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THE EFFECTS OF VEGETATIONAL SUCCESSION ON POPULATIONS OF WEEVILS (CURCULIONIDAE).

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THE EFFECTS OF VEGETATIONAL SUCCESSION ON POPULATIONS OF WEEVILS (CURCULIONIDAE).

List of Contents.

Abstract.

A single group of phytophagous insects, Curculionidae , (weevils), were studied on four successional limestone grassland sites of differing ages. Specimens were taken from the sites using a D-vac suction apparatus to estimate populations. The sites were surveyed by a point quadrat method, recording numbers of plant species, height classes and floral structures. An older hawthorn scrub site was also studied for comparison. Successional age correlated with the numbers of species and abundance of weevils, and accounted for 96% and 88% of the variation respectively.

Comparisons were made between measures of habitat diversity and weevil populations. Number of plant species and spatial diversity seemed to have some importance in determining the abundance of weevils. Numbers of plant species present, plant species diversity, spatial diversity, and architectural diversity all were factors which affected species numbers, but these factors are not necessarily independent and it was not possible to ascertain their inter-relationship. However, spatial diversity accounted for the greatest amount of the variation in numbers of weevil species (38%) and thus it was clear that other unmeasured factors were also important in determining the size of weevil populations.

The palatability of the flora of the different sites was estimated using Cepaea spp. and some conclusions were made.

Introduction

Superabundance in insects is only rarely more than a temporary phenomenon. There are exceptions to this generalisation, for example *Aptinothrips* spp. and *Holocaphis* spp. on *Holcus mollis*, (McNeil and Southwood, 1978) and (Lawton and McNeil, 1979) are examples. Many factors influence the numbers of species, abundance, and diversity of insects on vegetation. Amongst these are food availability, palatability and the suitability of the habitat, as well as the effects of predators, parasitoids, and environmental conditions. For example, plant feeding insects do not have to become abundant to be food limited since the biochemistry of plant secondary metabolites often severely limits the ability of herbivores to exploit plants as food. Most herbivorous insects are specialist feeders exploiting a very restricted range of plants, for example leafhoppers on grassland, (Waloff and Solomon 1973).

Even on one host, insects are often confined to particular parts of a plant, especially those with a high nutritional status, or they are restricted to narrow windows of host suitability in time, (Feeney, 1976). A plant may be only nutritionally suitable for short periods of time or once alerted to insect attack biochemical or other changes may render it less palatable. Haukioja, (1982), has shown that resistance to herbivory increases in white birch following damage by the geometrid defoliator *Epirrita autumnata* . Indeed the response can be so strong as to reduce the potential reproductive output of *Epirrita* by half.

Palatability varies between species because of differing phytochemical and other defences against herbivory, but even within species there is polymorphism between close neighbours. Herbivory may also act as a biological switch to activate dormant innate defenses so that two otherwise similar plant communities may differ in palatability merely as a consequence of differing insect herbivore loads. Finally the growth stage of the plant further affects palatability.

Plant material en masse is not a particularly attractive resource. Sap is rich in sucrose and low in amino acids, so it is amino acid levels which influence the numbers and type of insect that can exploit plants directly. Herbivores have evolutionarily responded to this problem in various ways. The secretions of quantities of honeydew by aphids is to dispose of excess sucrose accumulated in order to obtain sufficient protein. Strophingia ericae is a minute psyllid bug which feeds directly below the leaf growing tips of Calluna and is able to draw on the amino acids which are being transported to the sites of manufacture of new leaves, (Hodkinson, 1973).

Seasonal changes and variations in maturity of the plants affect the population of herbivores that can be supported. There is a general decrease in the energy/protein ratio of plant tissue with seasonal age, and an increase in sucrose and structural carbohydrate, (Morrison, 1949). A gross measurement of the potential calorific value of the tissue, although this does fall with age, masks the extent of the decrease in nitrogen content.

Even the measurement of energy/protein ratios is a fairly crude estimate of the resource value of plant tissues to any insect. Soluble nitrogen is the biologically significant factor, but this may fluctuate greatly and is difficult to measure. Nitrogen content is highest in meristematic tissues but damage by insects results in more irreversible damage in this area than other tissues, (Hodkinson and Hughes, 1982), and hence rarely is exploited. Young tissues such as leaf buds and young leaves and shoots, which are in a state of growth, have a high nitrogen content and during such growth phases the phloem will contain amino acids mobilised from storage organs. However the phloem is located within the plant and requires special adaptations to exploit it. Exploitation of young tissues is hampered by low apparency, (Feeney, 1976), growth stages are often short lived, and the biology of an insect herbivore that exploits high nitrogen phases will reflect this. Such phases are well documented; in the Northern Treeline Birch the total leaf nitrogen fell from 3% dry weight to 1% dry weight in three months, (June to September), (Haukioja et al, 1978). Holcis mollis shoots formed either in autumn or spring have higher nitrogen levels than existing shoots, (McNeil 1973). In conclusion merely the plants relative maturity will affect its attractiveness to an insect herbivore. On these grounds alone one would predict variations in herbivore load with successional status.

Often plants control insect herbivore load by other ways than merely passive nutritional status. Interactions between Epirrita autumnata and Betula involve complex defensive reactions by the plant, and it appears here the plant regulates the productivity of insects, (Haukioja, 1980).

Even if plant tissue contains broadly the right quantities of energy and nutritive materials in a suitable mixture it does not mean that it is either;

i) actually suitable, or

ii) available to a particular insect population since there are specific barriers to plant consumerism as well as more general ones.

Plant material has low energy and protein to mass ratios; it is not a satisfactory strategy for insects to feed on plant material which is also elusive or unpredictable. In other words most plant's nutritive qualities are poor. If animals are to feed on general plant material they must be able to compensate for this by consuming relatively large quantities of food, and they must be assured of its consistent availability. If plant material is elusive or unpredictable an insect will find it evolutionarily difficult to exploit unless it is of unusual nutritive value, such as underground storage organs, seed pods etc. The ease of location of a particular resource, eg; leafbuds, has been defined by Feeney, (1976), as apparency. Greater apparency results from large plants rather than small ones, with a regular distribution rather than ramdomly spaced. If plants occur at high density they are apparent, or if they occur frequently or with temporal regularity. In a temperate forest deciduous leaves of the dominant tree species are apparent to insect herbivores on all these accounts although young leaves to a lesser extent than older ones.

Apparent	Non-Apparent
woody perennial	annual
climax species	pioneer
common species	rare species
mature leaves	young leaves
bark or stems	leaves
evergreen species	deciduous species

(after Hodkinson and Hughes, 1984).

The importance of apparency to plant-insect interactions is illustrated by the high degree of variability in the timing of bud burst between individual oaks within a forest, by which the risks to insect populations are greatly increased, (Satchel, 1962) (Feeney, 1970). In this example there is an effective decrease in apparency.

There are other barriers to consumerism by insects than that of reduced plant apparency. Many plants have organs to repel insects, and the production of toxins by plants is common. Trace compound barriers such as alkaloids, eg: nicotine, cocaine, quinine are one type of barrier. They are fairly specific in their effect on insects and are commoner in herbs than trees.

An alternative strategy is to produce dosage dependant chemical barriers, such as tannins, resins, silica. Effectiveness on active herbivore consumers is dependent on the concentrations found in the plant or the stand, but generally they occur at much higher concentrations than trace-compound chemicals. They are therefore energetically costly to produce and have a more general effect.

Again the presence of these chemicals is seasonally variable. Secondary chemicals perform other functions than defense and evidence of their defensive effect is difficult to prove. However, defoliation by the bud moth Zeiraphera results in delayed leaf flush in Larix decidua. The new leaves are lower in nitrogen, higher in fibre and resin content, (Baltensweiler et al, 1977). Clearly there is a complex and specific habitat template necessary for the phytophagous insect, (Southwood et al, 1979), and many factors will affect the herbivore load of a particular vegetational stand.

Plant chemistry and defense will have an important influence on insect diversity for even when comparing two similar plots quite close to each other, we have seen there may be marked differences. Spacial dimensions of the habitat may also be important. 'Bird species diversity' has been long associated with measures of habitat structure, (MacArthur, 1957). Correlations between the microhabitat of the phytophagus insect and its abundance and diversity have only been made recently. Southwood et al, (1979), have devised a measure of spacial diversity making distinctions between the foliage-height diversity and architectural diversity. For as Lawton, (1978), has pointed out, there seems to be a clear difference between merely changes in density of the habitat and its architectural structure of differing types of plant structures, eg; leafbuds, leaves, flowers, stalks. He has stated that 'there must be more ways to make a living on a bush than a bluebell'. Stinson and Brown, (1983), have shown the abundance and diversity of leafhoppers are correlated to the architectural diversity of the habitat, see also Waloff and Solomon, (1968).

Spatial effects can be various, larger plots of natural stands of the same plant have more insect species, (richer animal communities), (Rigby and Lawton 1981), but small or isolated plots frequently have greater numbers of herbivores, and certainly measurably more eggs laid by females than larger ones. (Jones, 1977; Ives, 1978; Zalucki and Kitching, 1982). The surrounding vegetation strongly influences the herbivore populations; when there are different species of plant, ie. mixed stands, there is less colonisation and a lower rate of population growth causing the herbivorous insect to be less abundant. (Tahvanain and Root, 1972; Root, 1973; Cromartie, 1975). Thus the population dynamics of insects may vary from one habitat patch to the next. It is also true that different herbivore species attack different plants of the similar distributions in different ways, for example Pieris rapae, Phyllotreta striolata and P. cruciferae, all behave differently given similar plant densities in their attack of Brassica, plants (Cromartie, 1975). (Iwao, 1971; Singer, 1972; Whittaker et al, 1979). Kareiva's, (1982), analysis of the dispersal of the flea beetle, (Phyllotreta), showed dispersal rates increased as distances between patches declined. Thus the beetles foraging was optimal in relation to the quality of the host plants, only when these were close together.

Richlef's, (1973), has emphasised the 'many functional and structural attributes of community change during its successional development'. Such changes alter the habitat so that the same species strategy will no longer match with the altered habitat template, as a result animal communities will be driven to change in parallel with the vegetation.

Historically, 'from the work of numerous ecologists most notably Clements, (1916), and Watt, (1947), it is now generally accepted that most types of vegetation are subject to temporal changes in both species composition and in the relative importance of constituent life forms', (Grime, 1979). This may be cyclic as in seasonal variation but successional changes, progressive in nature, will also occur. Stands of different successional age will differ in height, maturity, species composition, plant chemistry, and possibly colonisation by invertebrate species. However, even without the factor of colonisation there will be inherent differences sufficient to influence animal communities (Brown, 1982). Indeed, in localised areas, where dispersal is not an important component of colonisation, colonisation itself will be a very minor factor, and it will be the suitability of a particular habitat to a species trying to establish itself that will be significant.

If herbivore popluations will be influenced in a number of ways by the vegetation, they will also exert their own effects, including successional ones on the vegetation. Indeed this reflects the traditional view of plant-herbivore interactions as factors limiting the growth of their host species. Janzen, (1970), has described how in the tropics the level of insect and vertebrate predation around a parent tree is such that it affects the distribution of establishing seedlings, which he suggests may account for the diversity of tree species in equitorial rainforest:- (a suggestion that Hubbel, (1980), has since refuted following studies in Costa Rica). The feeding of the beetle _Gastrophysa viridula_ is important in the competitive interaction between two dock species, _Rumex obtusifolius_ and _R. crispus_.

Levels of feeding by *Gastrophysa*, which had no effect when either species was grown in isolation, resulted in extensive damage when the species were competing. In effect this is a result of differing strategies to light grazing. *Rumex crispus* responded by reducing its root to shoot ratio dry weight ratio from 2.14 to 1.69, making more material to compensate for consumption. In contrast *R. obtusifolius* increased the ratio from 1.18 to 3.57, essentially protecting material from surface grazing. *R. obtusifolius* appeared to show severe reductions in seed numbers and the weight of each seed. Under the pressure of this consumerism, *R. crispus* appeared to be at a competitive advantage. (Bentley and Whittaker, 1979. Bentley et al, 1980).

The aims of this project are to look for successional changes within a habitat and attempt to correlate this with the status of an animal community. Measures of habitat diversity are used and are as follows; plant species diversity, the structural or foliage-height diversity (which essentially is the density of the habitat) and the architectural diversity. Plots of similar soil type, slope and aspect but of differing age and successional development were chosen to show how these measurements of habitat varied with time. The insect population at each of these sites was sampled using D-vac apparatus, members of the Coleopteran group Curculionidae extracted, counted and identified, so that these habitat changes could be compared with the abundance and diversity of an animal community.

Methods and Materials.

Within the area of a limestone quarry, a range of sites differing age and of secondary successional status were selected. A D-vac apparatus was used to extract insect populations from 10 square feet samples of each site.[2] Point quadrats were used to discover the number of plant species present. The pin used in this method was marked so that additionally a measure of height and density of the foliage could be made. The numbers of plant structures touching the pin were also recorded.

The Study Area.

The site selected for a study had to have a selection of areas in the same locality and of similar soil type, aspect, and slope, but of a differing age and at differing stages of secondary succession. Wingate Quarry Local Nature Reserve, owned by Durham County Council was chosen. It is a site of importance as a refuge for the grassland flora that were once common in the meadows of the magnesium limestone ridge which runs N.E. to S.W. through the County of Durham. The quarry has had a history of working going back to the last century. However, magnesium quarrying ceased in the 1930's, only to be resumed after the Second World War. The quarry was in part used for stocking mined coal but following its purchase by the County Council in 1978 it was fenced and partly regraded.

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[2] See page 19 for further details.

Selecting Sites.

As a result of the intermittent activity it was possible to select several sites of differing successional age. On one site there was hawthorn scrub, which was estimated to date from the mid 1950's, (pers. comm. Mr. S. Scoffin, warden). In this study it was assumed to be at least 20 years old, although in fact this was probably an underestimate. The site is divided by a path running through the quarry, to the west of this the quarry is periodically grazed as a management practice, to the east it is retained in an ungrazed state, although periodic clearing of emergent hawthorn is used to keep the rich magnesium limestone flora intact. It was possible to identify five main sites, which on consultation with Mr. Scoffin, I was able to age as follows:-

i) a mid-successional site which had been ungrazed, although some clearance had occured in the ten years since it had been regraded.

ii) a younger site which had through grazing been held at an earlier successional development and was estimated to be about six years old.

iii)and a site very similar to (i) described, except for being slightly more mature, and on which a little hawthorn was establishing, of an estimated age of 12 years.

iv) a final site recently cleared for maintenance was also selected, which was about 12 months old.

v) a twenty year old site, which had a developed hawthorn scrub and was used as a comparison to sites (i-iv).

The sites were 20 metres by 40 metres and marked out with wooden pegs. Each site, at the beginning of the study was given a number, but in this report from now on I shall refer to them only by successional age or description to avoid confusion. (see table 1). Map 1 gives an indication of the layout and aspect of the reserve; each site is marked.

A Vegetative Survey.

The vegetation was surveyed using a point quadrat technique. The location of each of the fifty quadrats taken at each site was chosen by throwing a small steel pin at random over my shoulder. Where the pin landed a longer steel pin was vertically inserted into the vegetation. Using preprinted record sheets the plant species touching the pin were recorded as standard for this technique, for example Muller-Dumbois and Ellenberg (1974).

The pin was marked from 5 cm away from the sharpened tip in increasing increments as shown in figure 1. This allowed the first 5 cm to penetrate the earth and keep the pin standing vertically without being held. The marking described intervals starting at 25 mm and increasing to 650 cm. The pin was 2.0 m long. These marked intervals were used to record the spatial elements of the habitat. (see figure 1.) Both the size and increase of the increments were chosen arbitarily, but the nature of the vegetation surveyed influenced this.

Using the markings the vegetation was divided up into a series of vertical layers. Each layer of each quadrat was scored either positive or negative according to whether there was vegetation touching the pin at this level. If there was more than one 'touch' in a single layer this could not be recorded in any special way. Should this occur repeatedly it would mask the true density of the vegetation, so it was important to select an appropriate scale on the pin in order that multiple touching was minimised throughout the pin's length. As a result of this need the broadly geometric scale described was chosen. The overall effect is to roughly measure the density by the number of occupied laminar within the vegetation. This is easier than recording the total number of touches of the pin at each quadrat and their position, an almost impossible task. An effect of this layer method is that as the vegetation becomes sparser the width of the layers becomes greater, as illustrated in figure 2. Conversely if the vegetation occupies most of the available volume, then each of the layers will be close together.

When the vegetation was too high to measure using the pin method a second technique was used. Firstly the pin was used as normal, as far as possible. Then lying on my back where the pin had been inserted I looked vertically upwards into the canopy through the view finder of a single lens reflex camera, with a split screen focusing aid. I focused the camera on the lowest piece of vegetation visible in the centre 'disc' of the screen, noting the species involved. This was in the event always hawthorn. Then using the scale on the lens barrel I read off the distance to which the camera was focused.

Finally I recorded the plant structure involved. Focusing up through the canopy I repeated this, until I had followed the line of the pin to the top of the canopy.

This method did involve certain errors since the core that the central portion of the split-screen took through the vegetation was larger than the pin, and it was difficult to hold the camera steady. Also the system viewed more vegetation at the top of the canopy than close to the lens due to the effects of perspective. However, the method was reliable, easy (although time consuming) and required no specially fabricated materials. I think it compared favourably, at least for the purposes of this study, with the use of scaffolding towers or weather balloons on wires as used in previous studies. In conclusion the method's inaccuracies were acceptable, particularly as the survey of hawthorn scrub was only intended as a comparison to the grassland sites.

As mentioned previously a record of all the plant structures touching the pin were recorded on printed record sheets. This provided a record of the architecture of the habitat, and would allow the calculation of a value for the architectural diversity of each site. Again multiple touches of the pin by the same type of structure were not treated in any special way. Plant structures were categorised after Southwood et al, (1979), with some ammendments. These are listed in Table 2. In particular a distinction between monocotyledon and dicotyledon stems and leaves were made, because these appeared to be structurally different, and were added to Southwood et al's (1979), list.

TABLE 2

List of Plant Structures Recorded.

dead wood > 10 cm diameter

dead wood > 2-10 cm diameter

dead wood < 2- 2 cm diameter

bark on dead wood > 10 cm diameter

bark on dead wood > 2-10 cm diameter

bark on dead wood < 2-2 cm diameter

bark on living wood > 10 cm diameter

bark on living wood > 2-10 cm diameter

bark on living wood < 2-2 cm diameter

green stems

leaves (monocotyledon)

petioles

leaf surface (upper) (not monocotyledon)

leaf surface (lower) (not monocotyledon)

leaf budscales

flowering stems

flowerbuds

open flowers

dead flowers, which are not,

- fruit/seeds
- old fruiting structures
- dead leaves (not monocotyledon)
- dead stems (not monocotyledon)

mosses, (epiphytic)
mosses, (soil surface)
lichens and algae, (epiphytic)
lichens and algae, (soil surface)
fungi fruiting bodies, (soil surface)
fungi fruiting bodies, (epiphytic)
After Southwood et al, (1979).

Sampling the Invertebrate Populations.

Samples were taken using a D-vac insect sampling apparatus. A petrol driven fan, allowed insects on the herbage to be sucked up through a funnel connected to the apparatus by wide tube. A cloth bag trapped the insects. The cone or funnel could be placed over a particular area of vegetation to permit collection from it. Since the cone was one square foot in cross-section, the ten random repetitions from each site allowed an area of ten square feet to be sampled. Collected insects were shaken from the cloth bag into a polythene bag. At this stage no sorting occured. The bag was sealed with plastic tape. A small glass specimen tube containing a filter paper soaked in ethyl acetate, or preferably a 5 mm layer of plaster of paris similarly soaked, was taped to the cut corner of the bag. Samples were kept in the shade until they were brought back to the laboratory for examination. Repeat treatments of the same vegetation failed to produce further specimens of Curculionidae, and I estimated that the method gave over 90% extraction from the herbage.

This is similar to other workers findings, (eg. Southwood, 1966; Dr. V.K. Brown, pers comm.) However, if the herbage was damp, sampling became impossible; the insects and leaf litter stuck to the vegetation and water droplets were sucked into the D-vac's collection bag, making the removal of collected samples difficult. As a consequence sample days were chosen for their dryness. Sampling was repeated four times during the study period of the summer 1984; on 30th May, 12th June, 26th June, and 19th July. These were roughly two week intervals although the exact dates were dictated by the weather. In addition in the hawthorn scrub where the vegetation was too tall to ensure complete extraction of all the weevils, by the use of suction apparatus, the plant material was additionally subsequently beaten and falling insects collected on a tray one foot square. This was repeated as necessary when collecting each sample from this site, however, some samples lacked vegetation tall enough to justify this additional method. Samples were added to those already collected at that site by the D-vac apparatus.

Bags of sampled insects were sorted by placing their contents in a large tray and brushing through the material. Curculionidae were easily removed and placed in 70% alcohol to which a few drops of glycerol had been added. This technique proved quite effective, sorting through samples for the second or third time failed to reveal further individuals. A binocular microscope was then used to identify individuals according to Joy, (1932). A species list is to be found in the appendix. Nomenclature is after Kloet and Hinks, (1977).

Estimating the level of Herbivory.

An attempt to gather information regarding the level of herbivory was also undertaken. This was done by estimating the numbers of snails (*Cepaea* spp.) ateach site. These were chosen on the basis that they are general herbivores and molluscs have been used previously by other workers to attempt to assess herbivory. (eg. Cates and Orians, 1975; Grime et al, 1968). Since they are wide spread and oligophagous it is maintained that they have no specialised adaption to specific anti-herbivore strategies. As the sites that were being compared were fairly similar, it seemed unlikely that snails were genetically predisposed to cope with one particular one and any natural bias in this biological assay method would be equivalent on each site.

At each plot twenty baited pitfall traps were set on the 15th June. This was done in a grid of four by five traps, spaced out at two metre 2 m intervals. Each trap comprised of a plastic cup sunk upto its rim into the earth. The bait used comprised of a sweet solution made up in the following mixture 7 parts beer, 2 parts fresh orange juice, 1 part water, to which half a kilo of sugar was added per gallon. Sufficient fluid was initially placed in each cup to form a depth of 5 cm. This was topped up twenty four hours later, after the snails were collected and removed. A final collection was made after a further twenty four hours. The total numbers of snails trapped at each plot during this period was then recorded.

The Handling of Data.

The University of Durham Computer was used to handle the raw data collected. A program which generated a range of diversity indices from the numbers and abundance of species was kindly supplied by Dr. B. Huntley, for which I am most grateful. This was used for the plant species and the structural and architectural components of the habitat as well as the species of Curculionidae found. The Statistical Package for Social Sciences was employed to perform statistical analysis. The New Gimms Version, (release 6), of the Gimms graphics package created the graphical representations of the findings of my study.

Results and Discussions.

The Relationship between Numbers of Species and Total Abundance of Curculionidae and Plant Succession.

Over 350 individual Curculionidae (weevils) were sorted and identified. The results of this D-vac sampling from five sites on four occasions is shown in table 3. There appeared to be no obvious pattern in the occurence of particular species or their abundance, except that (*Eutrichapion loti* Kirby) was by far the most frequently found. This species is easly distinguished by its characteristic shape and yellow appendages.

There was a clear increase in the number of weevil species taken at each time of sampling as the season progressed upto the final sample on 19th July. This is illustrated in the bar graph of figure 3. However, also apparent is the failure to collect any specimens in sampling on the 26th June. The cause of this was almost certainly the period of extremely wet weather in June. As a result the herbage remained too damp even on the apparently sunny day chosen for sampling, Data from this date was not used in analysis.

Through out the season only thirteen weevils were collected from the hawthorn scrub. This area had been selected for comparison but the numbers were so low that the results from this type of vegetation were not included in the statistical analysis.

The first examination of the total collection of Curculionidae from the three samples reveals an increase in the number of species found with increased maturity of the plot up to the age of twelve years, then a decline. This is shown in figure 4. where the total number of species found in samples taken at each site are plotted against the age of the site. This illustrates that at both late successional plots twelve species were found. One would expect this from their visual similarity, given that the numbers of species are determined, at least in part, by properties of the habitat itself. At the six year old site only half as many species were found. At the youngest plot (one year old) and the oldest (twenty years old), only three weevils species were found. Regression analysis confirmed the results as highly significant ($r = 0.98$, $p = 0.01$, *see 1.25). The twenty year old plot of hawthorn scrub is not included in this analysis. These statistics indicate a very close correlation between successional age and the number of weevil species within the grassland habitat.

Similar analysis of the total abundance of weevils (i.e. number of specimens) is also highly significant and this is plotted out on figure 5. ($r = 0.94$ $p = 0.01$ see 26.15). This again involved the summation of all the samples taken through the season, and the calculation of the total numbers of specimens taken at each successional site.

Of the four grasslands sites, the additive bar graph in figure 3. and associated data in table 3. illustrates that the youngest site had the lowest abundance of Curculionidae on every occasion of sampling as well as in total.

* standard error of the estimate.

The oldest grassland site studied, the twelve year old site had the greatest abundance of Curculionidae in total and on every occasion, except 19th July, when the ten year old plot had slightly larger numbers of weevils present. Whilst the ten and twelve year old plots do have the same numbers of species, the actual abundance of insects at the ten year old plot is considerably lower than the twelve year old one, with only nineteen more individuals collected than on the six year old plot.

These results indicate that successional age is closely correlated with the numbers of species and individuals of Curculionidae present in the habitat. Three possible explanations exist as to why this might be the case.

Firstly, one possibility is that the correlations observed are caused by genuine successional effects. That is the increase in weevil populations is caused by the establishment and increase in frequency of occurence of a particular plant species or suite of plant species. The plants may be important as food plants or represent some other essential resource, such as shelter.

Secondly, the effect observed may be the result of the increasing maturity of the plant stock with age. As all four plots do have weevils present possibly as their host plants increase in maturity, size, and biomass and number of individual plants, then so the numbers of weevils that can be supported increases.

This is not a succession effect since for this to happen there need be no replacement of plant species within the community with others, or change in the relative abundance of the various species in the flora.

Finally, however, as natural populations of insect herbivores are rarely food limited, (Lawton and McNeil, 1979), the marked changes in weevil populations observed may not be connected with the availability of food plants but with structural changes associated with successional development.

There also exists the possibility that the observed correlation between weevil species and numbers and plant succession is caused by the effect of the animals on the plant community.

It is documented that large herbivores, primarily vertebrates can affect plant community structure. Grazing of the alluvial plains and lower slopes of grassland pastures in Idaho by cattle is followed by the replacement of palatable Agropyron spicatum with the unpalatable Aristida longiseta. When this grazing becomes heavy and prolonged the palatable Agropyron will not recover even if the livestock are removed; recovery during the dry summer months is slow and autumnal regrowth depletes the Agropyron food reserves. A permanent change is therefore observed. (Evans and Tisdale, 1972).

Even invertebrates can have pronounced effects. The larvae of the frit fly Oscinella frit bores into the central shoots of Lolium multiflorum, Italian ryegrass.

Losses of ryegrass to Oscinella are 15 to 30% per year and its attack is a major factor in the replacement of ryegrass with other species in permanent grasslands (Clements, 1978). Yet there are fewer examples of herbivores actively changing the habitat to favour a particular food plant since their feeding normally puts these at a selective disadvantage.

In this study the possibility exists that weevils may have a similar effect on their habitat and food plants in particular. If this is the case, the greatest effect will be at the site with the greatest density. In this study this is the twelve year old plot but weevil numbers are still low, never rising above 10.8 weevils per square foot whenever a sample was taken. This low population, representing four species is unlikely to be able to have dramatic effects on the plant community. If there was an effect it would be most obvious in a plot older than the twelve year old plot, and no older grassland site than this has been studied. For these reasons we must conclude that weevils are not significantly affecting plant populations or succession in the studied plots.

To conclude, it seems that the correlation between numbers of species and abundance of weevils is due to the effect of the vegetation on these insects.

Species richness of weevils and the abundance or total numbers of individuals have used as a means of comparing insect populations. Whilst diversity measures and indices have been used in this study they have not been used as a means of measuring weevil population.

The decision is partly because, number of species and abundance are measures which have very clear meaning in the field, and it is easy to understand what these changes in weevil populations practically mean. But the decision is also an empirical one, since no meaningful relationships were derived by using a range of diversity measures of weevil populations when they were compared with the range of other data obtained.

Effect of Habitat Diversity of Weevil Populations

(using direct measurement of the habitat).

The aims of the project were to investigate the possible relationships between the species richness and abundance of Curculionidae and the nature of the vegetation. The vegetation was characterised by point quadrat measures of the numbers of plant species, height classes and plant structures present. Studying the vegetation in this way may help to explain why the weevil population correlates so closely with the successional age of the sites.

Measurements of the vegetation reveals no obvious link between plant species frequency and the weevil populations. No one plant seemed to occur in proportion to the appearance of weevils on the site. Dominant species were generally dominant on all sites. The exception was Lotus corniculatus, which did become less frequent in the older plots: occuring in 70% of the quadrats in the one year old plot, 34% in the six year old plot, 18% in the ten year old plot and 22% in the twelve year old plot. Trifolium species were relatively abundant in the six year old plot; for example T. medium occured in 24% of the quadrats in this plot and yet everywhere else frequency was below 2%.

In general no significant conclusions can be drawn from this the decline in Lotus corniculatus. With successional age is interesting since the information available suggests vetches and trefoils are the most important food plants (Joy 1932).

Incidentally this is further evidence that the effect of succession on weevil populations is not directly connected with food plants.

The abundance and numbers of species of weevils taken in each D-vac sample at each site, are plotted against numbers of plant species in figures 6. and 8. respectively. Since the number of plant species is given by the vegetative survey, its value will be the same on each of the samples made at the site. This results in a series of vertical lines of points which correspond to the different samples taken at each site.

For the abundance of weevils in each D-vac sample and the number of plant species a correlation coefficient was calculated using the data in table 4. and the graph shown in figure 6. This indicates there is a significant positive correlation between numbers of Curculionidae found in the site and the number of plant species present (r = 0.54, p = 0.015, see = 21.9). As previously discussed the hawthorn scrub of this twenty year old site (plot 2) is not included in this analysis.

The total numbers of Curculionidae specimens collected at each site (total abundance) also were plotted against the numbers of plant species recorded, (figure 7.) There is no significant relationship, but the figure illustrates the distribution, of weevils collected between the different sites.

When a similar comparison is made between the numbers of species of Curculionidae obtained at each sampling and the number of plant species present a value for the correlation coefficient of r = 0.44 is obtained. (p = 0.036 see = 2.216). This is a significant relationship and is shown in figure 8. The total numbers of species of Curculionidae obtained at each site is plotted against plant species present in figure 9. but because this reduces the points to only four no statistical analysis was possible.

In terms of flora the ten year plot has fewer species than the six year old plot. I find this suprising since visually the ten year old plot resembles closely the twelve year old site. Since single occurences of a species would alter the numbers of species present, some of this can be accounted for by random effects.

Similar comparisons were made between the number of height classes in the vegetation and the plant structures in the habitat and the numbers of species and abundance of weevils in the plots. However, in none of these four cases was there any significant relationship.

Figure 10. shows the total abundance of Curculionidae sampled against numbers of height classes in the habitat of each plot. The dotted line marked with a '?' indicates the possible relationship but statiscally this is not significant. There is a very small spread of numbers of height classes between sites; only five classes between the one year and twelve year old sites.

This is a product of the way height classes are recorded. A single touch in any point quadrat at a particular height class will cause that habitat to be scored for that class. This is also true for floral structures. In figure 10. we see only five classes separate the first year site from the twelve year old site. This effect could be predicted in the field, despite the differing overall appearances of the habitat, in that relatively quite tall plants such as Chrysanthemum leucatum were present in all the plots. Measuring the number of height classes does not record the spatial diversity of the habitat and one tall plant on the plot can weight results to show a large number of height classes.

Similarly the number of different types of plant structure ranged from seven to twelve in all the four grassland plots. The hawthorn scrub as one would except clearly had many more plant structures and height classes, and it was entirely dominated by hawthorn and the ground flora was totally different from the grassland studied.

Effect of Habitat Diversity on Species Richness and Abundance of Weevils.

(using diversity indices as measurements of the diversity of the habitat)

Stinson and Brown, (1983), looked at Auchenorrynchna on grassland and showed that most significant were the structural attributes of the habitat, which accounted for 79% of the species richness and 85% of total abundance. Of course there is no reason why weevils should be the same as leafhoppers but I decided that simple measures of numbers of plant species, height classes, or plant structures were too crude, since they took no account of the differing frequencies of occurence of different classes within these groups. For example *Lotus corniculatus* was present in all sites, but at differing frequencies of occurence.

A measure of diversity was required to overcome these problems. Several diversity indices were examined, including the Simpson and MacIntosh measures. However, historically the use of the Shannon Wiener index has been used in work of this type, and a treatise is given on its use by MacArthur and MacArthur, (1961). This index is based on information theory and is based on the form $H = -\sum^{s}_{i=1}(p_i)(\log_2 - p_i)$.

The index increases in value as diversity increases, both as the number of individuals or numbers of species increases. It is possible to measure the eveness of distribution of numbers of individuals in each species by using on equitability index.

This is essentially a ratio of diversity against maximum possible diversity and can be derived by dividing Shannon Weiner by log to the base 2 of the total number of species. Equitability ranges from 0-1. (for further information see Krebs, (1978).

Species richness and abundance of weevils were plotted against the diversity of the habitat, using the three measures previously described. (floral, spatial and architectural). Equitability was used as the index of diversity. Table 5. shows these indices for each plot.

The data indicated there was a significant correlation between plant species diversity and both the numbers of species or total abundance of weevils. A correlation coefficient was calculated between diversity and both the numbers of weevils and the number of species of weevils taken in the D-vac samples. This is shown in figures 11. and 12. Since each site had one value for diversity of the habitat, and several sample of weevils. The total number of weevil specimens and total number of weevil species are marked on the graphs by the use of a box symbol, but no statistical tests were applied to these values. In the case of the numbers of weevil species (Fig. 11.) $r = 0.426$, ($p = 0.04$, see = 2.23) which is a significant result.

The correlation coefficient for the numbers of individual weevils was $r = 0.355$ (Fig.12.) ($p = 0.08$ see = 24.12). This is a low level of significance, outside the 5% confidence level.

A similar analysis using habitat spatial diversity as a measure of the changes in the habitat also gave significant results. There was a significant relationship between numbers of Curculionidae individuals sampled and spatial diversity (r = 0.472 p = 0.02 see = 22.7) (Fig 13.)

The correlation coefficient for number of species of Curculionidae and spatial diversity of the habitat is (r = 0.617 p = 0.004 see = 1.946). These results are highly signifcant. (Fig. 14.)

A comparison was also made between habitat architectural diversity and weevil populations. The number of species of weevil were plotted against architectural diversity, the diversity indices calculated from each site from the measures of number of plant structures. This is shown in figure 15. and the relationship is shown to be significant (r = 4.487, p = 0.02, see = 2.16). The correlation coefficient was calculated for the abundance of weevil sampled and the habitat architectural diversity. This is shown in figure 16. There is no significant relationship, also the r^2 value is low so it would in any case only account for 12% of the variation between these two variables.

A summary of the results in this section is shown in table 6. From this it is clear that the most important factor determining both numbers of species and numbers of individual weevils is spatial diversity. The coefficient of determinations shown in table 6. as a percentage values, account for 38% of the variation in the number of weevil species and 22% of the variation in the number of weevil individuals by spatial diversity. This is the only measure of diversity studied which accounts for the variation in weevil abundance.

In addition both plant diversity (18%) and architectural diversity (23%) have a significant effect in determining the number of weevil species present but not their abundance. Of course regression analysis and coefficients of determination are not proof of causal relationships merely correlation.

The argument that diversity of habitat should affect weevils populations is a logical one, obviously the reverse is not. Certainly it is an attractive hypothesis to suggest that spatial diversity is important in affecting the numbers of individual weevils. Since this is in effect a measure of how much habitat is present. The greater the spatial diversity, generally the greater the density of the habitat and the more vegetation there is for the weevils to feed on and hide in. An important effect of spatial diversity may be that its increase may lower the apparency of weevils to predators and parasitoids.

Increased spatial diversity increased the numbers of herbivorous insects found in salt marshes studied by Cameron (1972). A low Salicornia sp. vegetation had thirty five species of insect herbivore, whilst the taller Spartina sp. stands studied had forty two species present.

As one would possibly expect, although spatial diversity seems important in determining the species richness of the Curculionidae community, plant species diversity and architectural diversity are also significant.

This can be explained, since increased species richness of the animal community requires a greater range of niches.

For these to exist a more diverse habitat with greater numbers of plant species, structural components and floral structures would be predicted. There is no easy way of separating these three measures of habitat diversity, since all three are certainly inter-related.

Comparison in the past between plant species diversity and insect species numbers have shown that this is not important in many cases. The diversity of Homopera on three old fields in southwest Michigan were studied. Variation of the diversity of the insects showed a 72% correlation with plant species, but insect species numbers showed a lower correlation (Murdoch et al, 1972). However, it was impossible to separate measures of plant species diversity from architecture.

In this study it has been possible to ascertain that in abundance of Curculionidae spatial diversity is the most important measure of the diversity of the habitat. In terms of species richness as with previous studies (Murdoch et al, 1972; Southwood et al, 1981; Stinson and Brown, 1983;) the greatest correlation between habitat diversity and herbivore species numbers has been with structural attributes in the community - in this case, with spatial diversity. In no cases in this study are the correlations as high as those for successional age of the habitat, which suggest that possibly other successional factors are operating to determine the size and composition of weevil populations.

Relationships between Measurements of Habitat Diversity and Successional Age.

It has been shown in this study that there is a strong correlation between both weevil species-richness and total abundance and the successional age of the habitat. Successional age accounts for 96% of the variation of the number of weevil species and 88% of the variation of numbers of weevils species. (r^2 values given as a percentages).

I have also shown that weevil populations are correlated with measures of habitat diversity such as floral, spatial and architectural structure. However, the values for the coefficient of determination are considerably lower for these relationships than those between weevil populations and successional age.

The measures of habitat diversity were taken as a means of exploring what attributes of the vegetation might be affecting weevil populations and also account for the importance of successional age. Two questions must now be asked. Firstly do the measures of habitat diversity used record the successional ageing, which has occured in the quarry studied? To answer this we must investigate whether the measures of habitat structure (such as numbers of plant species, height classes or floral structures) or habitat diveristy (such as plant species, spatial, or architectural diversity) correlate to the successional age of the sites studied.

The measurements of habitat structure were plotted directly against successional age, to assertain of any relationship exists. Correlation coefficients were calculated between successional age and the measures of habitat structure used, i.e. numbers of plant species, height classes and plant structures. The results are show in figures 17,18,19. In all three cases there were no significant relationships. Only the numbers of plant species showed any possible correlation with successional age, (figure 17.), but this was well outside the 0.05 confidence level and not significant.

Comparisons of plant species diversity, spatial diversity, and architectural diversity were also made against successional age. Again, as figures 20,21,22 indicate, there is no significant relationship between any of these. Only spatial diversity has any indication of any possible correlation with successional age and this is well outside acceptable confidence limits.

The results are surprising.Probably one would have predicted that the successional age of the site would have increased the diversity of the habitat, in the ways measured. However, the study was designed to observe what effect vegetational successional changes might have on weevil populations and had the major aim of the project been to investigate successional change itself, a different approach would have been justified.

Successional age of the plot accounts for a very large percentage of the variation of weevil populations.

There is no evidence that the measures of habitat diversity used are correlated to successional age. Therefore since the low values (below 40%) for coefficients of determination between habitat diversity and weevil populations cannot explain even part of the effect that successional age has on weevil species numbers or weevil abundance, we must ask a second question: what other factors could account for at least some of the reason why weevil populations correlate so strongly with successional age?

Successional changes will cause other changes to the habitat than merely habitat diversity. Composition of the plant community can change without necessarily altering diversity, if one plant is replaced by another. There may be changes in plant biochemistry, and palatabilty. An important factor may the rate of recruitment of weevils, merely as a result of colonisation. This may occur at such a rate to correlate quite closely with the successional development of the site. It is also the case that there may be some relationship between habitat diversity and successional age that has not been proved by the study, as previously discussed.

Some palatability experiments based on snail counts were also carried out. No snails were found on the first year plot, ninety on the six year old plot and over twice that number on the ten year old plot. Numbers fell to seventy four in the twelve year old plot and as few as thirteen Cepea spp. were found in the hawthorn scrub (Figure 23).

Whilst it is impossible to make any wide ranging conclusions from these results, several comments are possible. Levels of general herbivory are low initially. This is to be predicted, partly because there is less food available, but more importantly the resource is not apparent. Colonisation will also have to occur before a herbivore population can establish itself.

As the site matures, its vegetation becomes established, there is greater quantities of food available, because there are larger plants. There has been sufficient time for a snail population, to establish itself which may explain increased Cepaea spp. numbers. However, as yet little chemical or other defences have altered the palatability of the vegetation.

As the site becomes more mature, there is an increase in unpalatable plants which resist herbivory. As a result there is a decline in populations of general oligophagous herbivores such as snails. This effect is increased in the hawthorn scrub where the ground flora is either increasingly ephemeral, appearing only in spring or autumn or has evolved considerable anti-herbivore defences, as part of a stress tolerant regime. (Grime, 1979; Hodkinson and Hughes 1982). Other factors than palatabiltiy may and probably will determine the size of the snail population.

General Discussion.

Vegetational succession is a process in which a series of communities replace each other at a given location in a predictable sequence with the passing of time, providing the external environment conditions remain stable. Secondary succession begins in an already existing plant community as the result of disturbance on environmental change. The successional changes within the plant community are also likely to drive animal communities along a parallel course of successional change.

On the four grassland sites studied successional age accounted for 96% of the variation in the numbers of Curculionidae species and 88% of the variation of the abundance of individuals.

It is known that many factors affect insect populations; for example climatic factors, parasitoid and predator densities, disease, or a range of factors (Randolf, 1982; Whittaker, 1973). Changes in habitat diversity have been linked with species-richness and abundance of insects previously notably in Auchenorryncha (Stinson and Brown, 1983). Measures of habitat diversity have also been associated with successional change. Investigations into differences in Curculionidae populations being caused by changes in habitat diversity were made in this study.

The number of plant species present did correlate with the number of weevil species present (19% of the variation) and the results were significant.

There was also a positive significant correlation between number of plant species and the abundance of weevil species (29% of the variation).

Spatial diversity was important in accounting for the variation of both weevils species (38%) and number of individuals (22%).

Plant species diversity also was significant in determining the variation in number of species of weevils (18%) but not their abundance.

Architectural diversity accounted for some of the variation in the number of weevils species present, (23%) but not their abundance.

Since increasing the spatial diversity of the habitat, is in effect increasing the size of the habitat, we would expect that an increase in spatial diversity would cause increased insect abundance. However, the low value of the coefficients of determination indicates other factors are important in controlling weevil abundance.

As four measures of habitat accounted for variation in the number of species of weevils, the situation is more complex. Spatial diversity is again the strongest factor measured. It was, however, impossible to isolate the effects of these different measures of diversity and there is a strong possibility that they are linked.

Although the intuitive feeling remained that there ought to be a link between measures of habitat diversity and successional change there was no evidence for such a correlation.

Either habitat diversity, and successional age are independant factors affecting weevil populations, or more probably low numbers of sites surveyed did not allow me to substantiate such a relationship. Given more time, a refinement to the experiment would be to increase the number of sites surveyed, and more importantly increase the number of point quadrats taken to say two hundred. A survey of the vegetation could also have been taken after each D-vac sampling.

A short study of palatability using relative population sizes of *Cepaea* spp. which are large oligophagous herbivores also produced some interesting results. Populations were very low at the one year and twenty year old sites but two hundred and twenty two snails were collected at the ten year old site in baited pit fall traps. Although this is not conclusive, this fluctuation in population numbers suggests changes in palatability.

The whole area of insect herbivory is immensely complex, because there are so many subtle factors which operate on both plant and animal populations. One problem is thatit is particularly difficult to isolate the effects of a single factor from the action of the others. Clearly this project raises several interesting questions about the effect of the vegetation on weevil populations and insect populations in general, which would warrant further investigation.

Conclusions.

This study has established that numbers of weevil species and abundance are controlled by successional age of the habitat, in the sites studied. Habitat diversity is important in determining the number of weevil species present and spatial diversity of the habitat is particularly important. Spatial diversity also is important in explaining the variation in the abundance of weevil species. However, the results obtained suggested other factors than habitat diversity are operating. It was not possible to determine how independent were the different measures of habitat used. Nor was it possible to establish a relationship between variation in habitat diversity and successional age. It was felt that the study of a greater number of sites might have enabled the existence of such a relationship to have been tested more rigorously.

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APPENDIX I.

i) List of Weevils Species.

List of Weevils Species. Appendix i.

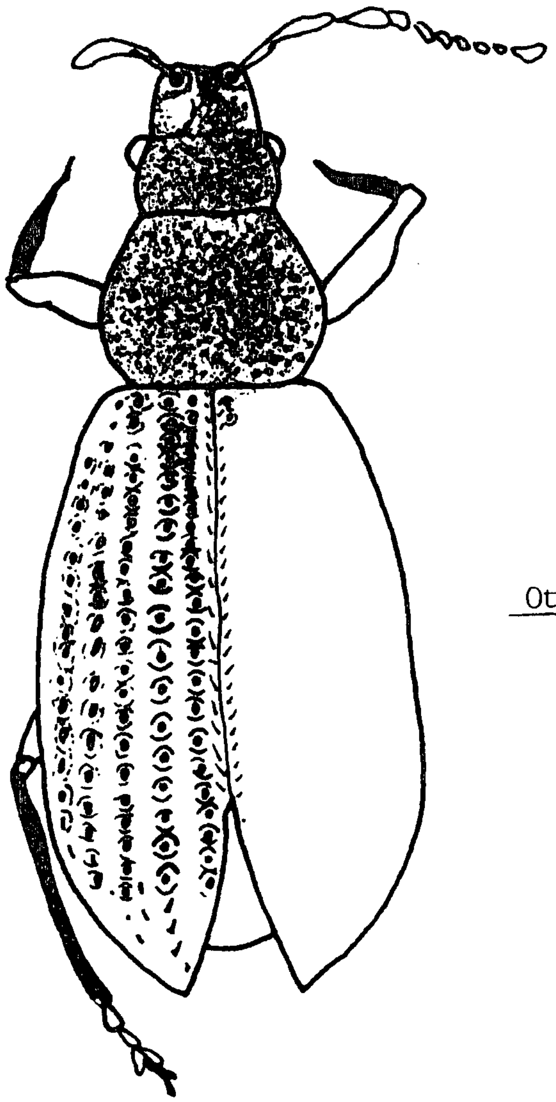
Below is a list of the weevils species found during the study. Identification was using Joy (1932), and nomenclature is after. Kloet and Hincks (1977).

Anchonidium unguiculare*
Eutrichapion loti.
Eutrichapion virens.
Protapion dissimile.
Nemoieus oblongus.
Omias mollinus*
Otiorhynchus morio*
Otiorhynchus raucus*
Pentarthrum huttoni*
Perapion sedi.
Phyllobius oblongus.
Phytobius comari*
Protapion assimile*
Protapion dissimile*
Sitona hispidulis*
Sitona sulcifrons*
Sciaphilus asperatus*
Synapion ebeninum.
Trachyphloeus lacticollis*
Tropiphorus tomentosus*

Three other other species were collected but refused to key out using Joy (1932). They were included in statistical analysis. Twenty three different species were collected in all. Species that are illustrated in the following pages are marked with a *. These drawing may prove a useful aid when using Joy (1932).

Anchonidium unguiculare

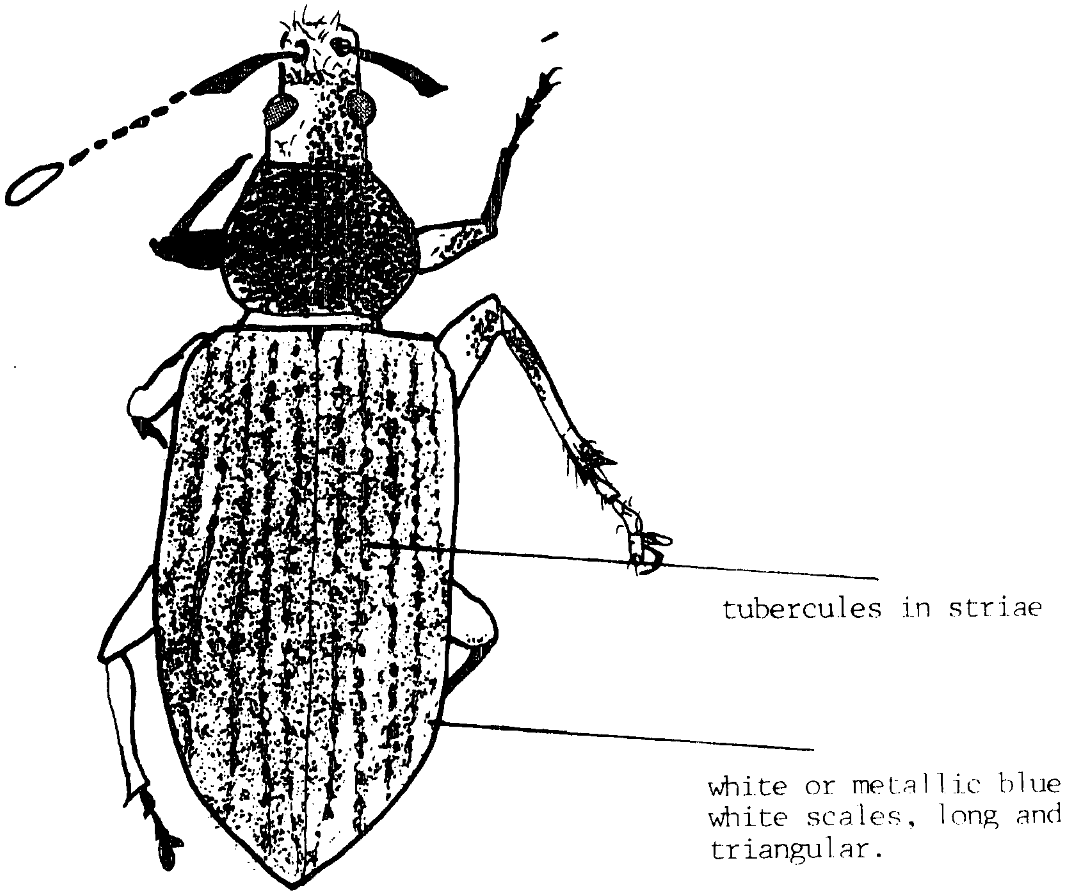
Omias mollinus



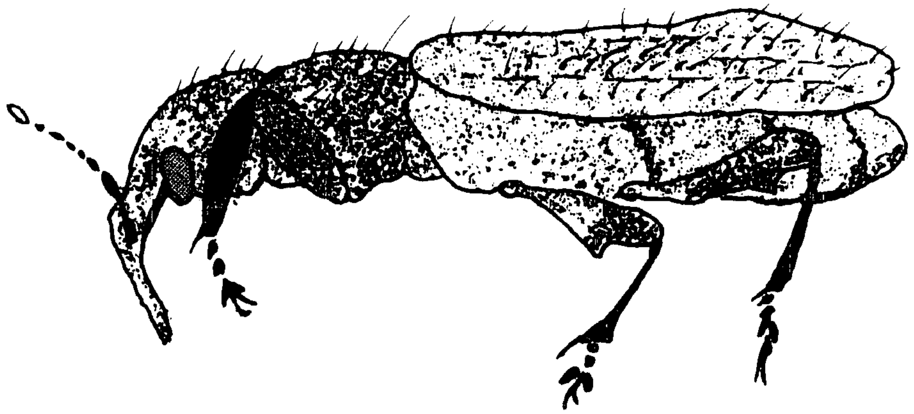
Elytra very black,
shiny and strongly punctured.

Otiorhynchus morio

Otiorhynchus raucus

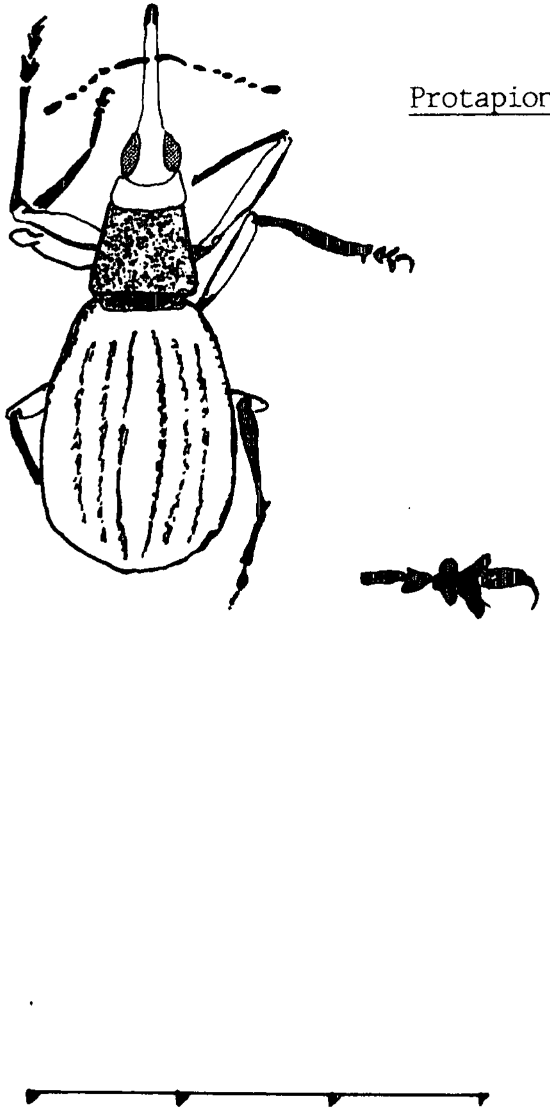


Pentarthrum huttoni

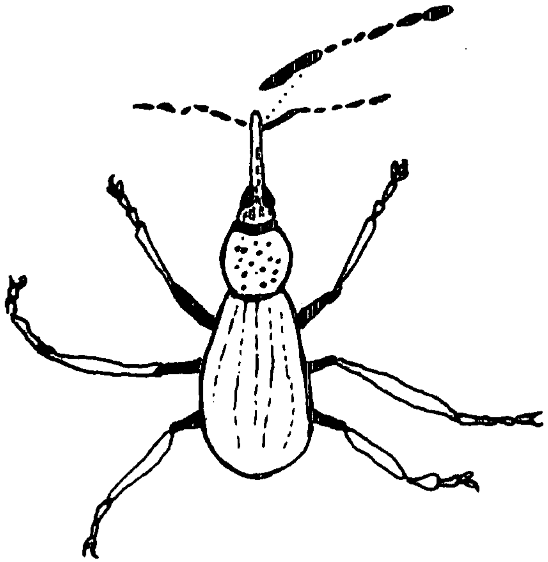


Pentarthrum huttoni

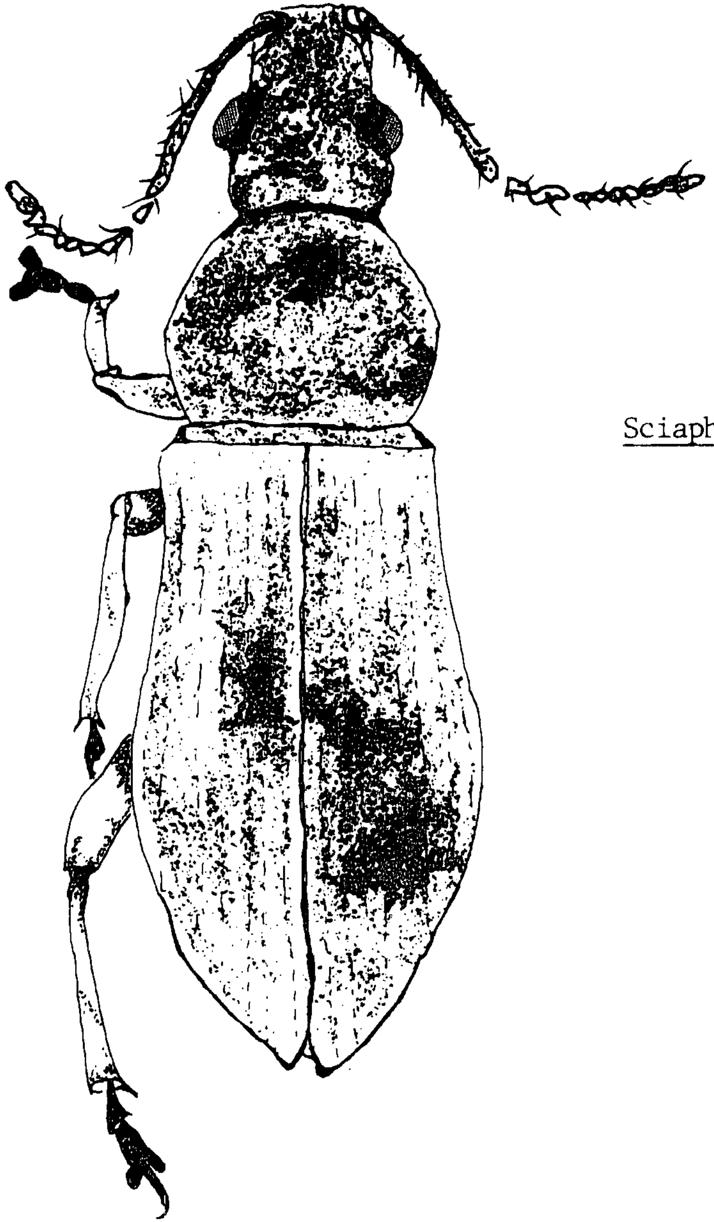
Phytobius comari



Protapion assimile



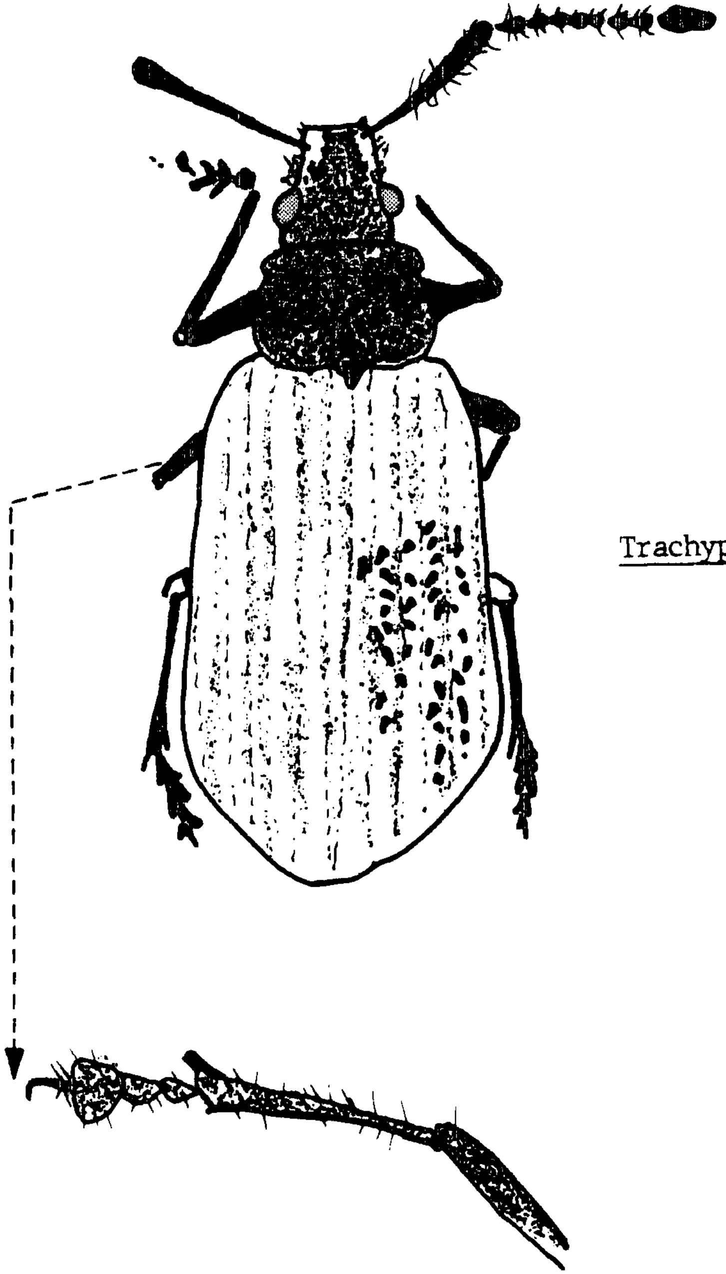
Protapion dissimile



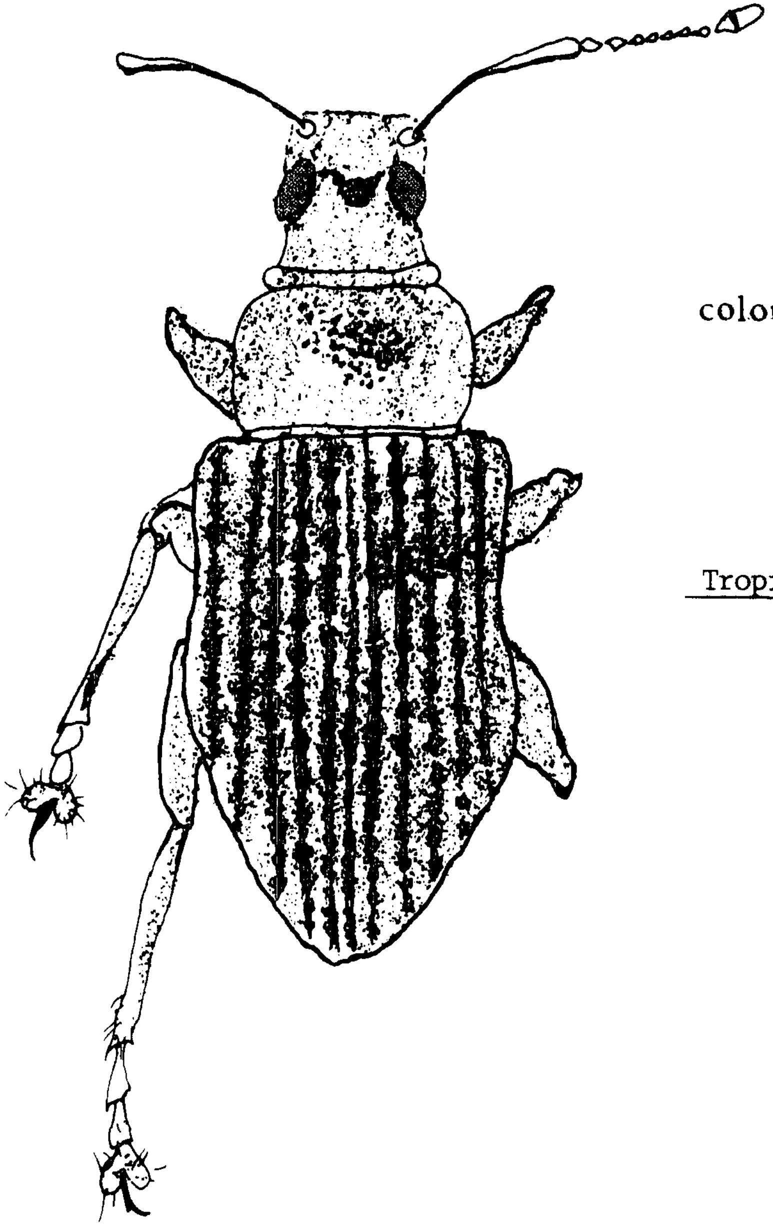
Sciaphilus asperatus

Sitona hispidulis

Sitona sulcifrons



Trachyphoeus lacticollis



colouration black with blue

<u>Tropiphorus tomentosus</u>

APPENDIX II.

ii) Figures Tables and Maps.

(in order refered to in text).

Table 1.

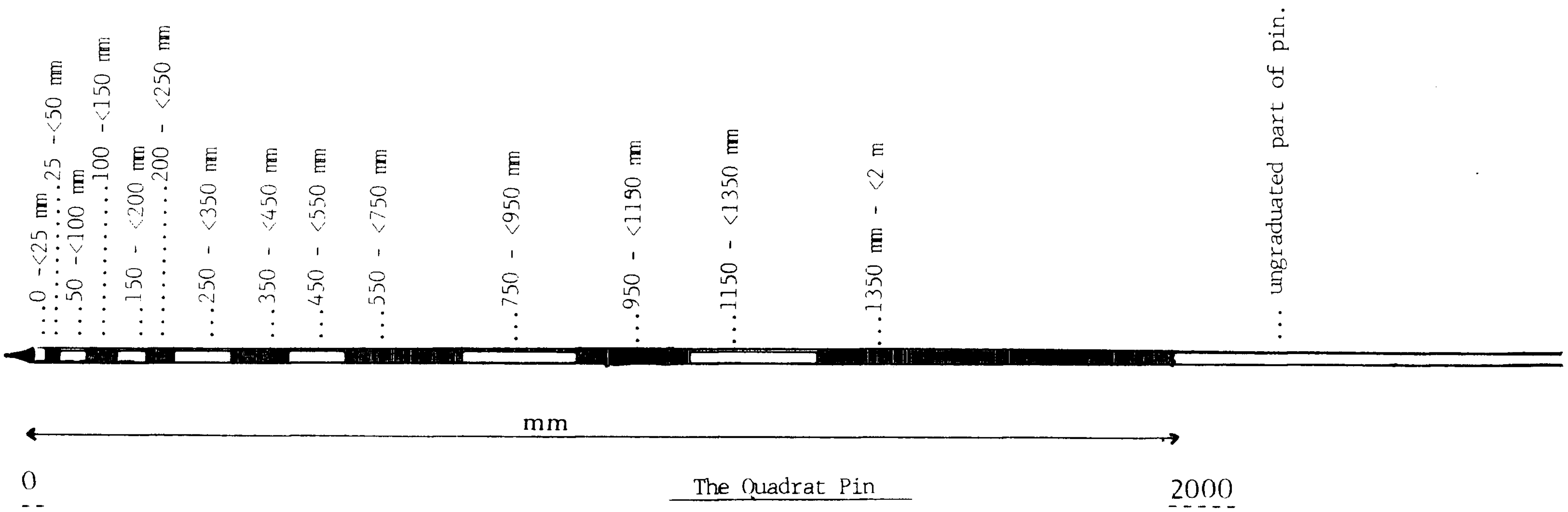
Sites Used in The Study

Successional Age	Description	(Site No.)
1	early successional grassland	5
6	mid sussuional grassland, (grazed)	3
10	late successional grassland	1
12	late successional grassland	4
20	grassland colonised by hawthorn scrub	2

* age in years.

Table showing description and age of the study plots used in the investigation. See text for details.

figure 1. Scale used on quadrat pin.



The Quadrat Pin

Diagram of the pin used for taking point quadrat measurements, with a scale marked on it to enable measures of foliage height diversity to be made.

Scale = 0.1

Layers used to measure spatial attributes of the habitat (see text for details).
n.b These layers are set as arbitrary values.

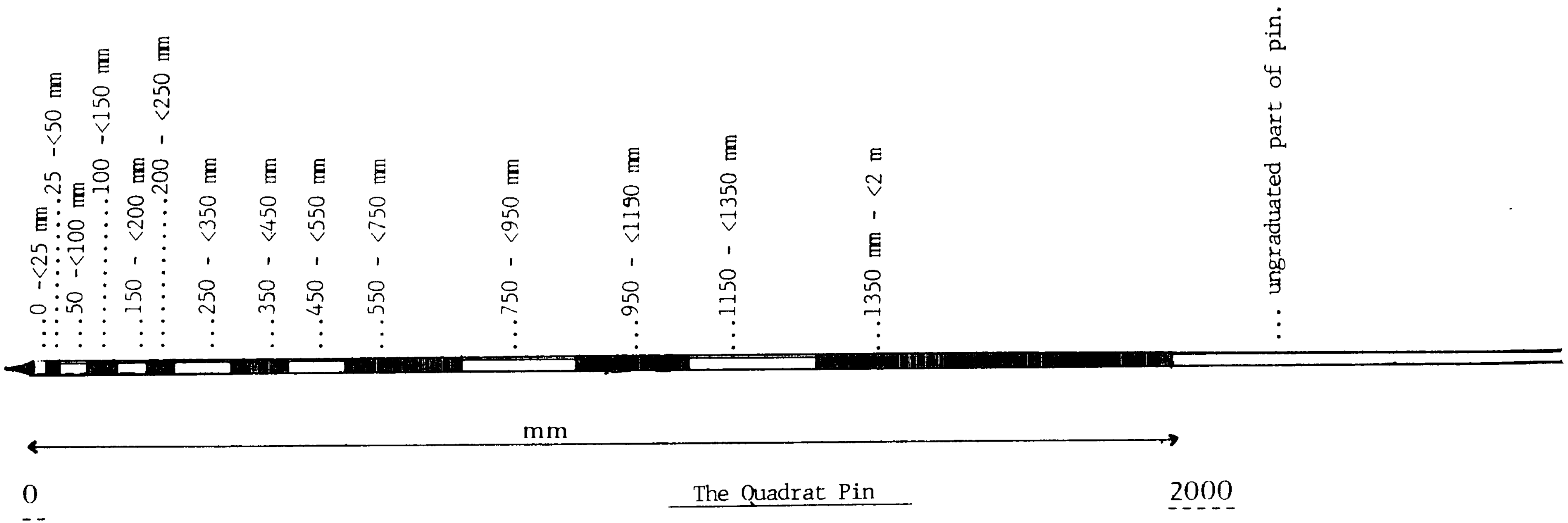
0 - <25 mm
25 - <50 mm
50 - <100 mm
100 - <150 mm
150 - <200 mm
200 - <250 mm

250 - <350 mm
350 - <450 mm
450 - <550 mm
550 - <750 mm
750 - <1150 mm
1150 - <1350 mm

1350 mm - <2 m
2 - <3 m
3 - <5 m
5 - <7 m
7 - <10 m
10 - 10+ m

This 19 height classes.

figure 1. Scale used on quadrat pin.



The Quadrat Pin

Diagram of the pin used for taking point quadrat measurements, with a scale marked on it to enable measures of foliage height diversity to be made.

Scale = 0.1

Layers used to measure spatial attributes of the habitat (see text for details).

n.b These layers are set as arbitrary values.

0 - <25 mm
25 - <50 mm
50 - <100 mm
100 - <150 mm
150 - <200 mm
200 - <250 mm
250 - <350 mm
350 - <450 mm
450 - <550 mm
550 - <750 mm
750 - <1150 mm
1150 - <1350 mm
1350 mm - <2 m
2 - <3 m
3 - <5 m
5 - <7 m
7 - <10 m
10 - 10+ m

This 19 height classes.

Sketch Map of Wingate Local Nature Reserve

Map1.

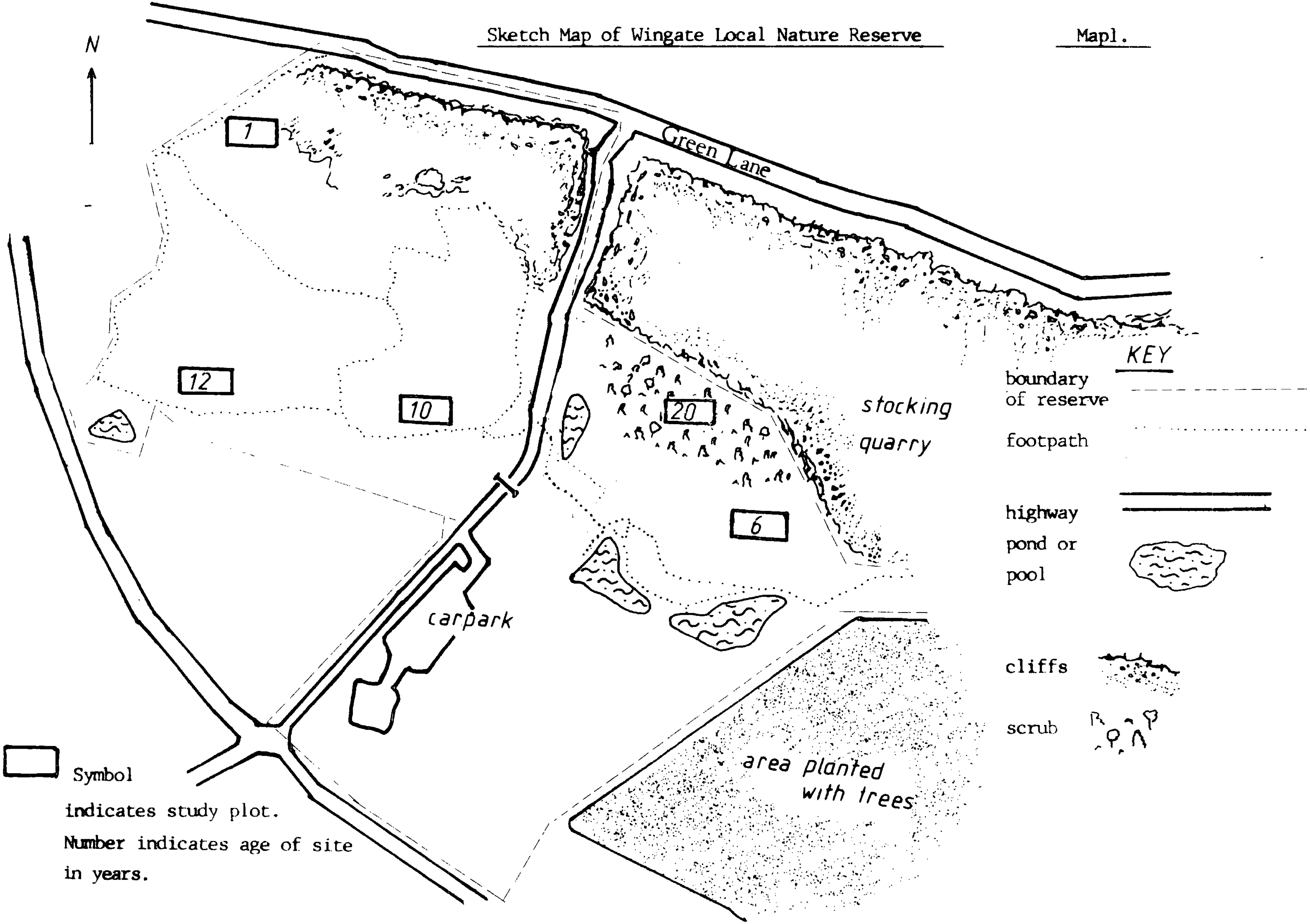
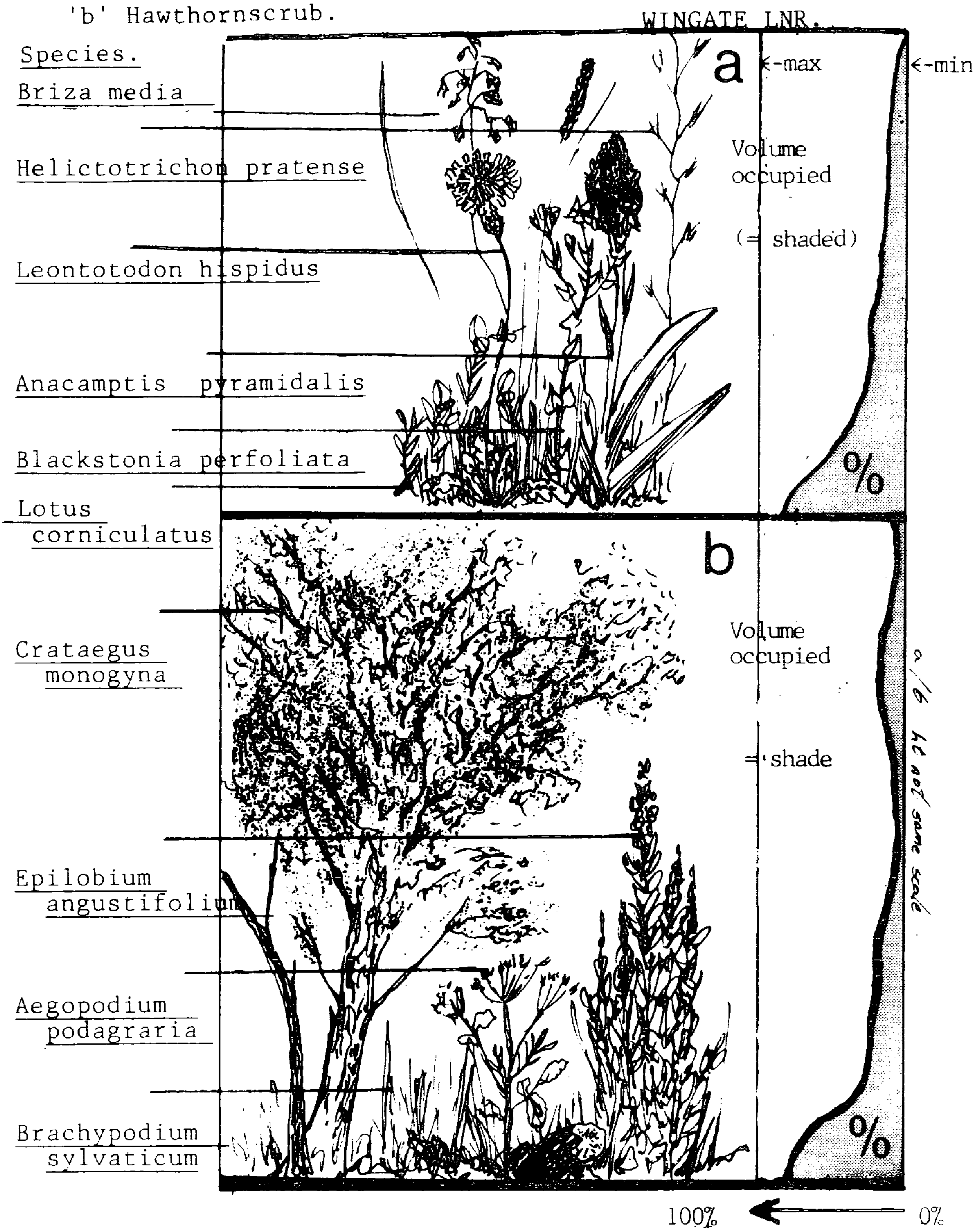


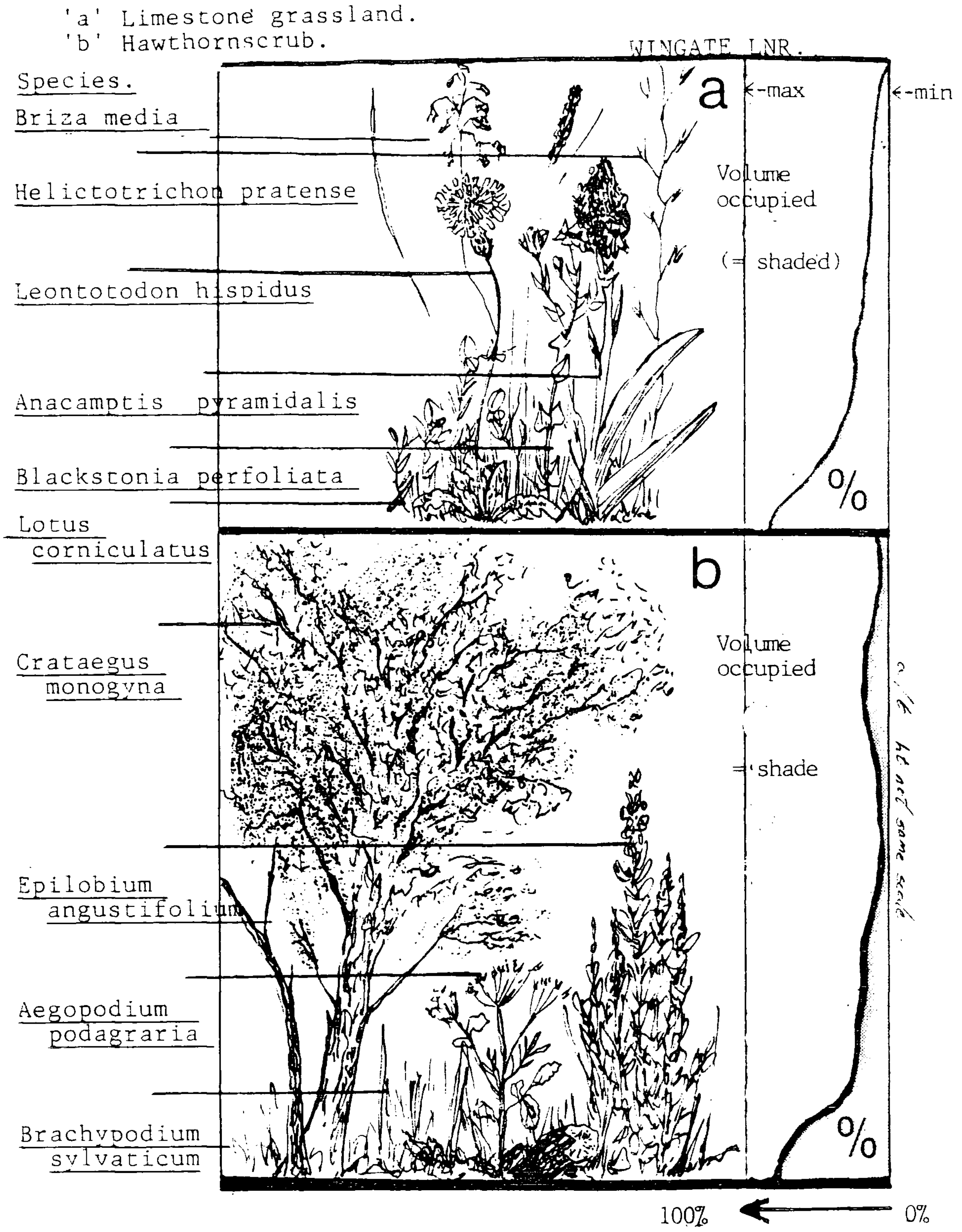
Figure 2. Changes in the Spatial Dimensions of the Habitat.

'a' Limestone grassland.
'b' Hawthornscrub.



The figure illustrates the habitat found at Wingate LNR., 'a' being the typical limestone grassland of the four sites (generalised), whilst 'b' is that of the hawthorn scrub. The right of the figure indicates the amount of volume occupied by vegetation. This is done by representing the volume between ground and top of the vegetation as an infinate series of laminars each of which can range from being empty to fully occupied and completely full of vegetational material. In both 'a' and 'b' the stand is the densest at ground level. This must be considered when devising a scale to measure spatial diversity of the habitat. Volume occupied is measured from 0-100 %.

Figure 2. Changes in the Spatial Dimensions of the Habitat.



The figure illustrates the habitat found at Wingate LNR., 'a' being the typical limestone grassland of the four sites (generalised), whilst 'b' is that of the hawthorn scrub. The right of the figure indicates the amount of volume occupied by vegetation. This is done by representing the volume between ground and top of the vegetation as an infinate series of laminars each of which can range from being empty to fully occupied and completely full of vegetational material. In both 'a' and 'b' the stand is the densest at ground level. This must be considered when devising a scale to measure spatial diversity of the habitat. Volume occupied is measured from 0-100 %.

Results of D-Vac Sampling

Table 3.

Date of Sampling	Successional Age of Sites in Years									
	1		6		10		12		20	
	#	sp	#	sp	#	sp	#	sp	#	sp
30.5.84	2	1	0	0	10	2	22	4	4	2
12.6.84	9	2	24	2	30	6	108	4	0	0
26.6.84	0	0	0	0	0	0	0	0	0	0
19.7.84	9	3	49	6	52	7	49	11	9	3
Total	20	3	73	6	92	12	179	12	13	3

nb./

number of individual weevils collected.

sp number of different species collected.

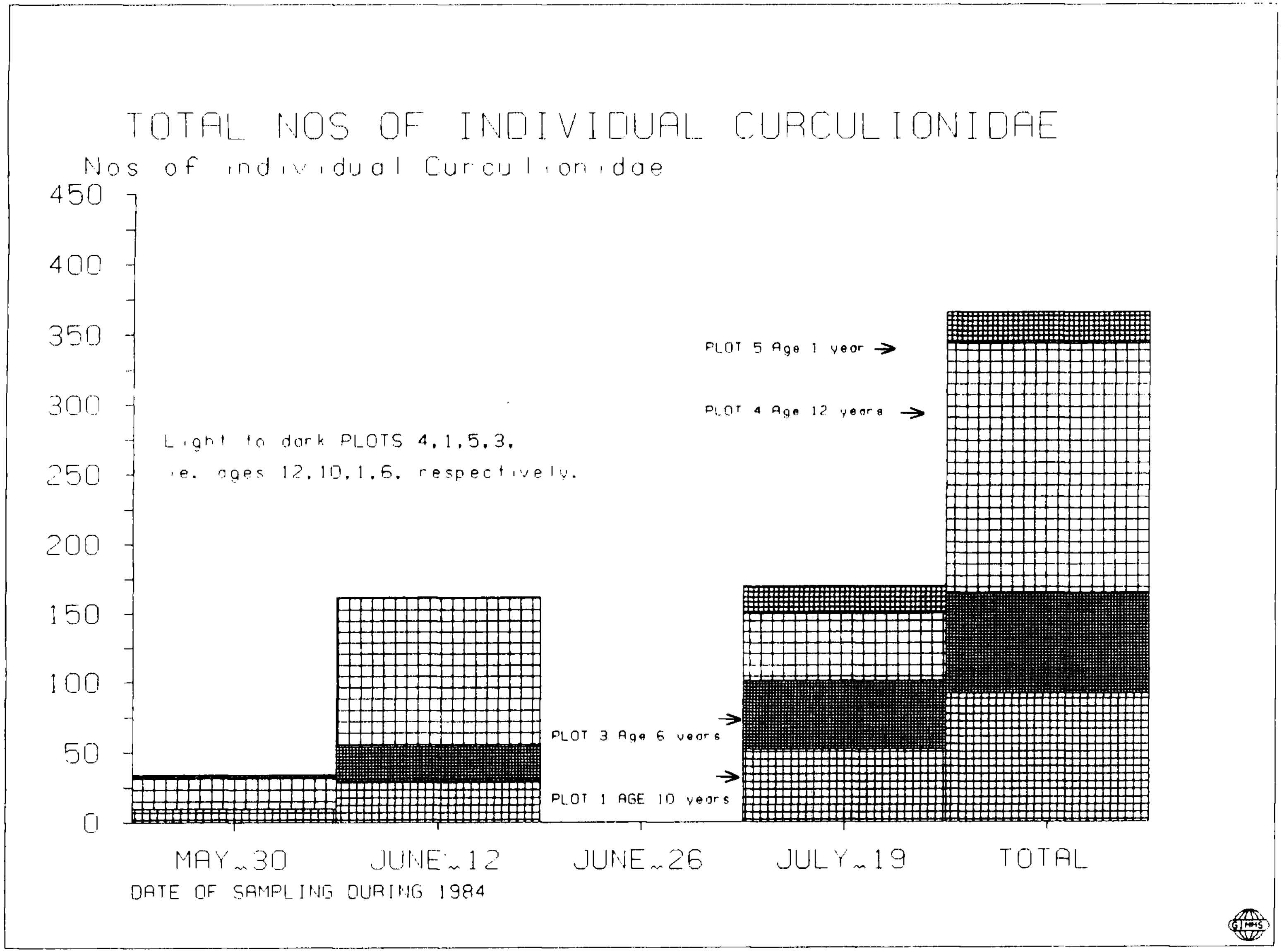

TOTAL NOS OF INDIVIDUAL CURCULIONIDAE
Nos of individual Curculionidae
450
400
350
300
250
200
150
100
50
0
Light to dark PLOTS 4,1,5,3,
ie. ages 12,10,1,6, respectively.
PLOT 5 Age 1 year →
PLOT 4 Age 12 years →
PLOT 3 Age 6 years →
PLOT 1 AGE 10 years →
MAY 30
JUNE 12
JUNE 26
JULY 19
TOTAL
DATE OF SAMPLING DURING 1984

Figure 3.

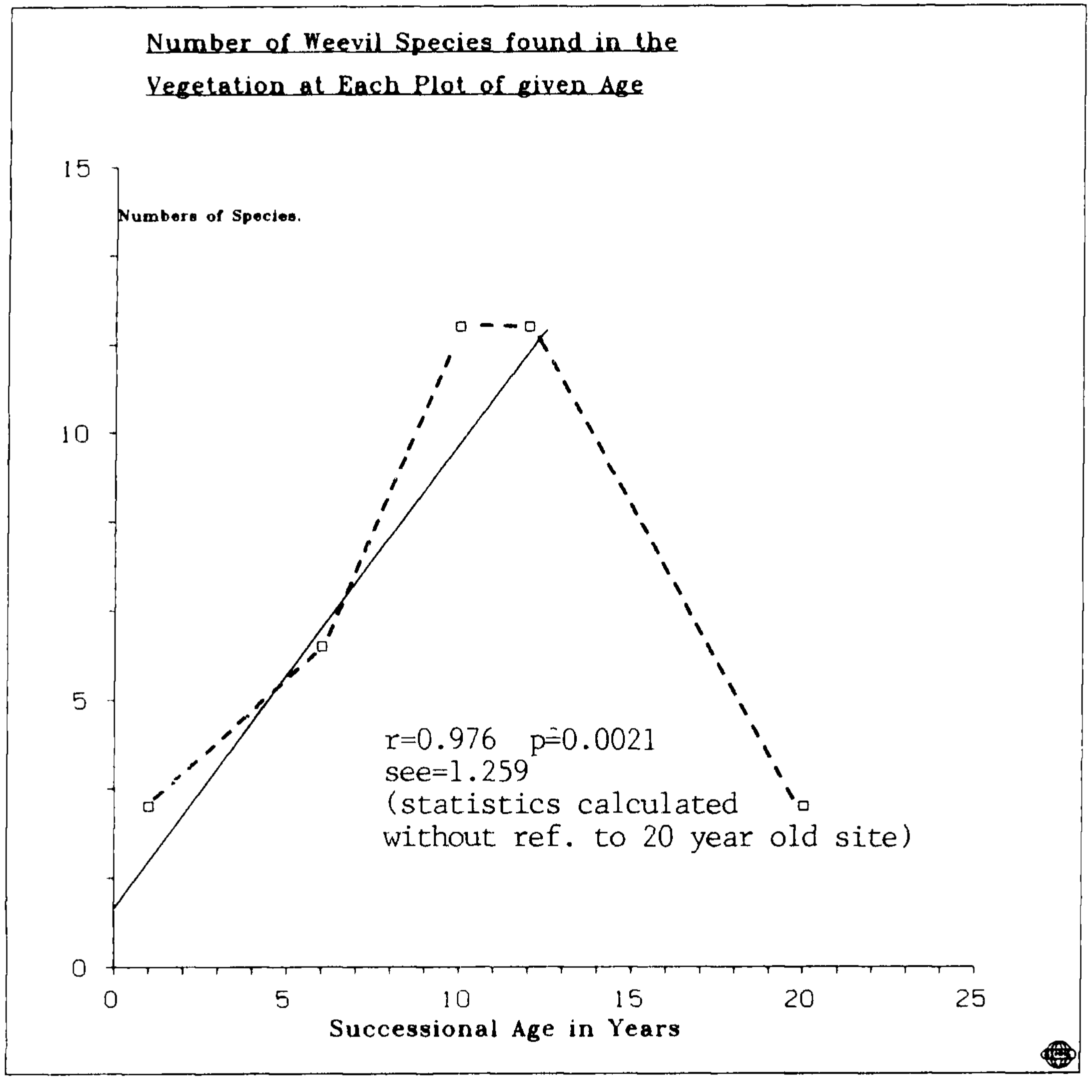
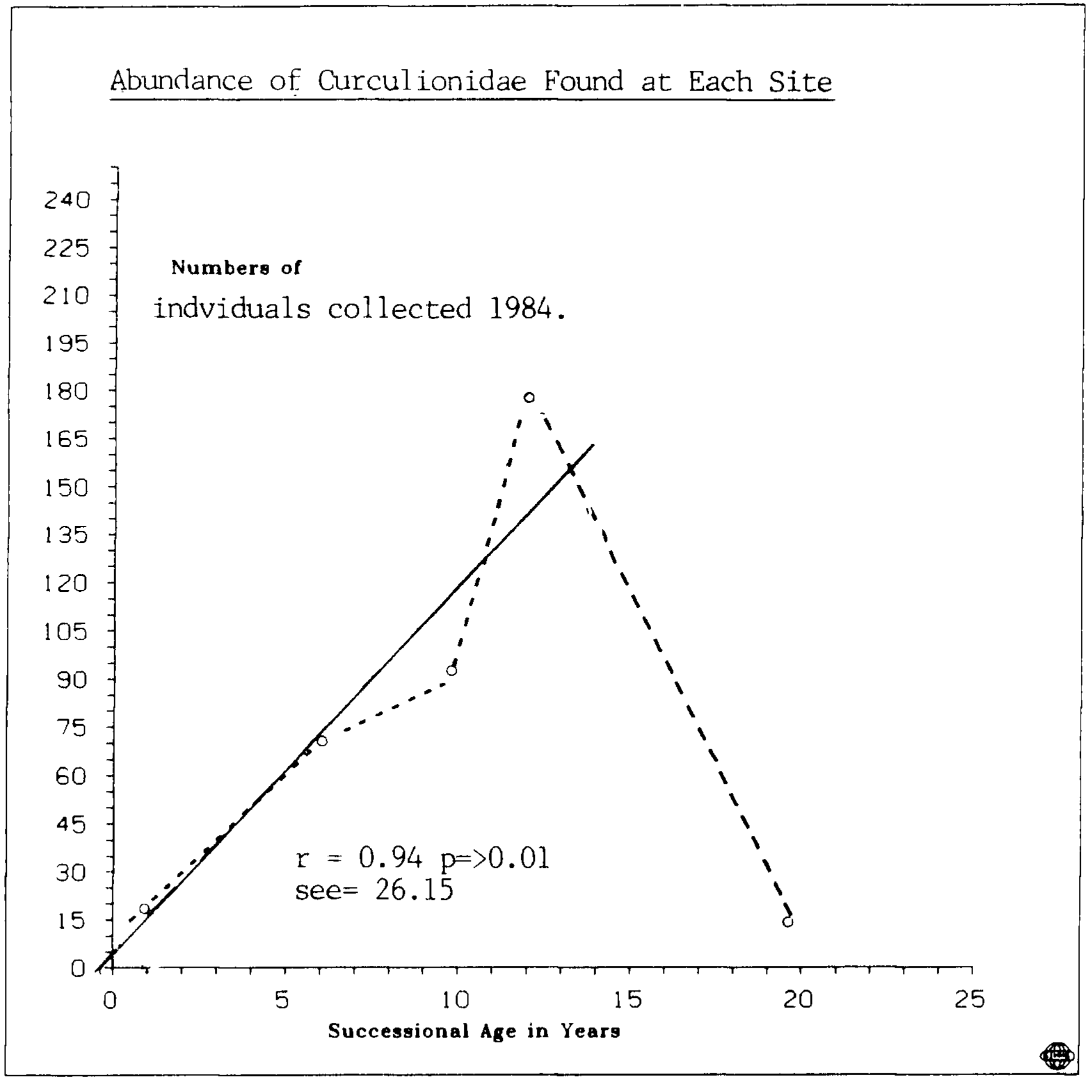

Number of Weevil Species found in the Vegetation at Each Plot of given Age
Numbers of Species.
15
10
5
0
0
5
10
15
20
25
Successional Age in Years
r=0.976 p=0.0021
see=1.259
(statistics calculated
without ref. to 20 year old site)

Figure 4

Figure 5.


Abundance of Curculionidae Found at Each Site
Numbers of
indviduals collected 1984.
240
225
210
195
180
165
150
135
120
105
90
75
60
45
30
15
0
r = 0.94 p=>0.01
see= 26.15
0
5
10
15
20
25
Successional Age in Years

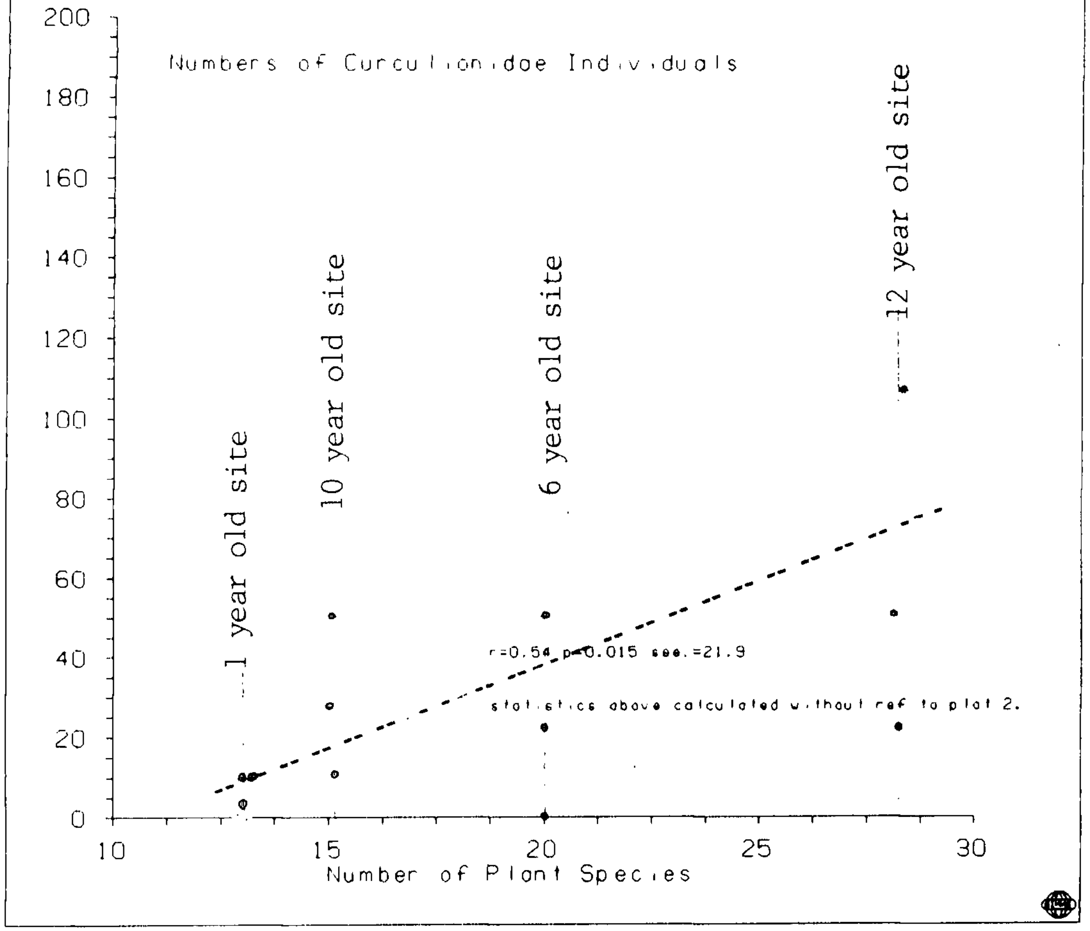
Results of Quadrat Data.

Table 4.

Successional age of the site.	number of plant species recorded	number of vegetational layers recorded	number of floral structures recorded
1	13	7	13
6	20	10	19
10	15	6	13
12	28	10	17
20	22	19	25

Figure 6.

Abundance of Curculionidae Sampled vs. Number of Plant Species In the Habitat of Each Plot



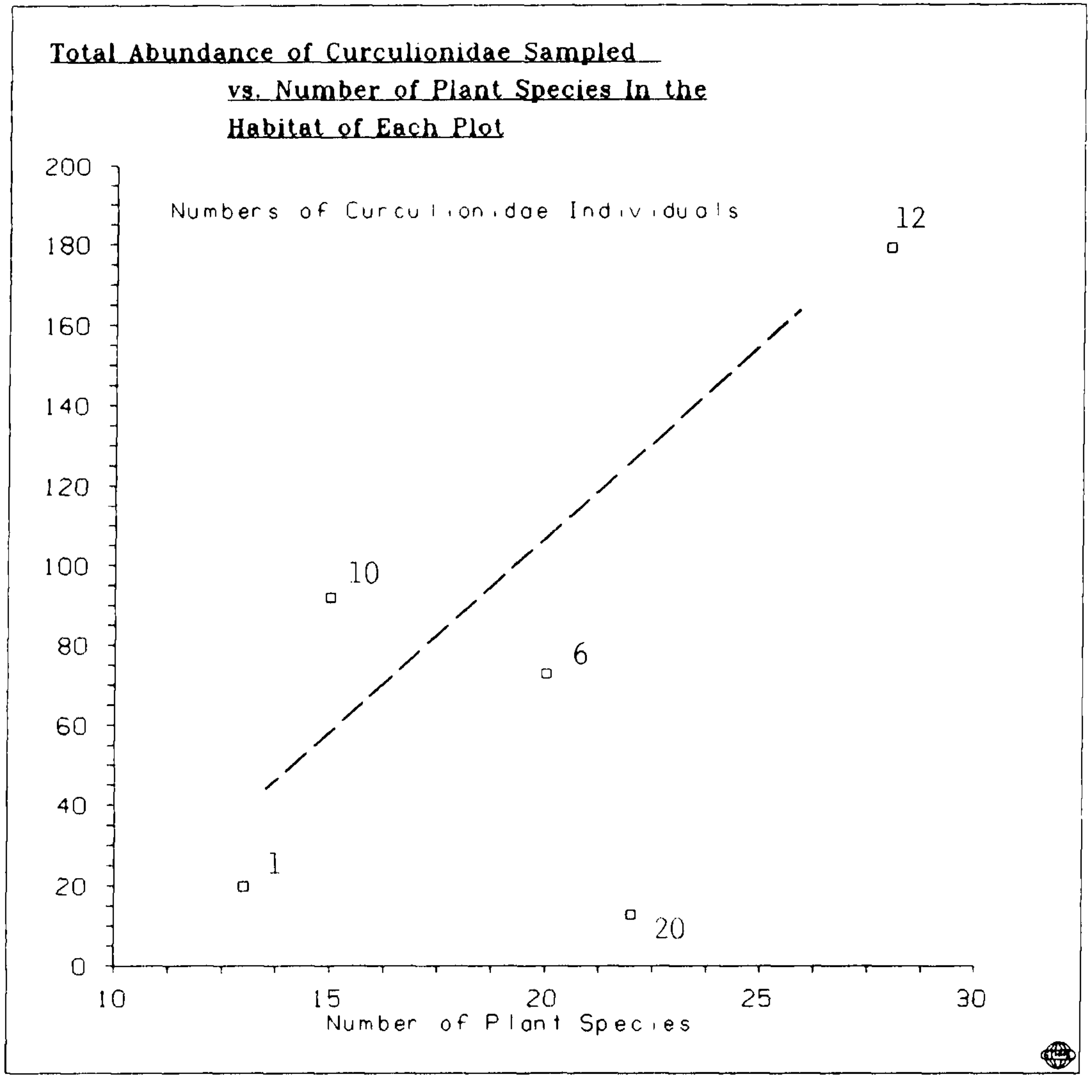


Figure 7.

numbers next to points indicates the successional age of the plots.

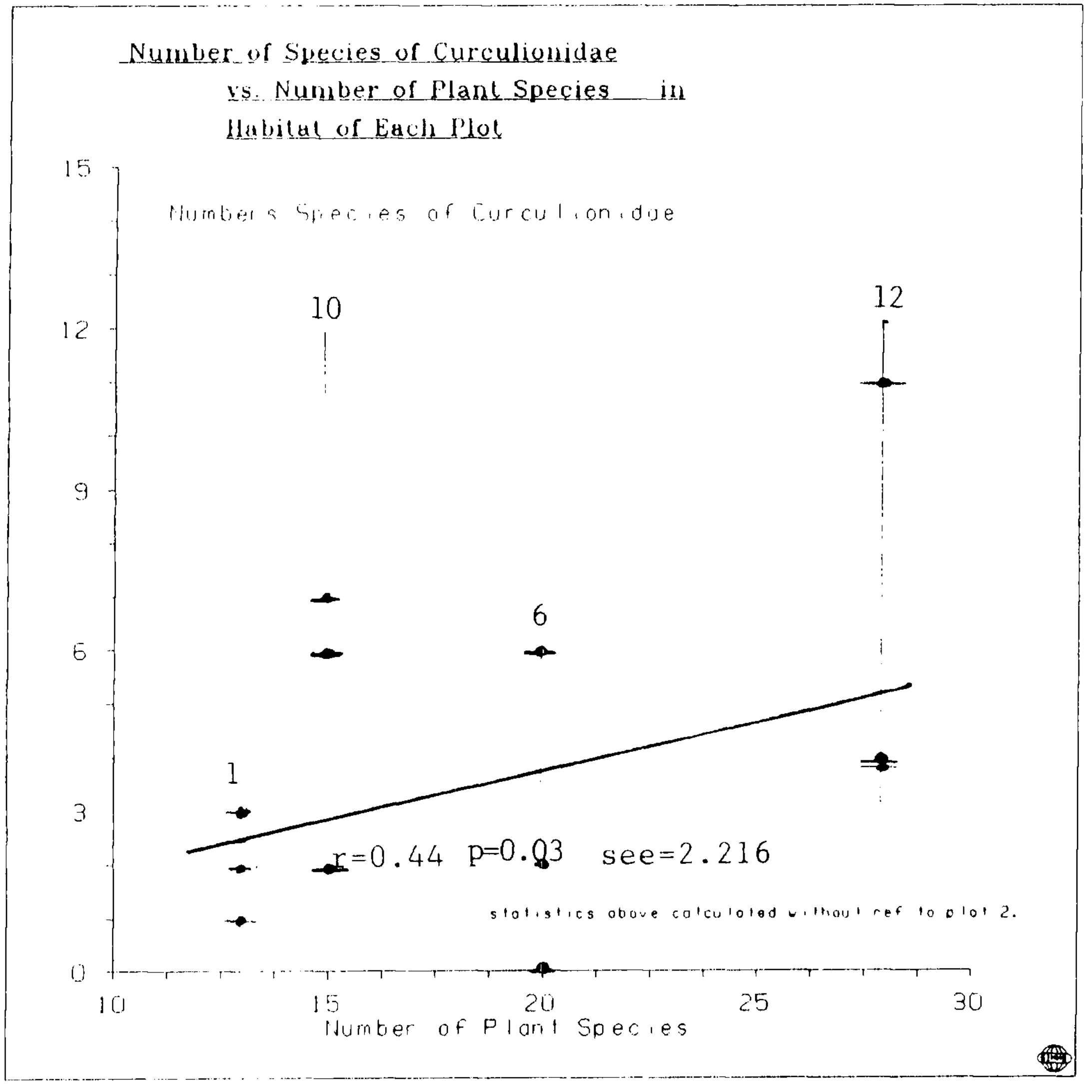


Figure 8.

Numbers next to points indicate the successional age of the plot at which the weevils species were collected. Age in years.

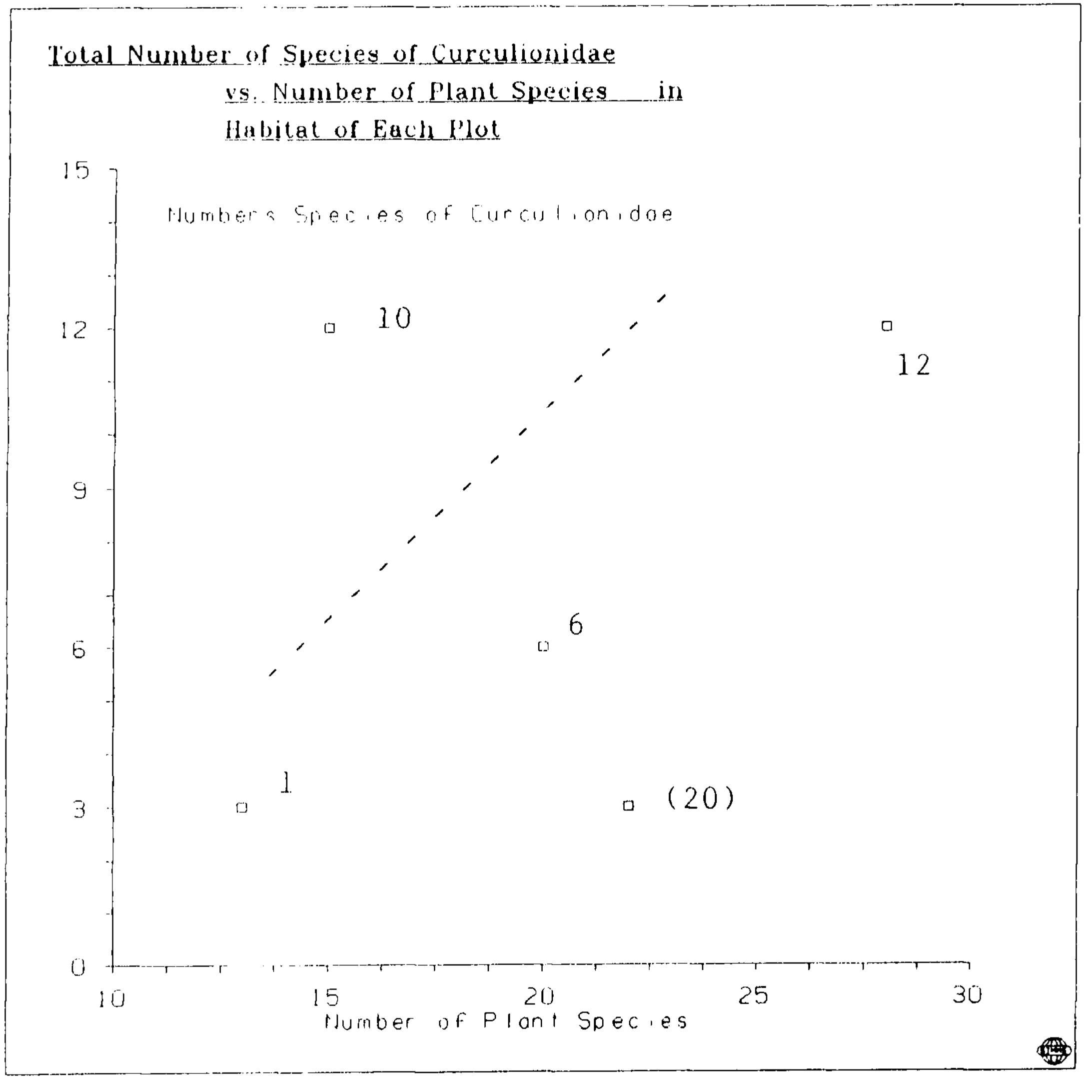

Total Number of Species of Curculionidae vs. Number of Plant Species in Habitat of Each Plot

Figure 9.

Numbers next to points indicate the successional age of the plot at which the weevils species were collected. Age in years.

Diversity of Sites Studied.

Table 5.

Successional Age of the Site in years	Index of Plant Species Diversity	Index of Spatial Diversity	Index of Floral Architecture
1	0.6481	0.8060	0.5118
6	0.8720	0.8610	0.7719
10	0.8233	0.9210	0.8152
12	0.8259	0.9150	0.7855
20	0.7290	0.8910	0.7855

Equitability is used as a measure of diversity.(see text)

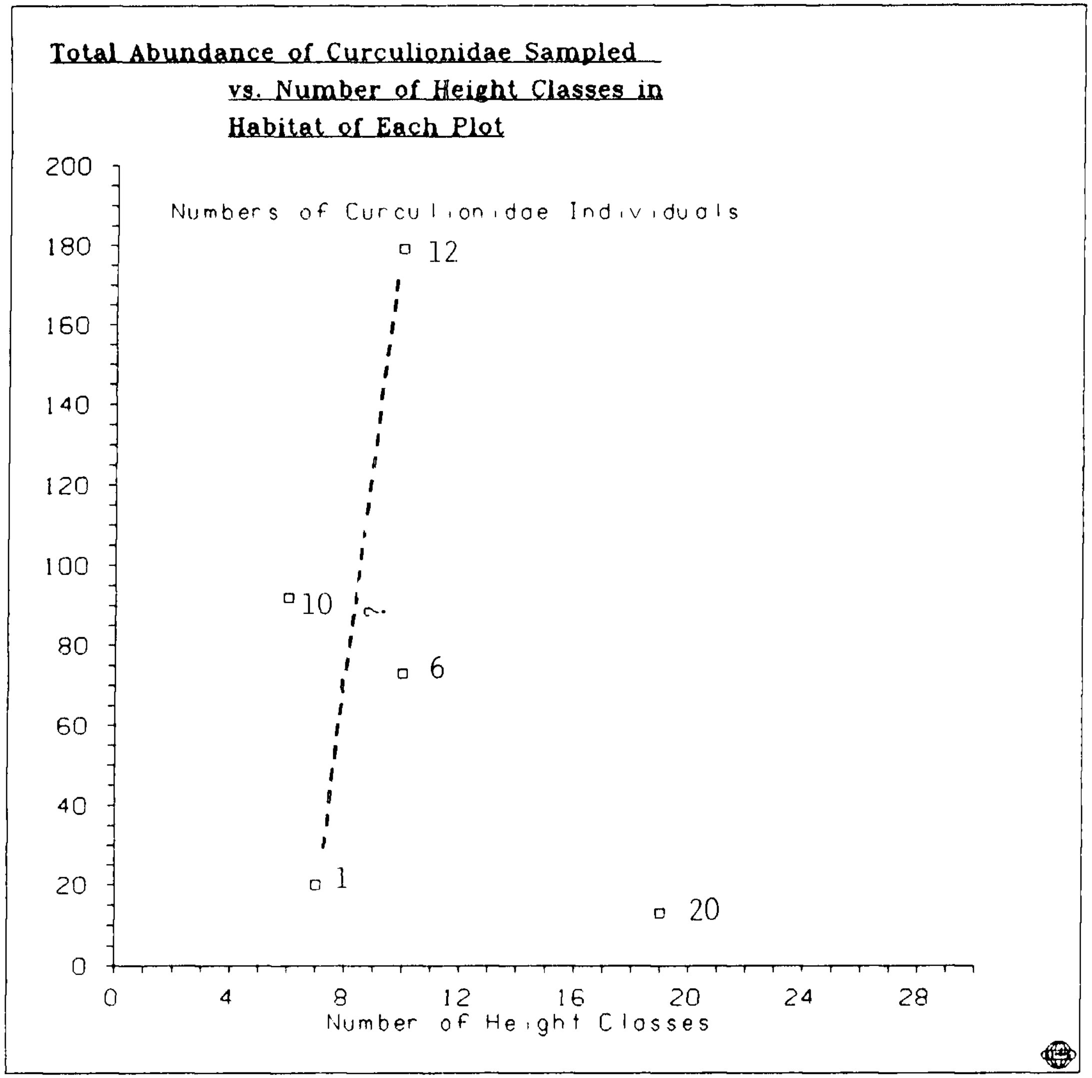
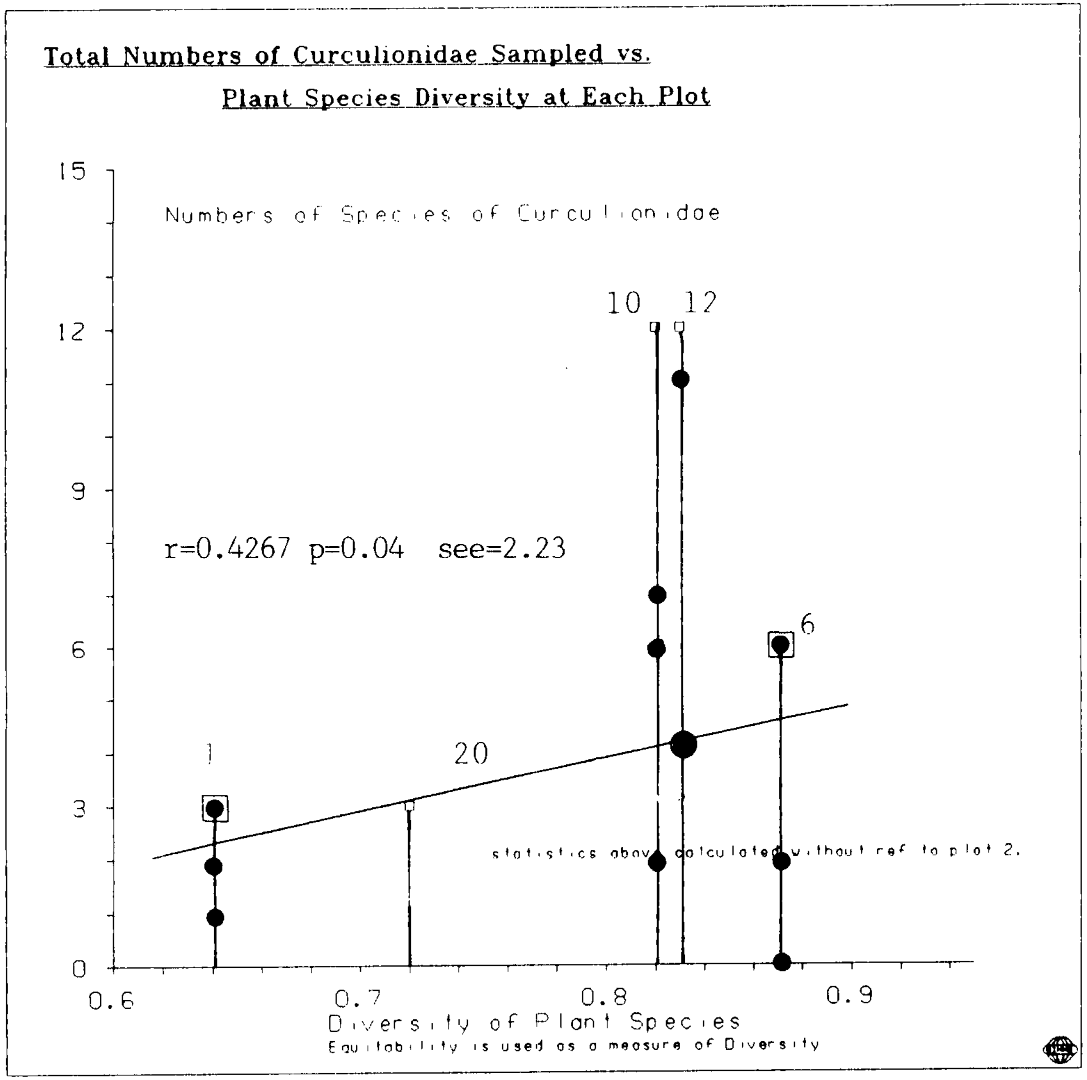

Total Abundance of Curculionidae Sampled vs. Number of Height Classes in Habitat of Each Plot

Figure 10.

numbers next to points indicate age of plots.

Figure 11.



Figures 11 - 16.

● numbers in D-vac sample of particular date

⬤ two points of same value

☐ total numbers sampled at paticular site

▣ both ● and ☐

statistics are based on correlation coefficient calculated from individual D-vac samples not total values. (see text for fuller explaination)

numbers next to points denote successional age in years of plot represented.

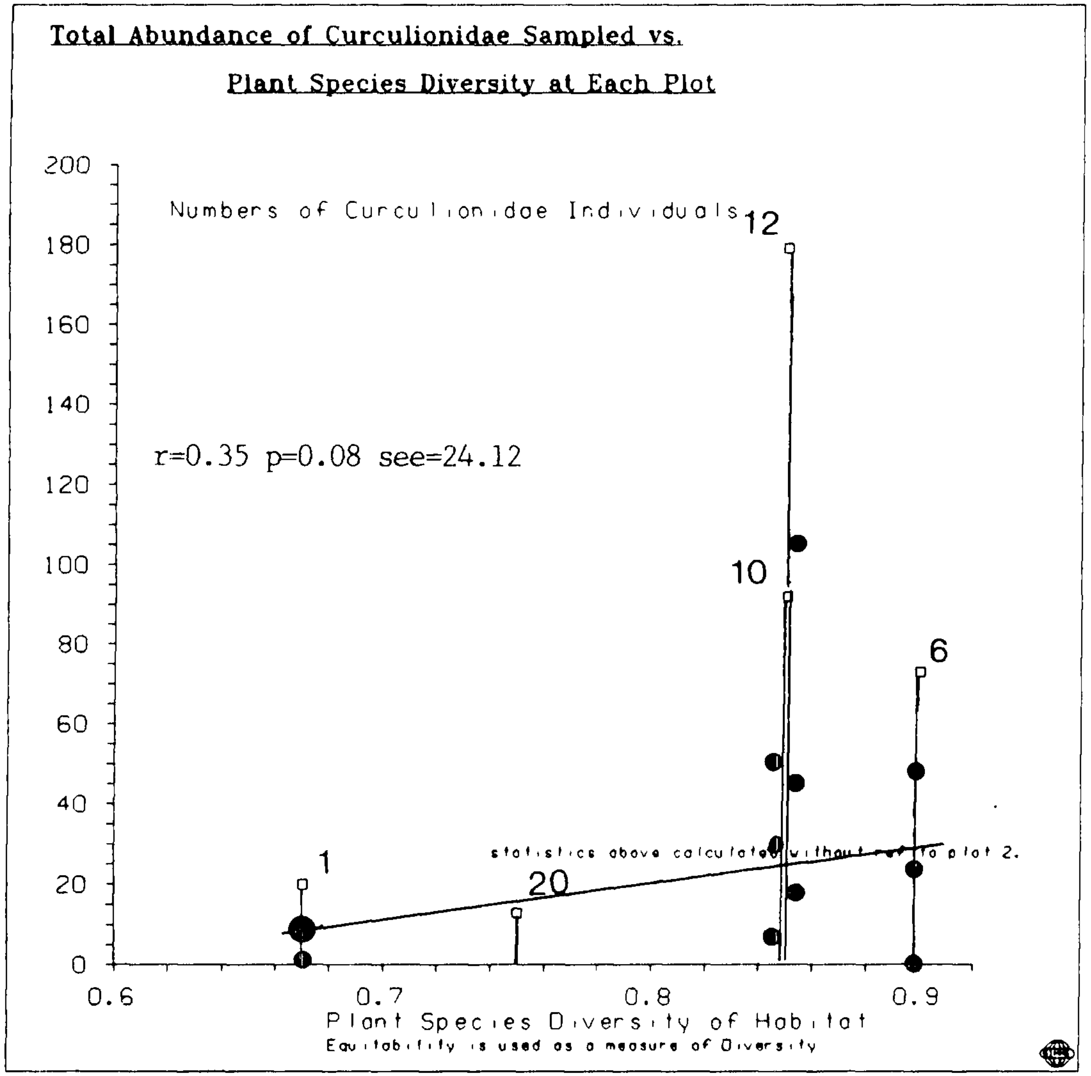

Total Abundance of Curculionidae Sampled vs.
Plant Species Diversity at Each Plot
Numbers of Curculionidae Individuals
r=0.35 p=0.08 see=24.12
statistics above calculated without ref to plot 2.
12
10
6
1
20
200
180
160
140
120
100
80
60
40
20
0
0.6
0.7
0.8
0.9
Plant Species Diversity of Habitat
Equitability is used as a measure of Diversity

Figure 12.

Total Abundance of Curculionidae Sampled vs.

Habitat Spatial Diversity at Each Plot

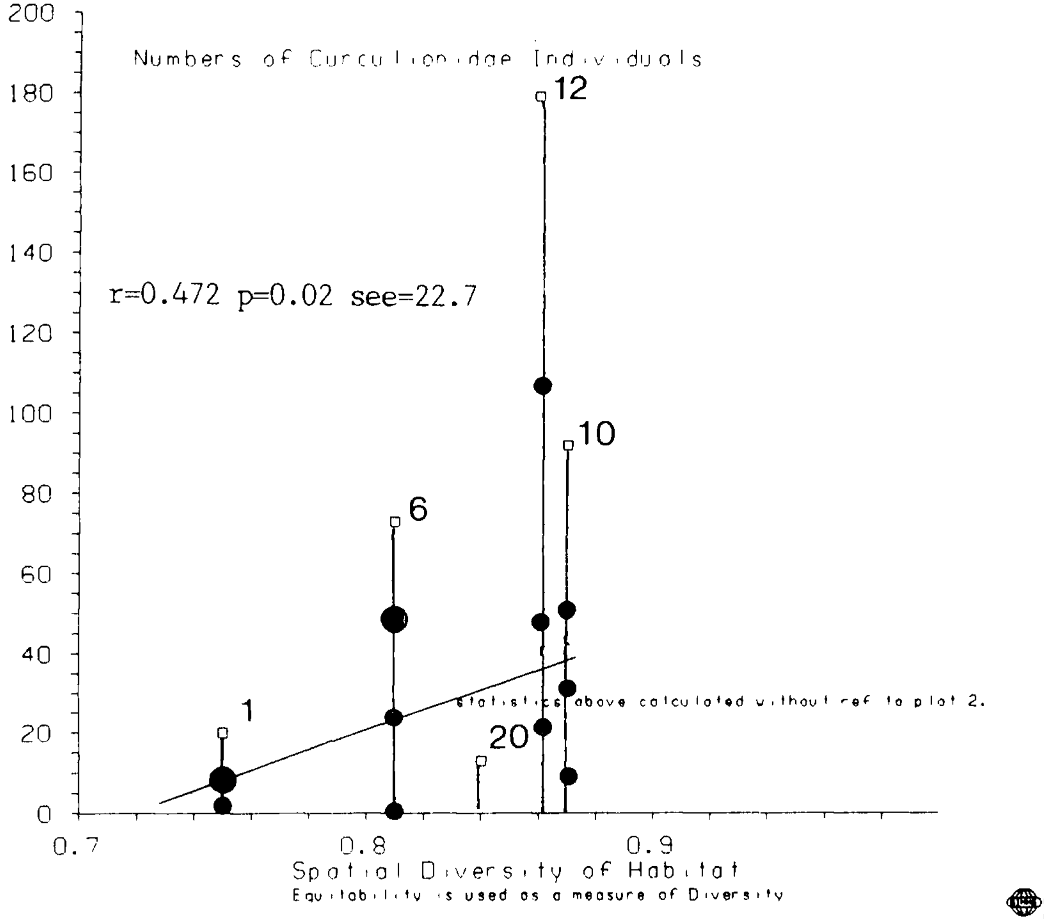
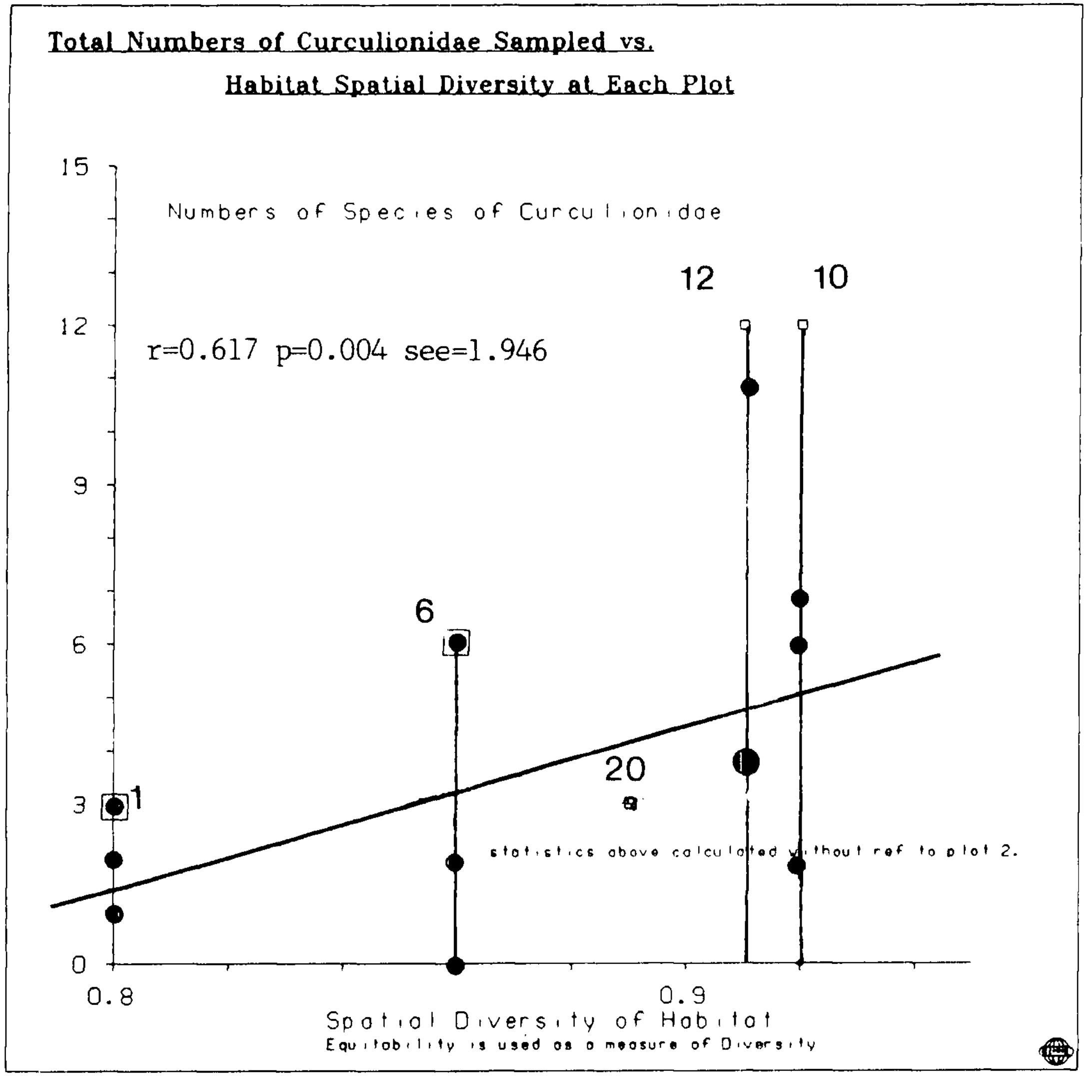
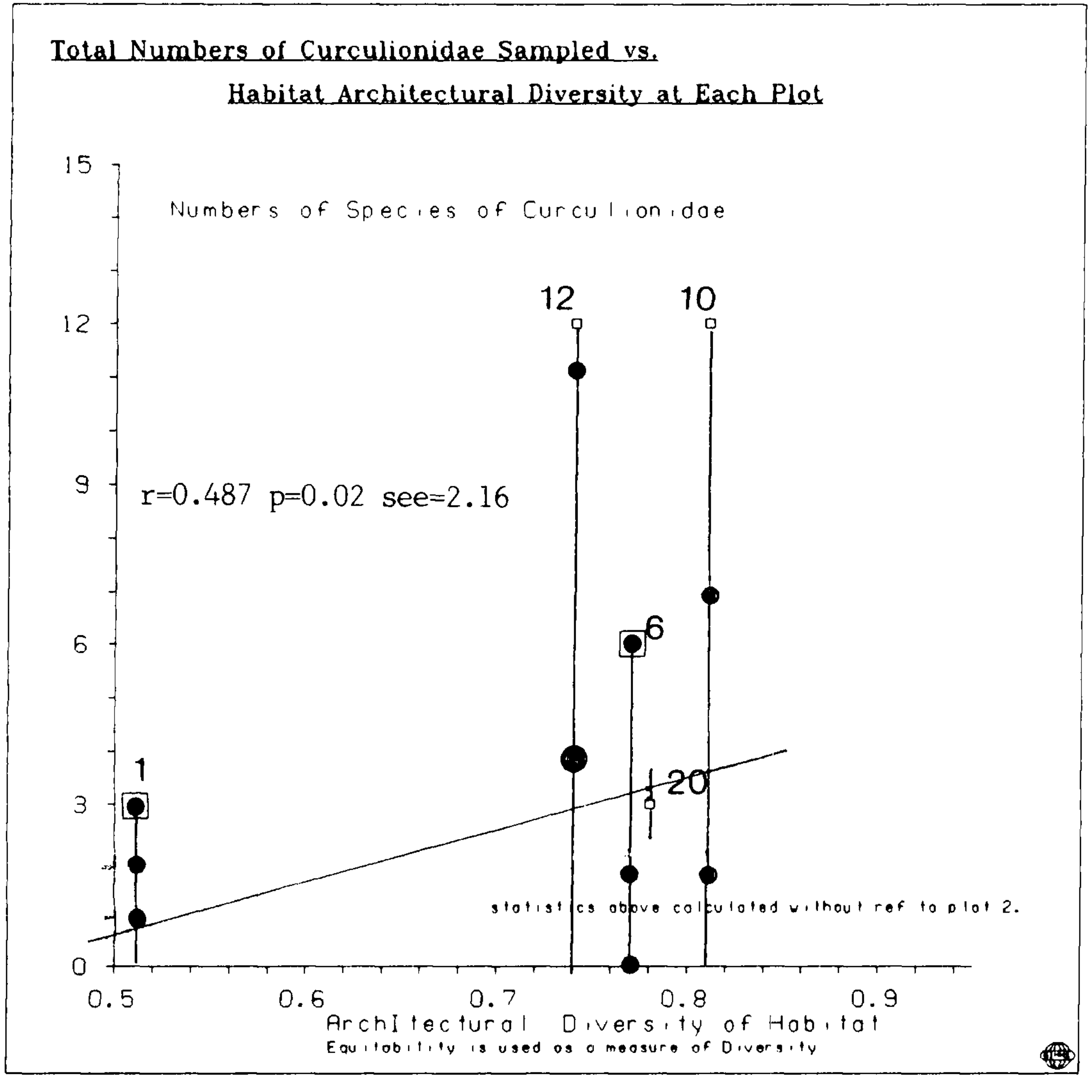


Figure 13



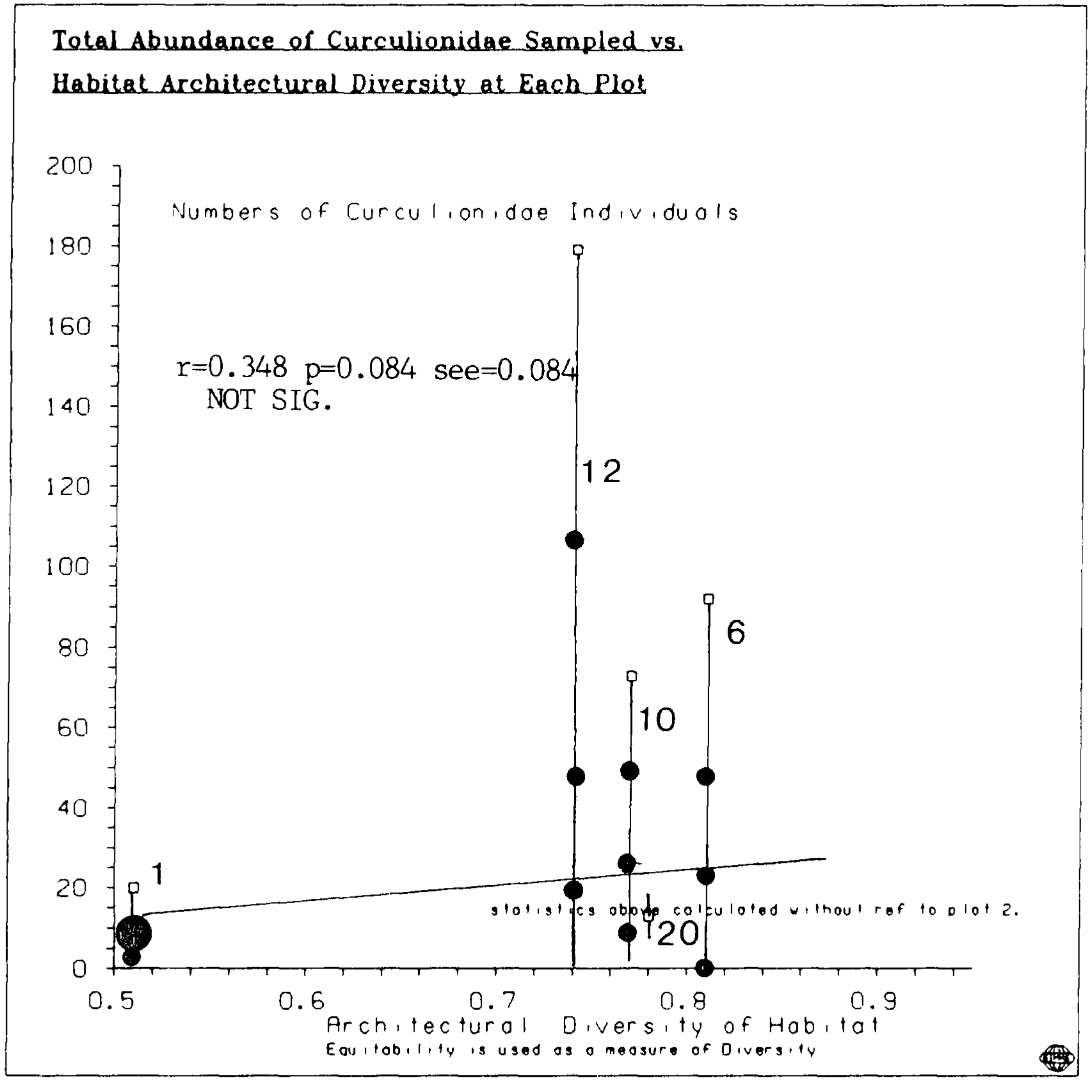
Total Numbers of Curculionidae Sampled vs. Habitat Spatial Diversity at Each Plot

Figure 14.



Total Numbers of Curculionidae Sampled vs. Habitat Architectural Diversity at Each Plot

Figure 15.



Total Abundance of Curculionidae Sampled vs. Habitat Architectural Diversity at Each Plot

Figure 16.

Table 6.

Effect of the Diversity of Habitat on Weevil Populations

Measure of Diversity	Number of Weevil Species (Species Richness)	Number of Weevil Individuals (Abundance)
Plant Diversity	18% SIG	NOT SIG
Habitat Structural Diversity	38% SIG	22% SIG
Architectural Diversity	23% SIG	NOT SIG

% are based on coefficient of determination, and relate to how much changes in the weevil populations can be explained by the various measures of diversity.
Significance is based on the 0.05 level.

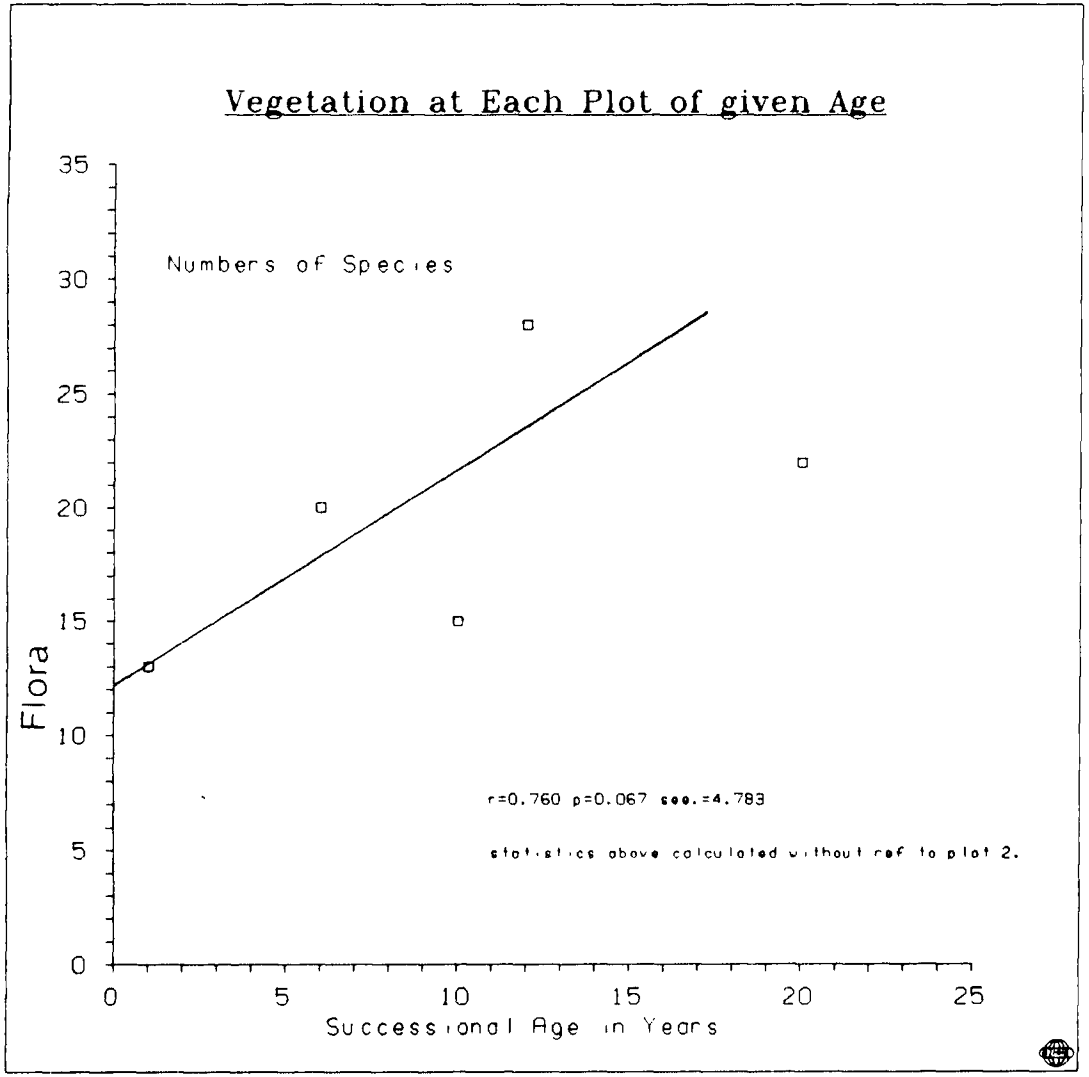

Vegetation at Each Plot of given Age
Numbers of Species
Flora
35
30
25
20
15
10
5
0
0
5
10
15
20
25
Successional Age in Years
r=0.760 p=0.067 see.=4.783
statistics above calculated without ref to plot 2.

Figure 17.

Figure 18.

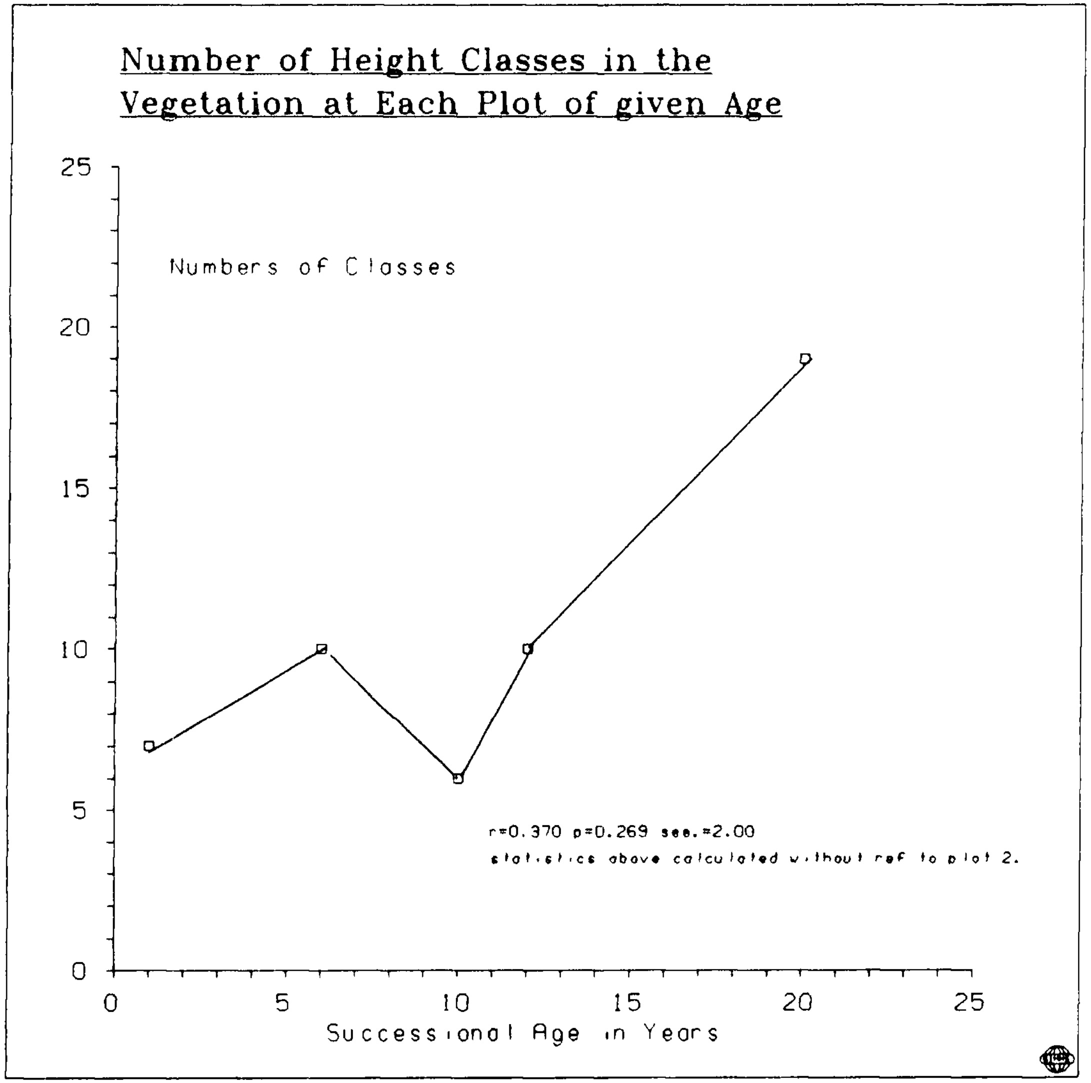
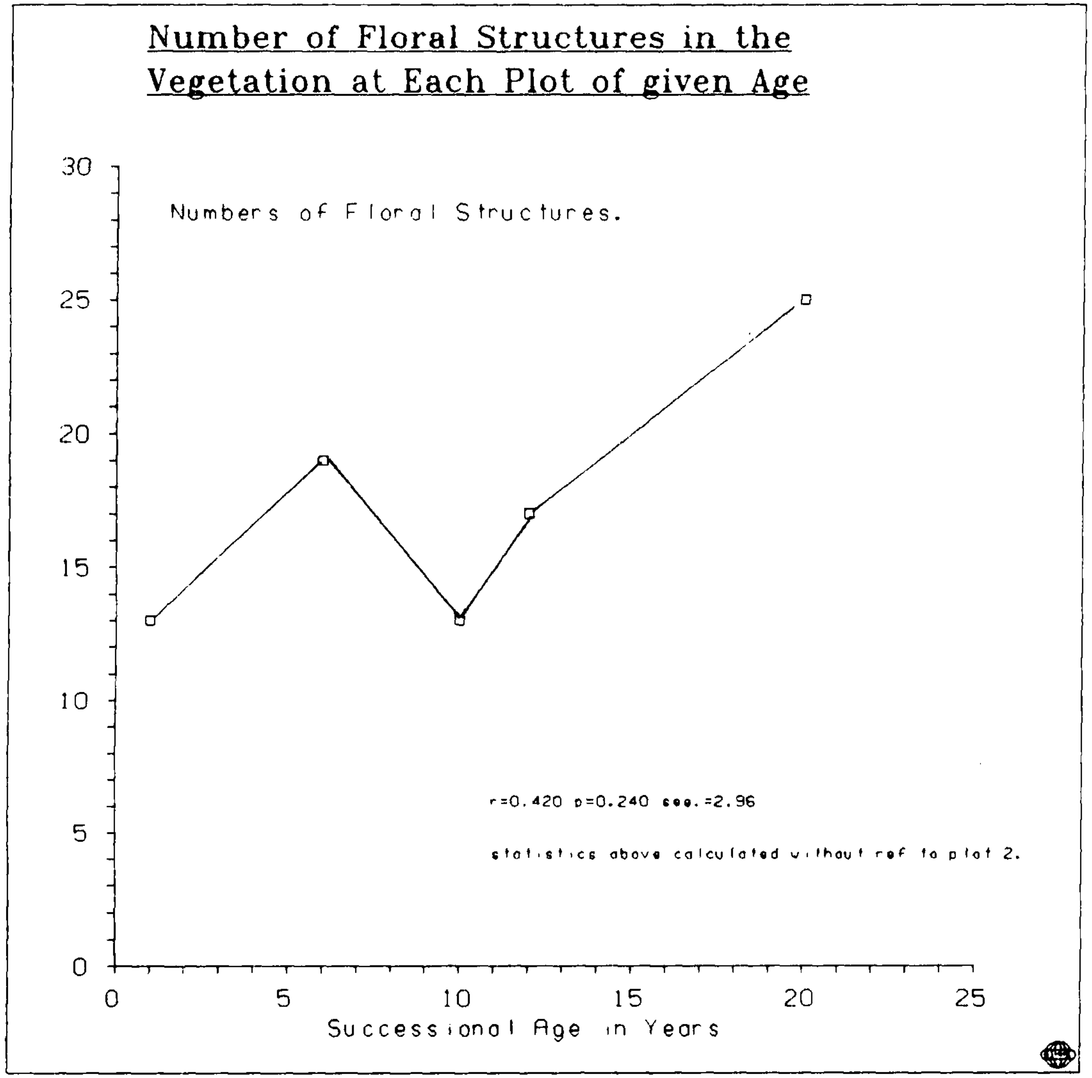

Number of Height Classes in the Vegetation at Each Plot of given Age
Numbers of Classes
25
20
15
10
5
0
0
5
10
15
20
25
Successional Age in Years
r=0.370 p=0.269 see.=2.00
statistics above calculated without ref to plot 2.

Figure 19.



Number of Floral Structures in the Vegetation at Each Plot of given Age

r=0.420 p=0.240 see.=2.96

statistics above calculated without ref to plot 2.

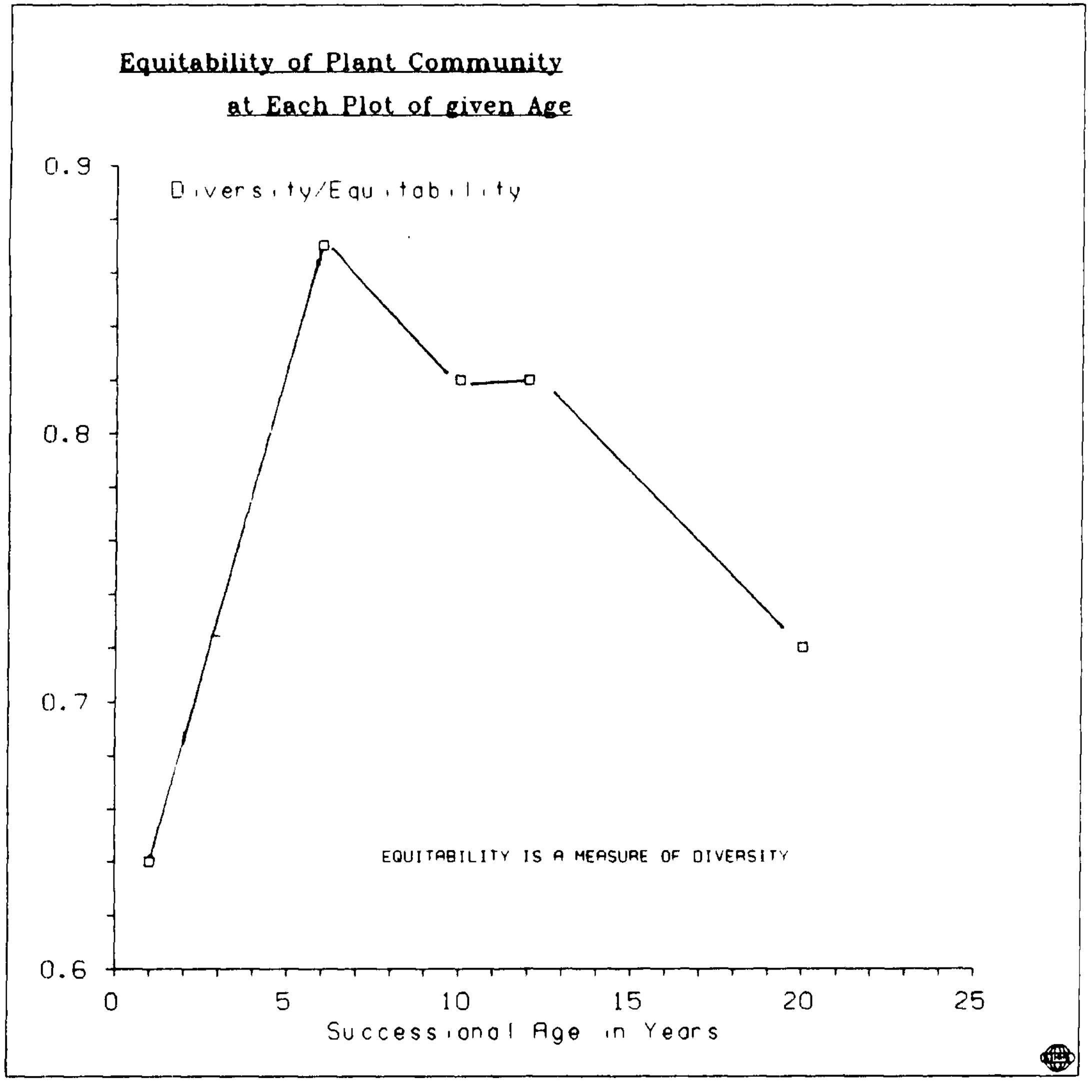
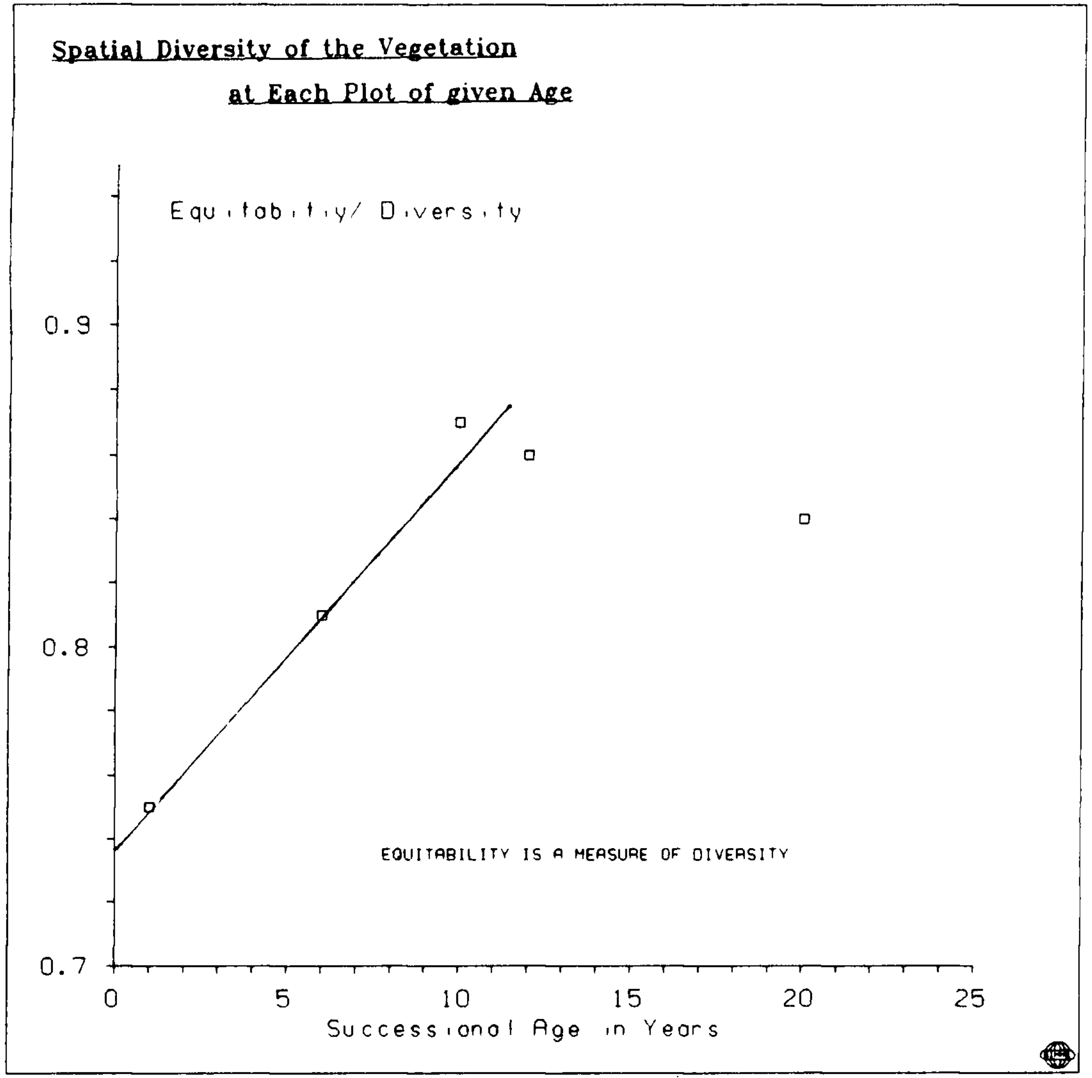

Equitability of Plant Community
at Each Plot of given Age
Diversity/Equitability
0.9
0.8
0.7
0.6
0
5
10
15
20
25
Successional Age in Years
EQUITABILITY IS A MEASURE OF DIVERSITY

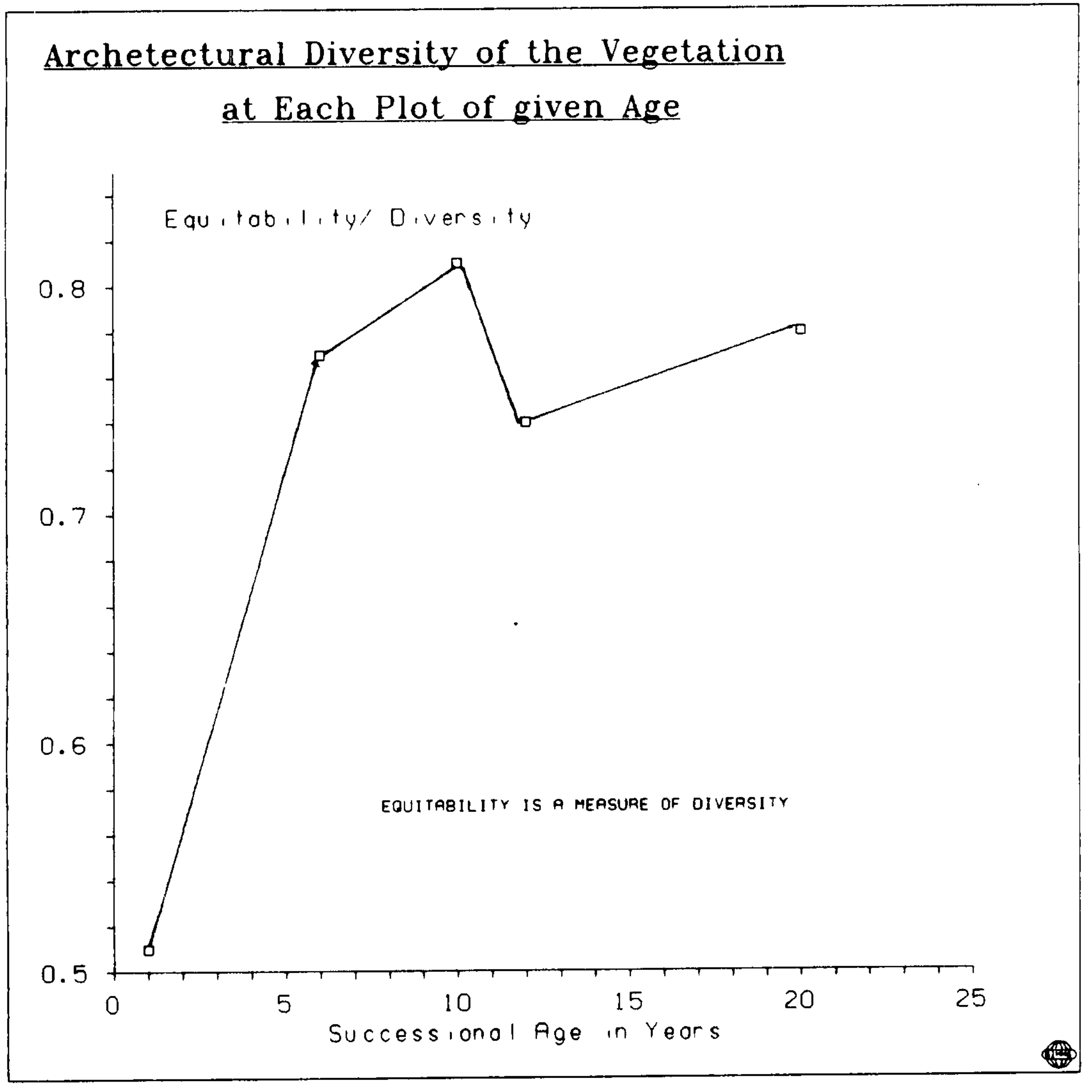
Figure 20.

Figure 21.



Spatial Diversity of the Vegetation at Each Plot of given Age

Figure 22.



Archetectural Diversity of the Vegetation
at Each Plot of given Age

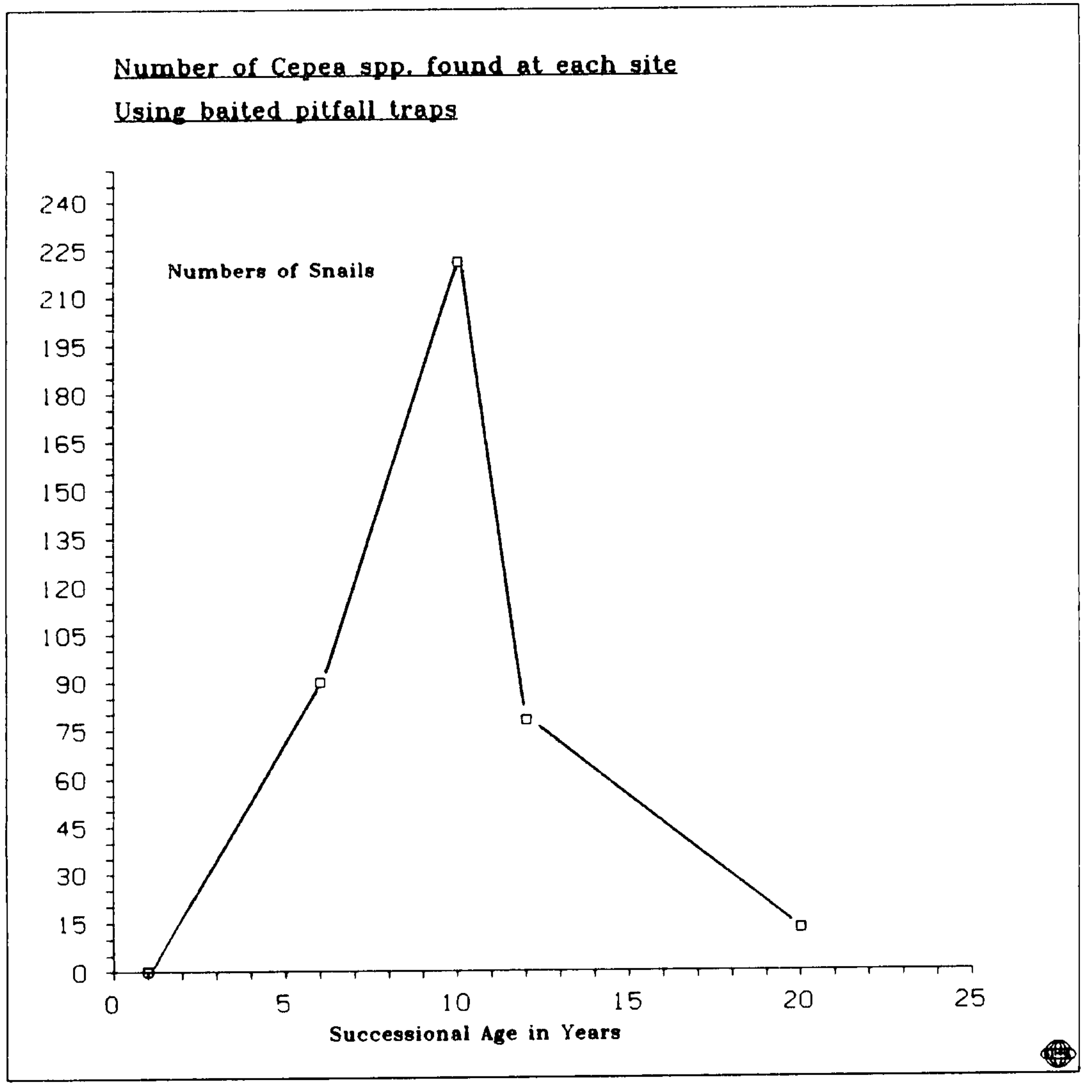

Number of Cepea spp. found at each site
Using baited pitfall traps
Numbers of Snails
240
225
210
195
180
165
150
135
120
105
90
75
60
45
30
15
0
0
5
10
15
20
25
Successional Age in Years

Figure 23.