Introgressive hybridization between *Crataegus monogyna* Jacq. and *C. laevigata* (Poiret) DC. in the Upper Thames Valley, England

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ABSTRACT

Where their ranges overlap in Britain, *Crataegus laevigata* (Poiret) DC. and *C. monogyna* Jacq. hybridize freely. The extent and causes of introgressive hybridization were investigated in the Upper Thames Valley by population sampling. Hybrid indices were calculated on the basis of leaf characters. A total of 1325 leaves from 265 trees in 17 populations was examined. The composition of *Crataegus* populations was strongly influenced by habitat, geology and management history. Evidence that coppicing reduced fecundity in the long-term was considered and this tended to encourage the introgression of *monogyna* genes into *laevigata* populations. With a reduction in the frequency of coppicing over the last 60 years, a gradual return to original taxon frequencies has occurred in a number of populations. It was suggested that differential insect grazing may have been responsible for the leaf character differences observed in the parental species.

INTRODUCTION

Two species of *Crataegus* occur wild in Britain. These are *Crataegus laevigata* (Poiret) DC. (the Midland Hawthorn) and *C. monogyna* Jacq. (the Common Hawthorn or May). These are generally accepted as good species and show a range of reliable, correlated characters (Franco 1968; Byatt 1975). Both species are shrubs or small trees growing to about 8 m, and commonly surviving to more than 100 years. Both are found widely in Europe where they are differentiated into a number of distinct geographical races. Those occurring in Britain are *C. laevigata* subsp. *laevigata* and *C. monogyna* subsp. *nordica* Franco. *C. monogyna* is a highly variable species in Europe and Browicz (1972) has suggested that interspecific hybridization has been partly responsible for this. Both species are diploid with $2n=2x=34$.

In Britain, *C. laevigata* is the rarer plant, occurring in 43/112 (or 38%) of vice-counties (Clapham *et al.*, 1962) whilst *C. monogyna* is found in all British vice-counties. Under natural conditions, the two species are ecologically isolated. *C. laevigata* is typically a woodland plant with a strong preference for clay and loam soils. This more or less restricts it to the clay soils of the English midlands and Kentish Weald where it is surrounded by limestones such as chalk, oolite and carboniferous limestone. In contrast, *C. monogyna* prefers open habitats and is a dominant scrub species. It is rare only on very acid soils such as peat.

Where their ranges overlap, these species regularly show introgressive hybridization resulting in a range of variants between the morphological extremes of the parental species. This 'hybrid swarm' results from successive crossing and back-crossing over several generations (Anderson 1949). Hybrids, i.e. plants which are intermediate in gross morphology between the parental morphs (Bradshaw 1971; Byatt 1975; Williams 1989), are also intermediate in leaf surface microanatomy, and in the occurrence of flavonoids (Gosler 1981). Byatt (1975) showed that *C. laevigata* occurred widely in the Kentish Weald but suggested that it had only crossed the chalk by introgression with *C. monogyna*. She suggested that introgression had been so widespread in that region that pure stands of *C. monogyna* could be found only on the chalk scarp slopes and that none of *C. laevigata* existed. Williams (1989) has found that hybridization between the two species has also been extensive in remnant hedges in the London Borough of Brent.

Anderson (1949) described a detailed genetic model of introgressive hybridization between two species. This identified three essential components. Firstly, the characters which allowed the recognition of introgression were controlled by polygenic complexes with a high degree of correspondence between the respective specific genomes. Secondly, there should be some 'hybridization' of the habitat which allowed a morphological transition to occur between the two species across an environmental gradient. The third factor was that which caused the initial contact between the two species. This was usually some environmental disturbance which might be natural (as described in *Iris* by Anderson) or might be due to human activity. Bradshaw (1953) showed that man's influence was the most important factor causing syntopy in the British Crataegi.

Anderson and his students worked mainly with annual and perennial herbs. These are relatively short-lived plants with a rapid life-cycle, but are frequently self-pollinated. Natural selection may act very rapidly in such a population so that significant changes in gene frequencies may be observed after only a few flowering seasons. In a small tree such as *Crataegus* which does not flower until it is 15 years old (or until 15 years have passed since coppicing) and may live 100 years, selection may act most strongly at a particular time in the life-cycle. The habitat may have little effect on an individual's survival but may significantly reduce its flower production or fruit-set. Hence the habitat may induce a differential specific fecundity which determines the morphological direction to which the population will move in subsequent generations.

Bradshaw (1971) showed that the British Crataegi were outbreeders showing between 30% and 59% fruit-set when cross-pollinated artificially, but only 2% fruit-set when selfed. Similarly, fruit-set was almost as high in interspecific crosses as in intraspecific ones. An examination of stained pollen showed no significant reduction of pollen stainability in hybrid plants, remaining above 95%. This established that full introgressive hybridization was genetically possible, and the need to outbreed greatly increased the probability of hybridization. Since *Crataegus* flowers are insect-pollinated (largely Hymenoptera and Diptera), vicinism (Grant 1971) plays an important part in producing the spatial distribution of variation observed in a population. Vicinism, longevity and differential fecundity may cause a departure from panmixis which may reduce the need for a smooth environmental gradient. Thus in *Crataegus*, the transition from open scrub habitats to closed woodland may involve too sudden a change in soil moisture, nutrients or available light to show a clinal change in morphology across the ecotone.

This paper considers the nature, extent and causes of introgressive hybridization between *C. laevigata* and *C. monogyna* in the Upper Thames Valley by the detailed analysis of selected populations. Agriculture is the principal land use in the region and fields have traditionally been bounded by hedges. In the north, fields tend to be smaller, and here, hedges may be associated with boundary ditches and/or banks indicating the great age of the boundary (Rackham 1987). The area is geologically diverse and of comparable age to the wealden beds of Kent and Sussex – so providing an interesting comparison with Byatt's (1975) survey of that region. Fig. 1 shows the drift geology and stratigraphy of the present study area (spanning some 135 million years). The soils reflect this geological series but are influenced also by the deposition of alluvium by the Thames and its tributaries. Little has been published on *Crataegus* hybridization in this area although the range of geology, and especially the close proximity of clays and limestones provides a unique opportunity for such a study.

MATERIALS AND METHODS

For present purposes, the Upper Thames Valley study area has been defined as that lying between northings 41/70 and 42/30 and between eastings 30 and 70 of the Ordnance Survey National Grid. This area covers some 2400 km^2 and includes all of the Thames between Reading and Oxford. The work was carried out during June 1981 by which time the foliage was mature, most flowering had ceased and fruits were forming. Seventeen populations were selected for sampling, and some attempt was made to include *C. laevigata* populations cited by Bowen (1968). Site details are given in Table 1, and their locations are shown in Fig. 1. In most cases, specimens were collected along transects oriented to run across any apparent woodland/scrub gradient. When sampling hedges, specimens were taken at 5 m intervals.

Two-year old twigs of up to 50 cm in length were cut from each of 15 (but see Table 1) trees in each
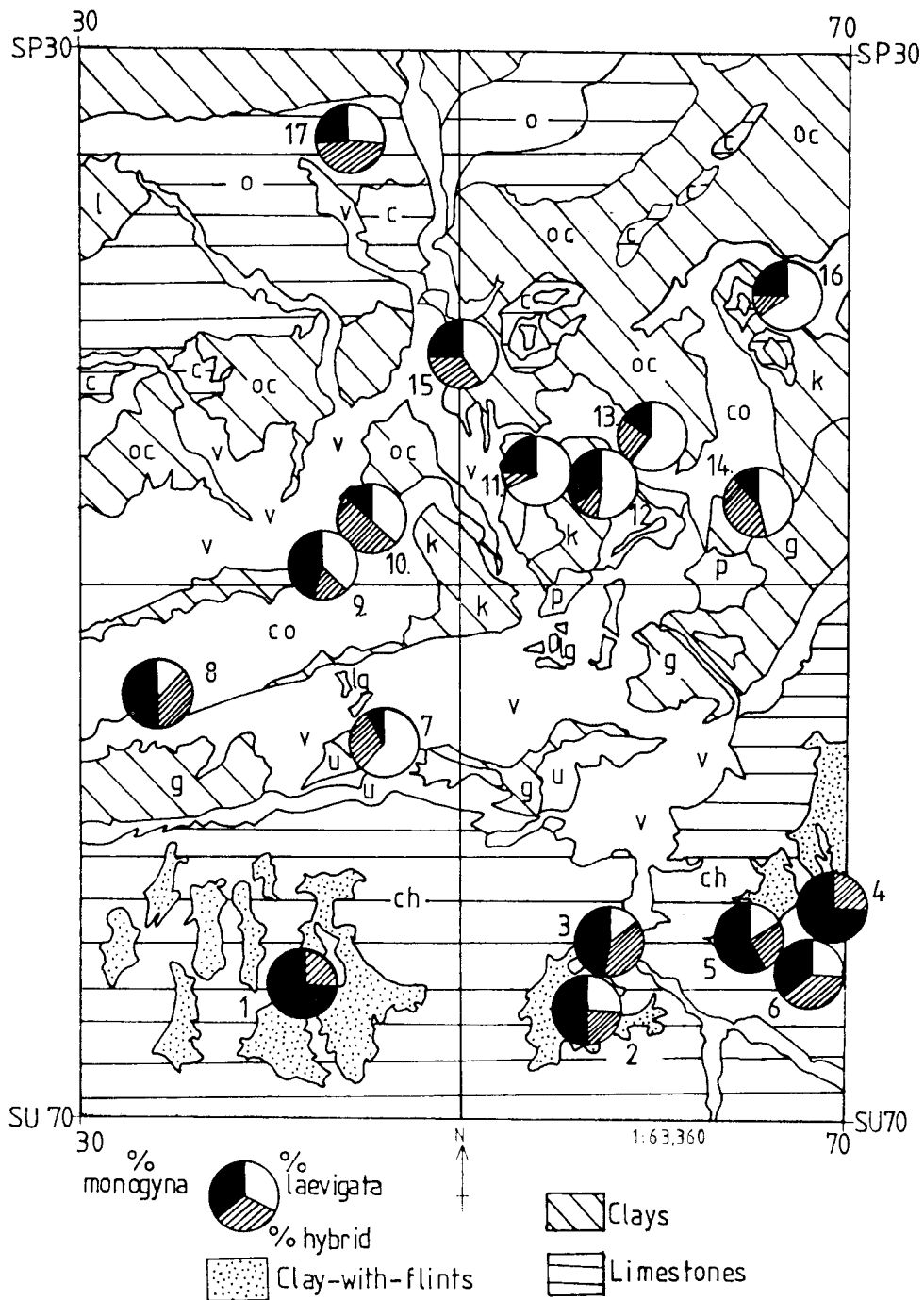
FIGURE 1. Map of the Thames Valley study area, showing the drift geology (based on Holmes & Wilson 1960) and the location of the sampled *Crataegus* populations (numbered 1 to 17 as in Table 1). The pie diagrams indicate the proportion of each taxon in the population. The geological strata are labelled as follows: V alluvium, Ch Chalk, U Upper Greensand, G Gault, Lg Lower Greensand, P Portland beds, K Kimmeridge, Co Corallian, Oc Oxford clays, C Cornbrash, O Great Oolite, L Lias.

TABLE 1. POPULATION DETAILS

	Population name	Grid ref.	n^a	Habitats[a]	No. of Shrubs	Description and notes
1	Brightwalton Common	41/422.806	15	H E W	7	Hedge along edge of Sycamore wood.
2	Ashampstead Green	41/561.773	15	H W	10	Old hedge along Beech wood.
3	Streatley Gold course	41/583.806	15	H	5	Open boundary hedge.
4	Cock's Hill	41/662.818	10	H E	10	Old hedge by Beech wood.
5	Exlade Street	41/661.815	15	H	9	Old hedge by Pine plantation.
6	Highland Wood	41/690.788	15	H W	9	Roadside hedge by Beech wood.
7	Steventon Village Wood	41/469.912	15	H W E	8	Deciduous coppiced wood.
8	Stanford-in-the-Vale	41/325.953	15	H W E	8	Hedge by wet wood on Corallian.
9	Appleton Lower Common	42/425.005	15	W H E	7	Ancient Oak wood.
10	Eaton Heath Wood	42/442.035	15	W H	5	Disturbed Oak wood.
11	Open Magdalen Wood-west	42/554.057	15	W H E S	9	Scrub and Oak wood.
12	Open Magdalen Wood-east	42/557.058	14	W H E S	9	Scrub and Oak wood.
13	Holton Wood	42/593.075	15	W H E	8	Coppiced wood.
14	Fernhill Wood	42/658.042	15	H E	4	Hedge running through wet wood.
15	Stratfield Brake	42/499.119	30	W H E S	8	Scrub and ancient Oak wood.
16	Rushbeds Wood	42/665.158	15	W H E	11	Ancient Oak wood.
17	Glympton Park Estate	42/433.238	15	H W	10	Sycamore coppice.

[a] n = sample size; Habitats: H hedge, E woodland edge, W wood, S scrub. See also Table 2.

population. These were taken from the southern side of the tree and were selected on the presence of short vegetative shoots required for leaf examination. No attempt was made to collect flowers or fruit consistently as these were often too high to sample, although a measure of total flower and fruit production was recorded (see points 4 and 5 below). Hence the present analyses are based largely on vegetative (and especially leaf) characters. Specimens were taken from below 2·5 m high. Although sampling was random with respect to the types of plants collected the sample sizes dictate that some caution should still be exercised in the interpretation of results of 'between-population' analyses. In the field, the following data were collected:

1. Transect location.
2. A preliminary determination of identity (L, H or M).
3. Girth of the bole at 30 cm height in uncoppiced trees, or at ground level if coppiced. This gave an indirect indication of tree age. Ages were later grouped into year classes as 1) < 15, 2) 16–30, 3) 31–50, 4) 51–75, 5) 76–100, 6) >100.
4. Flowering was scored on a six point scale so that a non-flowering tree scored '0', whilst a heavily flowering plant scored '5'. Although subjective, it was felt that reasonable relative estimates of flower production could be made which were comparable between trees.
5. Fruiting was scored in the same way as flowering.
6. Tree habit was scored as (1) Coppiced bole, (2) Pollarded bole, (3) Natural (unmanaged bole).
7. Style and/or pyrene number were recorded in all fruiting specimens.
8. The habitat of each specimen was recorded as scrub, edge, hedge, woodland or woodland clearing.
9. A shrub count was made in hedges which formed part of the sampled population.

The specimens were packed in presses and dried. In total, 265 specimens were collected.

In the laboratory, five undamaged leaves were selected from short vegetative shoots on each specimen. Where possible the oldest leaves were taken. A total of 1320 leaves was measured. Where fruit was present, the presence of hairs on the hypanthium was recorded. Where stipules were present they were recorded as 'monogyna-like' or 'laevigata-like'. The presence of variegated chlorosis indicative of iron deficiency was recorded. The amount of insect damage on the whole specimen was scored on a six-point scale (0–5, where 0 = all leaves complete, 5 = all leaves show some grazing damage). All other characters were scored on the five selected leaves. A hybrid index (I) was calculated for each specimen using the method described by Anderson (1949) where a
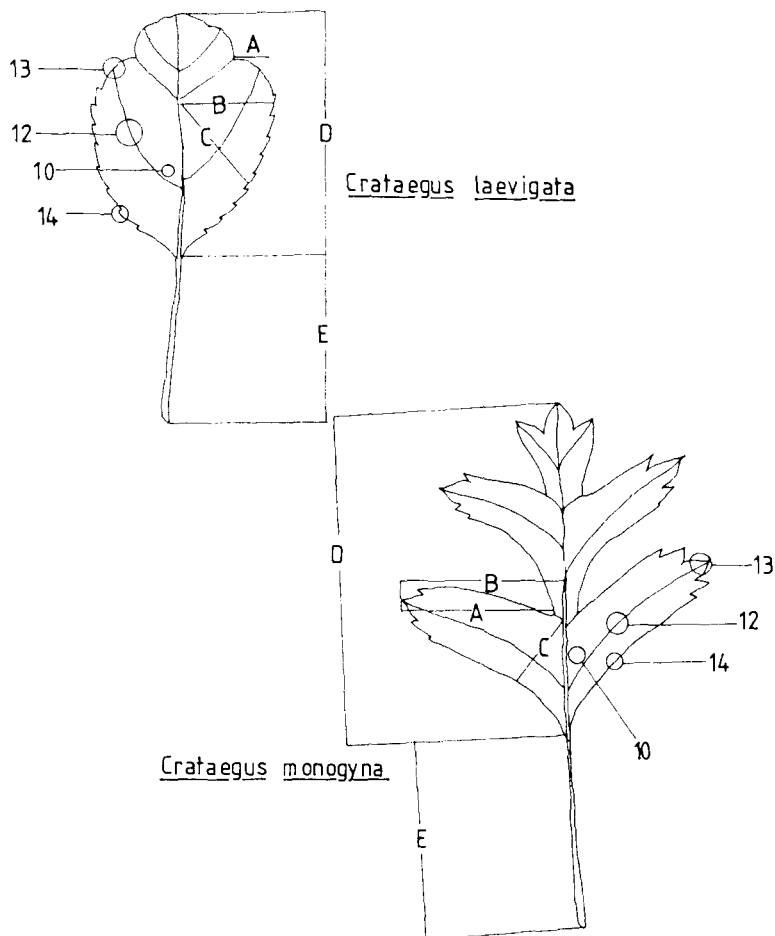
FIGURE 2. Diagram showing the leaf characters (A–E, and 10–14) used in the calculation of the hybrid index. The range of variation between the two species is indicated by the two leaves.

laevigata character state was scored as 0.0, and *monogyna* as 1·0. The full character list is as follows (see also Fig. 2):
  1. Fruit hypanthium villous or glabrous
  2. Depth of lowest leaf lobe sinus (mm) (A in Fig. 2)
  3. Lowest lobe length (mm) (B in Fig. 2)
  4. Lowest lobe width (mm) (C in Fig. 2)
  5. Length of leaf lamina (mm) (D in Fig. 2)
  6. Length of petiole (mm) (E in Fig. 2)
  7. Ratio A/B
  8. Ratio C/B
  9. Ratio E/D
 10. Hairs present in the vein axils of the abaxial lamina (I = 1·0)
     Hairs absent from the vein axils of the abaxial lamina (I = 0·0)
 11. Number of leaf lobes (subtended by a primary vein)
 12. Leaf veins curve upwards (I = 0.0)
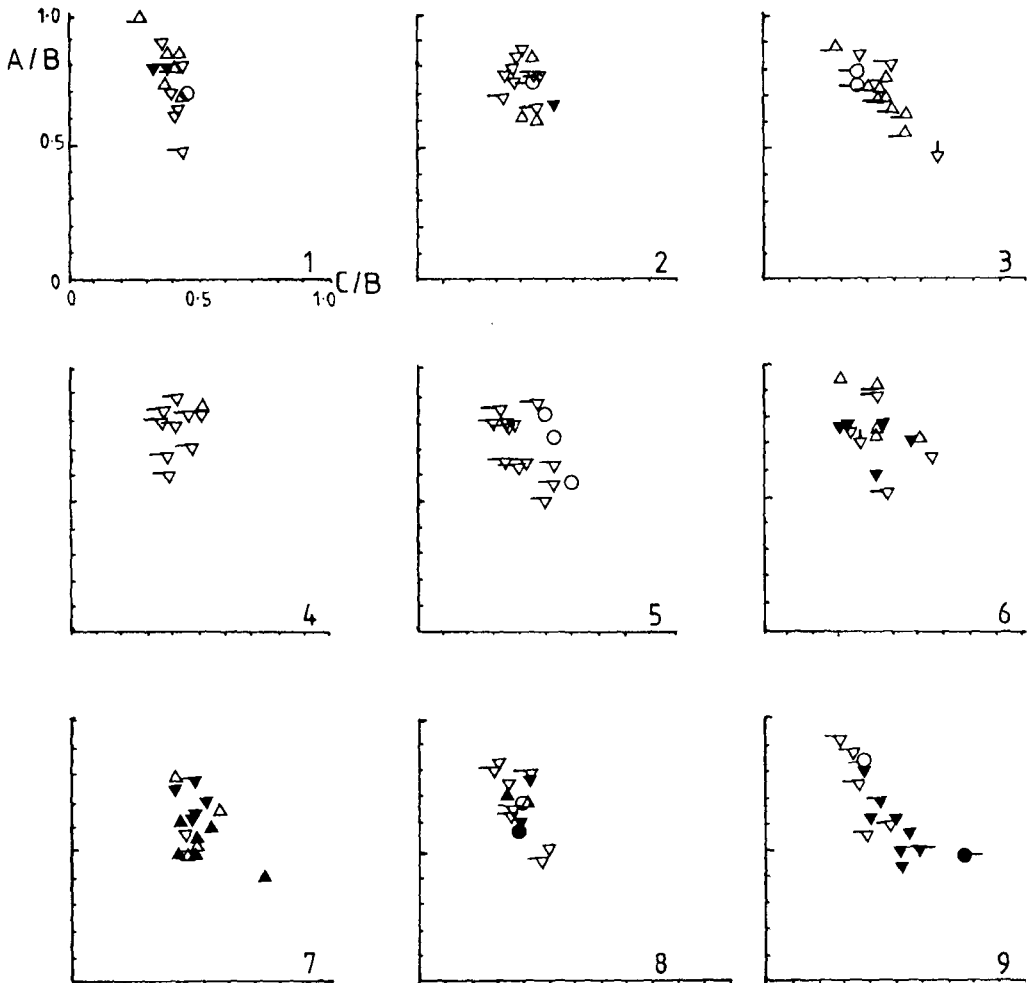   Leaf veins curve downwards (I = 1·0)

FIGURE 3. Scatter diagrams of the 17 populations showing ratio A/B plotted against C/B. See population 1 for details of axes. The following information is given for each tree: HABIT ▲ coppiced, ● pollarded, ▼ natural. FLOWER/FRUIT ● none, ─● flower with 1 style, ● 1 and 2 styles, ●─ 2 and 3 styles, ● flowers/fruit inaccessible. In plots 1–17, solid symbols denote a closed woodland habitat, open symbols an open habitat. The final diagram indicates the population means and their geology as □ Chalk and limestone, ▲ Upper Greensand, and ■ Clay communities. Means ± 1 S.E. are shown. Note that the axes are not as in the other diagrams.

13. Leaf lobe apex: rounded (I = 0·0)
                  : subobtuse (I = 0·5)
                  : acute (I = 1·0)
14. Leaf margin: serrate (I = 0·0)
                  : entire (I = 1·0)
15. Stipules if present *laevigata*-like
    Stipules if present *monogyna*-like

The hybrid index was calculated as the mean scores of characters 7, 10, 12, 13 and 14. These characters were chosen because, from previous studies, they were considered to be good diagnostic characters for the two species, and/or they could be assessed for every specimen, and because the index was to be used in another study (not reported here) to assess the value of the other characters
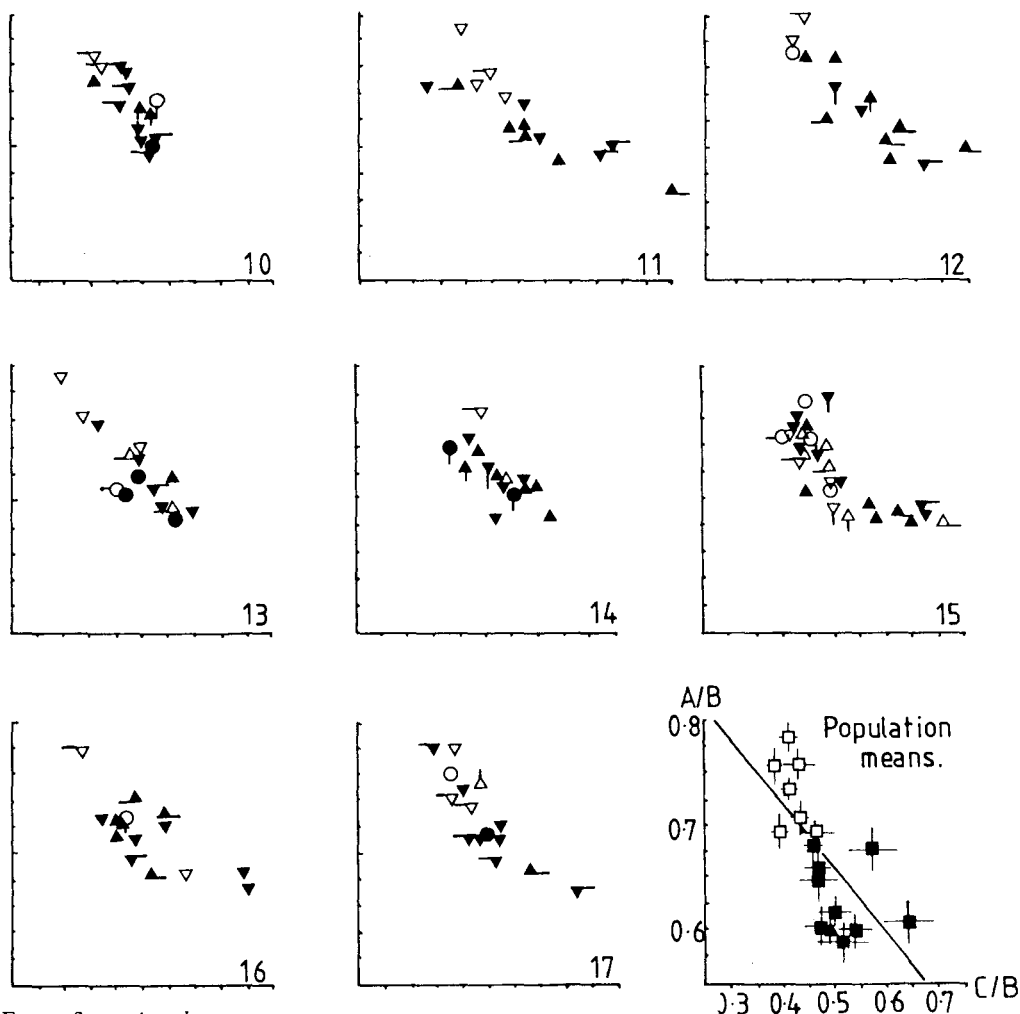
FIGURE 3. *continued.*

in specific diagnosis. In the analyses that follow *C. laevigata* is defined by a hybrid index (I) of <0·60, hybrids by I = 0·61–0·79 and *C. monogyna* by I >0·80. Statistical methods follow Sokal & Rohlf (1981) and terminology follows Stearn (1973).

RESULTS AND DISCUSSION

THE EXTENT OF HYBRIDIZATION IN THAMES VALLEY POPULATIONS

Fig. 3 shows scatter diagrams for leaf width and indentation for each population as described by Anderson (1949). The same characters (7 and 8) have been used as were used by Byatt (1975) for comparative purposes. Each point on the diagram shows the position of an individual plant relative to the axes together with its habit, habitat and style number (believed to be one of the most reliable characters). A population with a mean scatter in the upper left-hand corner of the diagram consists largely of *C. monogyna* whilst the lower right-hand corner represents *C. laevigata*. The plots have been presented in approximate geographical order from south to north. From these it is seen that chalk and limestone populations are strongly biased in favour of *C. monogyna* with considerably less

variation than populations containing *C. laevigata*. This is borne out by the hybrid index values presented in Table 2. Limestone populations showed a mean hybrid index of 0.76 ± 0.06 whilst that for clay populations was 0.57 ± 0.07. This difference was highly signficant ($t_{15} = 6.03$, $p < 0.001$). As in the Weald, there were no pure *C. laevigata* populations although pure *C. monogyna* populations were frequent. *C. laevigata* populations showed a strong preference for clay soils but were considerably hybridized.

These diagrams also show a clear habitat shift across the morphological range of the hybrid complex. Hence *Crataegus* populations in the region showed the same pattern of morphological variation and of geological and habitat preference that was found by Byatt in the Weald. Fig. 1 shows the proportion of each type in each population. The percentage of hybrids (as much as 40% in population 3 and 6) in chalkland populations suggests that both species were present here. Byatt (1975) found a similar situation in the Weald. She suggested that either hybridization had occurred between distant populations, or that these populations formerly contained *C. laevigata* and that introgression followed by strong directional selection had produced a *monogyna*-like population. For such a sudden change in selection pressure to operate there must have been considerable habitat change. It is possible that *C. laevigata* was formerly restricted to the clay-with-flints deposits which locally cap the chalk. However, Byatt found no *C. laevigata* in populations on the clay-with-flints, and it is unlikely that hybridization would occur between trees more than 30 metres apart (Grant 1971).

An alternative hypothesis might be put forward. Most chalkland sampling was done in hedgerows because very little *Crataegus* could be found in the beechwoods of the region. Since these hedges were almost certainly planted, it is likely that cuttings had to be brought from the clay vales due to the scarcity of suitable shrubs in the local woodlands for taking cuttings. The lowland trees may have come from pure or hybridized *C. laevigata* populations, in which case gene flow was due to man. However, there is some evidence (though slight) from Ashampstead Green (pop. 2) that *C. laevigata* may be derived from populations on the clay-with-flints. This woodland population lies on that deposit and shows a significantly lower hybrid index than the surrounding hedge trees (Table 2).

FACTORS AFFECTING FITNESS OF *C. MONOGYNA* AND *C. LAEVIGATA*
I am here concerned with the factors affecting habitat preference and the causes of introgression in the British Crataegi. Since fruit production in *Crataegus* gives a good measure of fitness I shall consider the effects of predation and habitat on fruit production as equivalent to their role in determining fitness although there are other components of fitness which have not been assessed.

TABLE 2. MEAN HYBRID INDEX VALUES BY HABITATS FOR 17 *CRATAEGUS* POPULATIONS IN THE UPPER THAMES VALLEY

| Population | Substrate | Mean hybrid index | | | t value between wood and hedge |
		Woodland	Hedge	Scrub	
1	limestone	0.89	0.84	—	0.74 ns
2	clay & flint	0.43	0.79	—	4.04 p<0.01
3	limestone	—	0.73	—	—
4	limestone	—	0.84	—	—
5	limestone	—	0.77	—	—
6	limestone	0.71	0.73	—	0.25 ns
7	sandstone	0.56	0.42	—	1.08 ns
8	limestone	0.83	0.75	—	1.18 ns
9	clay	0.65	0.88	—	2.78 p<0.05
10	clay	0.60	0.86	—	3.35 p<0.01
11	clay	0.44	0.42	0.87	0.14 ns
12	clay	0.55	0.89	0.88	40.20 p<0.001
13	clay	0.46	0.80	—	3.53 p<0.01
14	clay	0.49	0.76	—	2.46 p<0.05
15	clay	0.43	0.55	0.81	1.01 ns
16	clay	0.47	0.89	—	3.86 p<0.01
17	limestone	0.74	0.58	—	1.31 ns

Predation here refers to insect grazing damage to leaves and flowers, rather than fruit loss to birds and mammals which is largely beneficial in dispersing seed.

More than 100 invertebrate species are specifically associated with *Crataegus* in Britain (Pollard *et al.* 1974). Most of these are herbivores, feeding on fruits, flowers and leaves. Some, such as the hoverfly *Episyrphus balteatus* (Degeer), require pollen in their diet. The case-bearing caterpillar *Coleophora coracipennella* (Hübner) (Lepidoptera) also feeds on pollen. This moth larva burrows into young flower buds through one of the closed petals. Once inside, it feeds on the developing style, anthers and pollen. *Coleophora* may be detected in unopened buds by the small entry hole left near the base of one of the petals. A brief survey showed that as many as 20% of flowers on some *C. laevigata* in Open Magdalen Wood (pop. ref. 12) had been sterilised in this way. Predation was as high in some scrub *C. monogyna* trees in the same population.

Pollard *et al.* (1974) suggested that woodland edge and scrub trees maintained a greater diversity of invertebrates than did woodland trees. If true, *C. monogyna* might be under stronger selection pressure to evolve resistance to predators than is *C. laevigata*. In the present survey, insect damage was often observed as cavities in the leaf lamina in the vein axil region. This was equally frequent in both species although plants with an open sinus tended to be less damaged. Insect eggs were frequently found in the axils of leaf veins and, again, an open leaf sinus appeared to reduce this. Hence it is possible that the open leaf sinus, axillary hairs and possibly the cuticular wax of *C. monogyna* are adaptations to reduce insect grazing. To test whether insect grazing could influence future gene frequencies in the population through an effect on fecundity, I plotted the mean fruiting scores of the 171 mature (more than 24 years old) trees against their scores of insect grazing damage (see Methods). The results are presented in Fig. 4. There is a strong negative correlation between insect damage and fruit score ($r_{169} = -0.342$, $P<0.001$). Although this is highly suggestive, it is not clear whether this is a causal relationship nor indeed which might be the dependent variable. It is possible that the reduction in leaf area caused by selection for an open leaf sinus has reduced the ability of *C. monogyna* to colonise closed woodland habitats. Gosler (1981) found that for a given leaf length, *C. monogyna* leaves had a smaller lamina area and that the difference was greatest at the mean leaf length. Note also that the relationship is essentially similar in both the parental and hybrid morphs. However, although there is no significant difference in the mean grazing scores of the three morphs, the correlation was weaker in *C. monogyna* ($r_{85} = -0.286$, $p<0.01$) than in either the hybrids ($r_{45} = -0.466$, $p<0.001$) or *C. laevigata* ($r_{35} = -0.407$, $p<0.05$) and the slopes differed significantly (see Fig. 4B). This suggests that fruit production in *C. monogyna* was affected less by insect grazing than it was in the other taxa. This may help to explain the differences in fitness observed between the two species.

Table 3 shows the mean fruiting scores for mature trees of each parental type and hybrids in open and closed habitats on clay soils. In woodland there was no significant difference in fruit production between the parental species. In open habitats fruit production was significantly poorer in *C. laevigata* then in *C. monogyna*. However, *C. monogyna* showed a significant reduction in fruit production in woodland compared with that in open habitats whilst *C. laevigata* fruited significantly better in woodland than in open habitats. In both habitats hybrids were intermediate to the parental species in fruit production, although in open habitats *C. monogyna* trees were not significantly more productive than hybrids ($t_{18} = 1.71$, n.s.). We may therefore expect selection to favour introgression

TABLE 3. FRUIT SCORES OF MATURE *CRATAEGUS* IN OPEN AND CLOSED HABITATS ON CLAY SOILS

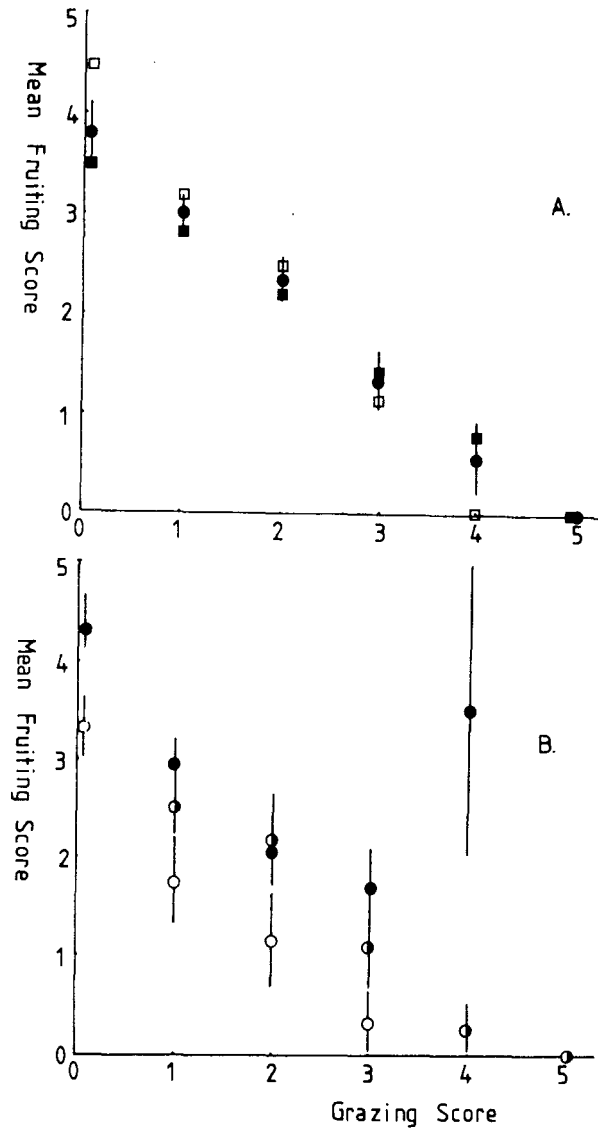|	*C. laevigata*	hybrids	*C. monogyna*
Mean fruiting score	n=22	n=12	n=6
in woodland:	2·09±1·44	1·83±1·40	1·17±2·04
	Difference between parental sp. means	$t_{26}=1.04$ n.s.	
in hedges and scrub:	n=5	n=7	n=14
	0·5 ±0·84	2·86±1·78	4·07±0·83
	Difference between parental sp. means	$t_{17}=8.18$ p<0.001.	
t difference between	3·28 p<0·01	1·31 n.s.	3·36 p<0·01
habitats. d.f.:	25	17	18

FIGURE 4. The relationship between insect damage (grazing) to leaves and fruiting score measured on 171 mature trees. A. shows the mean ± 1 S.E. for each grazing score for all trees combined (●). The regression of fruiting score on insect grazing was highly significant ($F_{1,169}$=21·93, p<0·001). In addition, the group means of populations on clays (■) and limestone (□) are also shown. B. shows the relationship between fruiting score and grazing damage in the two species and their hybrids separately. Means ± 1 S.E. are given for C. laevigata (○), for hybrids (◐), and for C. monogyna (●). The three were defined according to their hybrid index values (see methods). The regression equations for each were also significant ($F_{1,34}$ = 8·1, p<0·01; $F_{1,45}$ = 12·23, p<0·01; $F_{1,85}$ = 7·51, p<0·01 respectively). However, note that the slope for C. monogyna was significantly less than that of C. laevigata (t_{122} = 5·01, p<0·01); see text.

in woodland habitats but *C. monogyna* in open habitats, hence the question remains of why woodland populations on clay are not totally hybridized. Evidence that *C. laevigata* regeneration is occurring comes from an examination of the age structures of the populations.

Fig. 5 shows the age structure of the seventeen populations as kite diagrams. Each diagram shows the proportion of trees in each of the six age classes (see methods) together with the percentage of each type in each age class. Triangular diagrams with the apex at the top indicate a predominance of young plants in the population. These are mostly woodland populations with active regeneration. Triangular diagrams with the apex at the base show no regeneration and are largely hedge and scrub populations in which young plants are removed by grazing cattle or rabbits. The stable age distribution lies between these two extremes. These diagrams illustrate the changes that have taken place over time in the frequencies of the three groups in each population. Essentially four situations are suggested by these figures, although, as stated earlier, sample sizes dictate that some caution be exercised in the interpretation of these diagrams:

1. Populations showing approximately equal proportions of taxa with no changes over time, e.g. 6 and (to some extent) 15.
2. Populations in which hybridization has been extensive following the introduction of a second species, e.g. 3 and 7.
3. Woodland populations in which *C. laevigata* has been favoured over hybrids following introgression, e.g. 11, 13, and 16.
4. Scrub and hedge populations in which *C. monogyna* has been favoured over hybrids, e.g. 1 and 4.

Some indication of when introgression began is given by the age of the oldest hybrids in a population. Table 4 shows the age of the oldest trees in each population. Although these were rarely hybrids, Table 4 suggests that hybridization was initiated in most populations more than 50 years ago. Since hybrids do not dominate woodland populations this suggests that other factors are operating. The differences in age structure described above have probably resulted largely from differences in habitat and management policy. In many woodlands, coppicing was discontinued more than fifty years ago. This might explain the small number of recently hybridized populations in the area.

Since coppicing affects the woodland trees more than those of the surrounding hedge or woodland edge, it has undoubtedly reduced the fecundity of *C. laevigata* relative to *C. monogyna*. Coppicing may have a long-lasting effect on trees. To assess the effect of coppicing on fruit production, fruit scores were standardized for tree age, the openness of the habitat, and insect damage using the regression equation:

Fruit score $= 0{\cdot}323 + 0{\cdot}0276$ Age $- 0{\cdot}454$ Insect $+ 0{\cdot}669$ Habitat

This equation was derived from a stepwise multiple regression analysis in which these predictors each explained a significant proportion of the variation in fruit score (together with tree habit explaining $30{\cdot}23\%$ in all). The mean fruiting score for uncoppiced trees, after standardizing for age, habitat and grazing damage was $1{\cdot}86\pm0{\cdot}93$ (n=159), significantly higher than that for coppiced and pollarded trees of $1{\cdot}43\pm1{\cdot}05$ (n=104) ($t_{261}=3{\cdot}33$, p<0·001). However, this might be compensated for partly by the tendency for coppicing to increase the tree's longevity (Rackham 1987). In the present study the mean age of coppiced boles in woodland was $52{\cdot}5\pm31{\cdot}5$ (n=78) which was

TABLE 4. THE AGE OF THE OLDEST TREES IN *CRATAEGUS* POPULATIONS OF THE THAMES VALLEY

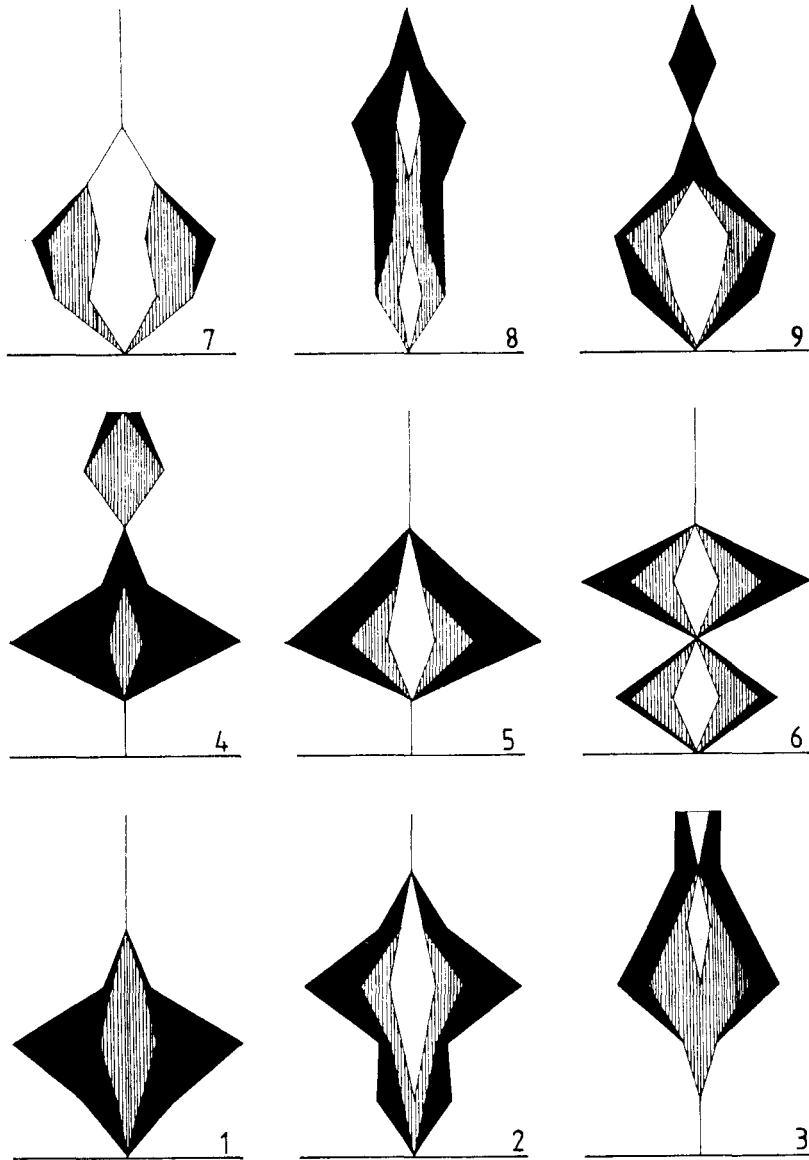| Age of oldest trees (yrs) (grouped into classes)	Number of populations		
	C. laevigata	hybrids	*C. monogyna*
0–15	0	0	0
16–30	2	0	0
31–50	3	4	6
51–75	3	6	2
76–100	2	1	2
101+	3	6	1

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FIGURE 5. Kite diagrams showing the age structure of 17 *Crataegus* populations. Each diagram shows the percentage of all specimens in a given age class, and the percentage of each type in each age class. The final diagram is a key. See text for further details.

significantly older than the mean for unmanaged woodland trees of $26 \cdot 1 \pm 20 \cdot 6$ (n=33) ($t_{109}=4 \cdot 45$, p<0.001). However, these results are biassed by the fact that coppicing was discontinued many years ago in most populations, so that the effect of coppicing on longevity cannot be assessed with confidence.

Table 2 shows the mean hybrid index values for open and closed habitats in each population. In most woodland populations on non-calcareous soils there is a significant difference between index values in the wood and in the surrounding boundary hedge. However in populations 7, 11 and 15
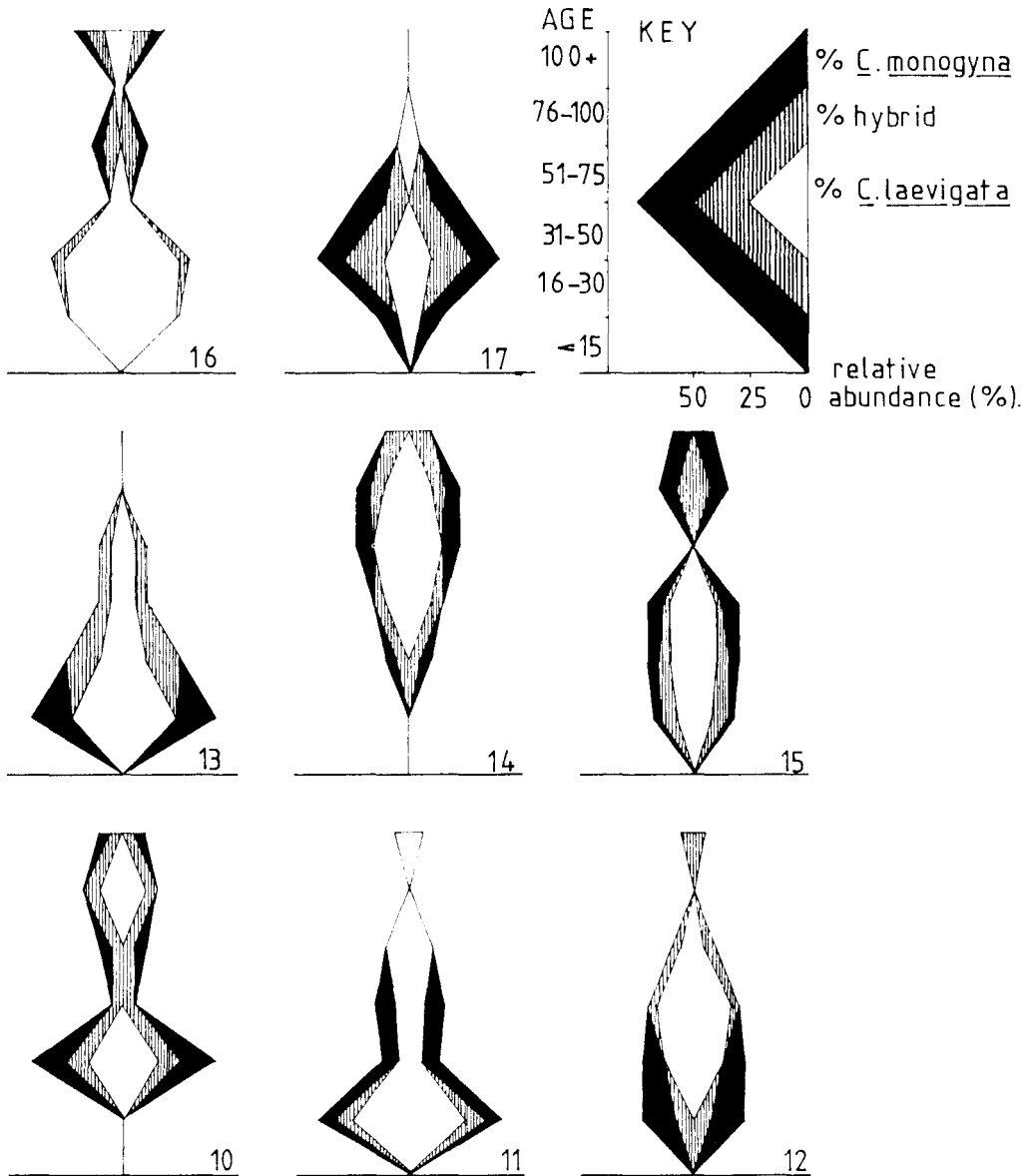
FIGURE 5. *continued.*

which are old woodlands, surrounded by ancient hedges with high shrub diversity suggesting great age (Pollard *et al.* 1974) and therefore probably planted from cuttings taken from within the wood, there was no significant difference and the low hybrid index values supports the view that *C. laevigata* is indicative of an old hedge (Bradshaw 1971). Most chalkland woodland populations have undoubtedly developed from hedges as they show no difference in morphology from the planted hedge populations. This is particularly well illustrated by the age structure of the Highland Wood population (6) in Fig. 5. Here a young woodland population has grown up from seed from a nearby hedge (this may be assumed as the next nearest *Crataegus* source was over 1 km away) on the edge of a Beech wood. The frequencies of *Crataegus* taxa in the hedge and woodland were identical.

CONCLUSION

Crataegus laevigata and *C. monogyna* are adapted both anatomically and ecologically to distinct habitats but hybridize readily where their ranges overlap in the Upper Thames Valley. However, in many hybridizing populations, hybrids have not replaced the parental species totally. Two principal factors have contributed to the introgression of *C. monogyna* genes into *C. laevigata* populations in the Upper Thames Valley. These are extensive woodland coppicing, which has reduced the fecundity of the woodland *C. laevigata* trees both in the short and longer term, and the planting of *C. monogyna* boundary hedges. The cessation of coppicing in most woodland populations has allowed some slow return to the original frequencies of the species in many woods. This contrasts with Byatt's (1975) study of introgression in the Weald which predicted a general breakdown in recognisable specific boundaries in these two species.

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