILLE (1940), and in which the leaf characters are associated with the distinctive unilateral branching habit. In this case, however, more samples are needed before drawing definite conclusions.

Especially in Essex, there is a series of elms differing from the preceding in the rather larger tooth size. These have been designated the COLCHESTER and LAYER groups. The differentiation between these groups, based on the larger tooth number of the latter, remains in the present analysis, where 16 A-clusters contain COLCHESTER samples but no LAYER samples, 10 A-clusters the converse, while only 2 A-clusters contain some of each. The status of this assemblage, which is intermediate biometrically between the small-toothed class considered above and the large-toothed elms characteristic of Suffolk remains uncertain. Intergradation certainly occurs between it and both the other assemblages. The geographical distribution of the various groups does not support the notion that these intermediate groups are in general of hybrid origin, though this is feasible in some cases. The various Hertfordshire groups with teeth of intermediate size, HUNSDON, TEWIN, THERFIELD and THROCKING, all appear to be related to the COLCHESTER group, and all occur in A-clusters together with COLCHESTER samples.

Most of the small CHRISHALL group of Essex, in which intermediate tooth size is combined with high values for relative petiole length and relative asymmetry reappears in one cluster, A4.1.2.2, and would seem worthy of retention. The BRAUGHING group of Hertfordshire, which has an unusual combination of very high values for relative petiole length but very low values for relative asymmetry, has already been mentioned to show how an apparently homogeneous group can be dispersed in different D clusters. None the less, it does retain its identity and has every appearance of constituting a well-defined natural group.

Of other groups with similar characteristics, the Sussex sample for the Pevensey levels resembles the COLCHESTER elms. It occurs in cluster A2.2.13, together with a COLCHESTER sample.

Only one sample was obtained from Cornwall, which came into A2.2.2.2, a rather heterogeneous cluster. More material from Cornwall would be necessary before discussing the relationships of this population .

The Essex and Hertfordshire elms with teeth of intermediate size might well be the product of a single introduction, or perhaps two if the BRAUGHING group did not evolve *in situ*. The Sussex and Cornwall populations seem likely to represent two different introductions.

One of the best-defined assemblages of *Um* is the group of large-toothed elms occupying most of Suffolk, much of Norfolk and well distributed over the Fenland, where it has been designated as group ELY. It also extends into northern Essex, where it was designated the NEWPORT group. It corresponds to most of B1.3.10, B1.3.11, B4.2.2, B5.1.4, B5.2.1, B5.2.2, B5.2.3 and B5.5.2.

One of the difficulties concerning this group is its apparent relationship with the CARLTON group of Bedfordshire and some of the putative *Umg* hybrids. The Bedfordshire group is geographically separate from the main population of large-toothed elms and its similarities to them seem to result from convergent development. The distinction from the putative *Umg* hybrids is, however, more difficult, since the large-toothed elms come into direct geographical contact with the extensive hybridisation zone of *Umg* that extends right across Essex and passes over into southern Suffolk.

It is probable that local variants can be distinguished within this extensive population, for instance A5.5.2.2, which comprises an assemblage with exceptionally large teeth, occurring in particular around the headwaters of the River Stour in western Suffolk.

The putative hybrids between *Ulmus minor* and *U. glabra (Umg)* form an extensive and highly variable assemblage.

What are almost certainly F_1 hybrids are clusters B1.3.12, B1.3.13, some of B5.4.6 and B5.5.1, D6, B7.1.4 and C7.2, excluding most of B7.2.5. Most of the hybrids occur in the hybridisation zone that extends from western Hertfordshire, right across Essex to south-east Suffolk. The Essex samples had previously been allocated to the three groups, BOXTED, BRAINTREE and STEBBING, but these are not distinguishable in the present analysis. The assemblage includes the Dutch Elm, an imported clone introduced in the seventeenth century and planted quite extensively throughout England, but the Essex hybrid swarm, includes elms which, though similar to the Dutch elm in many respects, are almost certainly of local origin. Sporadic F_1 *Umg* hybrids occur elsewhere.

A more difficult assemblage group is the group of putative back crosses of F_1 *Umg* to *Um*. These are difficult to separate from large-leaved *Um* since the limits of variation of this species in the absence of *Ug* are not known. The status of some of the intermediates between *Um* and F_1 *Umg* cannot in some cases be decided with certainty. Typical clusters of this sort are B5.2.4 and B5.4.3. Essex elms of this sort were previously divided into the three groups, COGGLESHALL, HALLINGBURY and RIDGEWELL, but again, the present analysis conflates these groups.

It seems probable that some, at least, of the SAWBRIDGEWORTH group of Hertfordshire elms, previously considered as large-leaved forms of *Um*, should be regarded as *Umg* hybrids. They appear in the same A-clusters as Essex samples regarded as *Umg* hybrids and, geographically, they would represent the western end of the *Umg* hybridisation zone of Essex.

The final taxa to be considered are the putative hybrids *Ulmus minor* × *procera (Ump)* and *Ulmus procera* × *glabra (Upg)*. There were seven of the first and two of the second. These few samples are widely scattered in the present analysis, which does nothing either to confirm or cast doubt on their putative hybrid status.

It is worth marking that the present analysis frequently confirms the relative remote affinities of some of the samples which had previously proved difficult to place. In the case of *Um*, the Ampthill sample, from Bedfordshire, constitutes a one-membered B-cluster, B5.4.1, while four Fenland samples, one from Spalding, two from Thorney and one from Tydd St. Giles, each constituted a one-membered A-cluster, respectively A4.2.3.1, A5.3.2.1, A7.1.4.5 and A4.2.3.2. In each case, no affinity with any English elm population had been apparent and it was suspected that each was of recent introduction from the European mainland, probably France. The present analysis is quite consonant with this supposition. Several of the putative F_1 *Umg* hybrids also appeared relatively isolated in the previous analysis, such as one of the Copford samples from Essex; it reappears relatively isolated in the present analysis, where it constitutes the one-membered A-cluster A4.2.2.3.

Conclusions

The present study shows that the results of the analytic technique used in this paper, principal-component analysis followed by clustering with severe distance restrictions, must be interpreted with great care since the variance of the whole population has been shown to be heterogeneous and the wide but continuous variation encountered may be unfavourable for clustering techniques. The lowest order A-clusters have proved the most meaningful taxonomically and the higher-order clusters became progressively less useful. The technique, however, has proved of value in confirming previous groupings, in introducing some corrections to previous groupings, and in suggesting comparisons between samples which might otherwise not have been made. In fact, the technique is a useful taxonomic probe when used in conjunction with, rather than replacing, other taxonomic methods.

As regards the English elm population, it is apparent that this is extremely variable but that very few discontinuities occur within it. The great difficulty that taxonomists have encountered with *Ulmus* is thus seen to result from the complexity of the situation in the field, and not, as so often in taxonomy, from artificial problems created by taxonomic methodology. It is apparent that much parallel variation has occurred and that many recognisable variants are polyphyletic. Many of the variants are quite narrowly localised. The English elm population consists mainly of four principal taxa: *U. glabra, U. procera, U. minor* and the *U. minor* × *U. glabra* hybrids. Of these, *U. minor* and the *U. minor* × *U. glabra* hybrids show the most extensive variation. However, the variation shows so little discontinuity that any taxonomic splitting of either *U. minor* or the hybrid assemblages would probably be imprudent. The limits of variation of the four major taxa are wide and convergence between them has occurred. In some cases, as with *U. minor* and *U. glabra,* hybridisation is in part responsible. In other cases, as with the larger-toothed samples of *U. minor* and *U. procera,* this is unlikely.

Acknowledgements

The analyses described in this paper were carried out on the I. C. L. Sirius computer at the Forestry Commission Forest Research Station, Alice Holt.

Summary

Based on 1131 samples, representing practically the entire range of variations of *Ulmus* in England, an analysis was made of the variation of eight biometric foliar characters. The technique used was principal-component analysis, followed by clustering under severe distance restrictions. Four principal components accounted for most of the variation and the clustering generated 338 A-clusters, 80 B-clusters, 19 C-clusters, 7 D-clusters and 1 E-cluster. The material proved rather intractable to the analytic technique used, partly because the variance of the characters was highly heterogeneous, and partly because variation showed so little discontinuity that the clusters were liable to have little taxonomic significance.

Combining the present results, however, with previous work, it is inferred that the English elm population consists mainly of four principal taxa: *U. glabra,* approximately equivalent to two segments of one D-cluster; *U. procera,* roughly equivalent to most of one D-cluster and a small segment of another; *U. minor,* a highly variable taxon comprising most of four D-clusters; and *U. minor* × *U. glabra,* also highly variable and comprising all of one D-cluster and about one half of another. Considerable parallel variation appears to have occurred within taxa at the infraspecific level and specific limits have become blurred both by hybridisation and convergent variation.

Literature

Gower, J. C., and Ross, G. J. S.: Minimum spanning trees and single linkage cluster analysis. Applied Statistics 18, 54—64 (1969). — Melville, R.: Contributions to the study of British elms. — III. The Plot elm, *Ulmus Plotii* Druce. J. Bot. 78, 181—192 (1940). — Richens, R. H.: Studies on *Ulmus* II. The village elms of Cambridgeshire. Forestry 31, 132—146 (1958). — Richens, R. H.: Studies on *Ulmus* III. The village elms of Hertfordshire. Forestry 32, 138—154 (1959). —

RICHENS, R. H.: Studies on *Ulmus* IV. The village elms of Huntingdonshire and a new method for exploring taxonomic discontinuity. Forestry **34**, 47 foll. p. (1961 a). — RICHENS, R. H.: Studies on *Ulmus* V. The village elms of Bedfordshire. Forestry **34**, 181—200 (1961 b). — RICHENS, R. H.: Studies on *Ulmus* VI. Fenland elms. Forestry **38**, 225—235 (1965). — RICHENS, R. H.: Studies on *Ulmus* VII. Essex elms. Forestry **40**, 185—206 (1967). — SEAL, H.: Multivariate statistical analysis for biologists. Methuen, London (1964).

Progress in Breeding Pinus radiata Resistant to Dothistroma Needle Blight in East Africa

By M. H. IVORY and D. N. PATERSON[1])

(Received for publication December 6, 1968)

Introduction

Dothistroma needle blight was first recorded in East Africa in the Western Usambara Mountains of Tanzania during 1958 (ETHERIDGE, 1965), although the identity of the causal organism was not determined until 1962 (GIBSON, 1963). The disease later spread to all *Pinus radiata* D. DON growing areas in Kenya, Tanzania and Uganda causing severe defoliation and even deaths where annual rainfall exceeds 60 inches (GIBSON, 1965). In areas with less than 60 inches rainfall deaths did not occur but diameter and height growth were checked considerably (CHRISTENSEN and GIBSON, 1964).

After the preliminary experiments reported from Kenya (GIBSON *et al.*, 1964) investigations were directed towards the development of control measures based on fungicide and shade treatments to the young susceptible crop in Kenya (GIBSON, 1965; GIBSON *et al.*, 1966; GIBSON *et al.*, 1967) and in Tanzania (HOCKING and ETHERIDGE, 1967). These have shown that control by shade treatment is impractical (GIBSON *et al.*, 1967), but that aerial applications of copper-based fungicides are effective and practical (GIBSON *et al.*, 1966). This has been confirmed by airspray trials in New Zealand (GILMOUR, 1967) and in small scale trials in the U.S.A. (THOMAS and LINDBERG, 1954; PETERSON, 1967).

It was realised at the onset of these trials that protective measures would be expensive relative to the income derived from a timber crop (DRAPER and GIBSON, 1964). Cheaper methods of control were therefore sought. Of those considered, the development of cultivars of *P. radiata* resistant to blight was thought to be most appropriate for East African conditions. However, as it takes a considerable time to select and build up cultivars from tree crops, it was thought desirable to continue with the development of protective control measures so that *P. radiata* might be grown during the interim period. The breeding programme was begun in 1963 (GIBSON, 1965) and expanded during 1964 and 1965. The progress made up to June 1968 is reported in this paper.

Procedure and Results

(1) Selection of resistant trees

Tanganyika resistant selections (TR), Kimakia resistant 1 (KR1) and Kerita resistant selections (KR_{2-4}) were selected in 1963 and 1964 on the basis of resistance to needle blight alone. Kenya resistant selections (K. Res.) made during 1964—1965 were selected for blight resistance and certain desirable morphological characters such as vigour, good stem form, fine branches, low spiral grain and narrow crowns. This was completed in the same way as for normal plus tree selections (DYSON and PATERSON, 1966). Plus tree ramets (423, 935, 954 & R. from the capital territory of Australia) were used as controls because comparable grafted material was available at the time of setting up the field trials. The control trees (KUR) used in the later trials were chosen from E.A.A.F.R.O. estate as this was the nearest available source of trees of similar age to Kenya resistant selections. All were healthy so no estimate of their level of blight resistance could be made. Seedlings used as controls in one trial were taken at random from E.A.A.F.R.O. nursery stock.

A survey of 1,445 acres of *P. radiata* plantations made from 1964 to 1966 yielded 75 selections at a selection pressure of 1 resistant tree from 11,600 trees. Of these only 37 trees were considered acceptable for breeding work after eliminating those with severe stem defects and low production potential as described by PATERSON (1967). This gives a final selection intensity of 1 in 23,500.

(2) Assessments of select trees

In 1964 and 1965 thirteen resistant parent trees at Kerita forest station (K. Res.) were each compared with five random freegrowing neighbours using the criteria for selecting plus trees described by DYSON and PATERSON (1966) and PATERSON (1967). The results of this comparison are shown in *Table 1*. It can be seen that the select trees are 4 times less affected by disease, and three times greater in volume, with less stem defects and slightly heavier branching than their random neighbours. This association of greater size and low level of disease attack was also found when 33 resistant selections from Nabkoi 2C were compared with their random neighbours. *Fig. 1* shows that the resistant selections have a much lower degree of attack and a much greater volume than their neighbouring trees. A regres-

Table 1. — A comparison of 13 resistant selections with their 5 random neighbours at Kerita forest station.

Character	Mean of 13 selected trees	Mean of 65 random neighbour trees
Disease attack (%)	27.4	97.9**
Volume O.B. (cu. ft.)	15.5	5.2**
Ratio of stem to branch diameters	4.6	3.9**
Number of internodes	30.6	20.3**
Number of stem defects	3.2	3.9*
Internode length (ft.)	1.8	2.2N.S.
Grain angle B.H. (°)	2.2	3.1N.S.

** Significant at 1% level.
* Significant at 5% level.
N.S. Not significant.

[1]) Forest Pathologist and Tree Breeder respectively at the East African Agriculture and Forestry Research Organization, Muguga, Kenya.