Hybridization between *Crataegus monogyna* Jacq. and *C. laevigata* (Poiret) DC. in south-eastern England

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ABSTRACT

Hybridization between *C. monogyna* Jacq. and *C. laevigata* (Poiret) DC. (*C. oxyacanthoides* Thuill.) has been investigated in selected populations in south-eastern England. The results show that most populations now contain hybrids and it appears that hybridization has continued long enough for a new equilibrium to be reached with the environment, resulting in a strong similiarity between populations found on similar soils. The far-reaching effects of man's activities in the past appear to have progressed to a point where further disturbance will only have a marginal effect, e.g. possibly the destruction of the last habitats at present allowing the survival of pure *C. laevigata*.

The concept of the two species *C. monogyna* and *C. laevigata* is largely irrelevant in south-eastern England because most of the populations now existing in this region appear to be the result of varied degrees of introgressive hybridization. However, there is a possible exception on the chalk scarps, which may provide a refuge for pure *C. monogyna*.

INTRODUCTION

Where hybridization has not occurred the two species *C. monogyna* Jacq. and *C. laevigata* (Poiret) DC. are quite distinct and can be most readily distinguished by the characters shown in Table 1. Hybrids may be intermediate in each of the features given in Table 1 or may exhibit an assortment of parental characters.

TABLE 1. SOME DIAGNOSTIC CHARACTERS OF *C. MONOGYNA* AND *C. LAEVIGATA*

	C. monogyna	*C. laevigata*
Style or 'fruit-stone' number	1	2–3
Flower diameter	Up to 15 mm	Often more than 15 mm
Mature leaf-shape	Laciniate, often 5–7-lobed	Shallowly 3-lobed to ± entire
Lowest lateral leaf-sinus depth	Extending at least two-thirds to midrib	Extending less than two-thirds to midrib
Lowest leaf-lobe shape	Acute, longer than broad; margin entire or with a few teeth at apex	Obtuse, broader than long; margin serrate nearly to base

Representative leaves of the two species and of a hybrid are shown in Fig. 1.

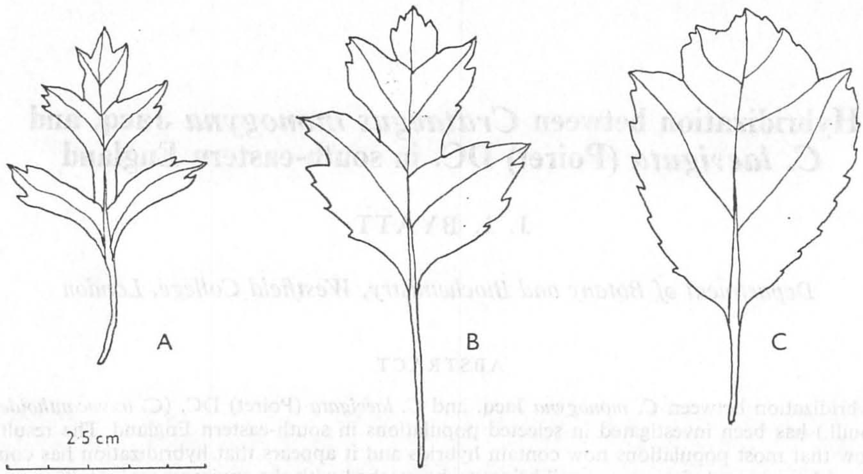


FIGURE 1. Representative leaves of *Crataegus monogyna* (A), *C. laevigata* (C), and their hybrid (B).

Although there is still little direct experimental evidence, it is normally assumed that species of *Crataegus* hybridize in nature wherever they are sympatric, since in such situations apparent hybrid swarms are common. For example, Franco (1968) stated of the genus in Europe that '. . . in regions where the areas of two taxa overlap, hybrids are commonly found'; and Browicz

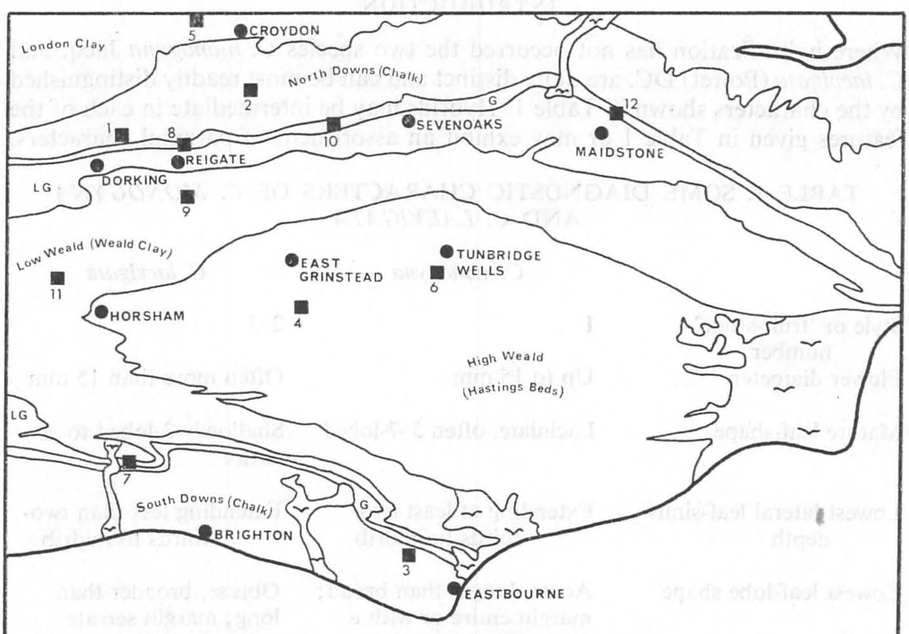


FIGURE 2. Sketch map showing position of 12 sites investigated. G = Gault Clay, LG = Lower Greensand.

(1972) described *C. monogyna* as an exceptionally variable species and said 'Some of this variation is certainly due to hybridization and, since it hybridizes freely with several species in both Sect. *Crataegus* and Sect. *Azaroli*, it is difficult to categorize the many forms which exist'. Bradshaw (1953) published histograms based on the degree of indentation of the leaves from several *Crataegus* populations in Cambridgeshire and Kent. He concluded that three of his diagrams represented hybrid populations.

Recently experimental evidence confirming some of the above conclusions has been provided by Bradshaw (1971), who investigated fruit-set in a series of crosses between *C. monogyna* and *C. laevigata*, and also looked at the pollen of both parental and intermediate types. The results showed that 30–59% fruit-set resulted from inter- or intra-specific cross-pollination but only 2% from self-pollination. Hence Bradshaw concluded that the two species are able to hybridize and, since he found no pollen sterility in hybrids, he suggested that the only barrier to hybridization is ecological. *C. monogyna* normally grows in the open and *C. laevigata* in woods.

The object of the present work was to investigate the degree to which hybridization has occurred between *C. monogyna* and *C. laevigata*, based on population studies in south-eastern England (Fig. 2).

METHODS

There are two major problems in studying *Crataegus* populations in south-eastern England: their ubiquity and their variability due to hybridization.

Scatter diagrams, as described by Anderson (1949), have been used in this investigation. Bradshaw (1953) selected a single feature, lateral sinus depth, which he said '. . . has always been held to be a good diagnostic character for the

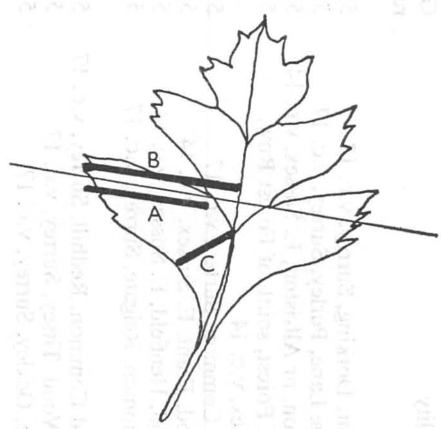


FIGURE 3. The three leaf measurements used.

A = Lowest lateral sinus depth.
B = Half leaf width.
C = Lowest leaf-lobe width.

Vertical axis on scatter diagrams $= \frac{A}{B}$

Horizontal axis on scatter diagrams $= \frac{C}{B}$

TABLE 2. DETAILS OF POPULATIONS SAMPLED

Population number	Locality	Grid reference	Soil-type	Community
1	View point, Dorking, Surrey, v.c. 17	51/18.51	Mainly Chalk	Mainly grassland & scrub
2	Old Lodge Lane, Purley, Surrey, v.c. 17	51/31.59	Mainly Chalk	Mainly scrub
3	Wilmington, nr Alfriston, E. Sussex, v.c. 14	51/53.03	Chalk	Grassland with limited scrub
4	Ashdown Forest, south of Forest Row, E. Sussex, v.c. 14	51/30.42	Ashdown Sand and loam	Mixed woodland by roadside
5	Mitcham Common, Surrey, v.c. 17	51/28.67	Gravel on London Clay	Grassland and scrub
6	Nap Wood, Frant, E. Sussex, v.c. 14	51/58.33	Mainly Tunbridge Wells Sand	Dry oakwood with *Betula*
7	Hoe Wood, Henfield, E. Sussex, v.c. 14	51/21.13	Gault Clay	Wet oakwood with *Corylus*
8	Wray Common, Reigate, Surrey, v.c. 17	51/26.51	Gault Clay	Wet oakwood with *Fraxinus*, and grassland
9	Earlswood Common, Redhill, Surrey, v.c. 17	51/26.48	Weald Clay	Wet oakwood with local *Betula*
10	Clacket Wood, Titsey, Surrey, v.c. 17	51/42.55	Gault Clay	Wet oakwood with *Corylus*
11	Van Lake, Ockley, Surrey, v.c. 17	51/15.39	Weald Clay	Wet oakwood with occasional *Fagus*, *Fraxinus* and *Corylus*
12	Horish Wood, Maidstone, W. Kent, v.c. 16	51/78.57	Gault Clay	Wet oakwood with *Corylus*

two species and is closely correlated with other diagnostic characters such as seed number, flowering time, growth-habit and flower size'. In this investigation the ratios of both lowest lateral sinus depth and lowest leaf-lobe width to one half the leaf width (Fig. 3) were used in constructing the scatter diagrams. Where practicable a third character, the style number, has been added to the diagrams. Since the number of styles or 'fruit-stones' is considered to be one of the main diagnostic features of *Crataegus* species, its close correlation with the leaf characters would seem to confirm the value of the vegetative characters chosen.

Ten leaves were collected from each of 15 plants in each of 12 populations, except in population 6 where only three plants could be found. The leaves were taken from vegetative short-shoots on two- or three-year old twigs, and whenever possible a mature plant was selected. As most populations consisted of large numbers of plants covering an extensive area, those sampled were selected at intervals along a rough line-transect, e.g. from one end of a wood to the other or from top to bottom of a scrub-covered hill, in order to collect as varied a sample as possible.

Selection of the populations to be investigated over such a wide area was at first made so as to cover a wide variety of the soil-types occurring in south-eastern England. In this way it was hoped to find out how far the two species were correlated with these soil-types and with the plant communities growing on them. Since it soon became apparent that hybridized communities were not difficult to find, efforts at a later stage were directed at sampling extra populations on soils and in communities which seemed more likely to yield 'pure' populations of the species concerned. The sites sampled are shown on the accompanying geological sketch-map of the area (Fig. 2), and further details are given in Table 2.

RESULTS

The primary results are shown in Fig. 4, which comprises scatter diagrams based on the two leaf characters and representing the 12 populations investigated. The populations numbered 1–12 have been arranged in order from nearest 'pure' *C. monogyna* to nearest 'pure' *C. laevigata*, and the two most distinct populations (1 and 12) have been plotted together to make comparisons easier. The scatter diagrams also show the mean value for each population. The position on the scatter diagrams of plants which appear very likely to be hybrids on the evidence of style or 'fruit-stone' numbers, i.e. those bearing some one- and some two-styled flowers on the same plant, or a mixture of fruits having one and two 'stones', are plotted together at the end of Fig. 4. Two analyses of these results were made (Table 3).

An initial analysis (left half of Table 3) was carried out based on the hypothesis that populations 1 and 12 (apart from the two rather isolated, less extreme plants in population 1) represent the two separate species, *C. monogyna* and *C. laevigata*. As will be seen from Fig. 4 there is an appreciable gap between these two populations, which might be taken to justify specific rank. Furthermore, population 12, although more variable than population 1, occupies a very isolated position if population means are considered.

Nevertheless the variability within populations, particularly populations 10 and 11, as well as population 12 itself, throws considerable doubt on the 'purity' of population 12. For example, some plants in populations 10–12, apparently

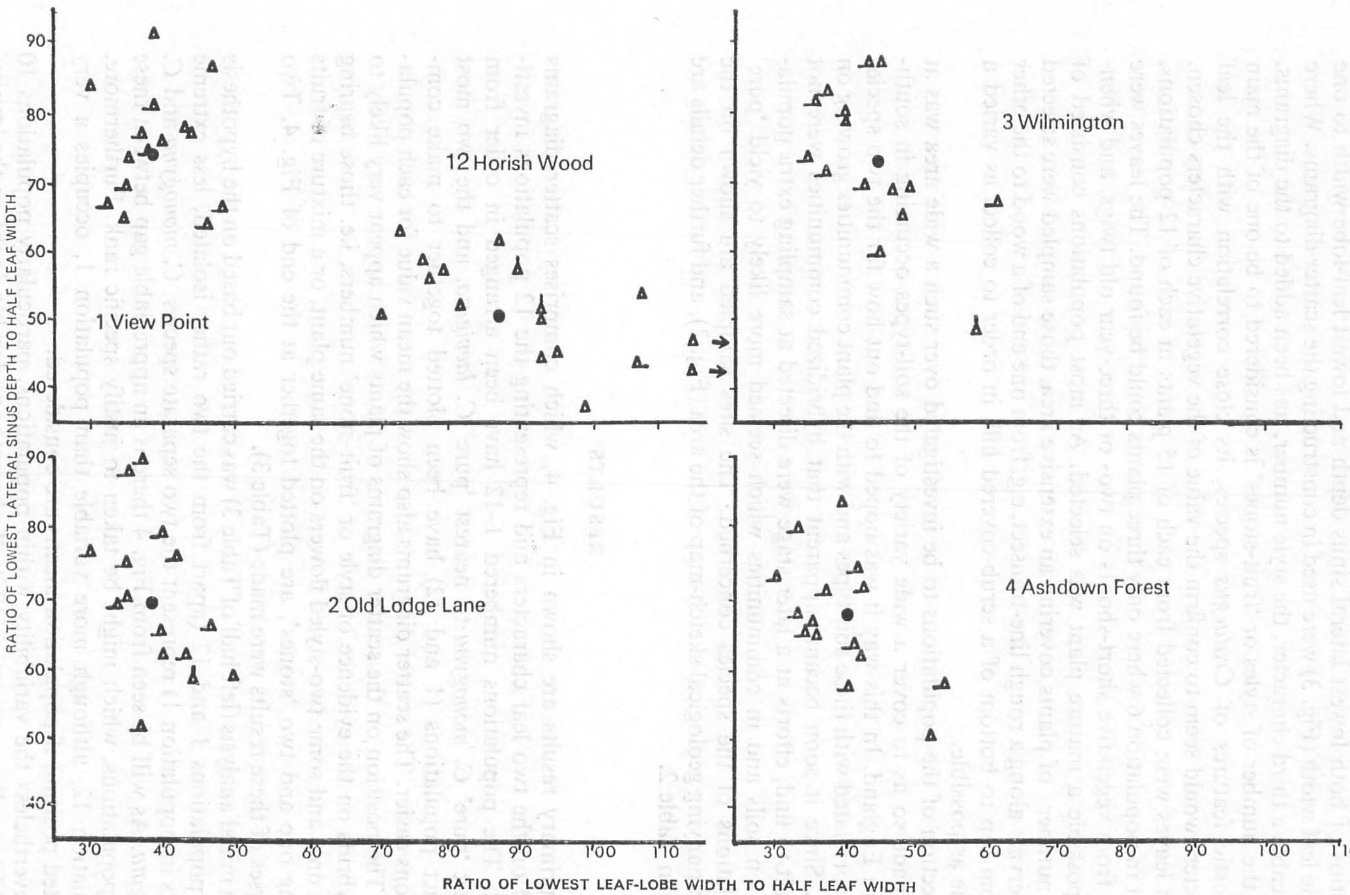
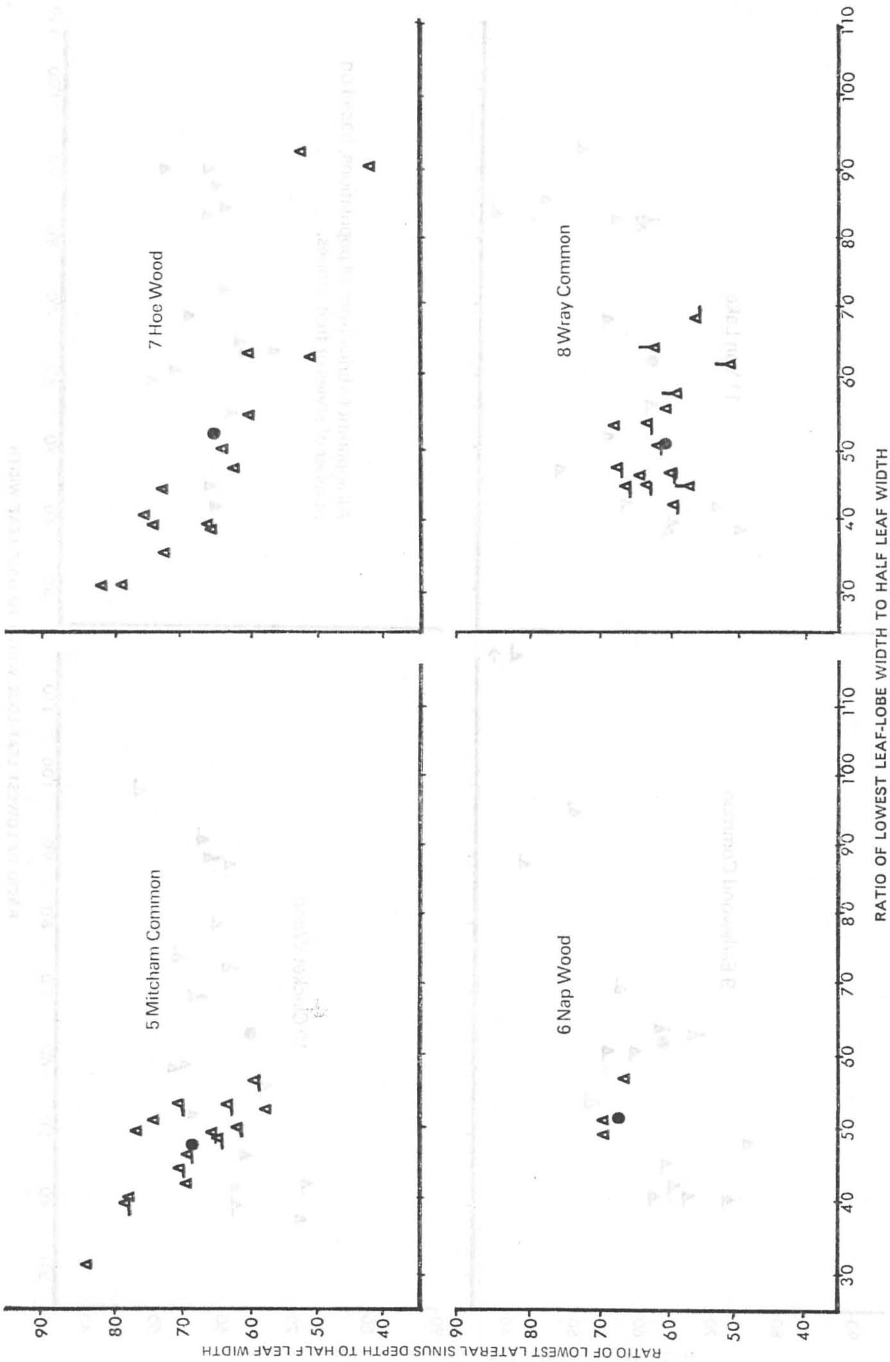


FIGURE 4. Scatter diagrams of the 12 populations.

Key ▲ Styles unknown ▲ One style ▲ Both one and two styles and/or forked styles ▲ Two or more styles ● Population mean


5 Mitcham Common
6 Nap Wood
7 Hoe Wood
8 Wray Common
RATIO OF LOWEST LEAF-LOBE WIDTH TO HALF LEAF WIDTH
RATIO OF LOWEST LATERAL SINUS DEPTH TO HALF LEAF WIDTH

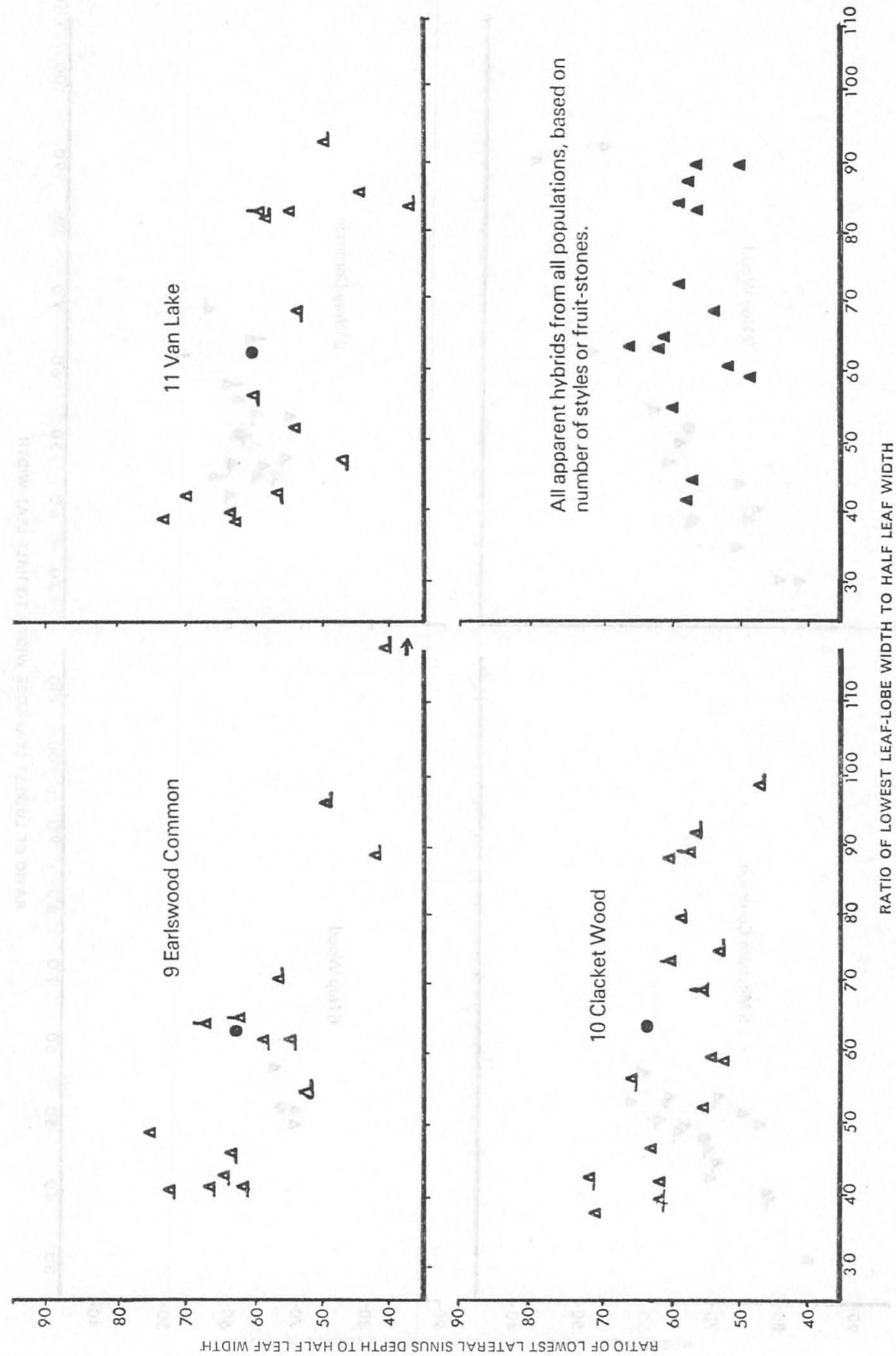

9 Earlswood Common
11 Van Lake
10 Clacket Wood
All apparent hybrids from all populations, based on number of styles or fruit-stones.
RATIO OF LOWEST LEAF-LOBE WIDTH TO HALF LEAF WIDTH
RATIO OF LOWEST LATERAL SINUS DEPTH TO HALF LEAF WIDTH

TABLE 3. COMPARATIVE ANALYSES OF POPULATIONS

See text for further explanation

Population number	Analysis 1				Analysis 2			
	No. of individual plants			Population structure	No. of individual plants			Population structure
	Group M *monogyna*-like	Group H Inter-mediate	Group L *laevigata*-like		Group M *monogyna*-like	Group H Inter-mediate	Group L *laevigata*-like	
1	13	2	—	MH	13	2	—	MH
2	8	7	—	MH	8	7	—	MH
3	8	7	—	MH	8	7	—	MH
4	10	5	—	MH	10	5	—	MH
5	3	12	—	MH	3	12	—	MH
6	—	3	—	H	—	3	—	H
7	5	8	2	MHL	5	9	1	MHL
8	—	15	—	H	—	15	—	H
9	1	10	4	MHL	1	11	3	MHL
10	2	7	8	MHL	2	14	1	MHL
11	1	7	7	MHL	2	11	2	MHL
12	—	—	17	L	—	10	7	HL

falling well within the range of *C. laevigata*, have some flowers with only one style; and the leaves of some plants, although resembling those of *C. laevigata* in the leaf characters plotted in Fig. 4, have other characters which are not typical of *C. laevigata*. Hence a second analysis (right half of Table 3) was made relying not on leaf characters, as in the first analysis, but on evidence of the number of styles or 'fruit-stones'. Using this criterion all the populations were again compared, but this time the two species were taken to include only those plants which fall well clear of the area of the scatter diagram in which hybrids occur. A comparison of the results of the two analyses (Table 3) shows that, while the circumscription of *C. monogyna* remains virtually unaltered, *C. laevigata* is in the second analysis represented by only a few plants forming parts of mainly hybrid populations. In Table 3 the individual plants forming the populations are shown as three groups: Group M (*C. monogyna*-like); Group H (hybrid); and Group L (*C. laevigata*-like).

DISCUSSION

Both these analyses and the population means show that most populations incline towards *C. monogyna*, there being a fairly continuous range of plants between group M and group H (populations 1–8). On the other hand populations 9–11 each contain many hybrid plants but with both species present in fairly small numbers. Populations 9 and 10 appear to have been subject to much human disturbance and dissection of the habitats and, while population 11 appears at present less disturbed, investigation has shown that it was also considerably interfered with in the past. It will be interesting to see whether the present population structure there is stable and allows *C. laevigata* to survive, providing there is no further major disturbance.

Whichever of the species limits discussed above approaches more nearly to the truth, it nevertheless remains that a major element in most of the populations is a hybrid one. On balance a higher proportion of the hybrids approach *C. monogyna* more closely than *C. laevigata*. On the lighter soils all the hybrids fall on the *C. monogyna* side of the diagram, while on clay soils there is usually a much wider spectrum of hybrids. This may result from the fact that *C. monogyna* is more frequently present and therefore more readily available for back-crossing, i.e. it is present in nine out of the twelve populations while *C. laevigata* is present in only five. On the other hand, it is possible that *C. laevigata*-like hybrids are being eliminated by unsuitable environmental conditions.

The correlation of population structure with soil-type is brought out strongly in Table 2, which shows that *C. laevigata* itself is entirely absent (even on its broader definition) from all the lighter soils, although hybrid plants are nearly always present. This correlation can be interpreted in various ways, e.g. *C. laevigata* was present in the past but has disappeared as a result of disturbance and clearance of suitable woodland habitats, or *C. laevigata* exists, or did exist, in sufficient proximity for gene-flow to have occurred. It seems quite probable that pure *C. laevigata* is excluded from these sites not so much by clearance of suitable habitats by man as because it is unsuited to the existing soil conditions, since in several places, even where woodland exists, *C. laevigata* is absent, e.g. population 4. It would appear, therefore, that light intensity is not the only factor limiting the distribution of *C. laevigata* in south-eastern England and it seems unlikely that it ever existed on the North and South Downs even in the past when they were possibly covered by forest. When *C. laevigata* does occur it is always on a clay soil, in this district either the Gault Clay or the Weald Clay, but apparently not on the Clay-with-flints. How far *C. laevigata* may have colonized the Tertiary Clays has not been studied in this investigation, although the existence of hybrid plants on Mitcham Common, Surrey, is suggestive.

C. monogyna appears to colonize a greater variety of soil-types and is absent from only three sites (6, 8 and 12). The wholly hybrid nature of populations 6 and 8 suggests that hybrids may be able to grow on soils unsuitable for both parents, although in the former site colonization is limited and may only have occurred because of the presence of a suitable local micro-habitat. Population 12 is unusual since the whole population consists of *C. laevigata* or *C. laevigata*-like hybrids, with the exception of one non-fruiting specimen of *C. monogyna* discovered since the scatter diagrams were constructed. In population 12 it seems possible that an artificial balance favouring *C. laevigata*, i.e. coppice with standards, has been maintained until very recently. In all those populations where *C. monogyna* does occur most plants are on lighter soils, especially the chalk and sandstones.

It is interesting that the more extreme variants of *C. monogyna*, i.e. those with very laciniate and often rather small leaves, have not been found on clay soils. It may be that these morphological characters are linked with physiological ones permitting colonization of the shallow, well-drained, warm soils of the chalk scarps where they are most often found, although more direct advantages may well be operating here. Lewis (1972) has found this to be so in the case of other macrophytes growing in dry situations. Indeed, the survival of distinct sympatric taxa of the genus *Crataegus*, in which the species hybridize so freely, can only occur if some stable association of characters is being continuously maintained by environmental selection. It appears very likely that *C. monogyna* may retain its identity in suitable habitats, while further encroachment and fragmentation of the last strongholds of *C. laevigata* will result in its replacement by hybrid populations more suited to the intermediate habitats created by man. Pure *C. laevigata* may well disappear although part of its genome will remain in introgressed *C. monogyna*.

It seems unlikely that any of the populations investigated do, in fact, wholly represent a pure species. The range of presumed hybridization is so wide that it may well be argued that all the populations, although not every individual specimen, have undergone introgression by genes from the other species. Although in some parts of the area considerable human interference with the vegetation has occurred only comparatively recently, all the sites investigated have been subject to intermittent disturbance by man over the last few centuries. Hybridization is therefore no new phenomenon; indeed, the continuous range of variation encountered in some populations suggests that it must have been occurring for several generations at least. While it is probable that some of the sites have not been continuously occupied by *Crataegus* in the past, it is likely that other suitable sites have existed nearby and that these have provided the parents for the existing communities. It is probable that in all populations genetic variability is very great owing to past hybridization and introgression, and that the limitation of phenotypes which is observed in the different populations is solely a result of environmental selection. If this is so, man's future contribution to the evolution of this genus in south-eastern England will be in habitat diversification rather than in providing an impetus for a greater mixing of the genotypes. Except for population 12, which still shows signs of past isolation from *C. monogyna*, most populations appear to have been hybridized over such a long period that the dominant factor at present determining population variability is the type and range of habitat available. Where the soil is a heavy clay the intermediate population tends towards *C. laevigata* and where the soil is light the population tends towards *C. monogyna*. Such a picture is of course over-simplified, as there is variation both between and within habitats.

This conclusion calls in question the existence of distinct species of *Crataegus* in south-eastern England. Studies in this area are not likely to give any assistance in delimiting the two species since the total variability of each cannot be distinguished in the presence of such widespread hybridization and introgression. As already noted, there is evidence of hybridization in what might have been thought to be a population of pure *C. laevigata*. Hence these plants might justifiably be considered to be either hybrids or pure *C. laevigata*. Thus we may detect evidence of hybridization up to a certain point by morphological characters, but beyond that point it is logical to suspect that introgression might have occurred although the outward signs are lacking. Hence, while studies in other areas where the two species are not sympatric might be very helpful in determining the limits of variability in the species, even if these limits are known they will not necessarily enable certain identification of the species and hybrids where hybridization and introgression have occurred.

If any pure populations of either species exist in south-eastern England the most likely candidates are those growing on the chalk scarps, where it is possible that environmental conditions are such that only plants with *C. monogyna* genotypes are able to survive. Hence, despite continuing disturbance leading to competition from hybrid populations, such situations may well remain the only refuge for *C. monogyna* in south-eastern England.

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