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REPRODUCTIVE STRATEGIES OF SIX
PERENNIAL PLANT SPECIES IN
RELATION TO A SUCCESSIONAL SERIES

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of the requirements for the degree
of M.Sc. in Advanced Ecology.

University of Durham

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ABSTRACT

Data are presented on the phenology of dry weight allocation of plant tissue to major component parts for six herbaceous perennials, in relation to a successional sequence. Individual reproductive effort is shown to be constant throughout the succession. Reproductive effort at the population level however is shown to be highest in an early successional quarry site and lowest in an ungrazed grassland site. Populations from the successional more advanced scrub site generally show a level of reproductive effort between the other two. Significant intra-specific differences between populations from the three sites are demonstrated for mean total plant dry weight, time of anthesis, leaf area and stem length. These are interpreted as plastic responses to environmental variables and the level of competition. Leaf palatability experiments show that leaves taken from different parts of the succession are not different in their palatability to a generalised herbivore.

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1.

INTRODUCTION

The concept that organisms may adopt fundamentally different strategies for survival and reproduction in a resource-limited environment was suggested by MacArthur and Wilson (1967). At one end of the spectrum where the environment is inherently unstable and changing, genotypes, and ultimately species will be selected that can attain a maximal population growth rate and start to reproduce at an early age. At the other extreme, where the environment is stable and the population size is close to the carrying capacity, there will be strong selection for genotypes that have a greater competitive ability, larger body size, delayed reproduction and fewer, larger progeny.

These two opposing forces were labelled r- and K- selection respectively, after the two parameters in the logistic equation. Pianka (1970) lists the correlates with these types of selection, emphasising that the two types represent the opposite ends of a broad continuum, with the majority of species in the natural environment being located fairly centrally.

An alternative to the MacArthur and Wilson concept has been put forward in the field of plant ecology by Grime (1974, 1977). He suggests that there are 3 fundamental determinants of vegetation: competition, stress and disturbance. Each represents a selective force that invokes a distinct strategy on the part of the plant: the competitive, stress-tolerant and ruderal strategies.

Following the many interesting questions raised by Harper (1967), several studies have been made on the relative levels of resources that plants allocate to reproduction. Harper and Ogden (1970) looked at allocation between the major components of a plant under varying levels of stress. Using Senecio vulgaris, they found that reproductive effort,



defined as $(\text{total seed production} / \text{total net production} \times 100)$ was maintained fairly constant (around 21%) under varying levels of stress and despite seven-fold differences in total plant weight. Under extreme levels of stress however, induced by small pot size, reproductive effort was severely curtailed and sometimes prevented altogether (no flowering).

Abrahamson and Gadgil (1973) demonstrated the different levels of reproductive effort shown by four members of the genus Solidago, occurring in three sites from woodland to open dry sites. They found that the greater reproductive effort exhibited in the more unstable environment (dry site) was more pronounced in comparisons between two distinct species than where two forms of the same species were compared.

Empirical evidence for intra-specific variation in reproductive effort was presented by Gadgil and Solbrig (1972) for various biotypes of Taraxacum officinale. Disturbed sites were characterised by individuals with higher seed production and lower competitive ability. In their analysis of whole communities, they found that the disturbed and unstable habitats contained a larger proportion of those T. officinale biotypes that allocate more resources to reproduction.

Hickman (1975) found complementary evidence in Polygonum cascadense. Again looking at the community as a whole, he showed that greatest allocation of resources to reproduction in this species was found in habitats with low species diversity and vegetative cover. Hickman concludes that these differences are environmentally induced and plastic rather than genetically determined.

Several other workers have demonstrated both inter- and intra-specific variation in reproductive effort in various plant species; Sterk (1975) in Anthyllis vulneraria. Gaines et al., (1974) in

Helianthus spp., Van Andel and Vera (1977) in Senecio sylvaticus and Chamaenerion angustifolium, Vasek and Clovis (1976) in Arctostaphylos glauca and Ogden (1974) in Tussilago farfara.

A possible correlate of the r-K strategy continuum is the proportion of resources (whether chemical or dry matter) that a plant allocates to the avoidance or repulsion of herbivores. The theoretical implications of the theory are that plants in stable habitats (at the K end of the spectrum), devoting fewer resources to reproduction, will be able to re-direct greater resources towards the physical avoidance (via thorns, hairs etc.) and chemical repulsion (toxins, tannins etc.) of grazing herbivores and parasites. This commitment to defence was estimated by Cates and Orians (1975) using short-term palatability of leaves to two slug species Arion ater and Agriolimax columbianus. Their results showed that early succession annuals, from a very unstable habitat, were significantly more palatable than late succession perennials.

Otte (1975) provides conflicting evidence for a different ecosystem and using different organisms. Using polyphagous grasshoppers (Schistocerca spp.) and plants along a succession in Texas, he found that edibility of plants from early successional stages was in fact less than that of late succession species.

Grime et al., (1968) list the palatability of 52 species of plant to the land-snail Cepaea nemoralis. Of the low percentage (20%) that were palatable to snails, a high proportion of species were associated with disturbed habitats and/or fertile soils.

This brief review of the literature published to date on reproductive effort in plants reveals a number of gaps. Firstly, few workers have confined themselves to the variation in resource allocation within species, most concentrating on closely-related species within a single

genus, or on the plant community as a whole. Also, most studies have involved looking at fundamentally different habitats that represent highly stable or unstable environments. Few studies have looked at the changes along a successional gradient of uniform environmental conditions, where the only variables are time and the stage of development of the plant community. The resultant induced differences in reproductive effort in a plant species, if any, are likely to be much smaller. Similarly most emphasis has been given to the monitoring of allocation of resources to reproductive versus non-reproductive plant structures. Such an approach may be too narrow. Information on all major plant parts, or modules, may be necessary to reveal not only what plant characters are plastic, but also how different allocations are facilitated by changes in the dimensions of the plant's supportive and photosynthetic structures. Finally, no one has, as yet, published any investigation into the intra-specific variability in leaf palatability to generalised herbivores. These aspects of reproductive strategies in plants form the back-bone of this paper.

2.

THE PAPER

This paper reports on work carried out from May to August 1978 on the phenology of dry matter allocation to major component parts in various species of limestone grassland plant, in relation to a successional sequence.

Six common herbaceous perennial species were chosen for the study. The succession was studied in detail at three stages of its development : early colonisation on an open quarry slope, ungrazed species-rich grassland and partly-closed-canopy, shaded Crataegus monogyna scrub.

Regular removals of samples of the above-ground parts of the six species were followed by separation into component parts, measurement of component dimensions, drying and weighing. This enables an analysis of how the allocation to reproductive and other structures varies over a growing season.

In addition, choice feeding experiments, using leaf samples from different sites, were done with the land-snail Cepaea nemoralis. This was done to ascertain whether individual plants from early successional stages were any more (as predicted by the Cates and Orians theory) or less palatable than samples of the same species from late seral stages.

3.

THE SAMPLE SITES

The three sample sites were all located on the magnesian limestone that outcrops in County Durham (Figure 1). The grassland and scrub sites were located within 250 metres of each other. However, the quarry site is 7 km apart from these other two. Since they are all on the same soil series however, this was not considered a problem, from the point of view of comparing the sites.

The open quarry site was located at Wingate Quarry, approximately 13 km S.E. of Durham (NZ 373,374) (Figure 2). The vegetation consists of an open colonising community characterised by Sesleria albicans, Epilobium angustifolium and Hieracium spp. The samples were taken from a 50 metre stretch of bank that had been created by quarrying earthworks. The bank is straight, 3.1m high and faces roughly S.W. (140°W), with an approximate average slope of 42°.

The ungrazed-grassland site was located at Thrislington Plantation, approximately 12 km S.S.E. of Durham (NZ 319,328) (Figure 3). This is listed as a Grade 1 SSSI in the Nature Conservation Review (Nature Conservancy Council, 1977) being considered as the best example of Magnesian Limestone grassland. The grassland is a species-rich Sesleria albicans type (Shimwell, 1968) with co-dominant Festuca ovina, supporting a number of rare species such as Epipactis atrorubens, Linum anglicum and Listera ovata. Samples were taken from the largest area of open grassland, on a gentle (6°) slope facing W.N.W. (79°W).

The scrub site was also located at Thrislington (Figure 3), approximately 250 metres N.W. of the previous site within a large area of well-advanced Crataegus monogyna scrub. Rosa pimpinellifolia is also relatively extensive. The field layer is dominated by Sesleria albicans

and includes some rarer species such as Linum anglicum and Anacamptis pyramidalis. The sampling site was located on flat ground, where C.monogyna produces extensive shade, but with small areas of open ground in-between.

Thrislington plantation, encompassing both the grassland and scrub sites is scheduled for quarrying within the next 50 years. The bank used for sampling at Wingate Quarry is also scheduled for removal and levelling within the next year (Doody, 1977).

FIGURE 1.

SYNOPTIC MAP OF SITES IN RELATION TO DURHAM

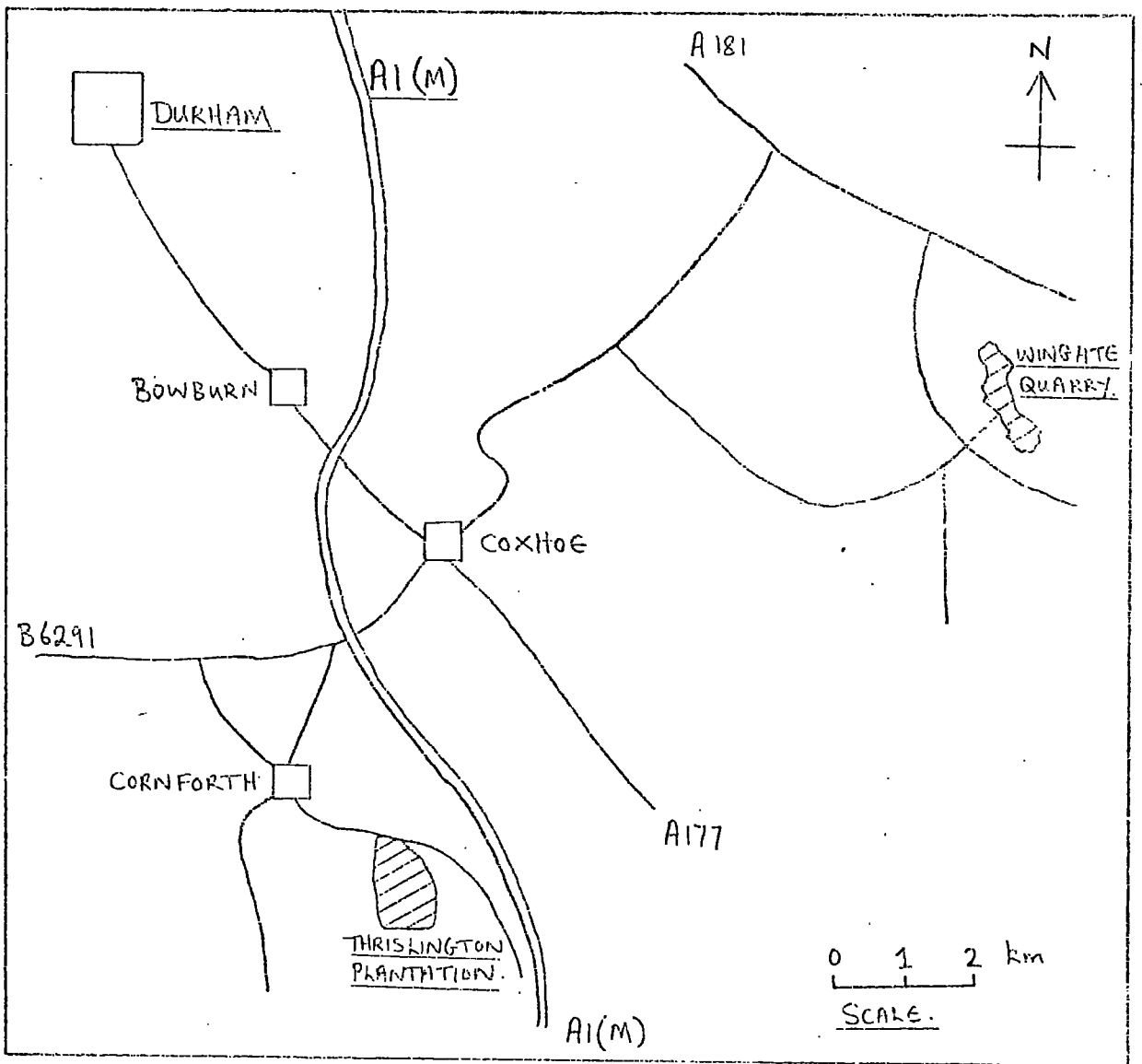


FIGURE 2.

WINGATE QUARRY SITE.

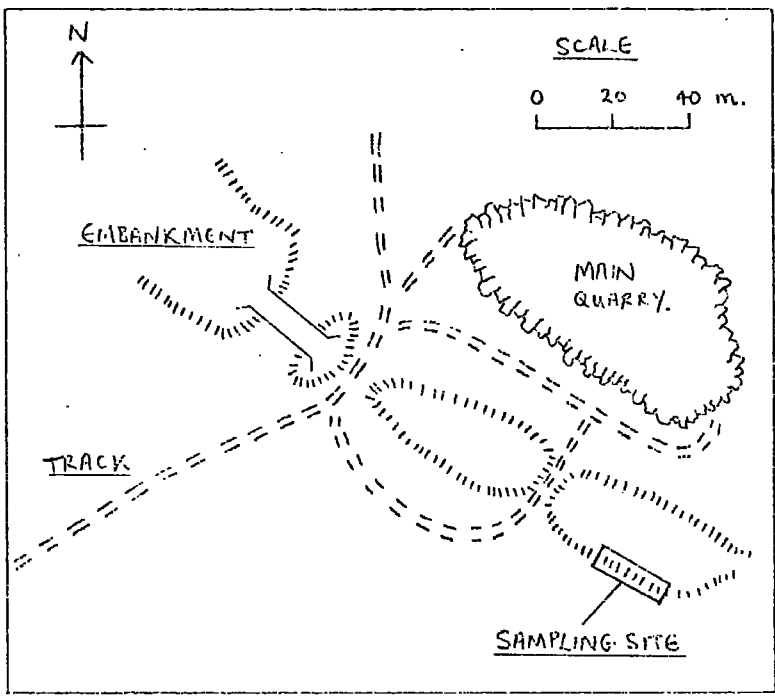


FIGURE 3.

THRISHINGTON GRASSLAND & SCRUB SITES.

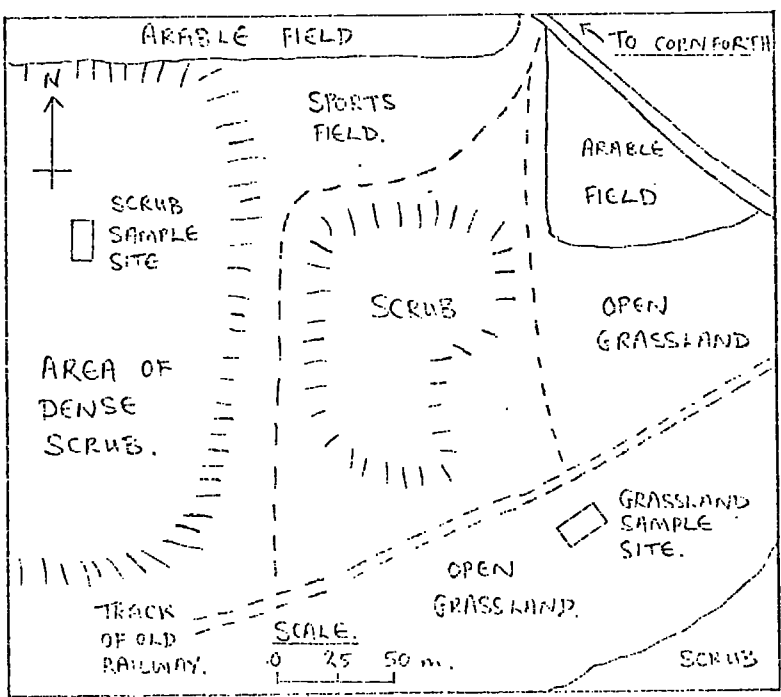


PLATE 1

THE QUARRY SITE

Wingate Quarry, Co. Durham

PLATE 2

THE GRASSLAND SITE

Thrislington Plantation, Co. Durham



PLATE 3

THE SCRUB SITE

Thrislington Plantation, Co. Durham



4.

CHOICE OF PLANT SPECIES

The choice of plant species was made using a set of criteria that would enable efficient sampling and analysis of plant material:

1. The species should be common and widespread in their general distribution and particularly abundant on the three sites concerned.
2. The species should be typical along the whole length of the succession.
3. Individual plants should be discreet and easily separated from one another. They therefore should be neither creeping (as in Hieracium pilosella) nor rhizomatous (as with most of the Gramineae).
4. The flowering parts of the plant should be easy to separate from the rest of the plant and should be of sufficient size to make individual weighings significant.
5. The seeds produced should be of sufficient size to make weighing practicable.

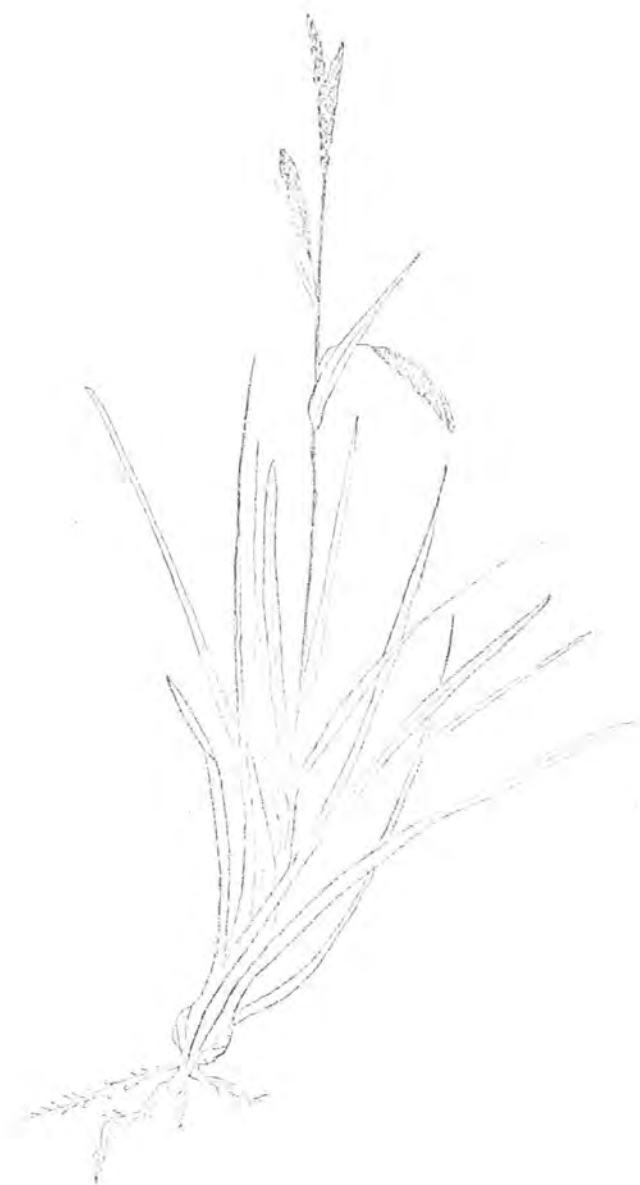
The six plant species chosen were:-

<u>Carex flacca</u> Schreb.	"Carnation Grass"
<u>Centaurea nigra</u> L.	"Lesser Knapweed"
<u>Leontodon hispidus</u> L.	"Rough Hawkbit"
<u>Plantago lanceolata</u> L.	"Ribwort"
<u>Plantago media</u> L.	"Hoary Plantain"
<u>Poterium sanguisorba</u> L.	"Salad Burnet"

All are medium to tall herbaceous perennials with relatively large seeds and inflorescences. Individual plants were, with some care, easily distinguishable from each other and therefore extractable. C. flacca, C. nigra and P. sanguisorba were less satisfactory in this respect since apparently separate above-ground parts were often found to be connected subterraneously. In such cases, a single above-ground stem was removed

as a sub-sample of the whole plant. Counting of the number of stems enabled the grossing-up of the data after analysis of component parts.

A problem concerning the range of the succession was encountered in the pilot survey. Representatives of the above species were found to be abundant in many quarry, grassland and scrub sites, but mostly absent in examples of the climax Fagus sylvatica woodland. In fact, there was a very sharp discontinuity between scrub and adjoining woodland sites (particularly noticeable at Thrislington) in terms of the species composition of the field layer. No species were found to be consistently represented in both areas. It was therefore decided to restrict the range of the succession studied to a gradient from open, disturbed quarry to well-developed scrub.

FIGURE 4.

CAREX FLACCA Schreb.

AFTER JEAMY & TUTIN (1968).

FIGURE 5.CENTAUREA NIGRA L.AFTER ROSS-CRAIG (1960-3)

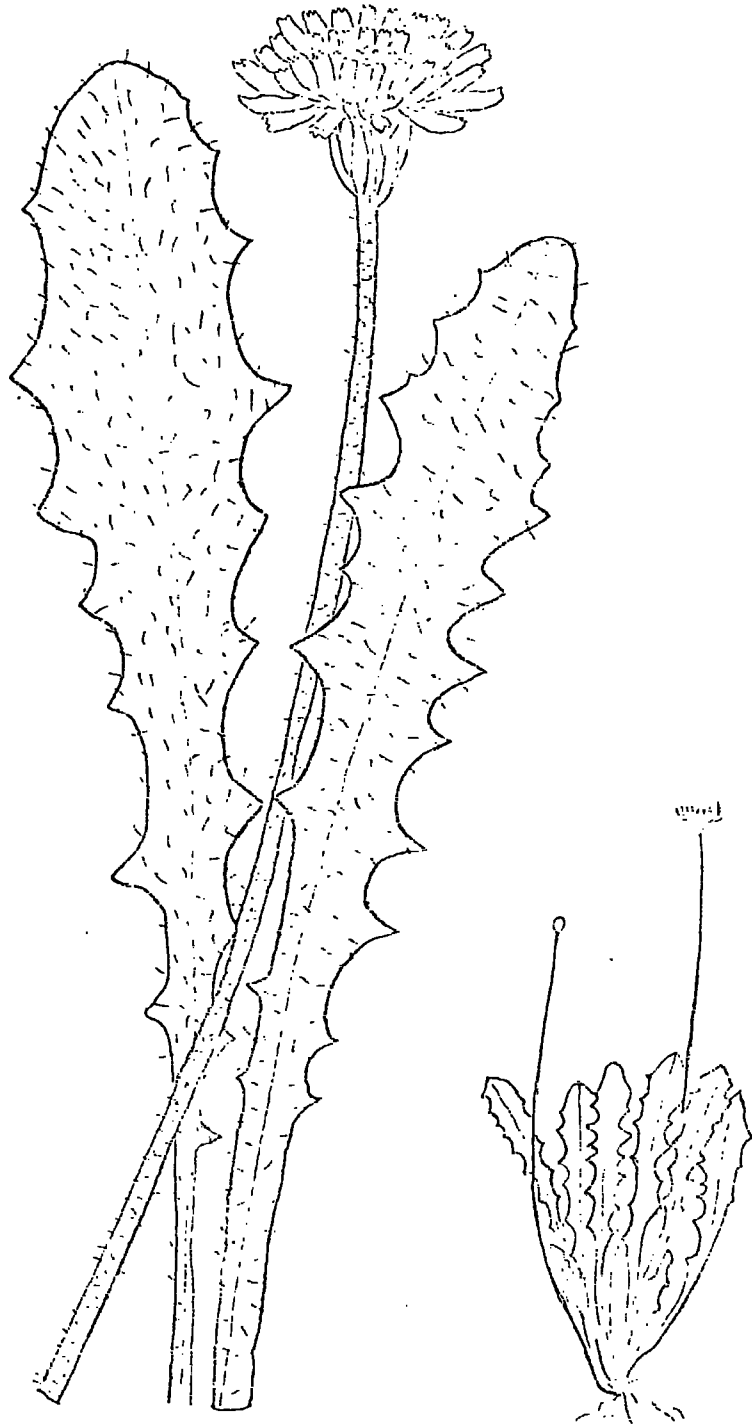
FIGURE 6.LEONTODON HISPIDUS L.AFTER ROSS-CRAIG: (1960-3)

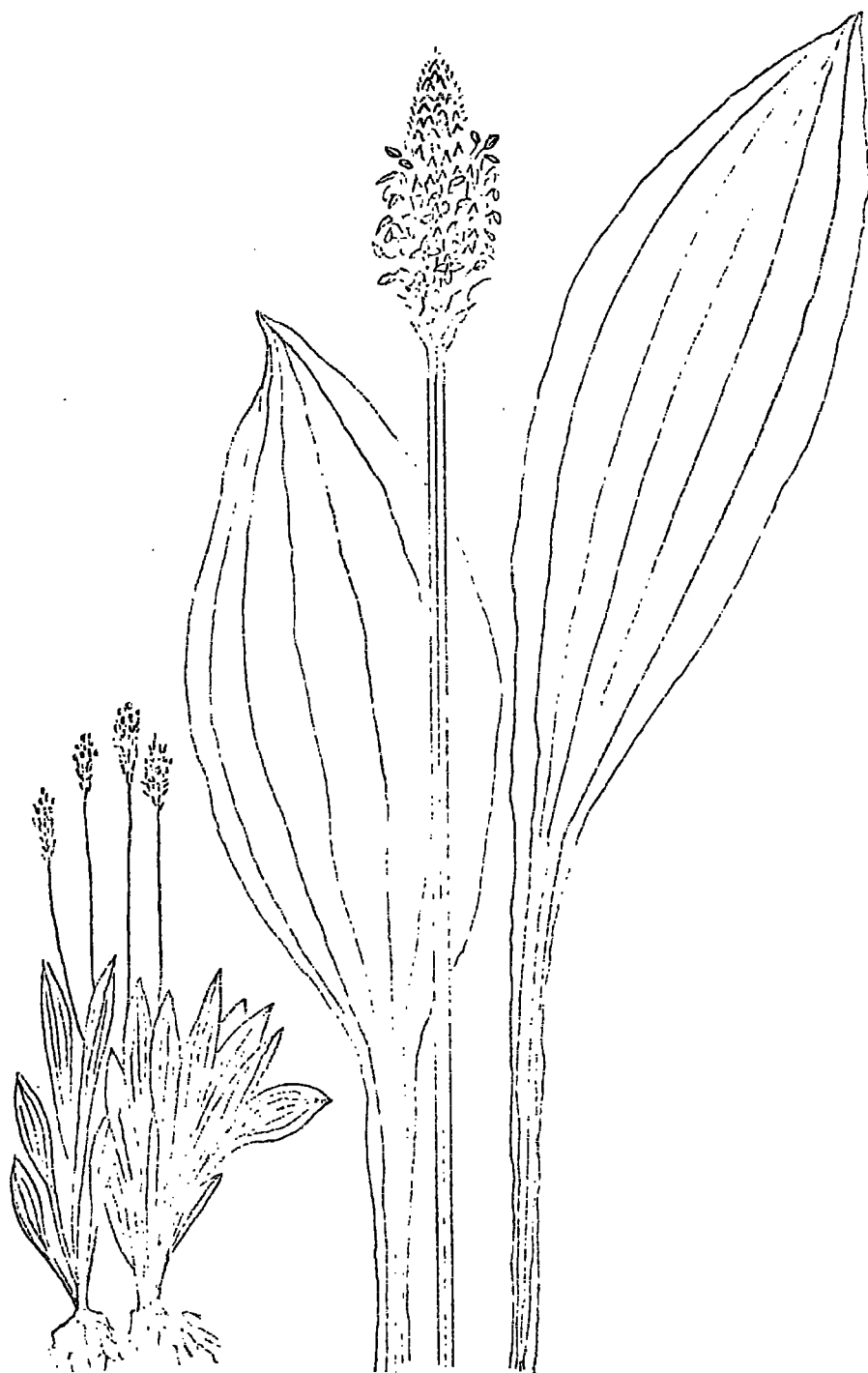
FIGURE 7.PLANTAGO LANCEOLATA L.AFTER ROSS-CRAIG (1960-3)

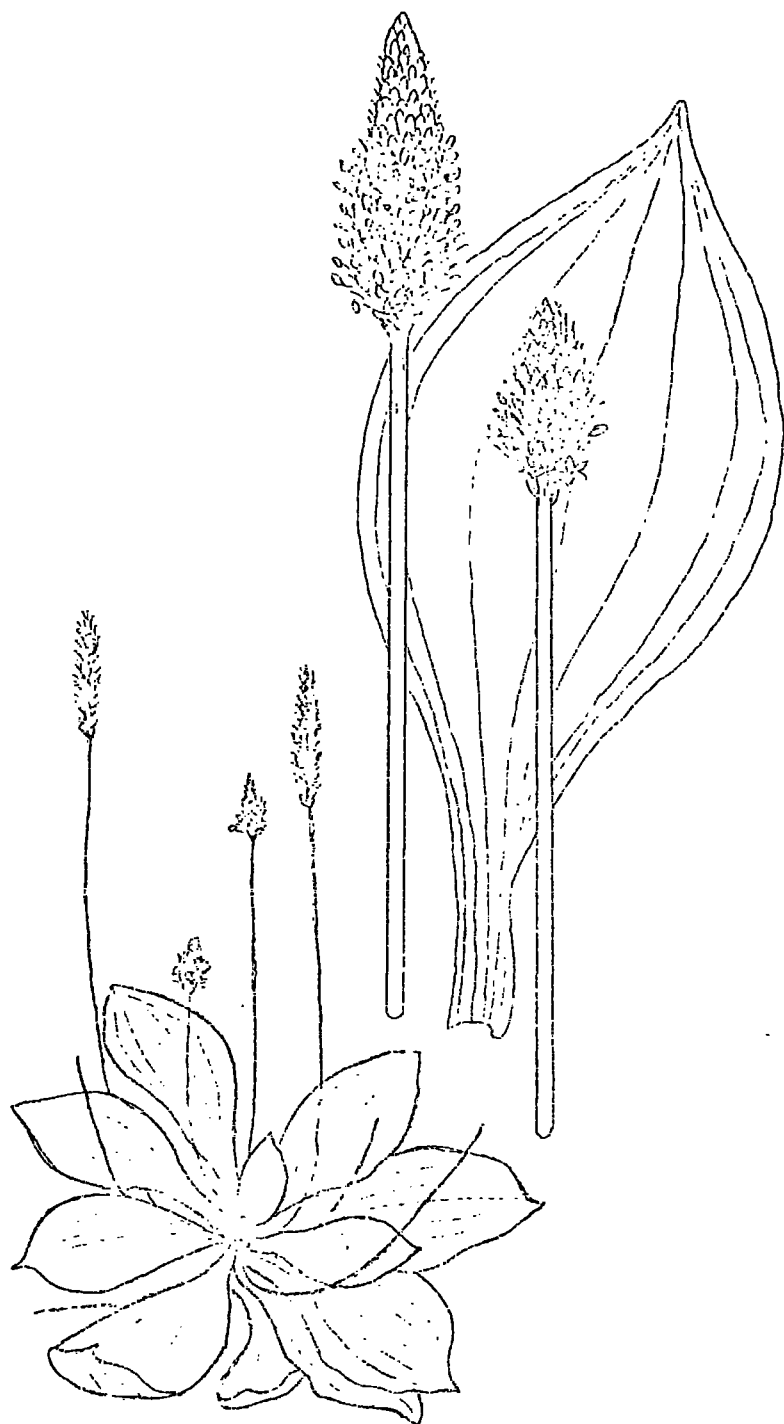
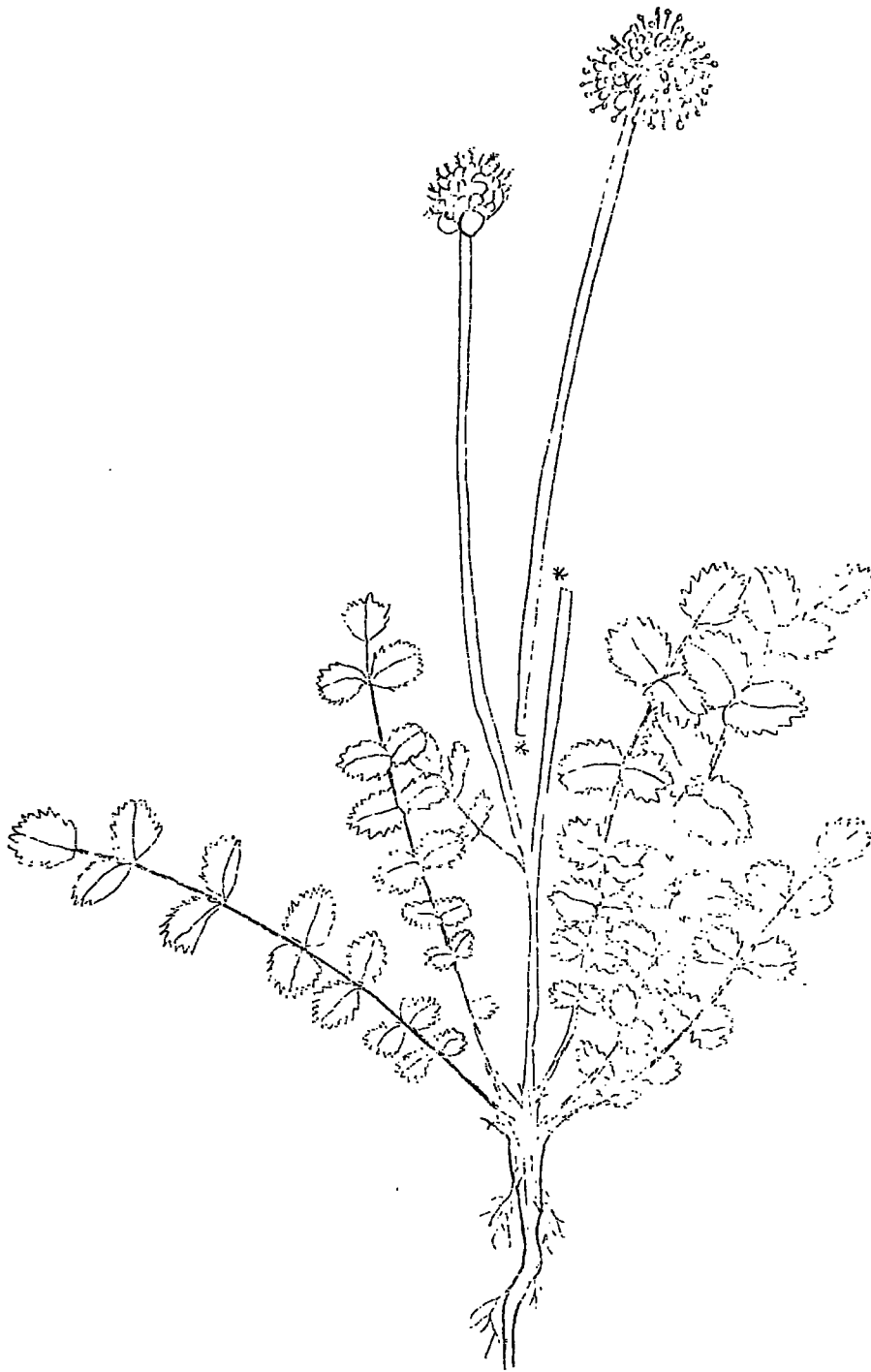
FIGURE 8.PLANTAGO MEDIA L.AFTER ROSS - CRUICK (1960-3)

FIGURE 9.POTERIUM SANGUISORBA L.AFTER ROSS-CRAIG (1960-3).

5.

SAMPLING

Permanent sampling plots were marked out in each of the three sites chosen. These were located centrally in relation to the extent of the selected habitat (Figures 2 and 3) and marked out with small pegs so that the same area was used for successive samples.

The sizes of the sampling areas were as follows:-

Quarry site	5 x 20 metres
Grassland site	10 x 20 metres
Scrub site	10 x 15 metres

Sampling involved the temporary laying of a tape to mark the four sides of the sampling rectangle. Random points within the square were located using random number tables (Rohlf and Sokal 1969). The nearest individual of the chosen species to the selected co-ordinate was then taken as a single sample.

Removal of all the above-ground parts (including dead plant material) was made by cutting as near as possible to ground level. Individual plants were placed in plastic bags and, on return to the laboratory, stored at 5°C. Analysis of the component parts was subsequently carried out within a week of sampling.

Sample size was at first maintained at 20 individual plants per species per site. Due however to the length of time needed to analyse the samples, this was later reduced to 15 individuals per species per site.

6.

FIELD DATA COLLECTION

Two extra sets of field data were collected at each site.

The first was a species list of each of the three sites. Using random points within the permanent plot, all species were recorded as present or absent within 100 quadrats, using a 10cm x 10cm frame. The relative abundances of each species, as shown by the number of occurrences, are given for each site in Table 1.

In addition, data was collected on the flowering status of the six species at each site. This was done to supplement the data collected in the analysis of component parts. For each species, 50 individuals were located by taking 50 randomly-directed paces and recording the individual nearest to the front of the recorder's shoe. Though not as statistically rigorous as the use of random number tables, this method is far quicker and thus widely used in plant ecology. The flowering status of each individual was scored using the following code:-

0. No inflorescence at all
1. Bud
2. "Early flowering" stage. Flower just opening
3. "Full flowering" stage.
4. "Late flowering" stage. Petals decaying
5. Unripe seeds within capsule or pappus
6. Ripe seeds within capsule or pappus
7. Seeds or pappus starting to disperse
8. All seed dispersed. Stalk or flowering head bare.

TABLE 1

SPECIES LIST AND ABUNDANCE IN 100 QUADRATS FOR THREE STUDY SITES

	<u>Quarry Site</u>	<u>Grassland Site</u>	<u>Scrub Site</u>
<i>Achillea millefolium</i>	11	4	
<i>Agrimonia eupatoria</i>			9
<i>Anthriscus sylvestris</i>			3
<i>Anthyllis vulneraria</i>		9	
<i>Astragalus danicus</i>		11	
<i>Campanula rotundifolia</i>		8	11
<i>Centaurea nigra</i>	9	26	20
<i>Centaurea scabiosa</i>	13	21	11
<i>Chamaenerion angustifolium</i>	7		
<i>Cirsium arvense</i>	4		
<i>Conopodium majus</i>		6	9
<i>Crataegus monogyna</i>		7	7
<i>Crepis capillaris</i>	8		
<i>Dactylorhiza fuchsii</i>	7	7	6
<i>Epipactis atrorubens</i>		2	
<i>Euphrasia officinalis</i>		22	
<i>Fragaria vesca</i>	8		
<i>Galium verum</i>		6	10
<i>Gentianella amarella</i>		6	7
<i>Gymnadenia conopsea</i>	6	9	7
<i>Helianthemum chamaecistus</i>		21	
<i>Hieracium pilosella</i>	19	4	
<i>Hypericum perforatum</i>		7	5

<i>Hypochoeris radicata</i>	17		
<i>Leontodon hispidus</i>	16	28	28
<i>Linum catharticum</i>	14	22	19
<i>Linum anglicum</i>		5	
<i>Listera ovata</i>		7	6
<i>Lotus corniculatus</i>	10	13	16
<i>Medicago lupulina</i>	10	7	9
<i>Orchis mascula</i>			5
<i>Plantago lanceolata</i>	11	9	19
<i>Plantago media</i>	8	16	15
<i>Polygala vulgaris</i>		9	9
<i>Poterium sanguisorba</i>	13	10	18
<i>Primula veris</i>	6	4	10
<i>Prunella vulgaris</i>		8	10
<i>Ranunculus bulbosus</i>	9	5	5
<i>Rhinanthus minor</i>		11	15
<i>Rosa pimpinellifolia</i>			2
<i>Rubus fruticosus</i>	3	3	6
<i>Scabiosa columbaria</i>	9	10	7
<i>Senecio jacobaea</i>	11	1	
<i>Senecio vulgaris</i>	9		
<i>Silene dioica</i>			3
<i>Taraxacum officinale</i>	8		
<i>Thymus drucei</i>	6	5	
<i>Tragopogon pratensis</i>		3	8
<i>Trifolium pratense</i>	15	10	9
<i>Tussilago farfara</i>	12		
<i>Viola riviniana</i>			2

<i>Agrostis stolonifera</i>		7	
<i>Agrostis tenuis</i>	14	10	6
<i>Anthoxanthum odoratum</i>		13	
<i>Arrhenatherum elatius</i>		6	3
<i>Brachypodium sylvaticum</i>			2
<i>Briza media</i>	13	17	9
<i>Cynosurus cristatus</i>		13	
<i>Dactylis glomerata</i>	10	8	5
<i>Deschampsia caespitosa</i>			4
<i>Festuca rubra</i>	21	34	29
<i>Helictotrichon pratense</i>		2	
<i>Holcus lanatus</i>		6	9
<i>Koeleria cristata</i>		3	
<i>Lolium perenne</i>		5	
<i>Poa pratensis</i>		8	
<i>Sesleria albicans</i> *	19	41	31
<i>Carex flacca</i>	11	19	10
<i>Luzula campestris</i>			3
<hr/>			
Total number of species	34	52	44
Average species density per quadrat	3.67	5.54	4.37

- NOTES: 1. Nomenclature follows Clapham, Tutin and Warburg (1962)
2. Figures refer to the number of occurrences in 100 quadrats of sizes 10 x 10 cm.
3. * Sesleria albicans = S. caerulea Subsp. calcareo

7.

METHODS AND TECHNIQUESA. Analysis of Component Parts

The bulk of the work in the laboratory centred around the separation of each plant sampled from the field into its component parts. A list of these component parts, or modules (Harper, 1977) is given below:

- (i) Leaves
- (ii) Dead leaves
- (iii) Stems
- (iv) Inflorescences
- (v) Buds
- (vi) Shoots
- (vii) Seeds
- (viii) Stem leaves (Centaurea nigra only)

A number of extra measurements were also made to describe the physical dimensions of the plant more fully:

- (i) Maximal height
- (ii) Flowering scale (as described in Section 6)
- (iii) Length of each stem
- (iv) Length of each shoot
- (v) Diameter of each bud
- (vi) Maximum diameter or length of each inflorescence
- (vii) Length and breadth of each leaf

Since it was not possible to measure leaf area directly, this parameter was calculated from empirically-derived equations, relating leaf area to maximum length and maximum width of individual leaves.

Twenty-five randomly selected leaf samples were collected, for each

site. After measurement of maximum length (including petiole) and maximum width, the outline of each leaf was traced onto paper and cut out. Given the weight and area of a much larger, square piece of similar paper, the area of each leaf could be calculated from the weight of its paper equivalent (measured to four decimal places). The regression of leaf area on leaf length, width and the cross-product of length and width was calculated for four plant species at each of the three sites. The dimensions of leaf samples of Carex flacca were not significantly different between sites and were therefore grouped together.

The problem of leaf-area measurement was exacerbated in Poterium sanguisorba by the occurrence in this species of numerous (up to 25) leaflets on each pinnate leaf (Figure 9). Obviously these could not be measured individually for each plant sampled, so a similar regression to that above was derived for the relationship between the length of the pinnate leaf, the number of leaflets and the total leaf surface area. This was repeated for each of the three sites.

A further problem was encountered with trying to determine the leaf dimensions of the stem-leaves of Centaurea nigra. Near the top of the stem, these are often too small and too numerous to measure accurately when analysing many samples in a short time (Figure 5). It was therefore deemed more sensible to count all those leaves less than 4cm long and use an empirically-derived equation (relating number of side leaves to leaf area) to calculate their area. This figure could then be subsequently added to the main-leaf area.

Once separated into component parts, the plant material was placed in numbered envelopes, thus enabling many samples to be dried at the same time. Samples were dried at 105°C for at least 24 hours. A Mettler balance was used to record weights to four decimal places.

Once recorded, the variables were coded and punched onto computer cards. Subsequent analysis on the N.U.M.A.C. computer used programs drawn mostly from "Statistical Packages for the Social Sciences" (Nie et al., 1975)

B. Palatability Experiments

Tests on the relative palatabilities of plants from different stages of the succession involved the use of choice feeding experiments. The helicid land-snail Cepaea nemoralis L. was used as a generalised herbivore.

C. nemoralis has a number of inherent advantages in a study of this nature. It is, firstly, fairly ubiquitous in calcareous environments and was found in reasonable numbers in all three of the sites. It was most numerous at Wingate Quarry. As a herbivore it has been recorded eating a wide variety of plant species, but has fairly distinct food preferences (Grime et al., 1968).

As an animal for use in the laboratory, it is very easy to handle, since it is very drought resistant and tolerant of wide temperature fluctuations. Since it requires only a very small space in which to feed, it is ideal for choice experiments involving several replicates.

The amount of plant material consumed in 24 hours varies between 10 and 40 mg. dry weight (Grime et al., 1968). This order of magnitude is sufficiently large for accurate measurements to be made.

Grime et al., (1978) found that Leontodon hispidus was one of the seven most favoured (out of 52 possible) food plants for C. nemoralis in choice experiments. Using faecal analysis, Williamson (1976) found that L. hispidus and Poterium sanguisorba were the commonest species eaten, accounting, at the time of their maximum abundance, for 21.9%

and 10.9% respectively of adult faeces. The relative palatabilities of Carex flacca, Plantago lanceolata and P. media have been recorded as very low (Grime et al., 1968 and Williamson 1976). Centaurea nigra remains unstudied in this respect.

In view of previous findings by the above authors, it was decided to restrict the choice experiments to C. nemoralis feeding on Leontodon hispidus.

Forty adult C. nemoralis were collected from Wingate Quarry during August 1978. Individuals were collected and used irrespective of their shell banding and background colour. The snails were placed in circular glass dishes (diameter 15 cm and vertical sides, height 7 cm) with lids and kept in the laboratory at an even 20°C. While captive, they were fed on foliage of Hypochoeris radicata, another favoured food plant (Grime et al., 1968). The snails were then starved for 24 hrs. before use in the choice experiments.

Each choice experiment involved the presentation of three labelled samples of Leontodon hispidus leaf taken from three sites, for a period of 24 hours. The three leaves used in each experiment were selected for roughly similar size and cut neatly down the middle of the central midrib. One half of each leaf was used in the choice experiment itself; another half was dried at 105°C and weighed. At the end of the experiment, the dry weight of each half-leaf remaining was also determined. Making the assumption that both halves of the leaf are of equal dimensions and weight, it was thus possible to determine the dry weight of plant material consumed by the snail from each of the three leaves. This experiment had ten replicates and was repeated on four occasions using different C. nemoralis individuals.

From the dry weight figures for each experiment it was possible to

obtain the total amount of plant material eaten and the percentages of the total taken from each leaf. The basic palatability index used was therefore:-

$$\text{P.I.} = \frac{\text{dry weight of plant material taken from individual leaf}}{\text{total dry weight of all plant material consumed.}}$$

8.

RESULTSA. Plant Component Parts

Collections of the six plant species from the three sites were made at weekly intervals over a period lasting from 24th May to 9th August 1978. Twelve collections were therefore made, each consisting of eighteen samples (six species at three sites). Each sample in turn contained twenty (and later fifteen) individual plants.

The data on the weights of plant component parts (leaves, stems etc.) collected for each individual were converted into percentages of the total plant dry weight. The mean percentage allocated to each component part could then be calculated and plotted, cumulatively, for each weekly sample. The resultant patterns of mean dry weight allocation for the whole of each sample (i.e. representing the average for the entire population) are shown in Figures 10 to 15.

It is immediately apparent that there are fairly major intra-specific differences in the pattern of dry weight allocation when the sample is treated as a single homogenous population. With the exceptions of Carex flacca and Centaurea nigra, there are distinct differences in the pattern of dry weight allocation between the three sites. The main differences lie in the level of maximum reproductive effort achieved, the stage at which it is reached and the stage at which the growth of inflorescences starts. Reproductive effort is defined here as the percentage dry weight devoted to all reproductive organs (including buds, inflorescences and seeds).

The most marked differences in maximum reproductive effort are shown in Plantago lanceolata and Poterium sanguisorba between the quarry and grassland sites. Here the differences are 12% and 13% respectively,

representing increases of 52% and 56.5% from the grassland to the quarry site. Similar differences are shown in the times when this stage of peak reproductive effort is reached. Intervals of six and three weeks respectively between the quarry and grassland sites are shown by the above two species. Leontodon hispidus shows a corresponding difference of five weeks. Even greater differences between grassland and quarry sites are shown by the stages when production of reproductive structures first starts.

Table 2 gives a summary of the differences between the sites in these three respects. The significance of the differences between sites in terms of reproductive effort was tested using chi-square. The particular samples that gave the maximum population reproductive effort for each site (taken from Figures 10 - 15) were used for this comparison. Table 3 gives the results and a summarised ranking of the sites in terms of reproductive effort.

Four out of the six species (L. hispidus, P. lanceolata, P. media and Poterium sanguisorba) appear to follow the same rule, namely that reproductive effort is greatest in the quarry site, while the corresponding grassland populations contain plants with the smallest allocation to reproductive structures. The scrub site shows values between the other two sites.

NOTE: Most variables were recorded on an interval scale (reproductive effort, proportion of reproducing individuals etc.) but the data does not meet the normality and homoscedasticity assumptions of parametric statistical tests. The non-parametric tests used are taken from, and follow the notation of, Siegel (1956).

Carex flacca and Centaurea nigra appear to be exceptions to this pattern. The former shows a lack of significant differences between the three sites in terms of reproductive effort. C. nigra, though showing a significant difference between the three sites (in terms of reproductive effort), shows a different ordering. Lowest reproductive effort is found in the scrub site, with the grassland population occupying a mid-way position.

Although significant differences in reproductive effort between the three sites have been shown, it must be appreciated that these observations refer to the plant population of each species, taken as a whole. All the species studied are perennials and may therefore flower in some years and remain in a vegetative state in others. Completely random sampling of the population means that estimates of reproductive effort will be biased by inclusion of those individuals that do not flower at all. Although this is a good measure of the regenerative effort of the population as a whole, it is very different from the percentage of resources devoted to production on an individual scale.

Data collected (from both field observation and laboratory-analysed samples) on flowering stage (measured on a 0-8 ordinal scale) was used to show what proportion of the plant population actually attempts to reproduce. The data was divided into those individuals that remain in the vegetative state (coded 0) and those that exhibit some sort of reproductive structure (coded 1 to 8). Histograms for each sampling stage are shown in Figure 16.

As expected with perennials, a substantial percentage of the population in any one year remains in a vegetative state. There are, however, differences between the sites in terms of what proportion of the population attempts to flower. The significance of these differences

was tested using the Friedman two-way analysis of variance, the results of which are given with each graph. The three sites were treated together since the purpose was to demonstrate whether overall differences exist.

The results of the test show that the percentage of the population that attempts to flower does vary between the three sites for five out of six species. The five species that follow this pattern all show that the greatest percentage of plants in the vegetative state are found in the grassland habitat. The quarry habitat, at the other extreme, contains relatively few individuals that do not attempt to flower. The scrub site, located, in this respect, between the other two, contains roughly equal percentages of individuals from both sub-populations (the flowerers and non-flowerers). Carex flacca, the only exception, appears to be remarkably consistent in terms of resources allocated to reproduction generally, since it shows no difference between sites in terms of component parts or the percentage that produce a flowering spike.

The results so far suggest that differential reproductive effort between sites at the population level is chiefly explained by the differences in the proportion of the population that actually attempt to flower. Those individuals that do produce inflorescences or buds form a discrete sub-sample of the population.

Treating this sub-sample separately, the mean reproductive effort has been plotted against the mean total dry weight, for each weekly sample taken. Approximate boundary lines have been drawn to enclose those areas which include means from the same site. (Figure 17).

The positions of boundaries suggest that mean reproductive effort does not vary between sites. The differences between the three sets of means were tested using the Friedman two way analysis of variance

(with two degrees of freedom). This showed that the levels of reproductive effort for each species were statistically the same for all three populations.

As expected, the total dry weight means vary between the three sites, the significance of which was tested using the same statistic as above. The χ^2 values and the significance levels for both tests are given underneath each graph.

Significant differences in total dry weight were found for all species except Carex flacca. The order of increasing plant dry weight was the same (grassland-scrub-quarry) for four species, Centaurea nigra, Leontodon hispidus, Plantago media and Poterium sanguisorba. Differences between the grassland and scrub sites were less marked than between the scrub and quarry sites. Plantago lanceolata showed a different ordering (grassland-quarry-scrub), which reflects a reduced vigour in the open, disturbed quarry habitat.

Figures 10-15 (and Table 2 in summary) show that differences in the time of peak flowering are often quite large between populations of the same species. Though the overall phenology of flowering appears similar, sample populations from the three sites are often out of phase with one another. In order to test whether this asynchrony was significant or not, use was made of data collected (from both field observations and laboratory-analysed samples) on flowering stage, measured on a 0-8 ordinal scale (for summary see section 6). The means for each sub-sample, plotted against time (Figures 18-23) were compared between sites using the Wilcoxon matched-pairs signed-ranks test.

L. hispidus, P. lanceolata, P. media and P. sanguisorba all show that samples from the quarry site are significantly advanced, in terms of the flowering cycle, in relation to the other two habitats. All

four species show statistically synchronous grassland and scrub populations, despite the marginally earlier flowering (one week) of three scrub samples. C. flacca and C. nigra are slightly different in that they indicate that all three populations are in synchrony in this respect.

From the above findings, it appears that individual allocation of plant resources to reproductive structures does not vary between sites, even though the timing of the flowering cycle in one site may not be in synchrony with that in another. The marked differences in reproductive effort of the population treated as a whole appear to be due to varying percentages of the plant population indulging in flowering. It is thus pertinent to inquire as to what mechanism or factors control whether, in any one year, an individual commits itself to flowering and seed production or remains in a vegetative state. Does an individual have to attain a particular leaf-weight before it can attempt to flower? Is there, in fact, a critical threshold (which may vary between environments) below which individuals will never flower?

To test this hypothesis, individual plants from a single sample were plotted on a "percentage reproductive effort - total leaf dry weight" graph (Figure 24). The particular sample chosen in each case was the one which gave the maximum population reproductive effort (taken from Figures 10 to 15). The broad scatter of points in each case shows that there is no relationship between these two variables at an individual level. The two subsamples (of flowering and non-flowering individuals) overlap considerably in terms of leaf dry weight. Regression lines have not been fitted as these would give spurious correlations, which would not be significant.

FIGURE 10 A.

PLANT COMPONENT PARTS.

CAREX FLACCA QUARRY SITE

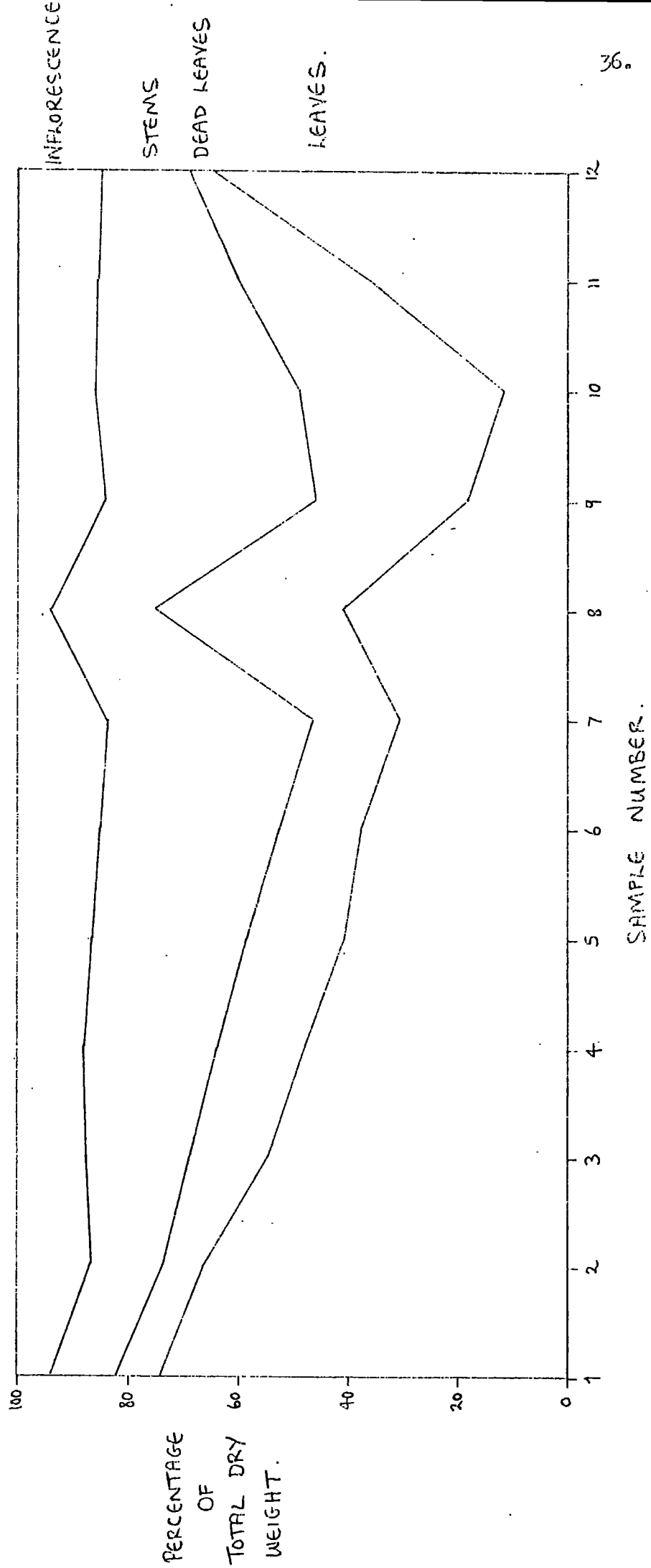


FIGURE 10 B. PLANT COMPONENT PARTS.

CAREX FLACCA.

GRASSLAND SITE.

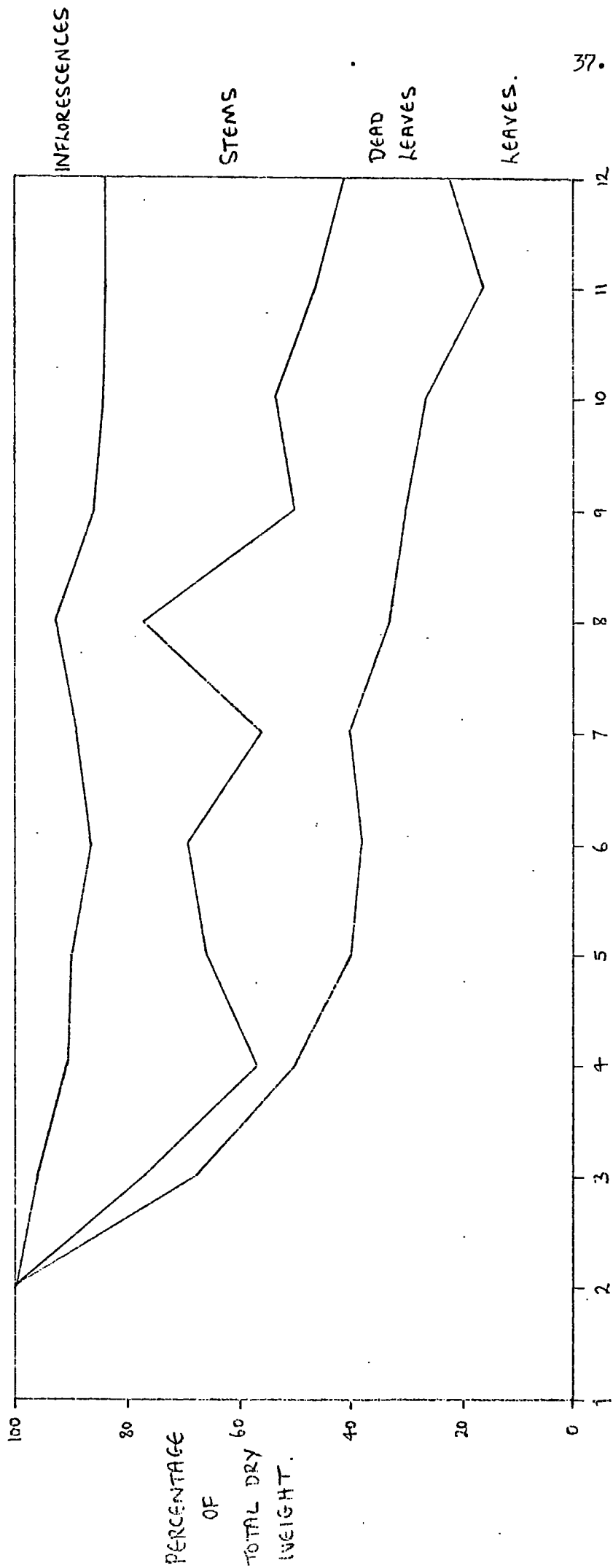


FIGURE 10 C. PLANT COMPONENT PARTS

CAREX FLACCA.

SCRUB SITE.

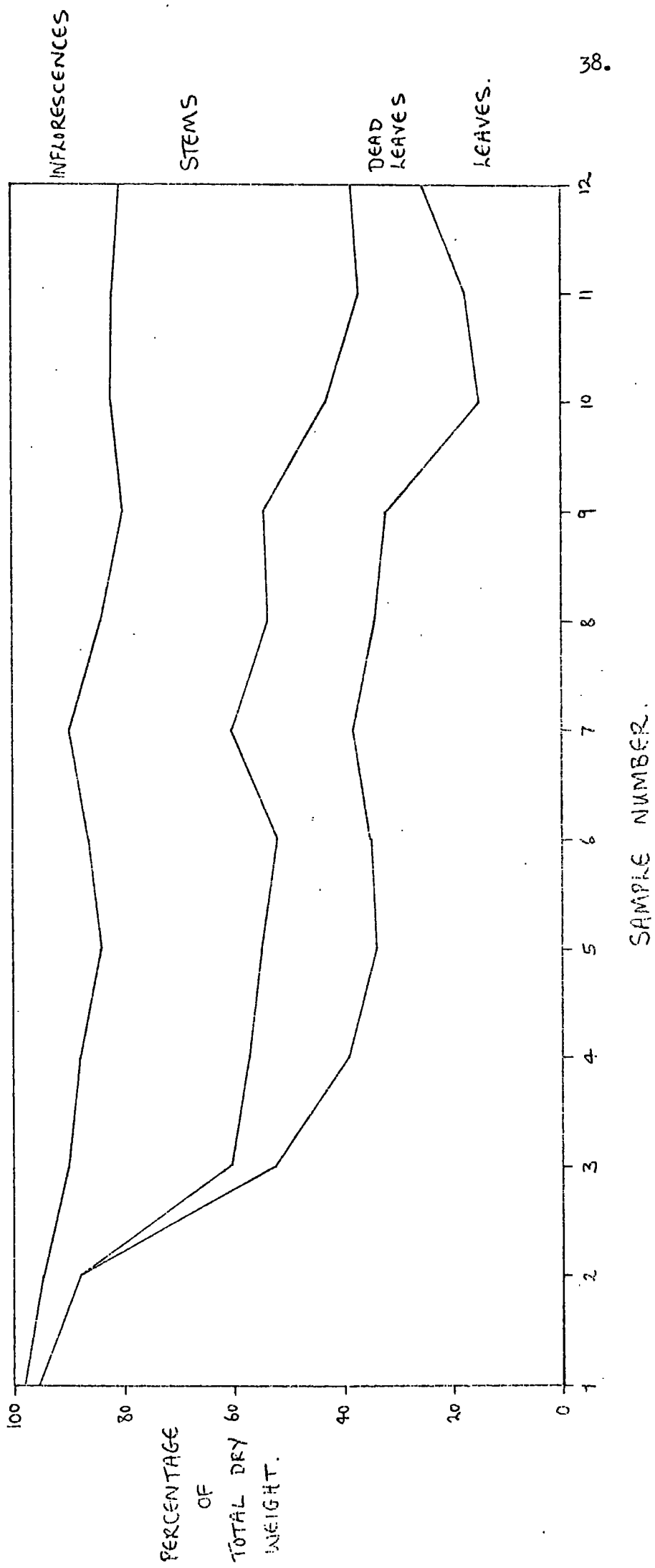


FIGURE 11 A.

PLANT COMPONENT PARTS

CENTAUREA NIGRA.

QUARRY SITE.

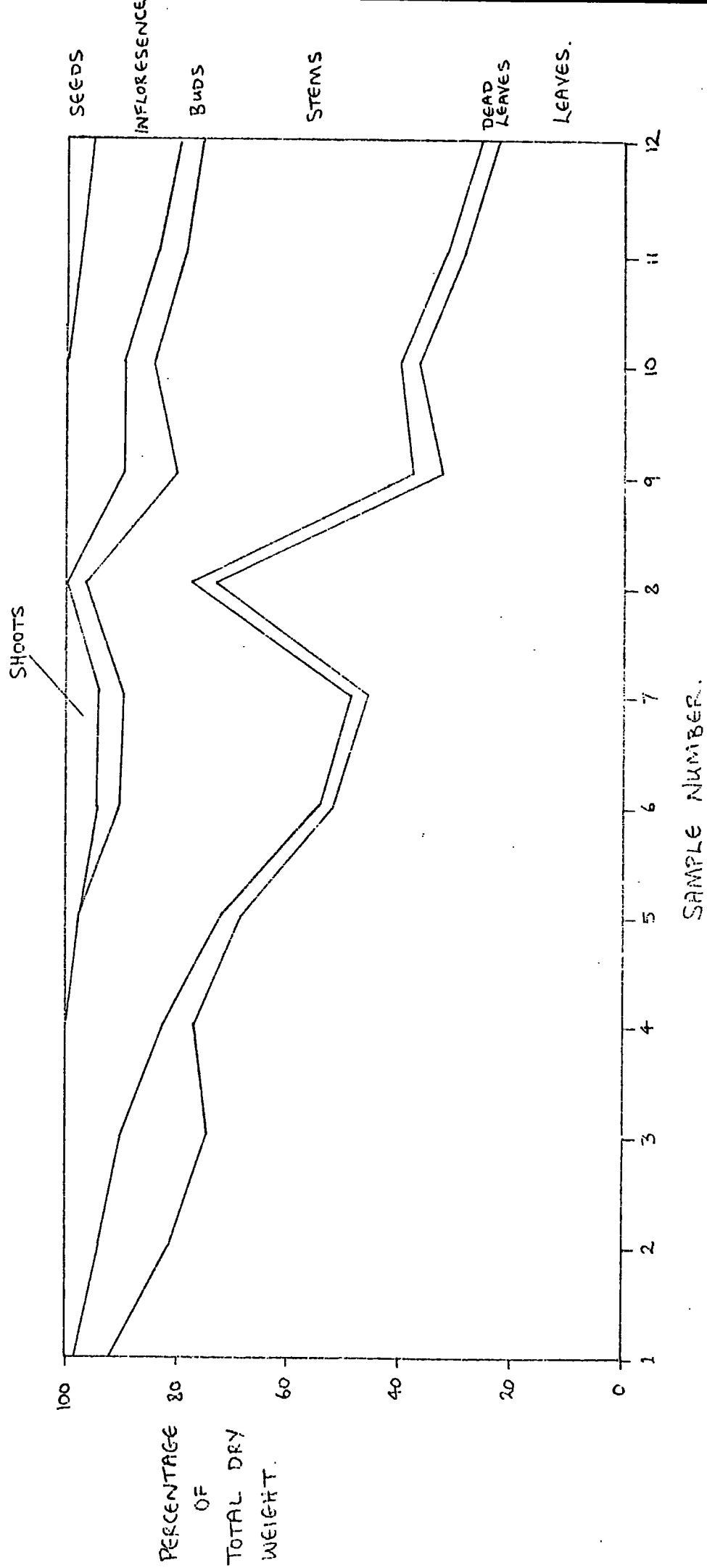
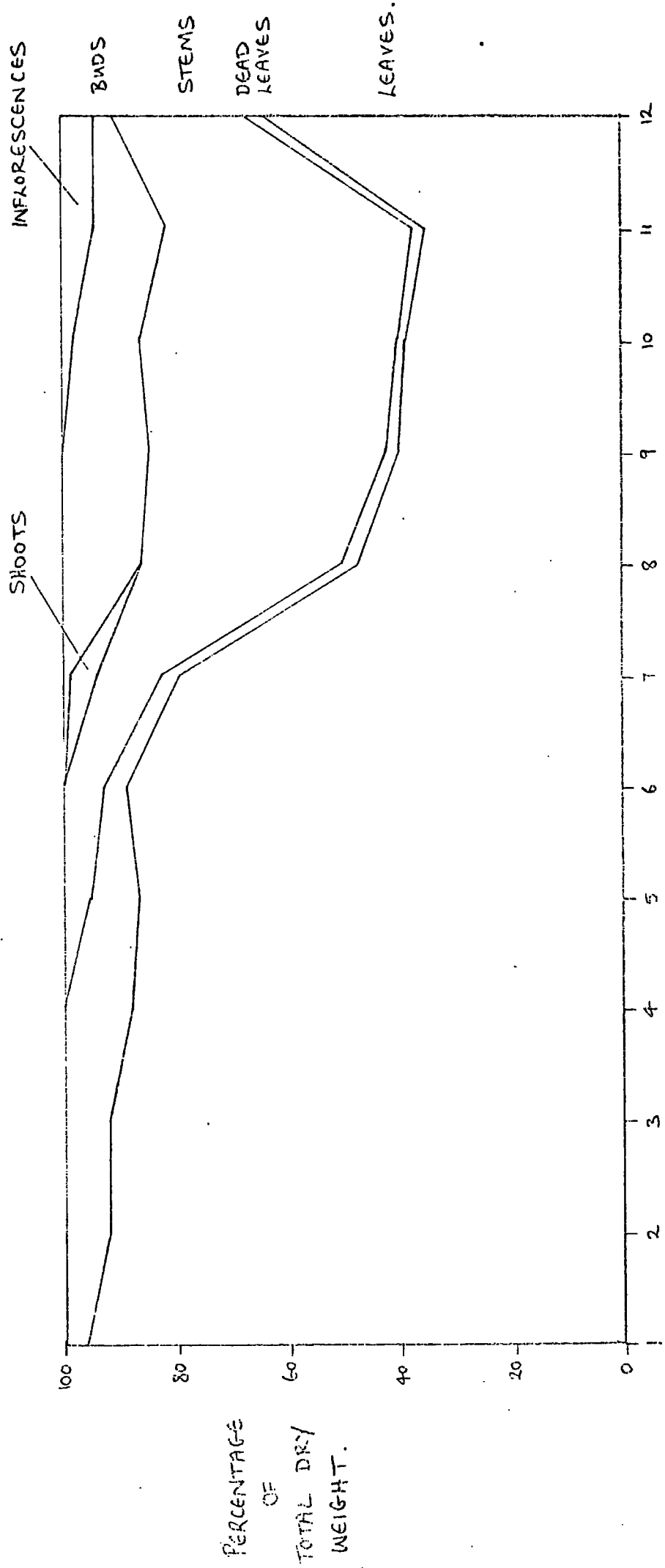


FIGURE 11 B PLANT COMPONENT PARTS

CENTAREA NIGRA.

GRASSLAND SITE.



PERCENTAGE
OF
TOTAL DRY
WEIGHT.

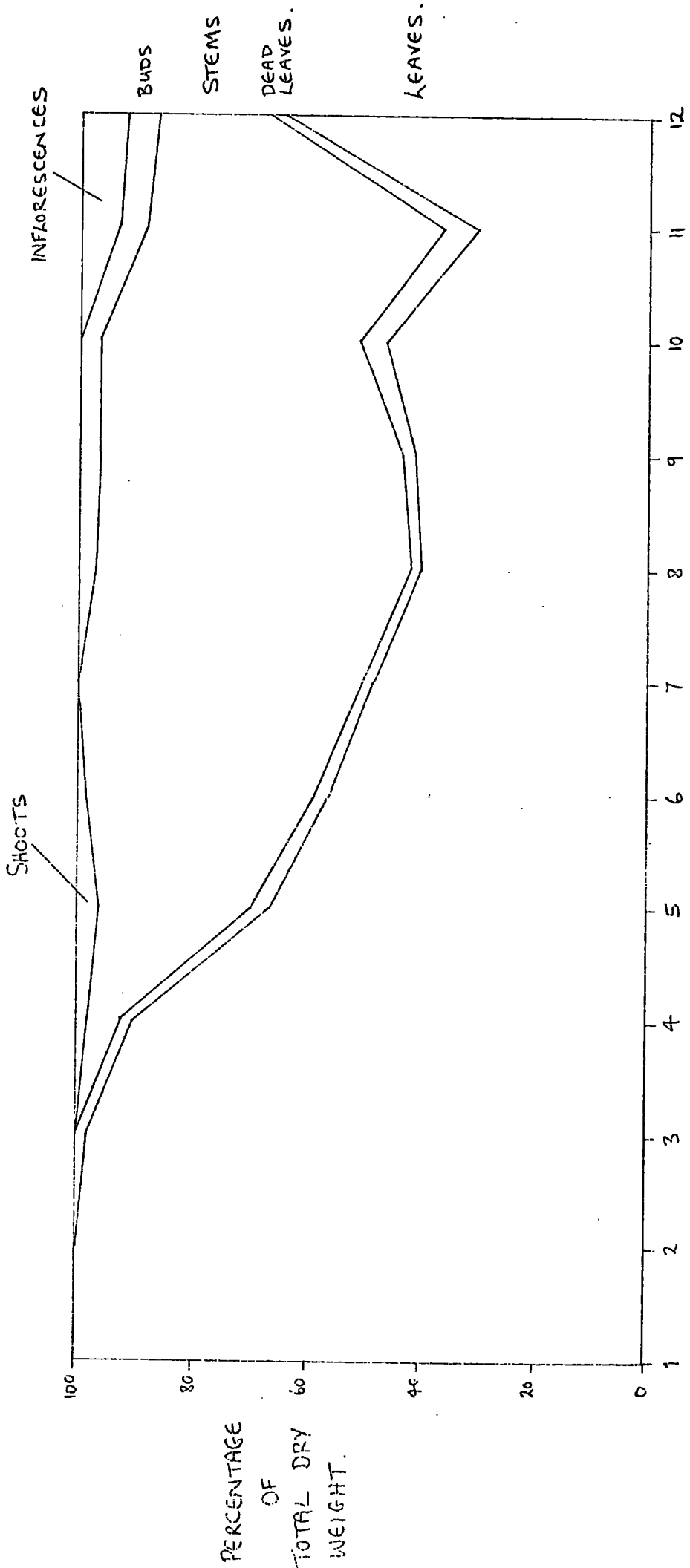
SAMPLE NUMBER.

FIGURE 11 C.

PLANT COMPONENT PARTS

CENTAUREA NIGRA.

SCRUB SITE.



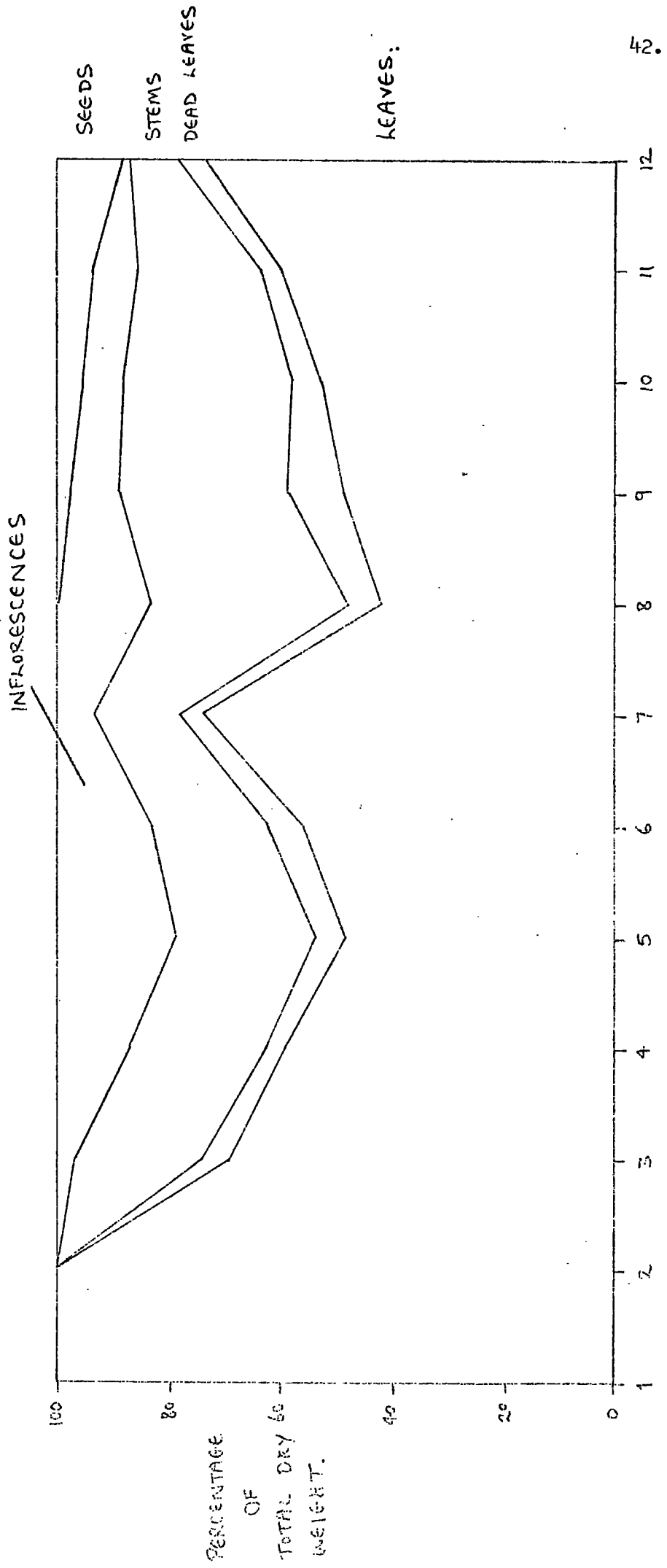
SAMPLE NUMBER.

FIGURE 12 A.

PLANT COMPONENT PARTS.

LEONTODON HISPIDUS.

QUARRY SITE.



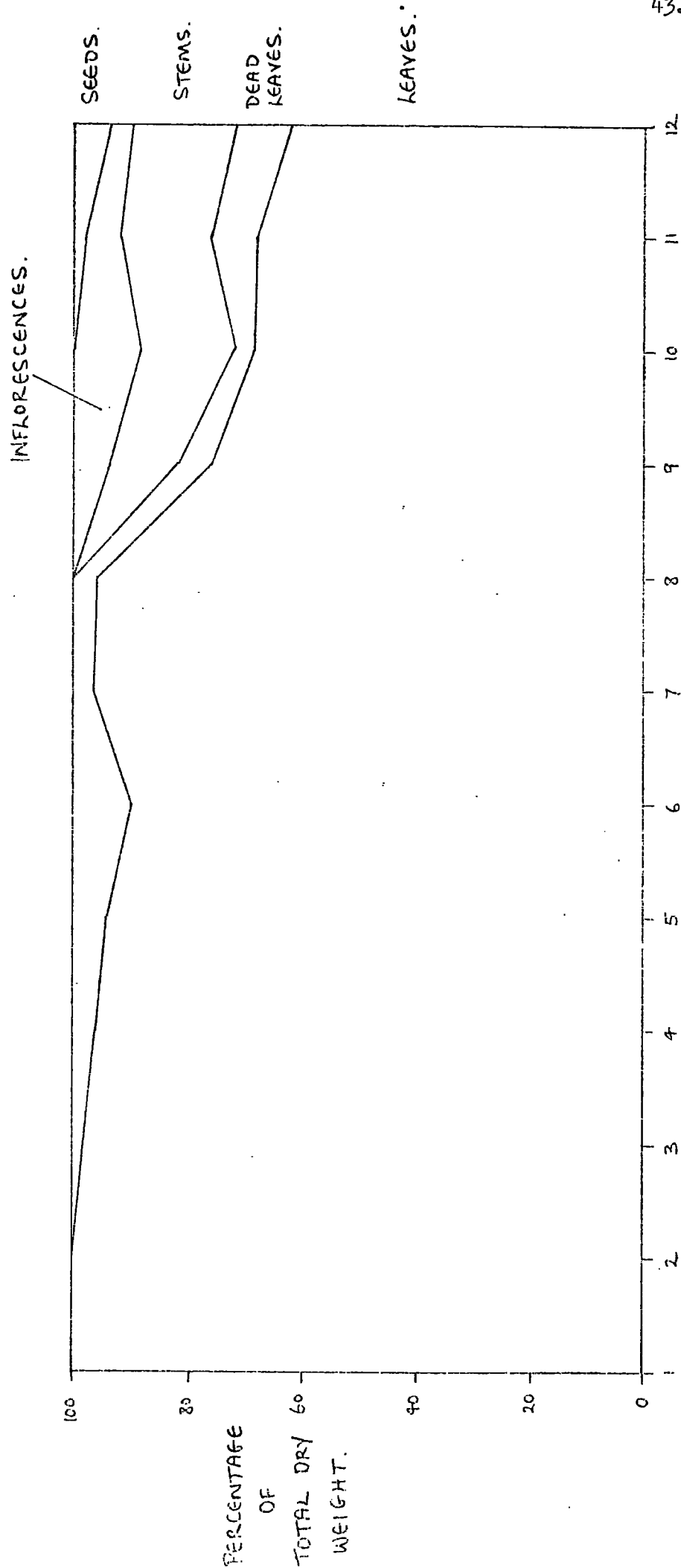
SAMPLE NUMBER.

FIGURE 12 B.

PLANT COMPONENT PARTS.

LEONTODON HISPIDUS

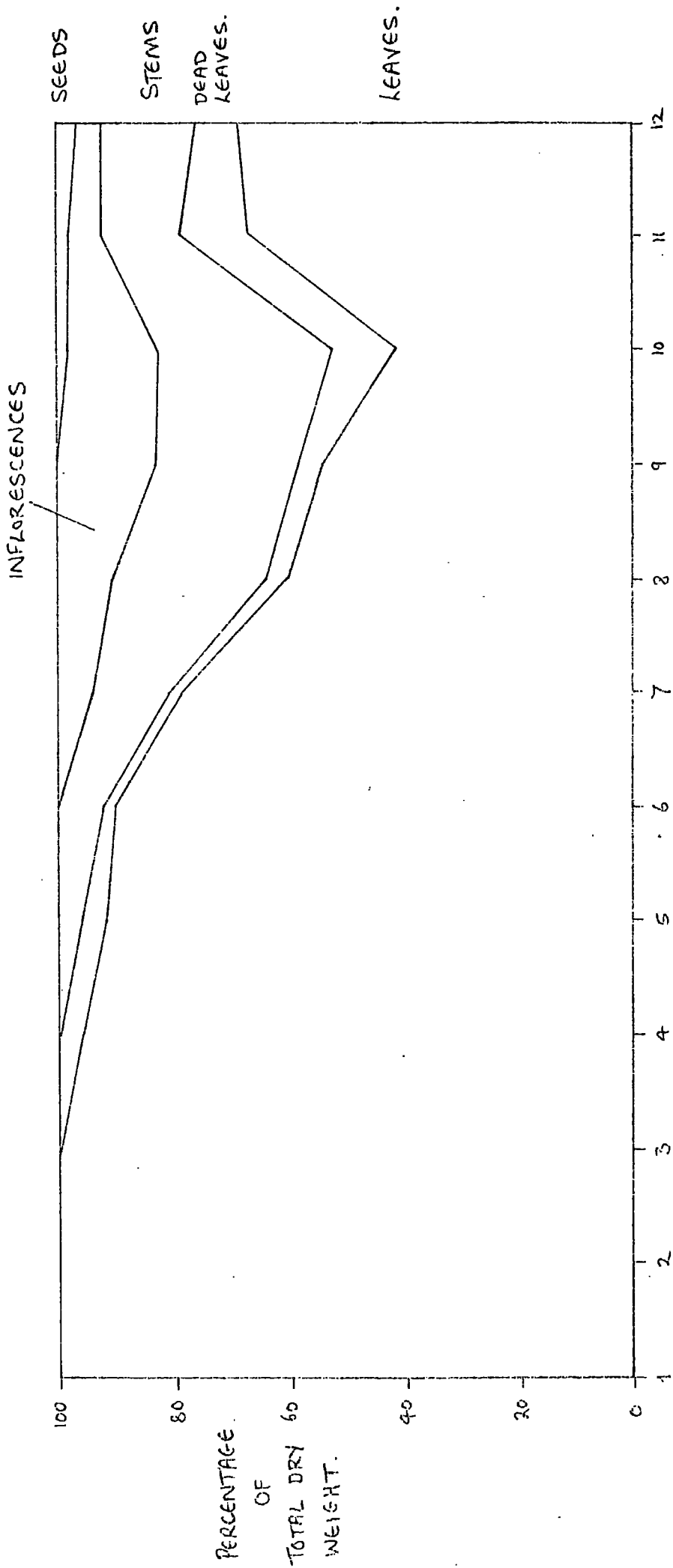
GRASSLAND SITE.



SAMPLE NUMBER.

FIGURE 12. C. PLANT COMPONENT PARTS.

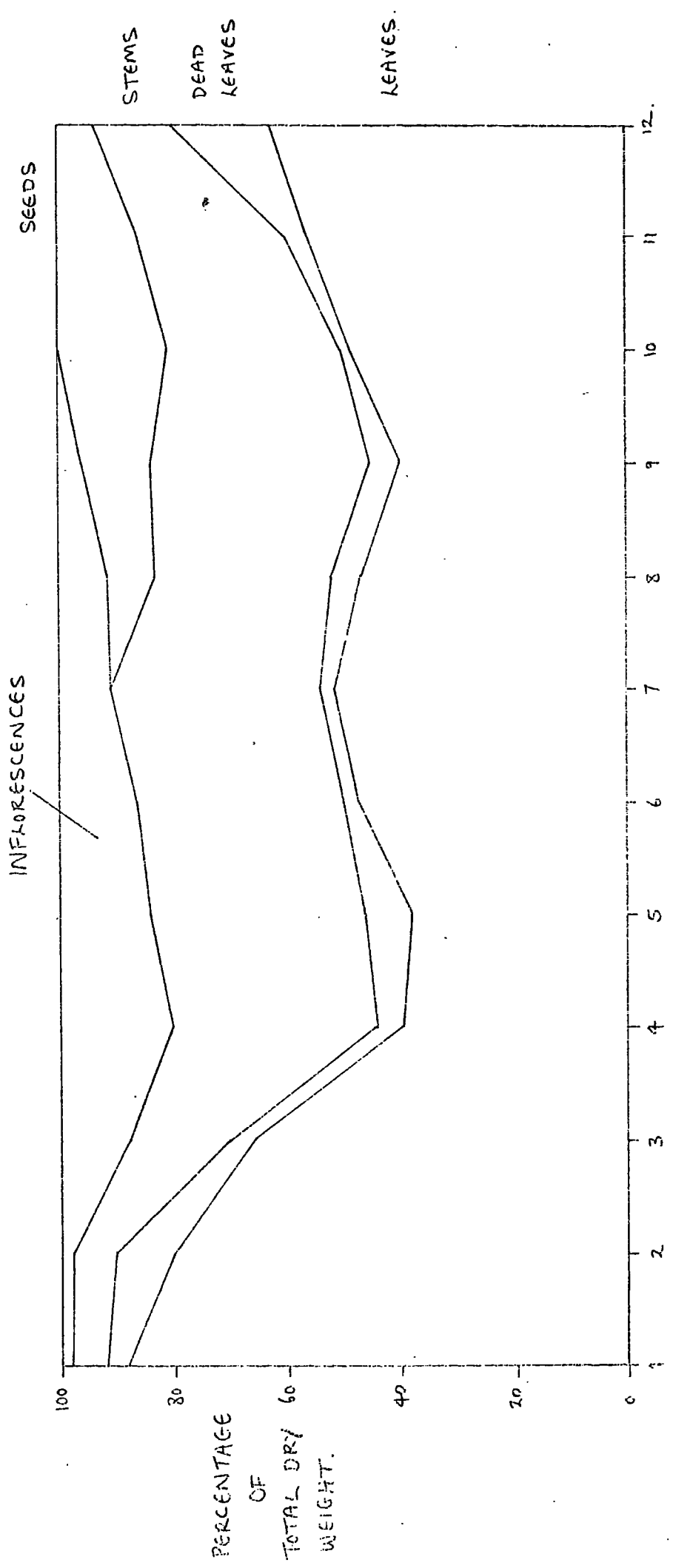
LEONTODON HISPIDUS SCRUB SITE.



SAMPLE NUMBER.

FIGURE 13 A. PLANT COMPONENT PARTS.

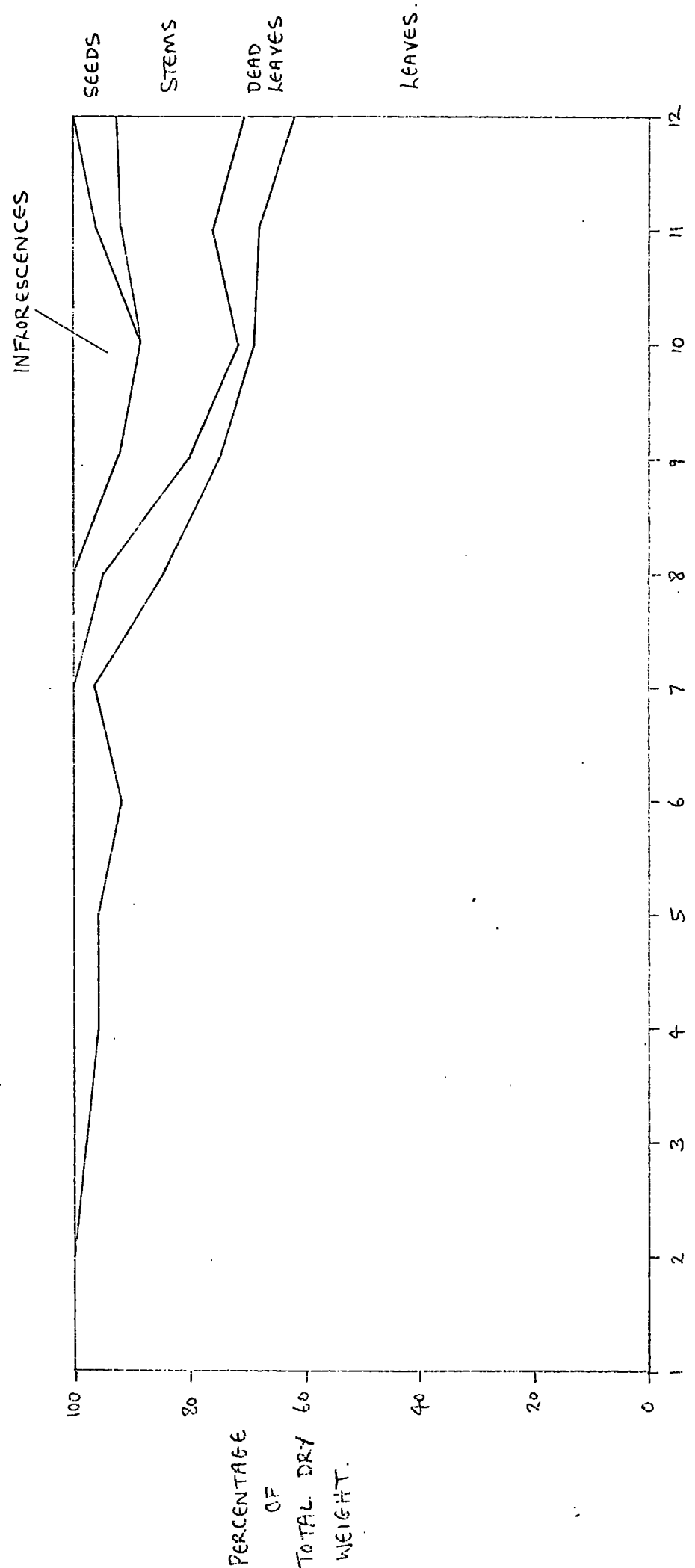
PLANTAGO LANCEOLATA. QUARRY SITE



SAMPLE NUMBER.

FIGURE 13 B. PLANT COMPONENT PARTS.

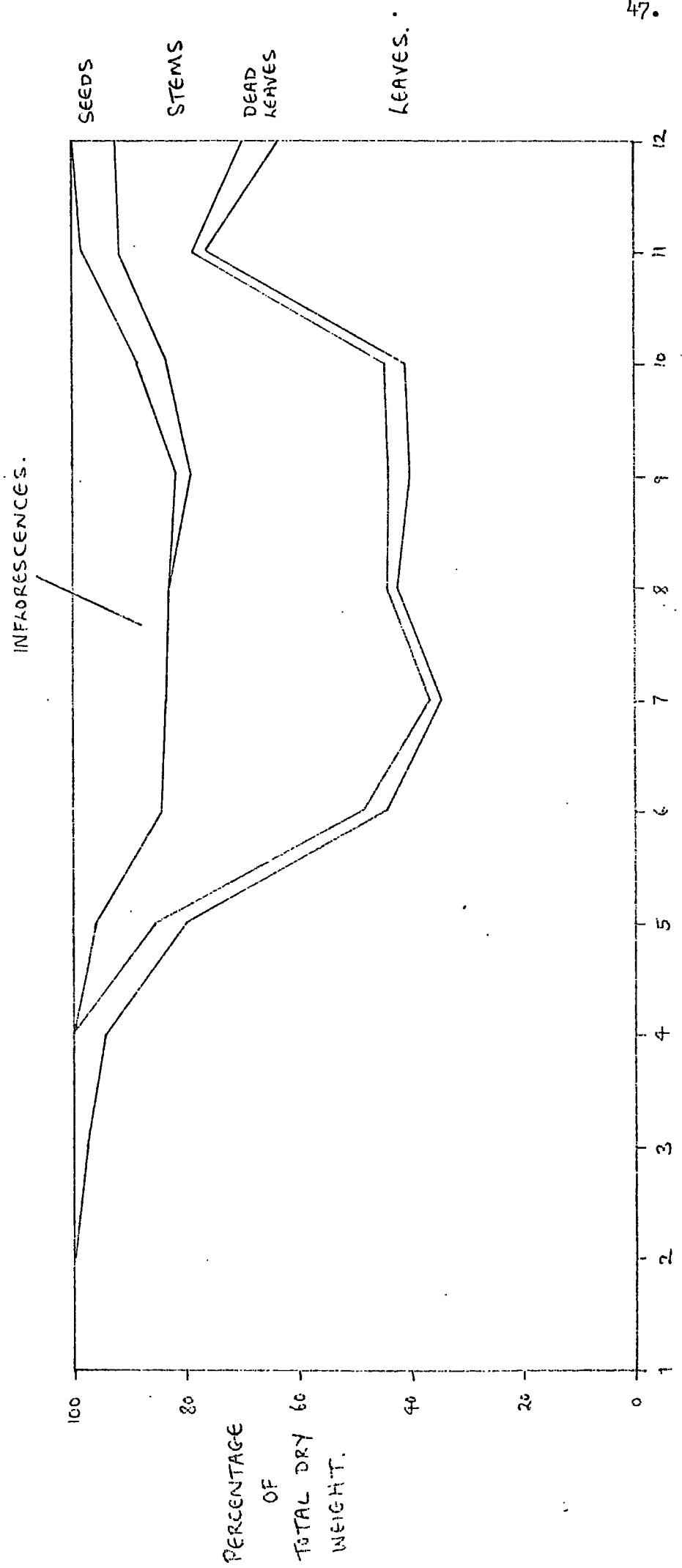
PLANTAGO LANCEOLATA. GRASSLAND SITE.



SAMPLE NUMBER.

FIGURE 13 C. PLANT COMPONENT PARTS.

PLANTAGO LANCEOLATA. SCRUB SITE.



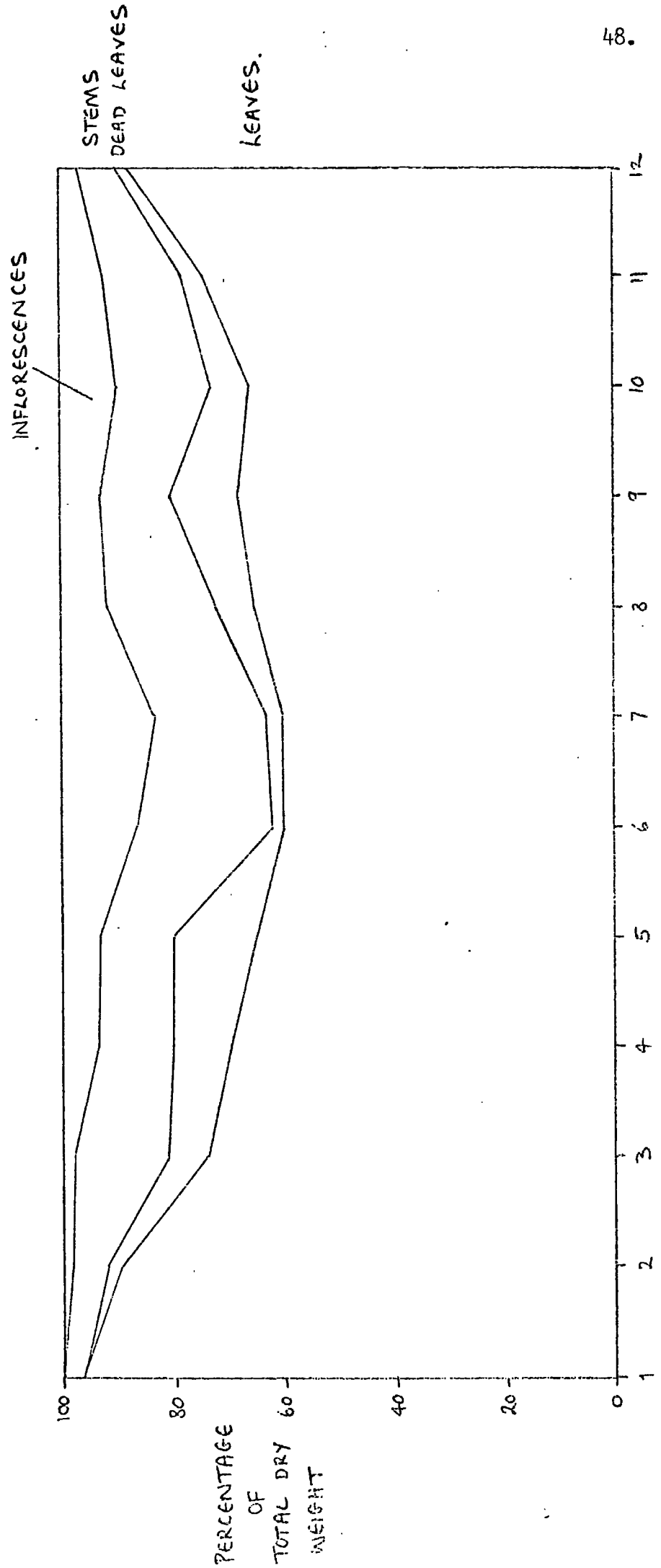
SAMPLE NUMBER

FIGURE 14 A.

PLANT COMPONENT PARTS.

PLANTAGO MEDIA

QUARRY SITE



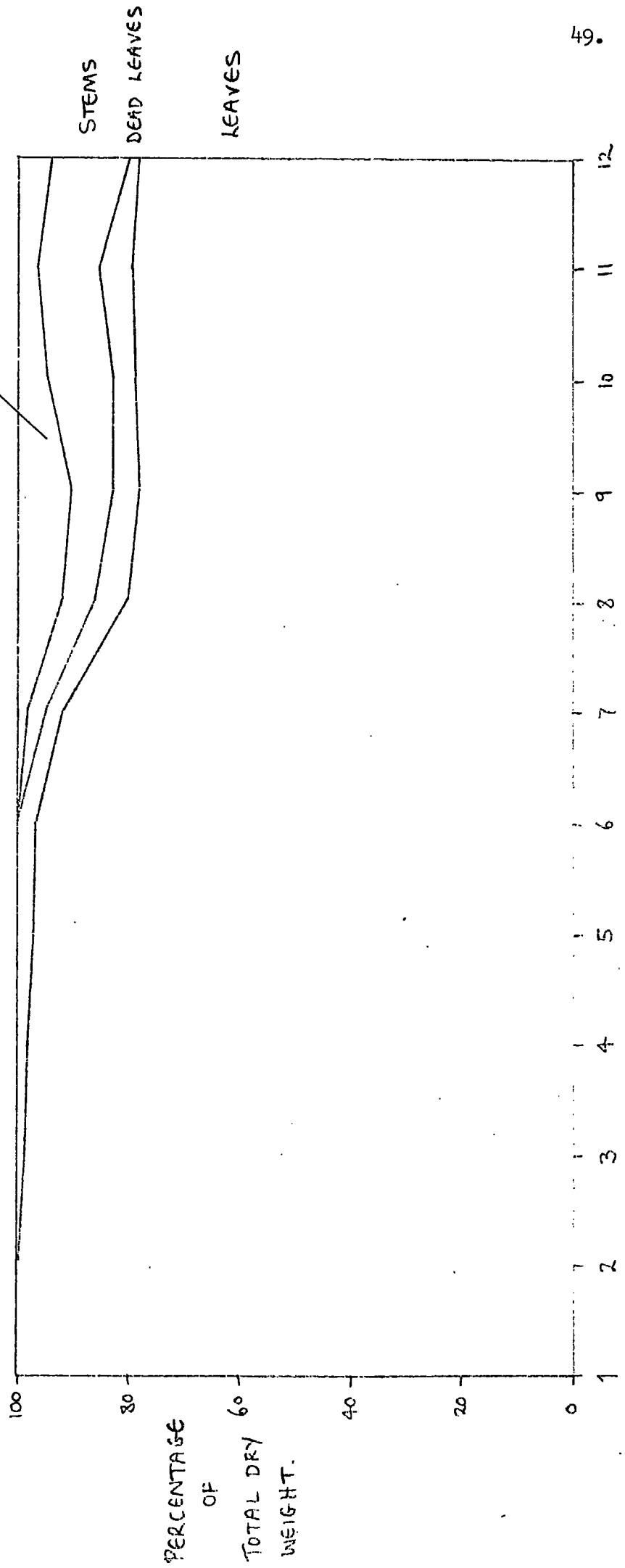
SAMPLE NUMBER.

FIGURE 14 B.

PLANT COMPONENT PARTS.

GRASSLAND SITE

PLANTAGO MEDIA



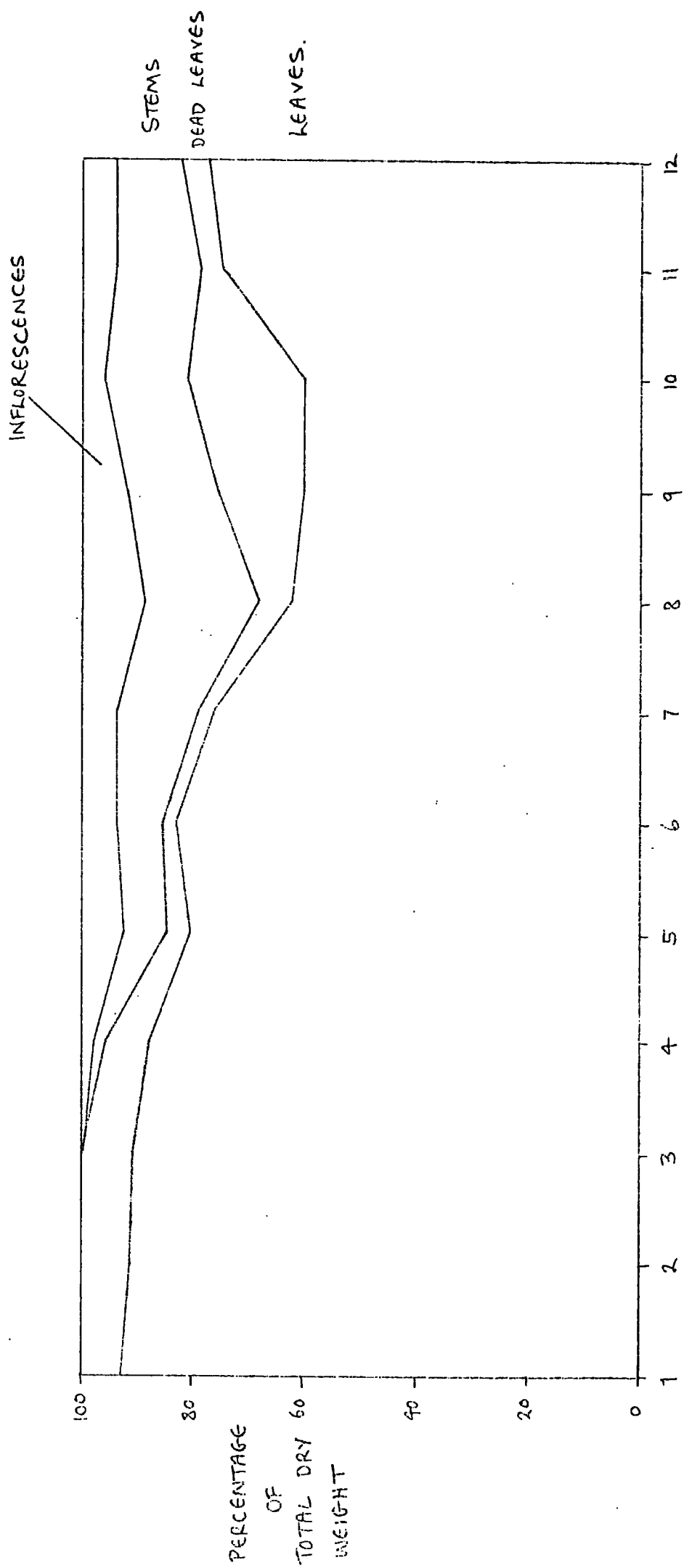
SAMPLE NUMBER.

FIGURE 14 C.

PLANT COMPONENT PARTS.

PLANTAGO MEDIA

SCRUB SITE.



SAMPLE NUMBER.

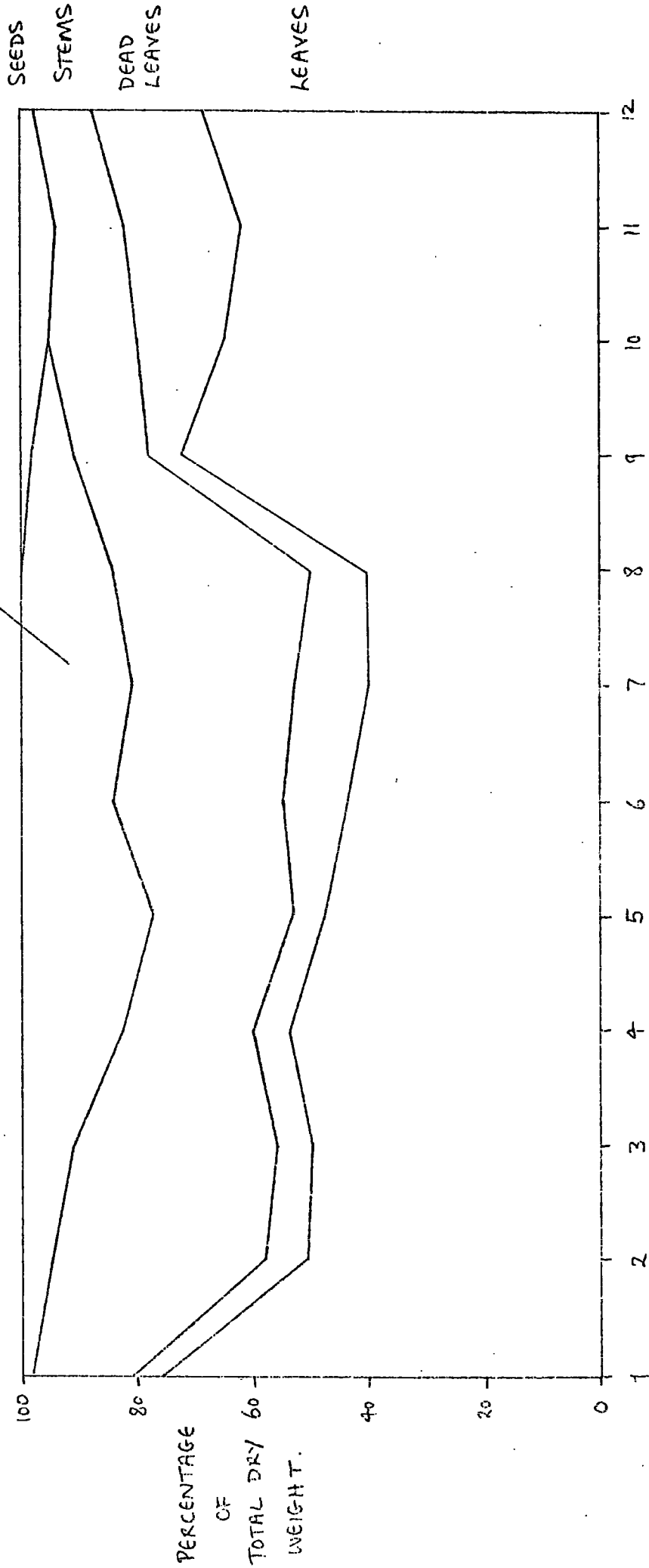
FIGURE 15 A.

PLANT COMPONENT PARTS.

POTERIUM SANGUISORBA

QUARRY SITE

INFLORESCENCES



SAMPLE NUMBER.

FIGURE 15 B. PLANT COMPONENT PARTS.

POTERIUM SANGUISORBA. GRASSLAND SAMPLE.

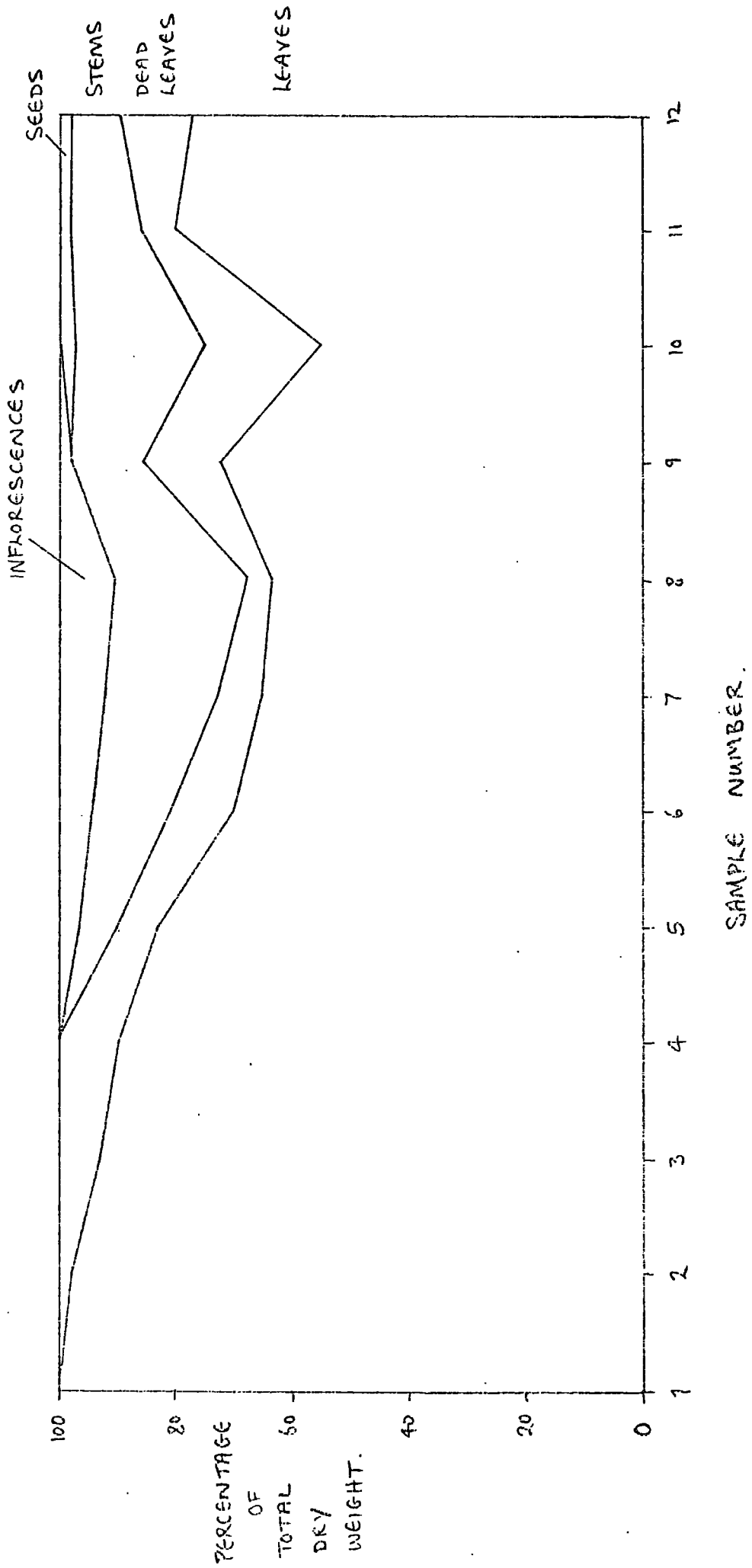
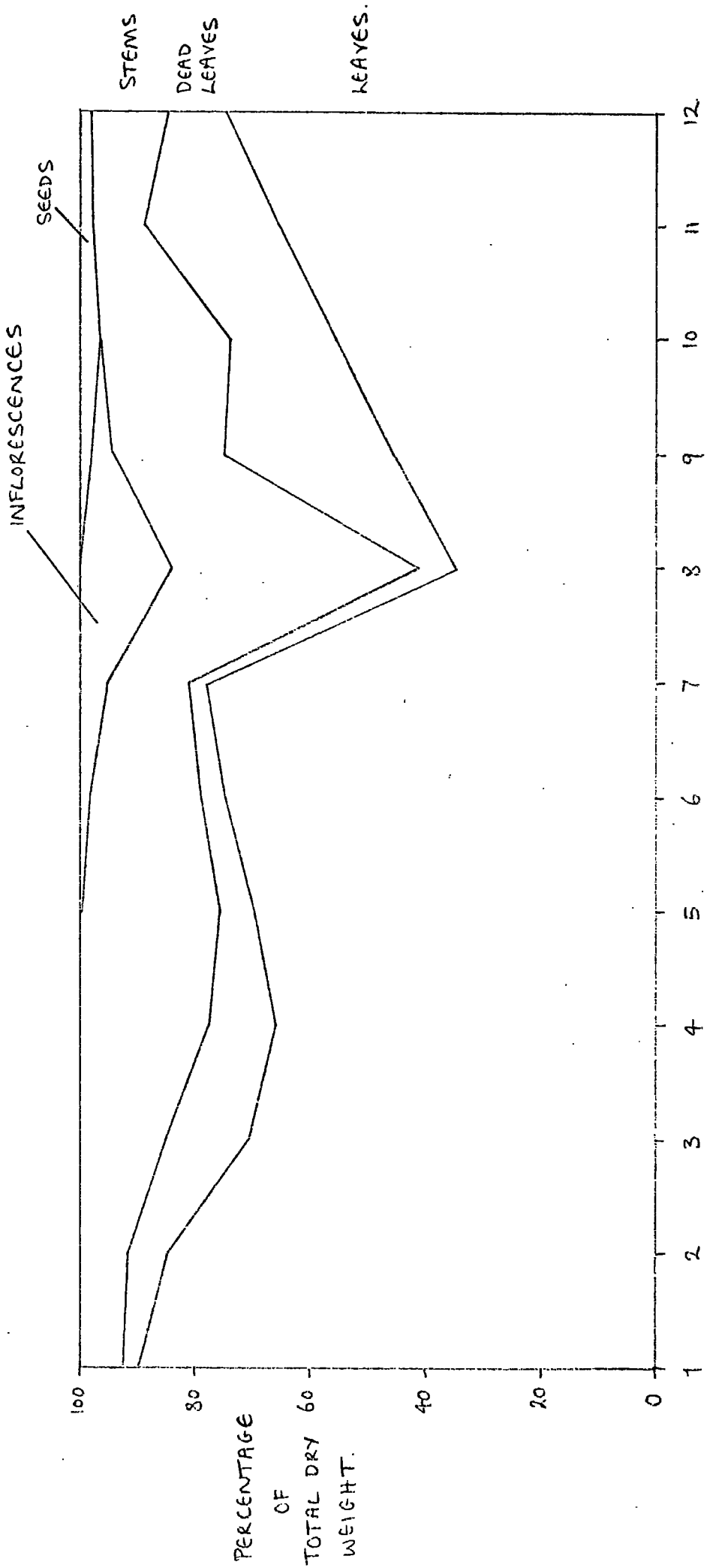


FIGURE 15 C.

PLANT COMPONENT PARTS.

POTERIUM SANGUISORBA

SCRUB SITE.



SAMPLE NUMBER.

TABLE 2Comparison of sites with respect to reproductive effort.

Species	Site	Maximum reproductive effort	Peak reproductive stage (sample number)	Start of reproductive effort (sample number)
Carex flacca	Q	16%	7	1
	G	16%	10	3
	S	19%	9	1
Centaurea nigra	Q	24%	12	9
	G	18%	11	7
	S	14%	12	11
Leontodon hispidus	Q	21%	5	3
	G	11%	10	9
	S	17%	9	7
Plantago lanceolata	Q	23%	4	1
	G	11%	10	9
	S	21%	9	5
Plantago media	Q	17%	7	2
	G	10%	9	7
	S	11%	8	4
Poterium sanguisorba	Q	23%	5	1
	G	10%	8	5
	S	16%	8	1

Note: Q, G, and S refer to quarry, grassland and scrub samples respectively.



Table 3CHI-SQUARE TEST ON DIFFERENCES IN REPRODUCTIVE EFFORT BETWEEN SITES

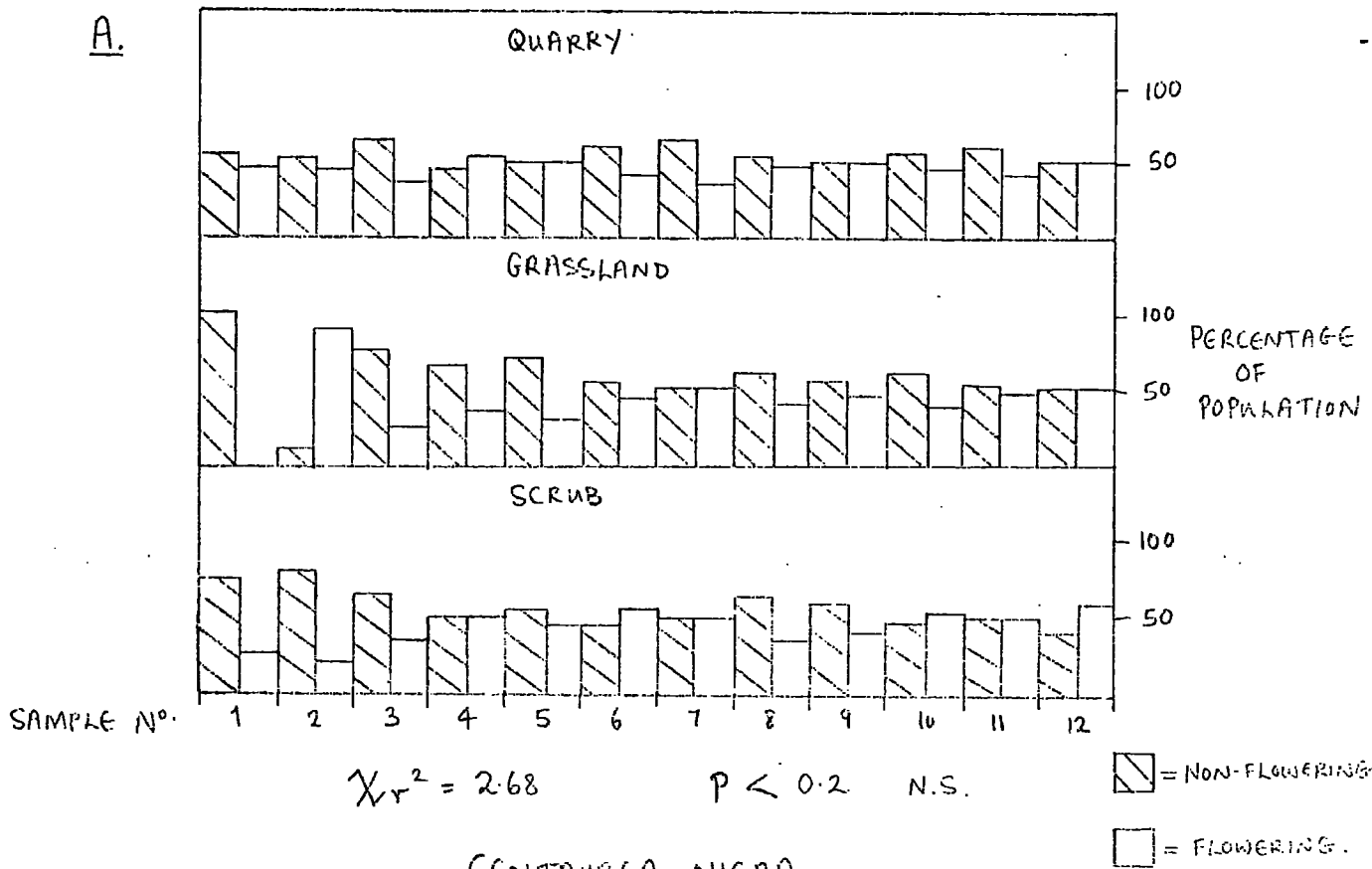
<u>Species</u>	<u>Chi-squared value</u>	<u>Significance level</u>
Carex flacca	16.2	N.S.
	Site ranking: Q = G = S	
Centaurea-nigra	46.8	P < 0.05
	Site ranking: Q > G > S	
Leontodon hispidus	68.7	P < 0.01
	Site ranking: Q > S > G	
Plantago lanceolata	49.4	P < 0.05
	Site ranking: Q > S > G	
Plantago media	51.0	P < 0.05
	Site ranking: Q > S > G	
Poterium sanguisorba	64.1	P < 0.01
	Site ranking: Q > S > G	

NOTE: ">" signs denote that the first site has a greater population reproductive effort than the second site (after the "greater-than" symbol).

PERCENTAGE OF POPULATION FLOWERING.

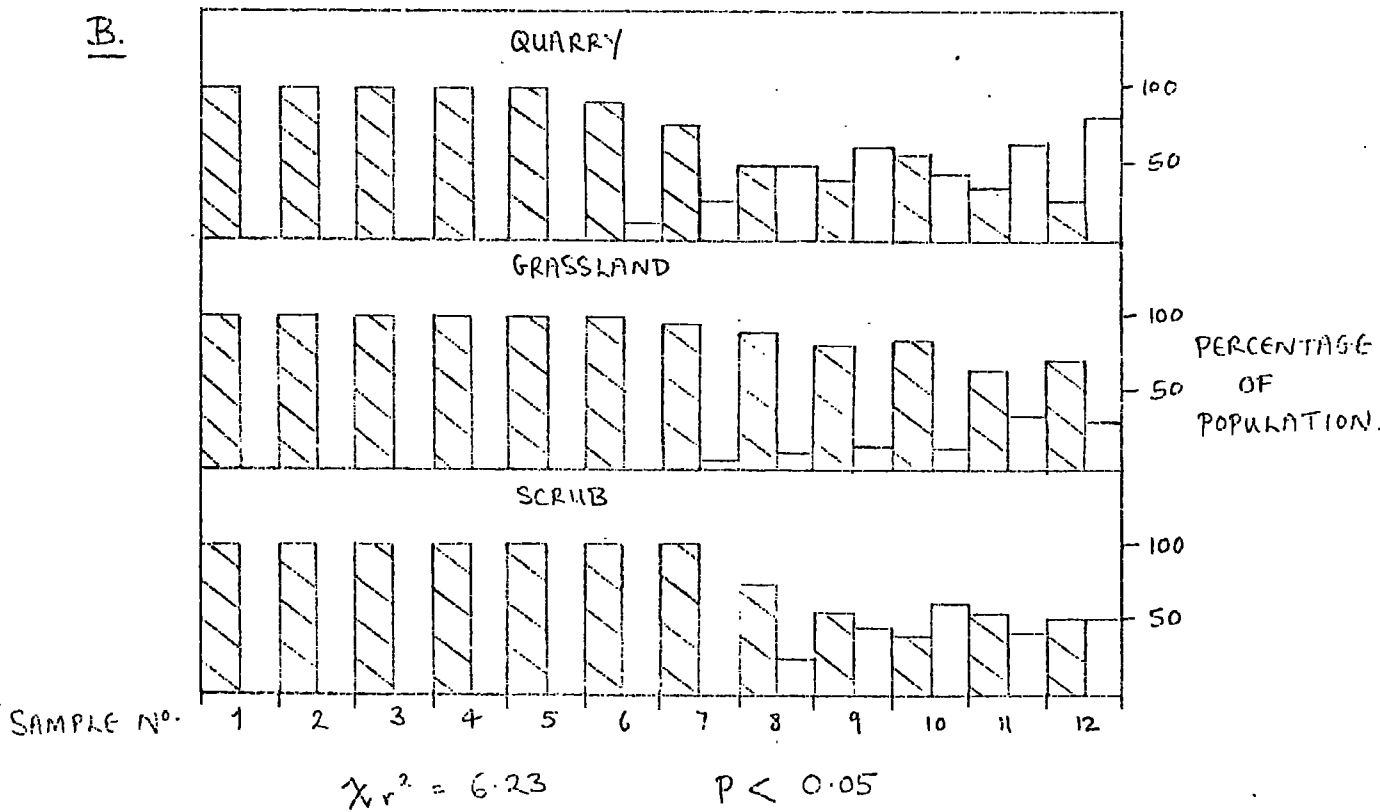
CAREX FLACCA

A.



CENTAUREA NIGRA

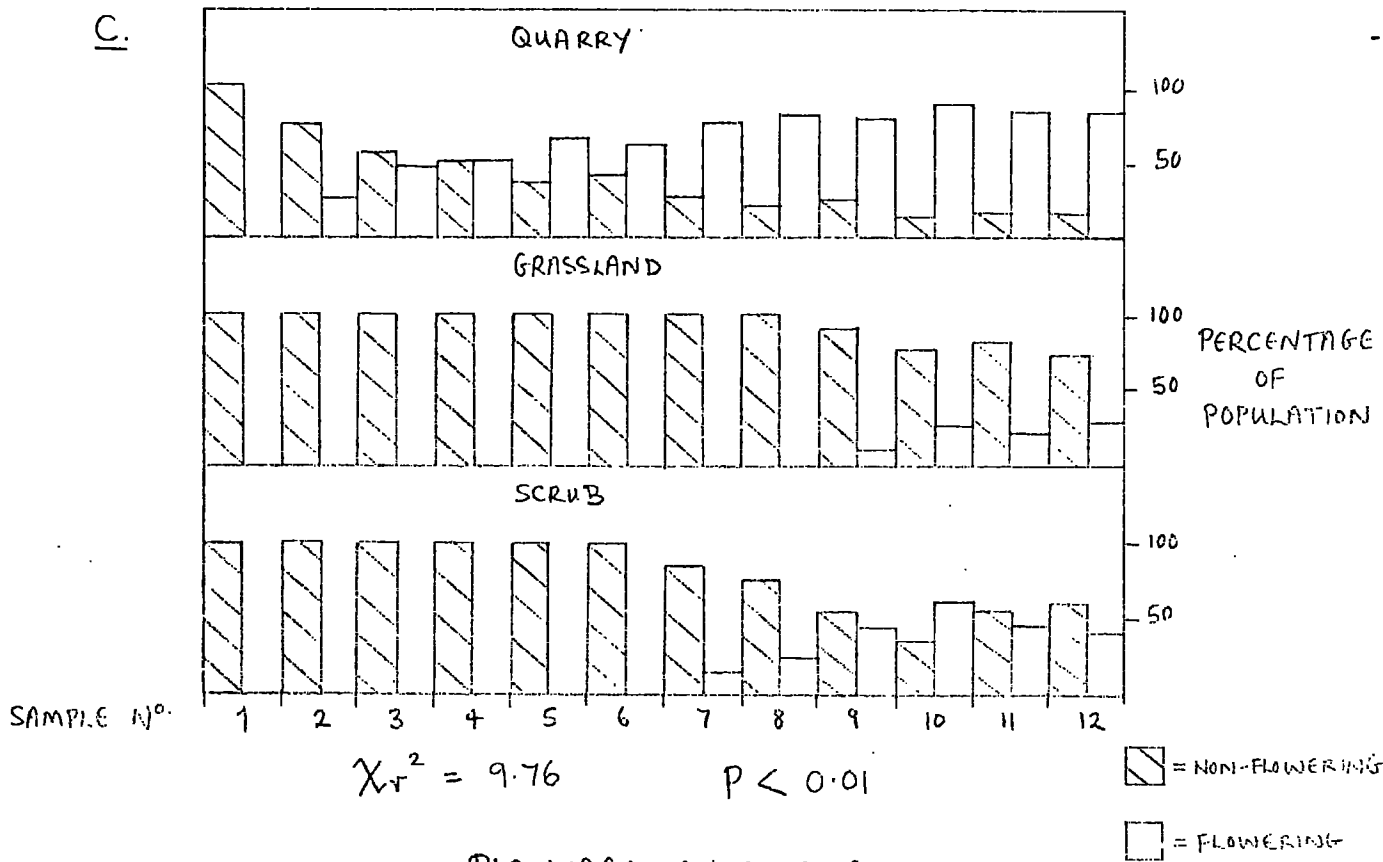
B.



PERCENTAGE OF POPULATION FLOWERING.

LEONTODON HISPIDUS

C.



PLANTAGO LANCEOLATA

D.

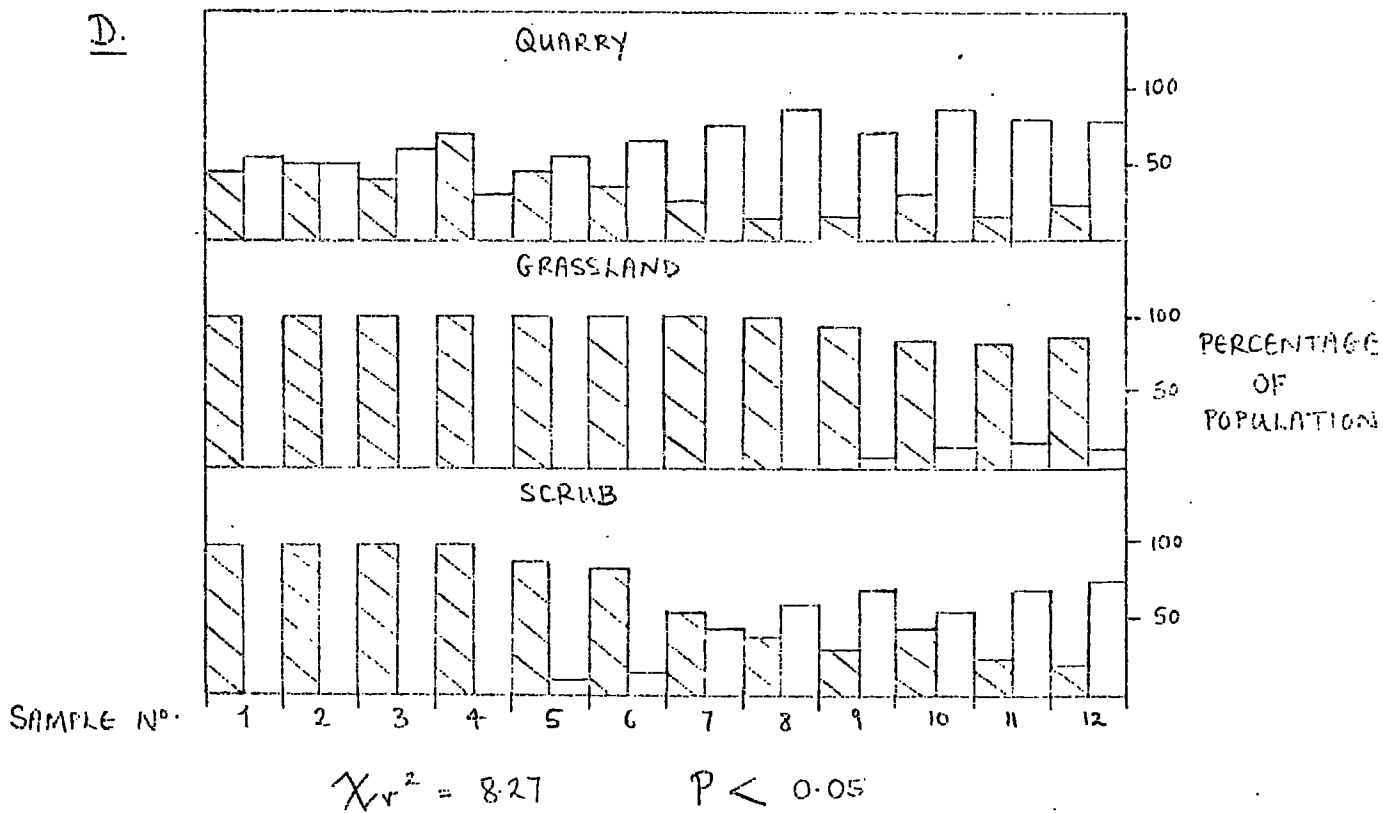
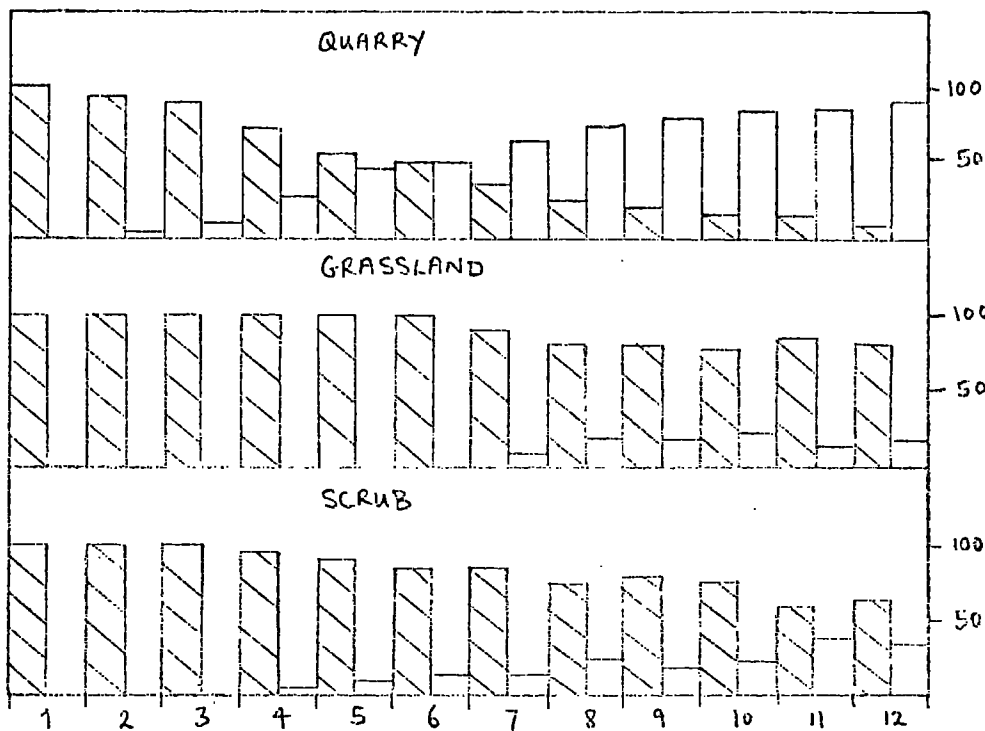


FIGURE 16 (CONT.)

PERCENTAGE OF POPULATION FLOWERING

PLANTAGO MEDIA

E.



PERCENTAGE OF POPULATION

SAMPLE N^o.

$\chi^2 = 10.74$

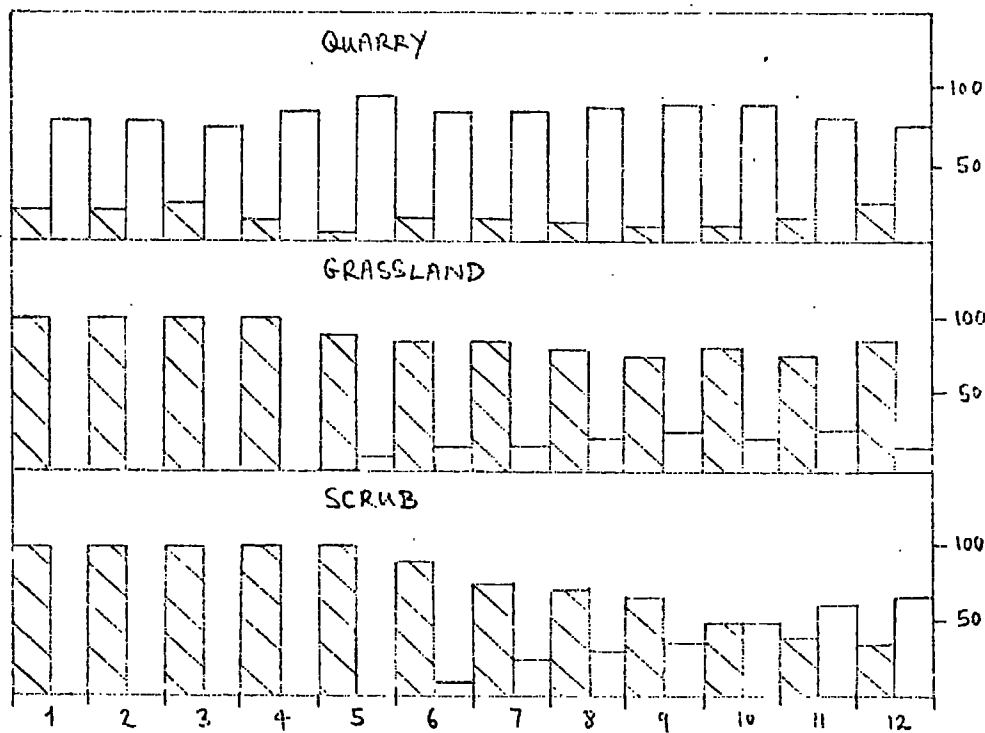
$P < 0.01$

▨ = NON-FLOWERING

□ = FLOWERING

POTERIUM SANGUISORBA

F.



PERCENTAGE OF POPULATION

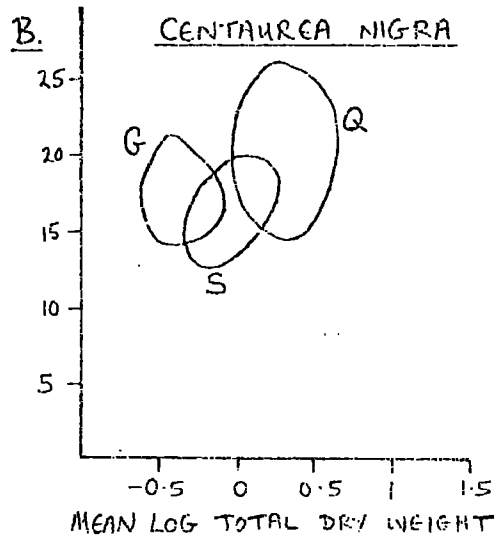
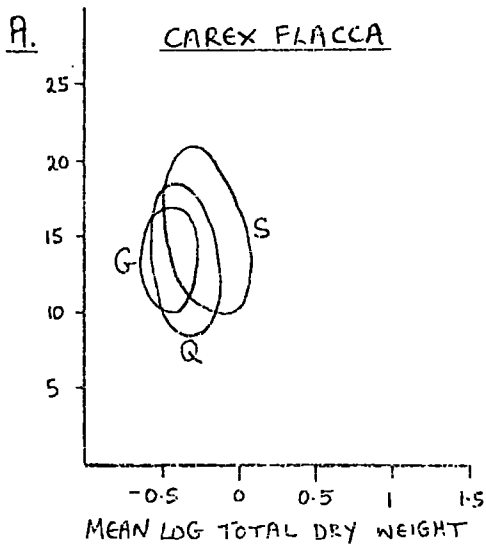
SAMPLE N^o.

$\chi^2 = 11.05$

$P < 0.01$

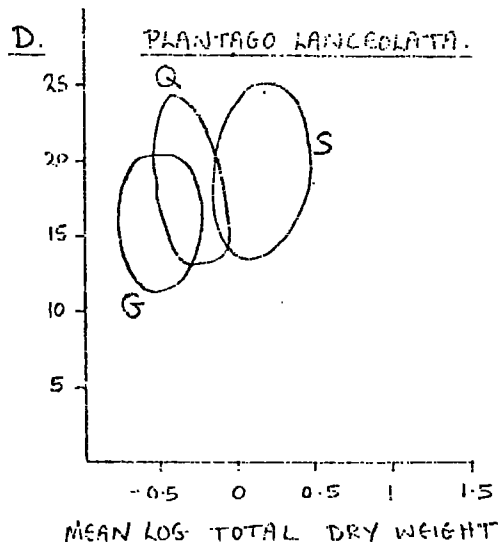
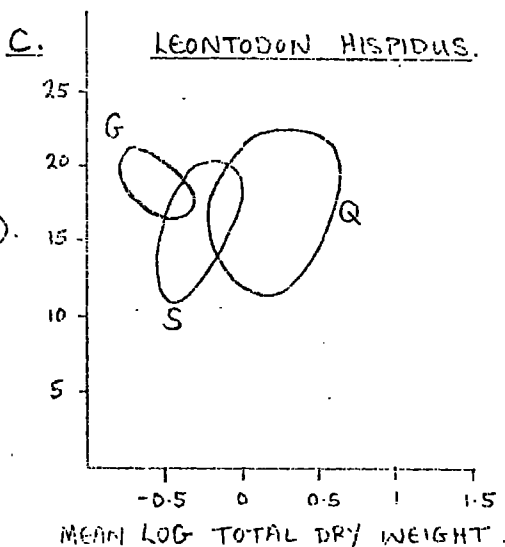
FIGURE 17.

REPRODUCTIVE EFFORT AND WEIGHT OF FLOWERING SUB-SAMPLE.



	χ^2	SIGNIFICANCE LEVEL.
REPRODUCTIVE EFFORT	6.16	N.S.
TOTAL DRY WEIGHT.	8.74	N.S.

	χ^2	SIGNIFICANCE LEVEL.
REPRODUCTIVE EFFORT	12.03	N.S.
TOTAL DRY WEIGHT.	15.37	$P < 0.05$

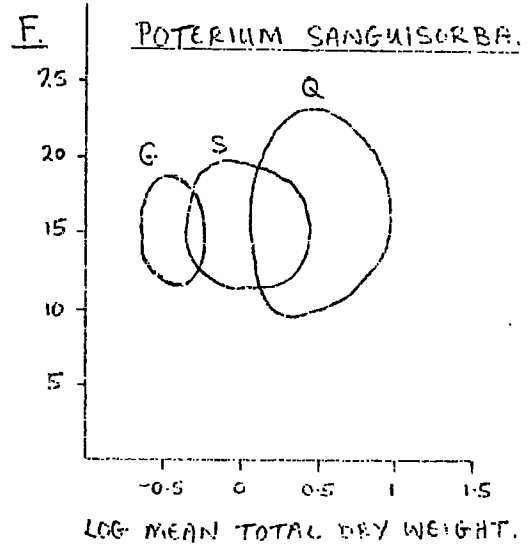
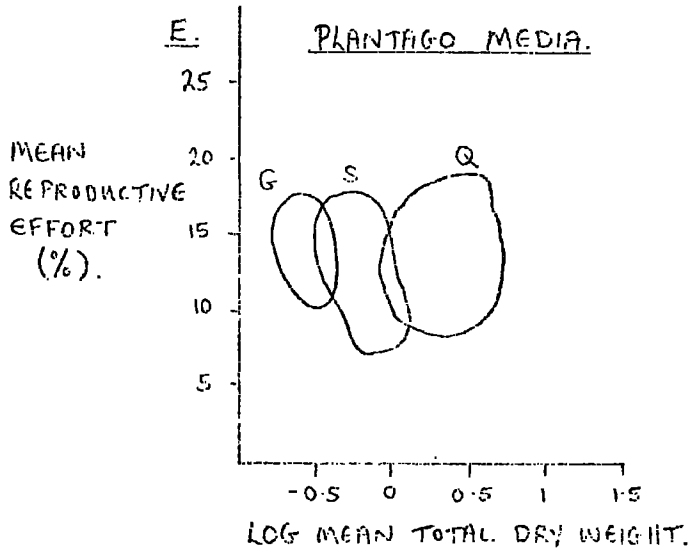


	χ^2	SIGNIFICANCE LEVEL.
REPRODUCTIVE EFFORT	5.30	N.S.
TOTAL DRY WEIGHT	23.6	$P < 0.01$

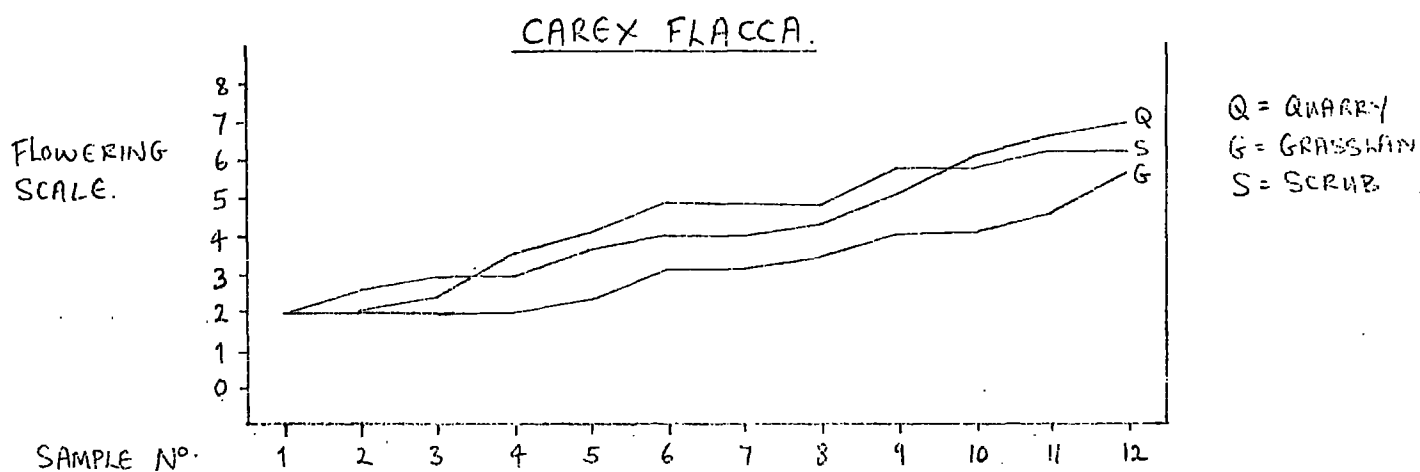
	χ^2	SIGNIFICANCE LEVEL.
REPRODUCTIVE EFFORT	8.91	N.S.
TOTAL DRY WEIGHT	20.08	$P < 0.05$

FIGURE 17 (CONT.)

REPRODUCTIVE EFFORT AND WEIGHT OF FLOWERING SUB-SAMPLE

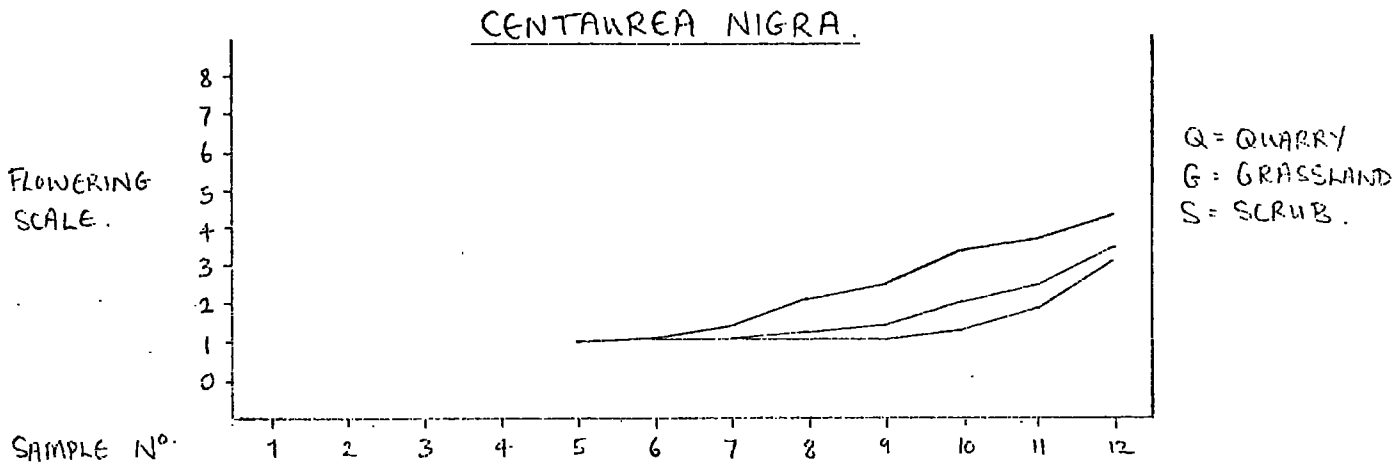


	χ^2	SIGNIFICANCE LEVEL.	χ^2	SIGNIFICANCE LEVEL.
REPRODUCTIVE EFFORT	4.39	N.S.	7.77	N.S.
TOTAL DRY WEIGHT	20.64	$P < 0.05$	25.71	$P < 0.01$

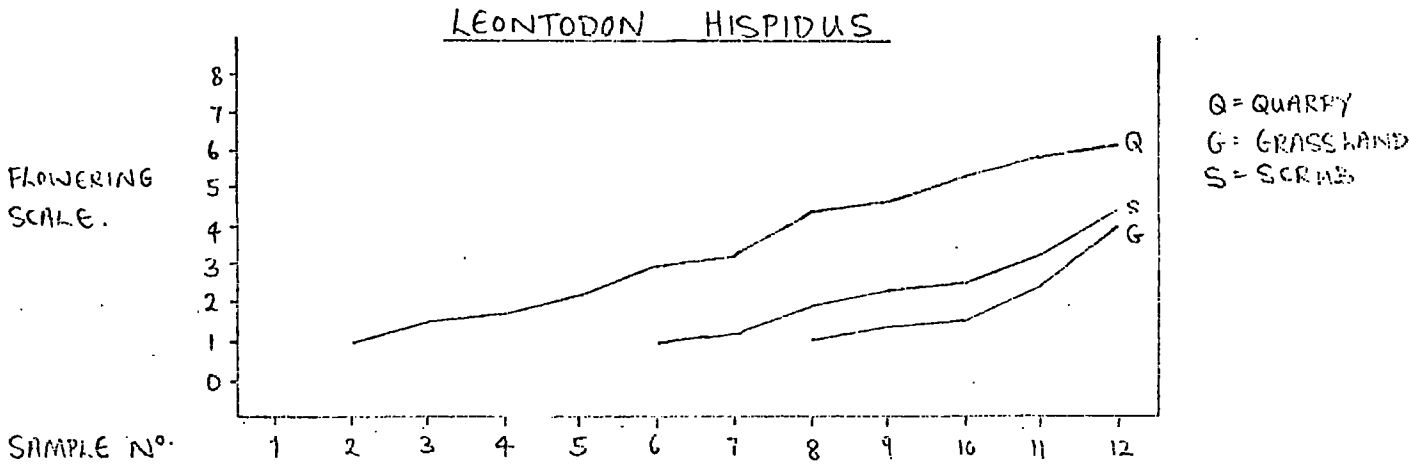
FIGURE 18THE PHENOLOGY OF FLOWERING.WILCOXON MATCHED-PAIRS SIGNED-RANKS TEST

<u>SITES COMPARED</u>	<u>T VALUE.</u>	<u>SIGNIFICANCE LEVEL</u>
QUARRY & GRASSLAND	16.1	N.S.
GRASSLAND & SCRUB	15.8	N.S.
SCRUB & QUARRY	16.3	N.S.

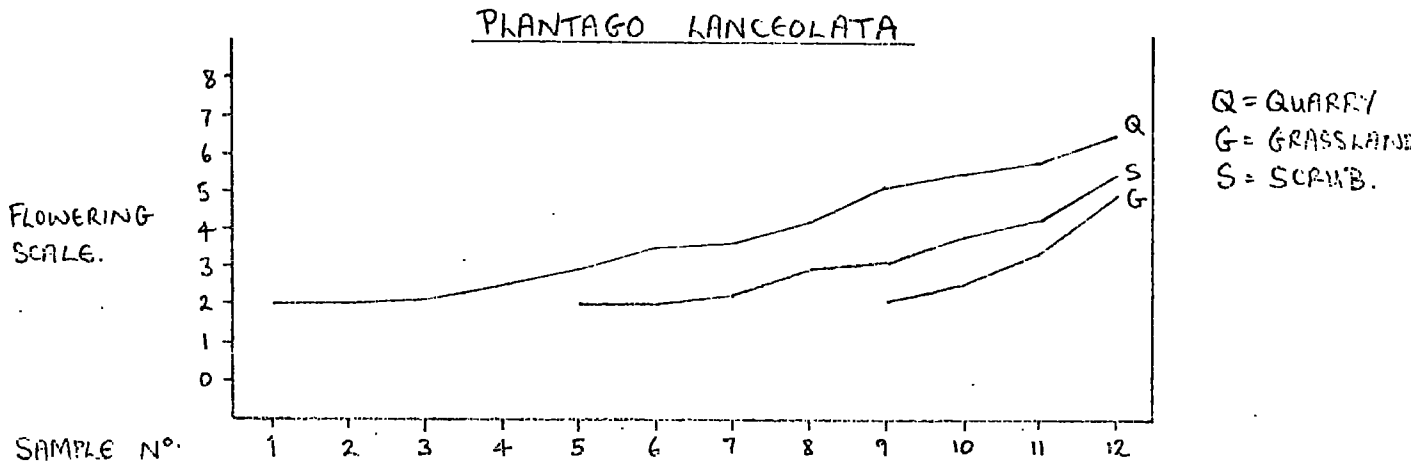
NOTE. FOR EXPLANATION OF FLOWERING SCALE, SEE SECTION 6.

FIGURE 19THE PHENOLOGY OF FLOWERING.WILCOXON MATCHED-PAIRS SIGNED-RANKS TEST

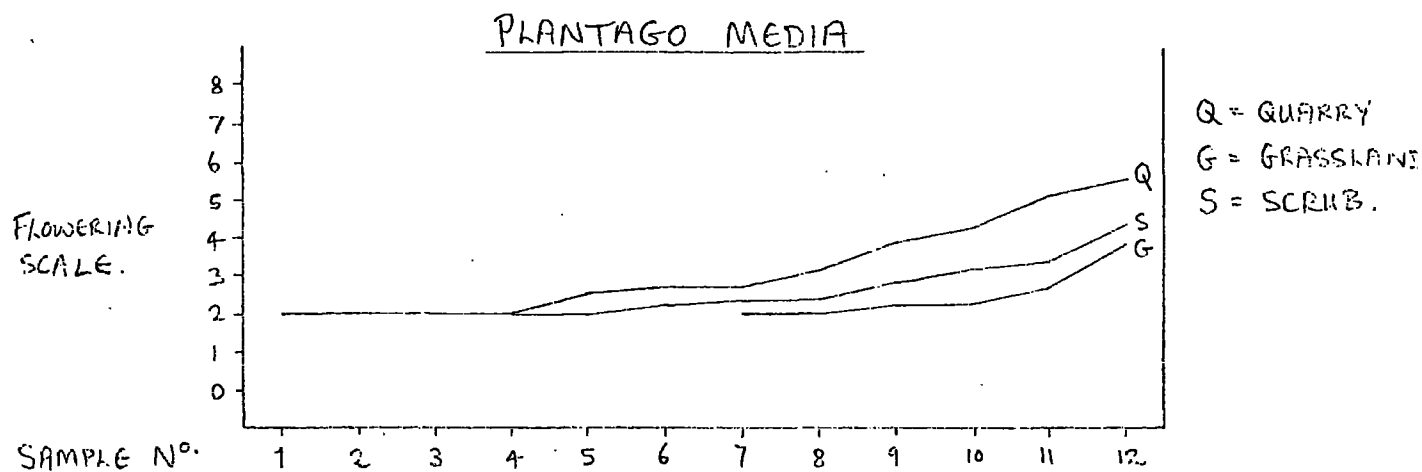
<u>SITES COMPARED</u>	<u>T VALUE</u>	<u>SIGNIFICANCE LEVEL</u>
QUARRY & GRASSLAND	14.0	N.S.
GRASSLAND & SCRUB	21.6	N.S.
SCRUB & QUARRY.	15.7	N.S.

FIGURE 20THE PHENOLOGY OF FLOWERING.WILCOXON MATCHED-PAIRS SIGNED-RANKS TEST.

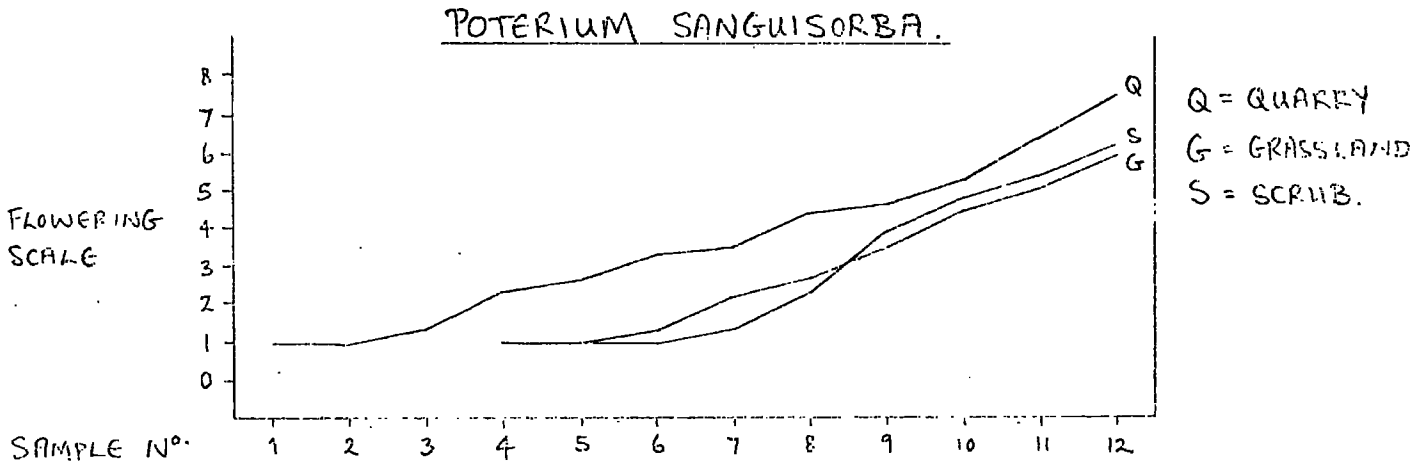
<u>SITES COMPARED</u>	<u>T VALUE</u>	<u>SIGNIFICANCE LEVEL</u>
QUARRY & GRASSLAND	8.7	$P < 0.02$
GRASSLAND & SCRUB	22.4	N.S
SCRUB & QUARRY.	11.9	$P < 0.05$

FIGURE 21THE PHENOLOGY OF FLOWERING.WILCOXON MATCHED-PAIRS SIGNED-RANKS TEST

<u>SITES COMPARED</u>	<u>T VALUE</u>	<u>SIGNIFICANCE LEVEL</u>
QUARRY & GRASSLAND	6.2	$P < 0.01$
GRASSLAND & SCRUB	17.3	N.S.
SCRUB & QUARRY	12.9	$P < 0.05$

FIGURE 22.THE PHENOLOGY OF FLOWERING.WILCOXON MATCHED-PAIRS SIGNED-RANKS TEST.

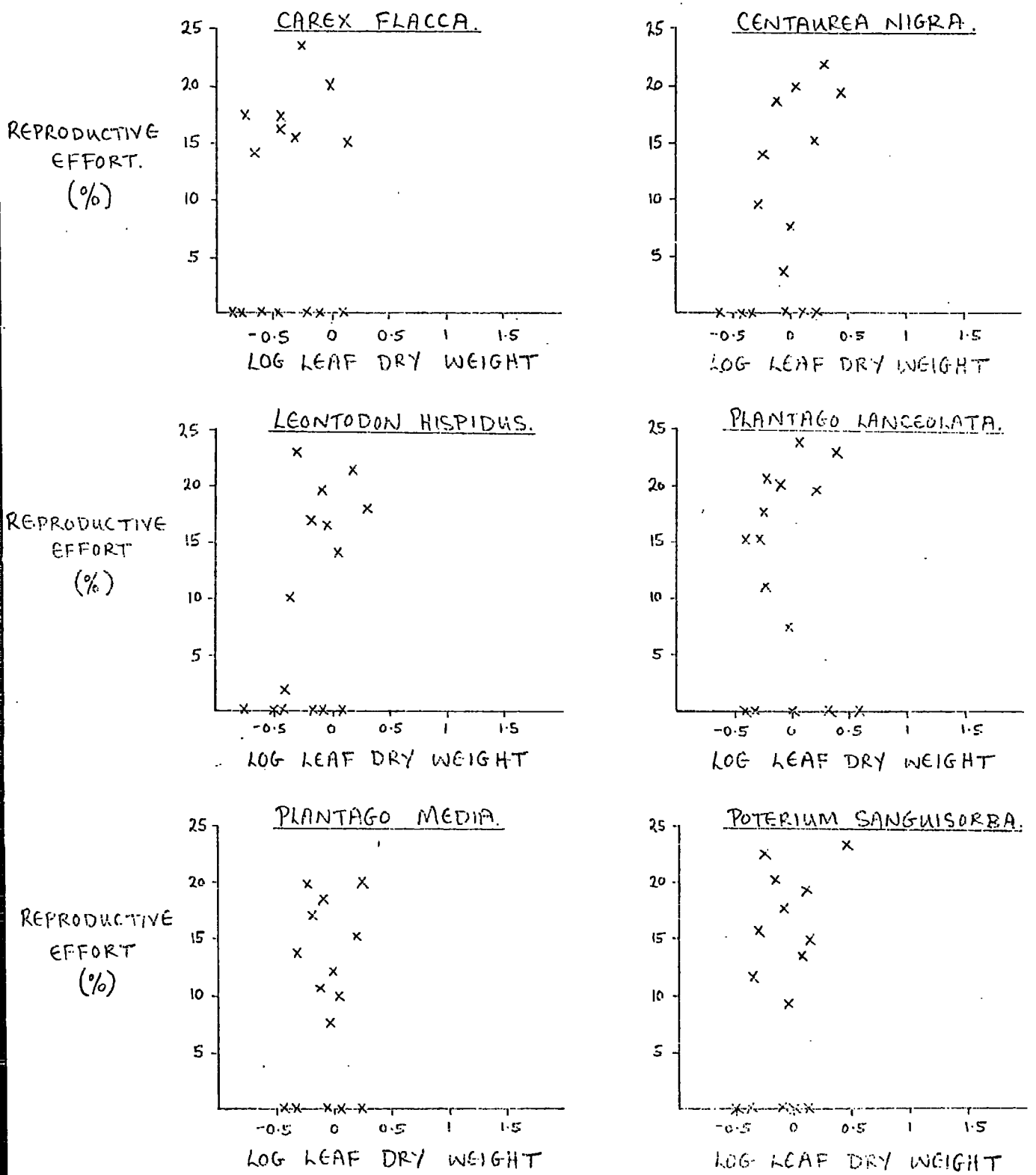
<u>SITES COMPARED</u>	<u>T VALUE</u>	<u>SIGNIFICANCE LEVEL</u>
QUARRY & GRASSLAND	12.6	$P < 0.05$
GRASSLAND & SCRUB	17.9	N.S.
SCRUB & QUARRY.	14.5	N.S.

FIGURE 23.THE PHENOLOGY OF FLOWERING.WILCOXON MATCHED-PAIRS SIGNED-RANKS TEST.

<u>SITES COMPARED</u>	<u>T VALUE</u>	<u>SIGNIFICANCE LEVEL</u>
QUARRY & GRASSLAND	10.9	$P < 0.05$
GRASSLAND & SCRUB	19.2	N.S.
SCRUB & QUARRY	10.3	$P < 0.05$

FIGURE 24.

INDIVIDUAL REPRODUCTIVE EFFORT AND LEAF WEIGHT.



B. Leaf Measurements

Leaf-area could not be directly measured for every plant analysed and therefore had to be calculated from measurements of maximum length and breadth, using empirically-derived equations. These equations, taken from the regression lines of twenty-five leaf samples for each species (see section 7) are given in Table 4. The regressions of leaf area on the cross product of length and breadth are given, since, in each case, they gave better correlation coefficients than regressions using length or breadth only. Separate equations are given for each of the three sites, apart from the case of Carex flacca, where the regression lines were almost identical. The equation for Poterium sanguisorba describes the regression line of leaf area on the cross-product of the length of the pinnate leaf and the number of leaflets. Though less direct, these two measurements still gave a correlation coefficient that was significant at the $P < 0.01$ level.

The problem of estimating the total leaf area of Gentiana nigra was complicated by the presence of numerous stem leaves (especially near the top of the flowering stem). Including only those leaves less than 4 cm in length, the regression of area on number of stem leaves was calculated using a random sample of 25 plants. The resultant correlation was significant at the $P < 0.05$ level. Area of stem leaves was added to the area of main leaves to give the total leaf area for each plant.

The phenologies for mean total leaf area are presented for the six species in Figures 25 - 30. This gives some interesting comparisons between species and between habitats.

Carex flacca shows no differentiation between sites in terms of leaf area, a result which accords with the findings in relation to reproductive effort. Furthermore, it shows very little variation in

leaf area over the whole period of study.

Four of the remaining species show a pattern of differentiation between the sites that directly accords with the measurements of total dry weight (Figure 17). This is that the smallest total leaf area occurs in the grassland, the greatest in the quarry and a mid-value in the scrub site. The species involved are Centaurea nigra, Leontodon hispidus, Plantago media and Poterium sanguisorba. The exception to this rule is P. lanceolata which records a lower peak leaf area in the quarry site than would be expected, judged in comparison with the above four species. This however accords with the data on total plant weight (Figure 17D).

The advanced growth season in the quarry site is shown in the leaf area phenologies for Leontodon hispidus and Plantago lanceolata. The leaf area graph starts to decline (due to the death of individual leaves) towards the latter end of the season. In P. lanceolata this is seen to such an extent that mean leaf area for the quarry plants finishes at a lower level than that for the grassland site.

The length breadth ratio of a leaf is a measure of its elongation. A mean ratio was calculated for five species from each site. The data (Table 5) were tested using Student's "t"-test which showed that significantly larger ratios (i.e. greater elongation) were found in the scrub populations of Leontodon hispidus and the two Plantago species.

This is seen as a plastic response to the higher levels of shade in this site.

TABLE 4

REGRESSION EQUATIONS FOR THE RELATIONSHIP BETWEEN LEAF AREA (A)
AND THE CROSS-PRODUCT OF LEAF LENGTH AND BREADTH (LB)

<u>Species</u>	<u>Site</u>	<u>Equation</u>	<u>Correlation</u> <u>coefficient,</u>	<u>Significance</u> <u>level</u>
			<u>r</u>	
<u>MAIN LEAVES</u>				
Carex flacca	All sites	$A = 0.51LB + 1.2$	0.98	$P < 0.0001$
Centaurea nigra	Quarry	$A = 0.48LB + 3.2$	0.99	$P < 0.0001$
	Grassland	$A = 0.41LB + 1.5$	0.98	$P < 0.0001$
	Scrub	$A = 0.38LB + 2.5$	0.94	$P < 0.01$
Leontodon hispidus	Quarry	$A = 0.59LB + 1.4$	0.99	$P < 0.0001$
	Grassland	$A = 0.56LB + 0.6$	0.95	$P < 0.0001$
	Scrub	$A = 0.38LB + 2.8$	0.98	$P < 0.0001$
Plantago lanceolata	Quarry	$A = 0.45LB + 0.4$	0.98	$P < 0.01$
	Grassland	$A = 0.52LB + 2.8$	0.95	$P < 0.001$
	Scrub	$A = 0.37LB + 3.4$	0.97	$P < 0.001$
Plantago media	Quarry	$A = 0.6 LB + 0.5$	0.99	$P < 0.0001$
	Grassland	$A = 0.59LB + 0.8$	0.99	$P < 0.0001$
	Scrub	$A = 0.42LB + 4.3$	0.99	$P < 0.0001$
Poterium sanguisorba	Quarry	$A = 0.17LN + 1.6$	0.94	$P < 0.01$
	Grassland	$A = 0.22LN + 3.9$	0.98	$P < 0.001$
	Scrub	$A = 0.23LN + 0.2$	0.96	$P < 0.01$

(Where LN = length of pinnate leaf x no. of leaflets)

STEM LEAVES

Centaurea nigra	All sites	$A = 1.3N + 0.8$	0.87	$P < 0.05$
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(Where N = no. of stem leaves < 4 cm long)

FIGURE 25.

PHENOLOGY OF MEAN LEAF AREA.

CAREX FLACCA.

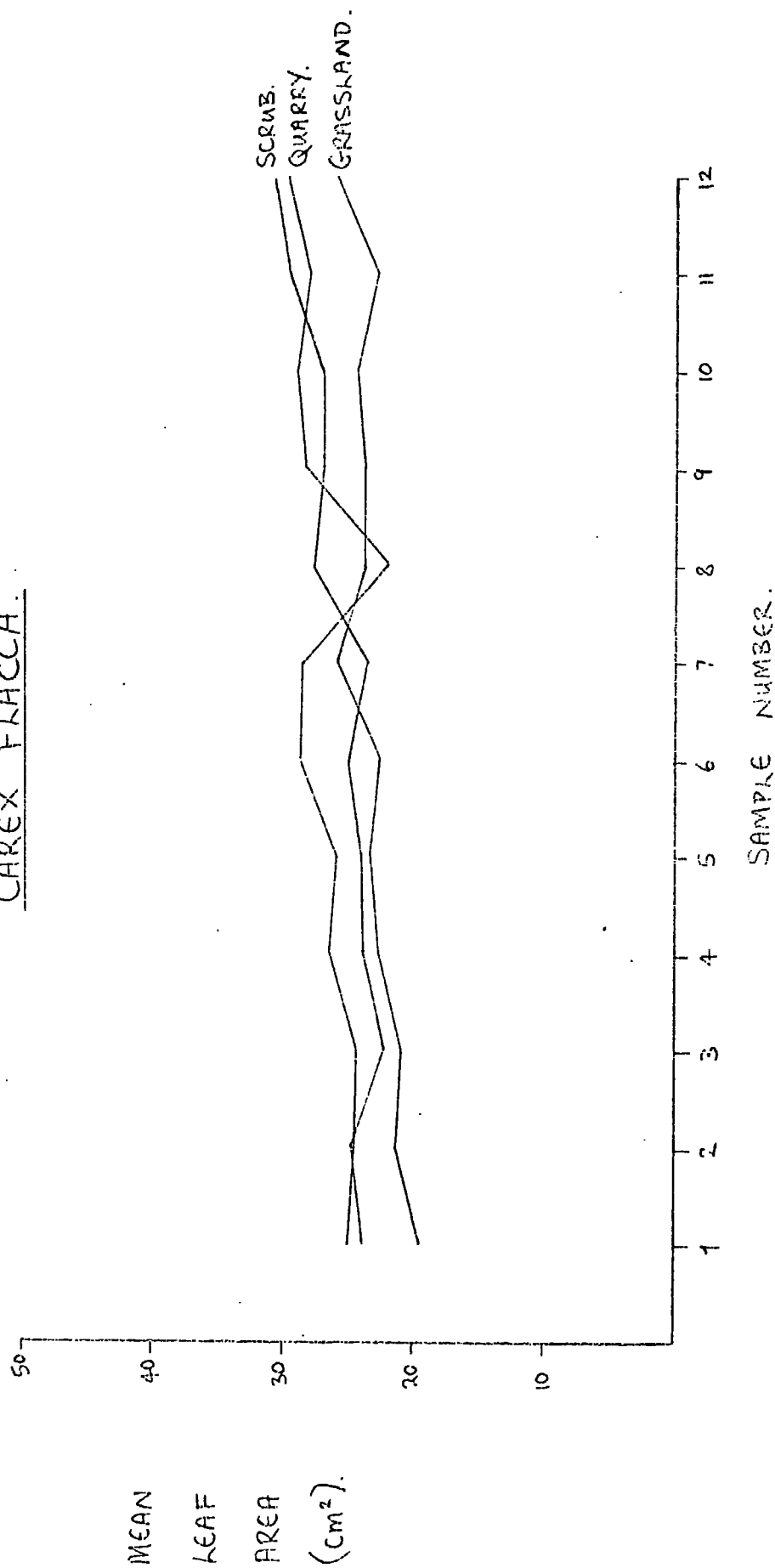


FIGURE 26.

PHENOLOGY OF MEAN LEAF AREA.

CENTAUREA NIGRA.

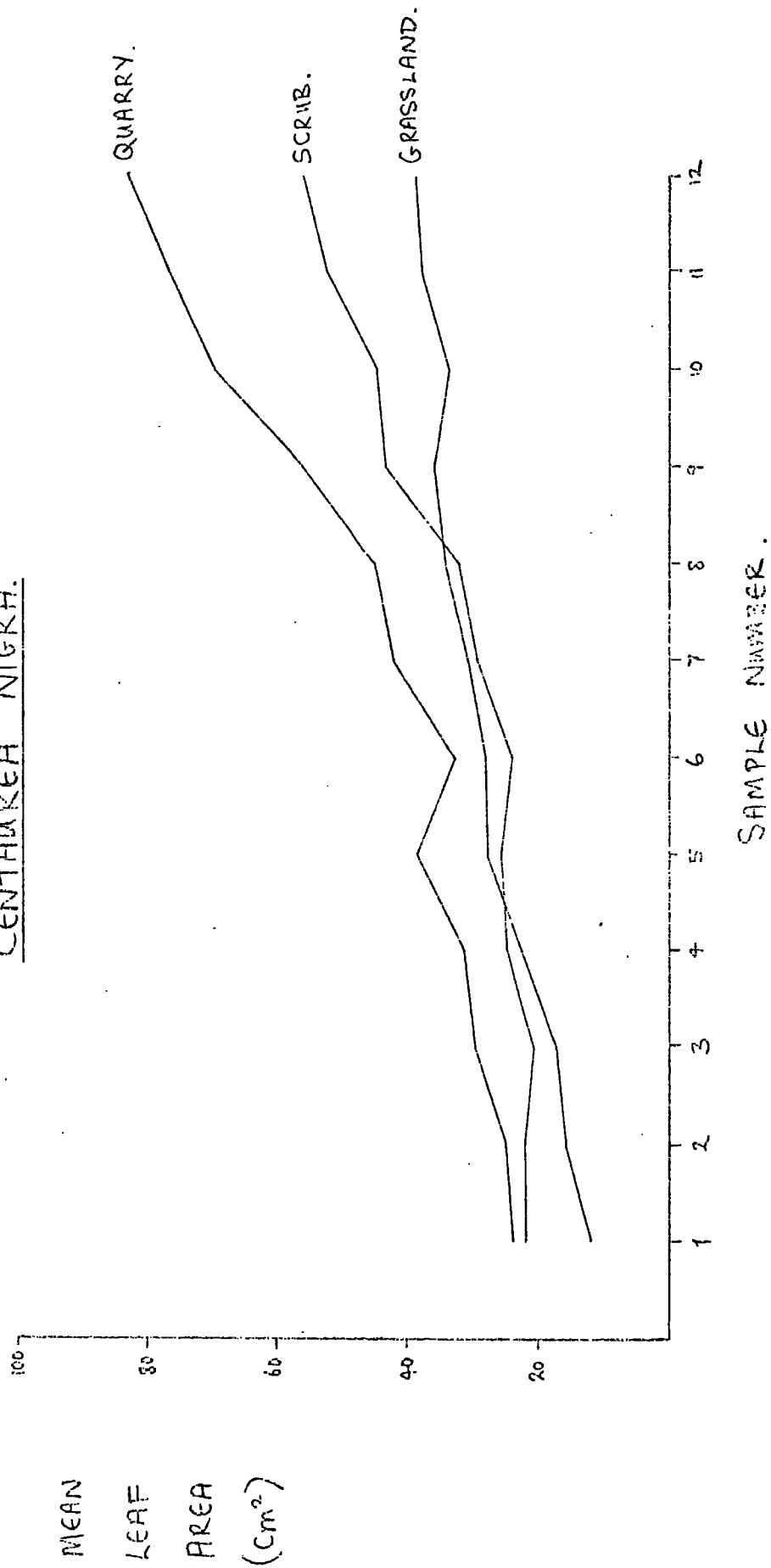
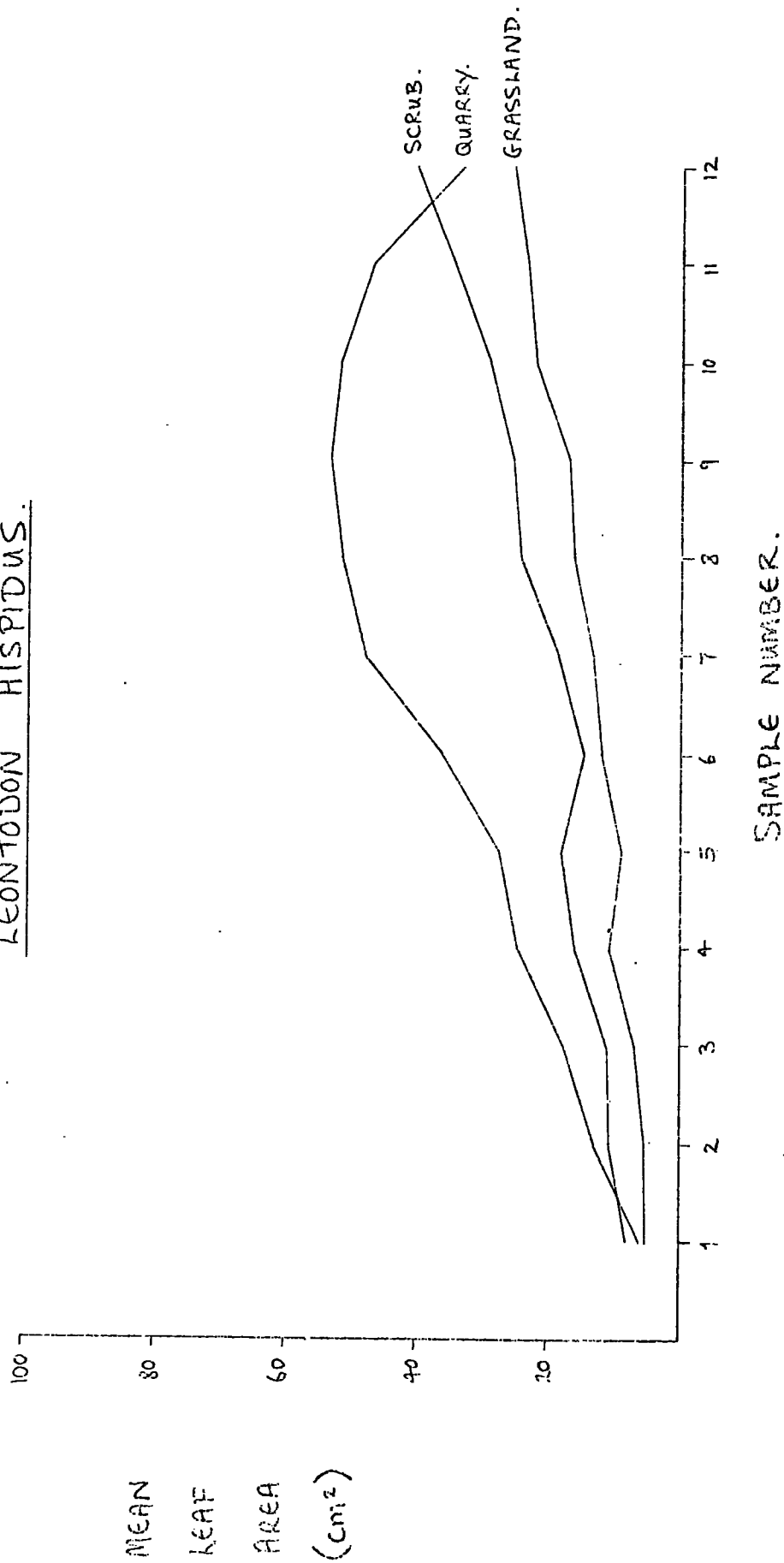


FIGURE 27.

PHENOLOGY OF MEAN LEAF AREA.

LEONTODON HISPIDUS.



SAMPLE NUMBER.

FIGURE 28.

PHENOLOGY OF MEAN LEAF AREA.

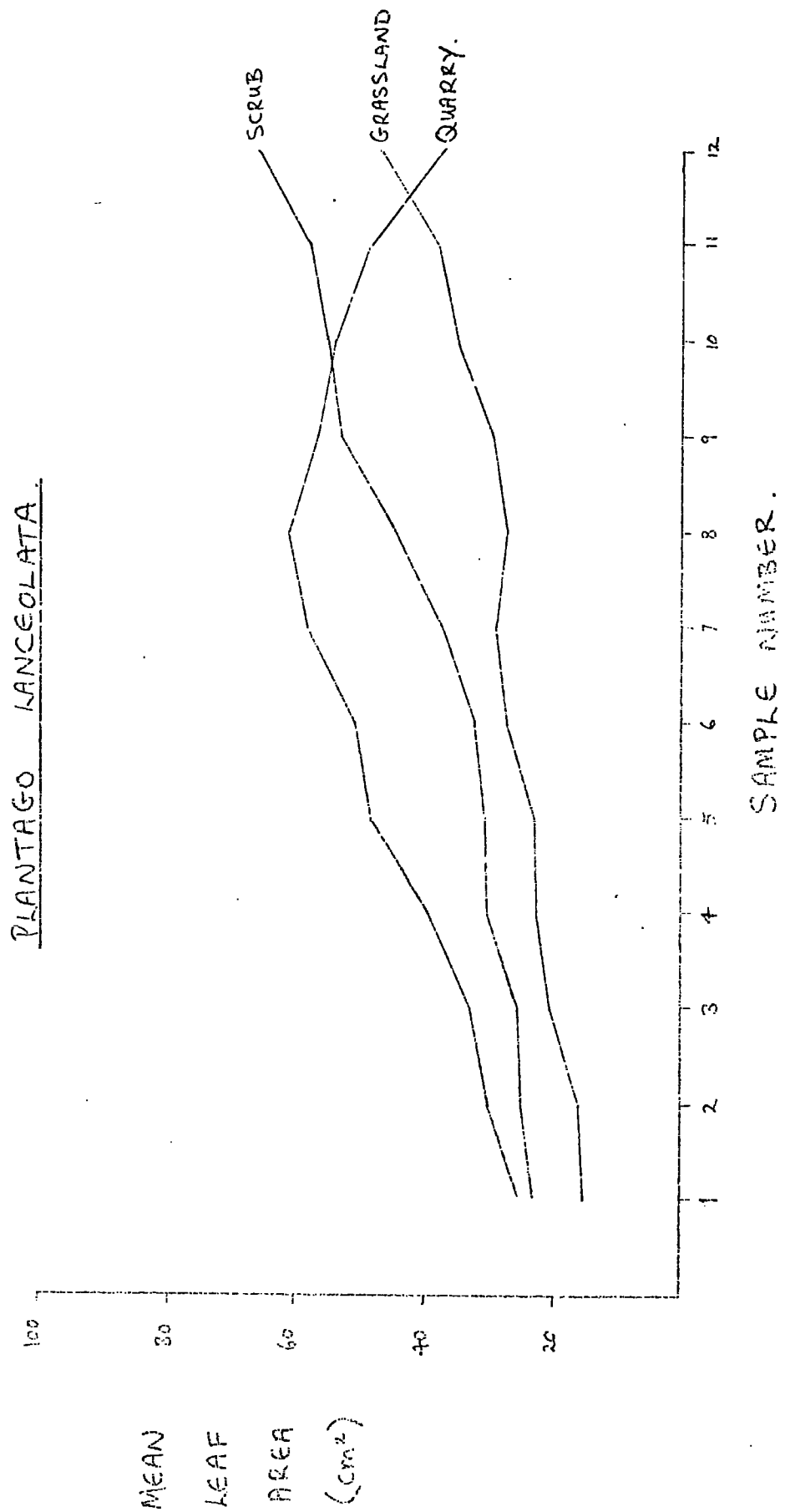


FIGURE 29.

PHENOLOGY OF MEAN LEAF AREA.

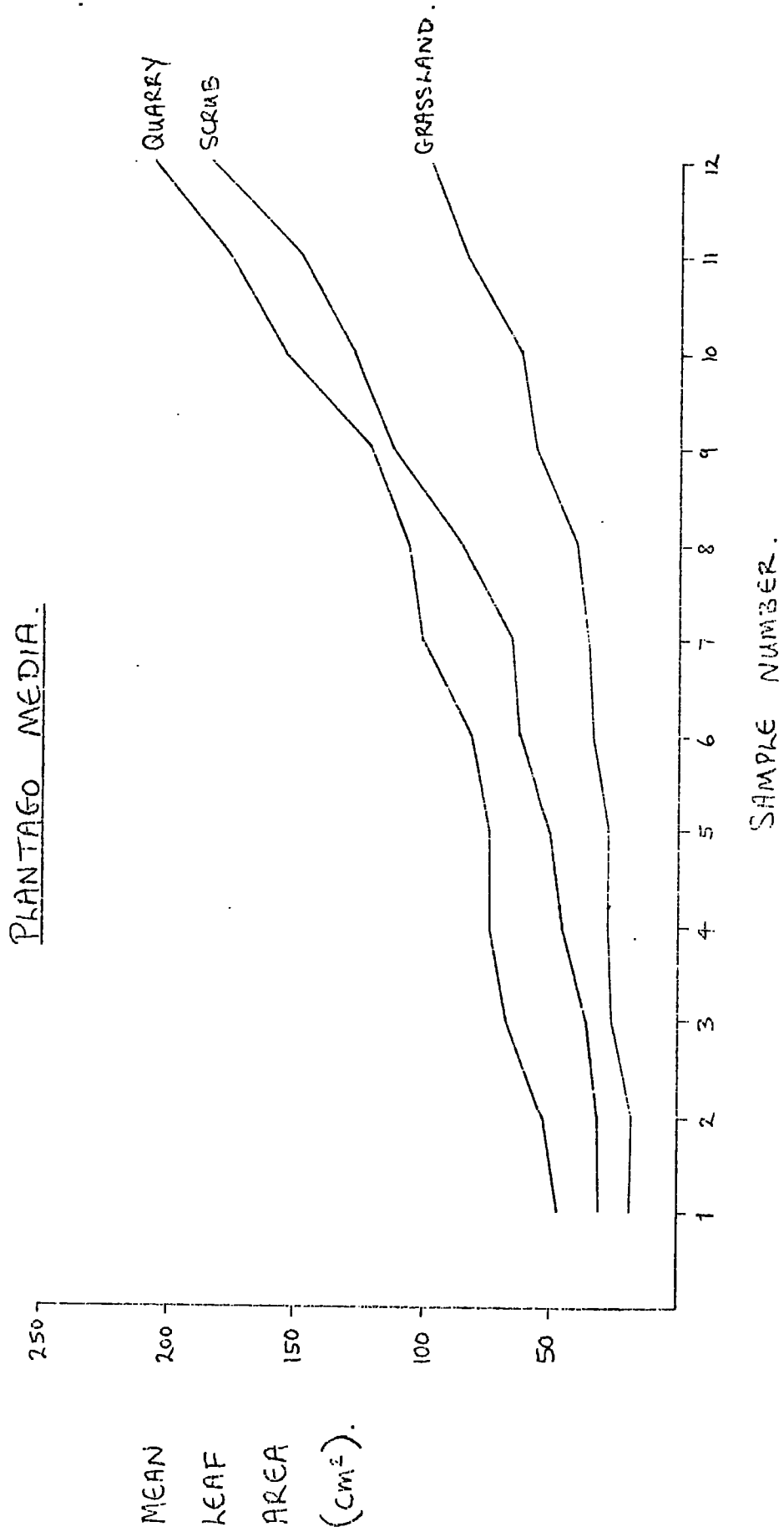


FIGURE 30.

PHENOLOGY OF MEAN LEAF AREA.

POTERIUM SANGUISORBA.

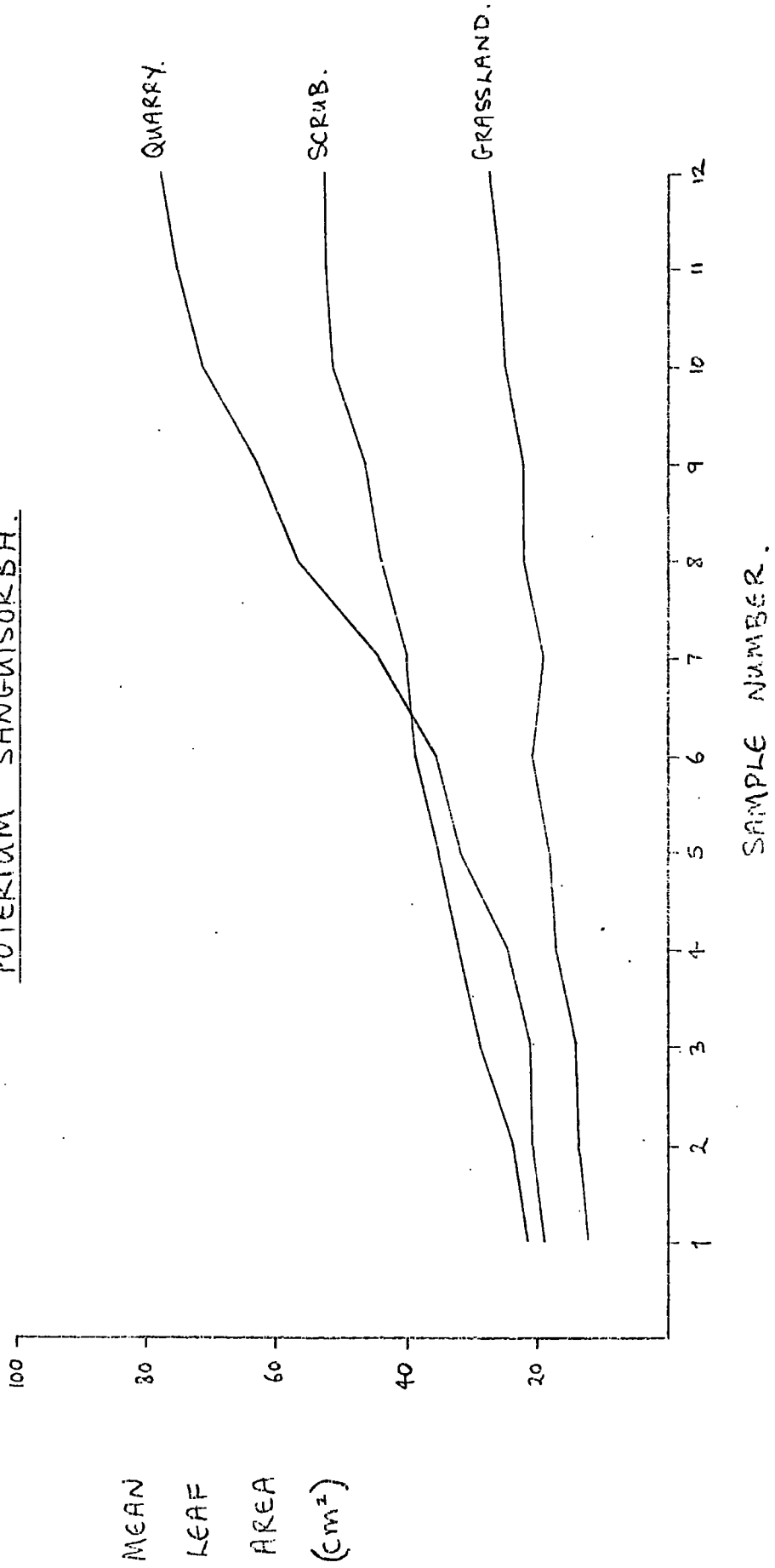


TABLE 5

LEAF LENGTH : BREADTH RATIOS

<u>Species</u>	<u>Site</u>	<u>Mean length : Breadth</u> <u>Ratio</u>
Carex flacca	Quarry	36.8
	Grassland	43.3
	Scrub	51.7
Centaurea nigra	Quarry	6.6
	Grassland	6.7
	Scrub	8.5
Leontoden hispidus	Quarry	13.5
	Grassland	11.8
	Scrub	18.2
Plantago lanceolata	Quarry	12.0
	Grassland	14.1
	Scrub	23.8
Plantago media	Quarry	2.5
	Grassland	2.6
	Scrub	4.1

SIGNIFICANT DIFFERENCES BETWEEN SITES USING STUDENT'S T-TEST

<u>Species</u>	<u>Sites Compared</u>	<u>T value</u>	<u>Significance level</u>
Leontodon hispidus	Scrub and Rest	2.98	P < 0.01
Plantago lanceolata	Scrub and Rest	4.12	P < 0.001
Plantago media	Scrub and Rest	3.87	P < 0.001

NOTE: Poterium sanguisorba not included since no measure was made of leaf breadth.

C. Stem Measurements

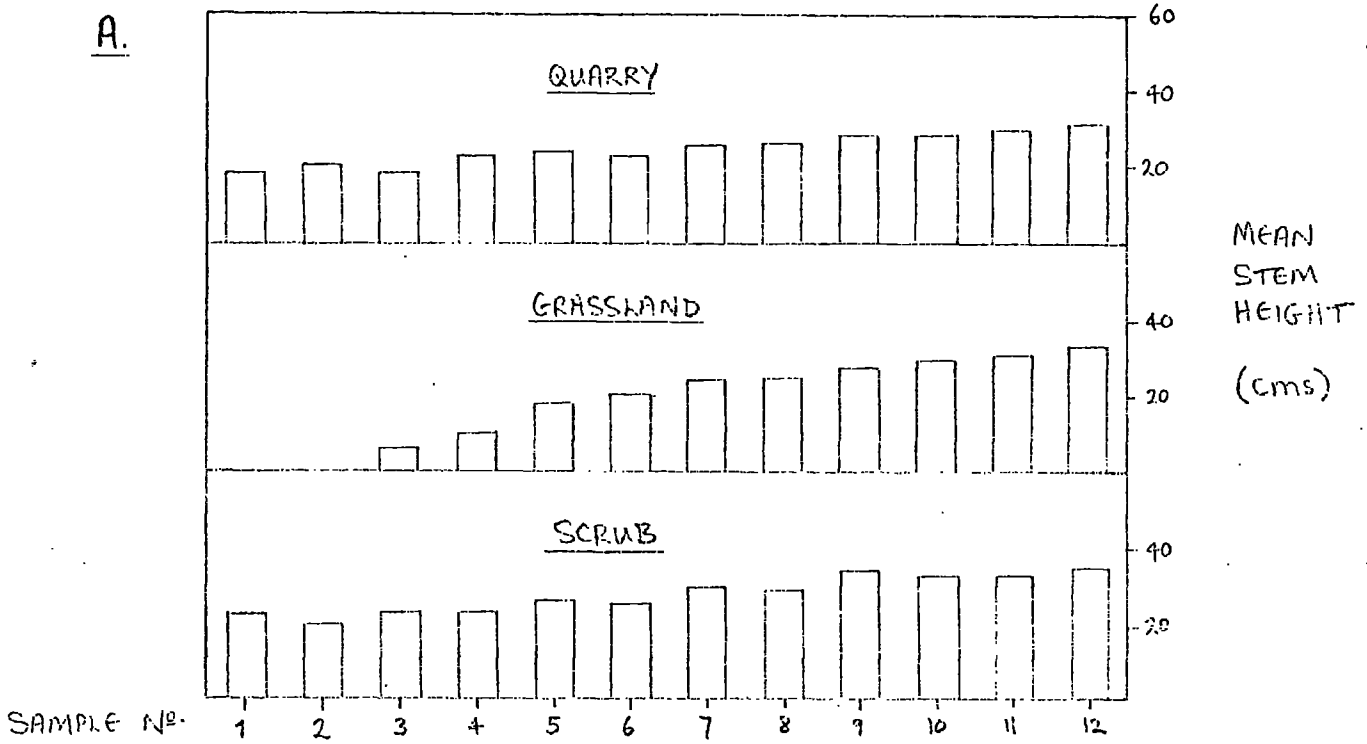
Data for mean stem heights for each site and species are presented in Figure 31. The differentiation between sites is clear for all species apart from Carex flacca. This species shows a very uniform mean stem height throughout. The other species appear to follow the same ordering in relation to sites. The grassland site contains populations with the shortest stems, while the scrub populations represent the opposite extreme in this respect. Samples from the quarry site show values in between the other two.

The greater height of stems in the scrub site is seen as a response to the greater shading effect induced by the Crataegus bushes. The general height of the field layer is greater in this site, showing that it is a general response on the part of all the herbaceous species to increased shade.

PHENOLOGY OF MEAN STEM HEIGHT.

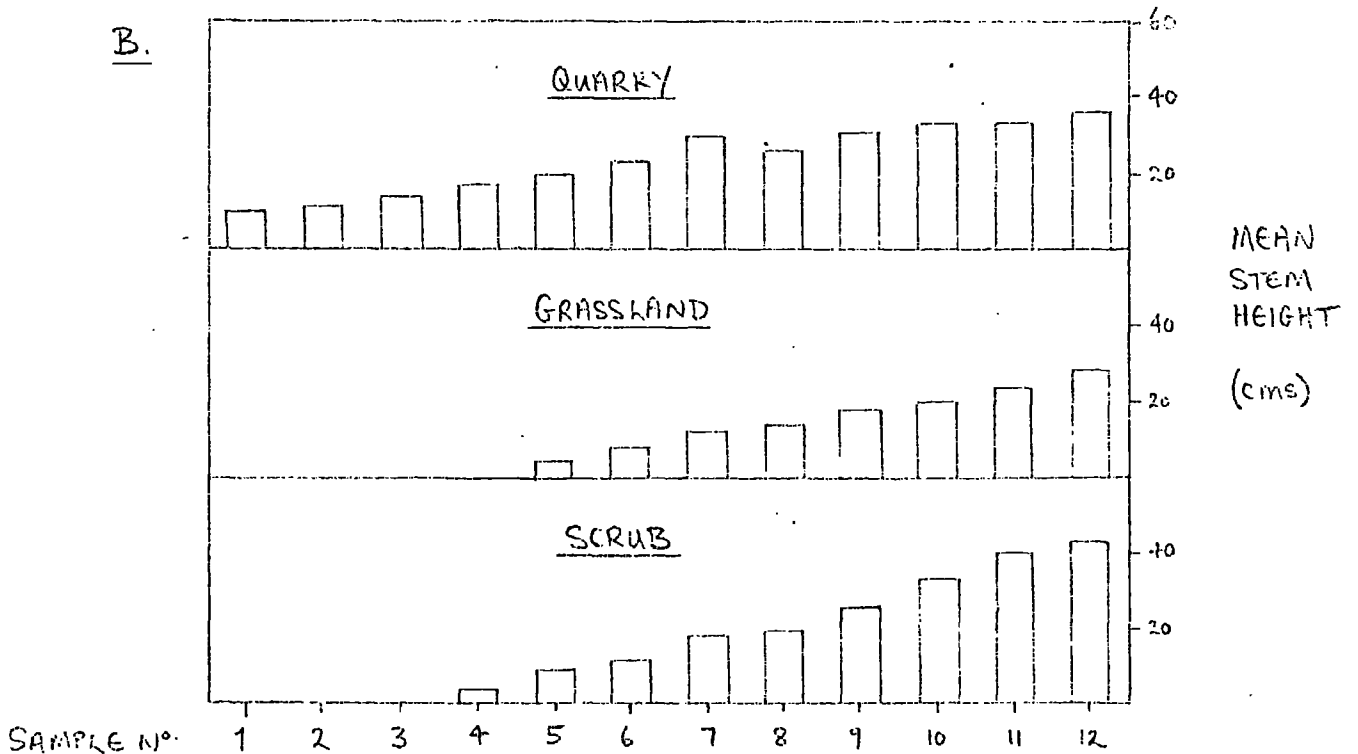
CAREX FLACCA.

A.



CENTAUREA NIGRA.

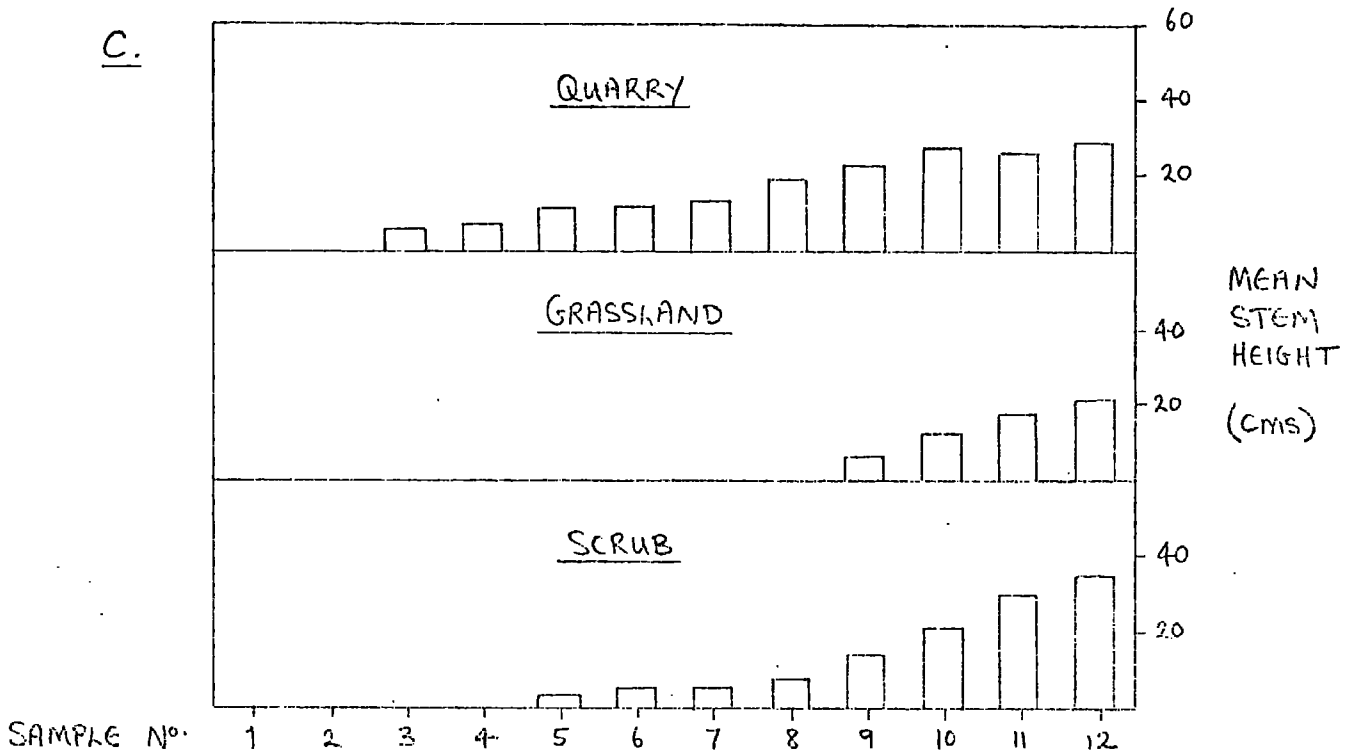
B.



PHENOLOGY OF MEAN STEM HEIGHT

LEONTODON HISPIDUS

C.



PLANTAGO LANCEOLATA

D.

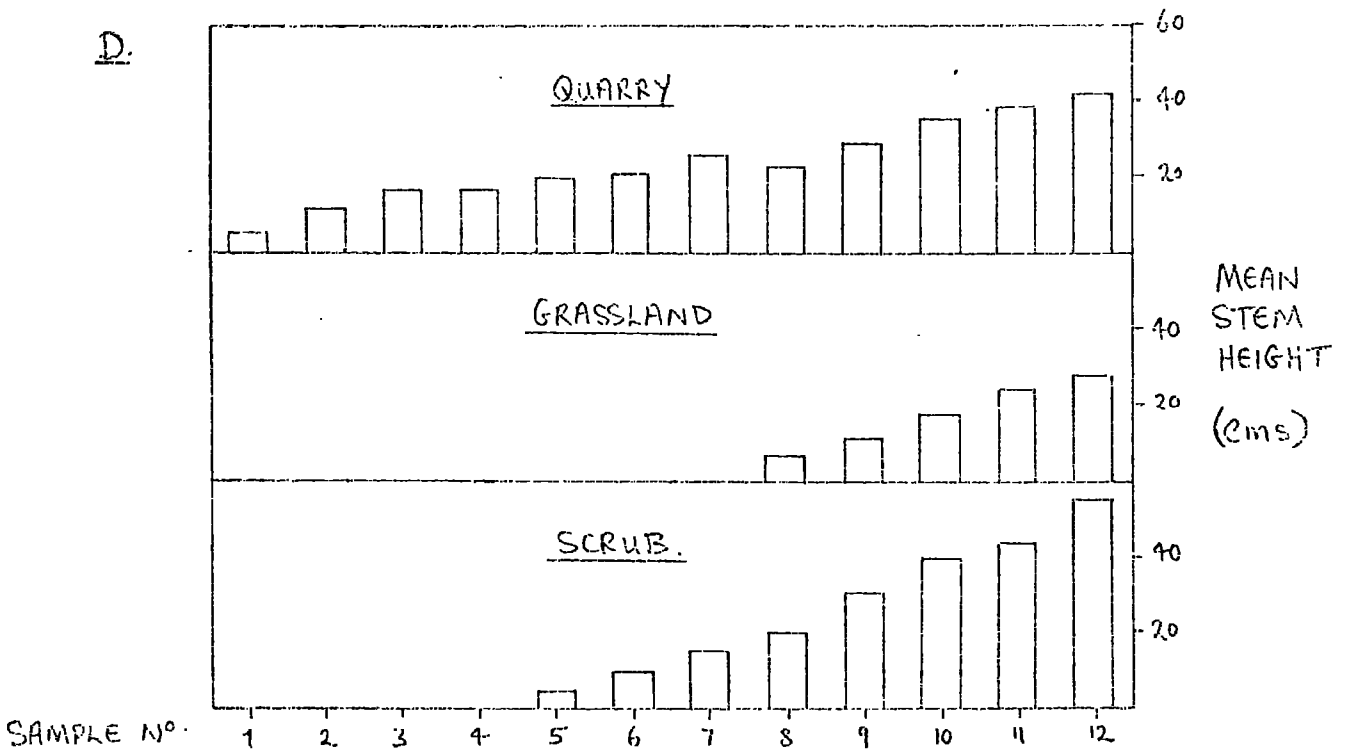
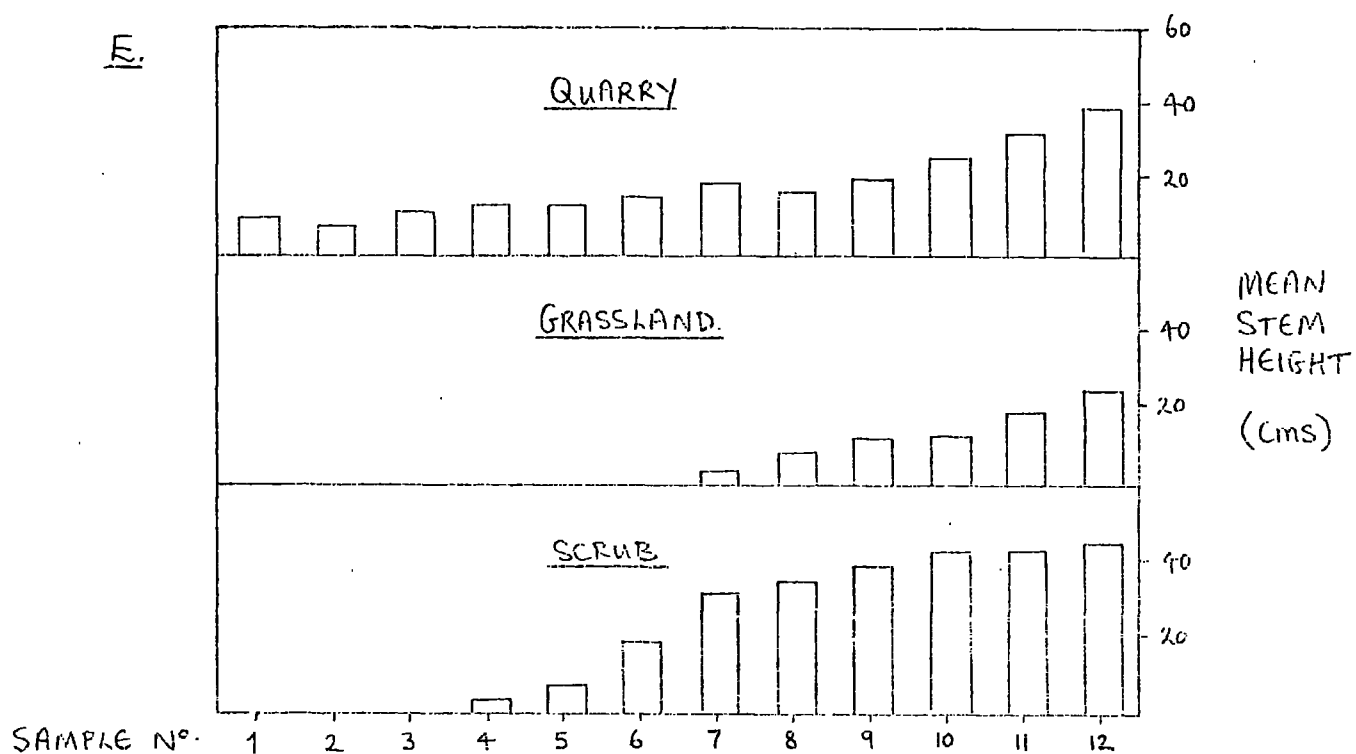


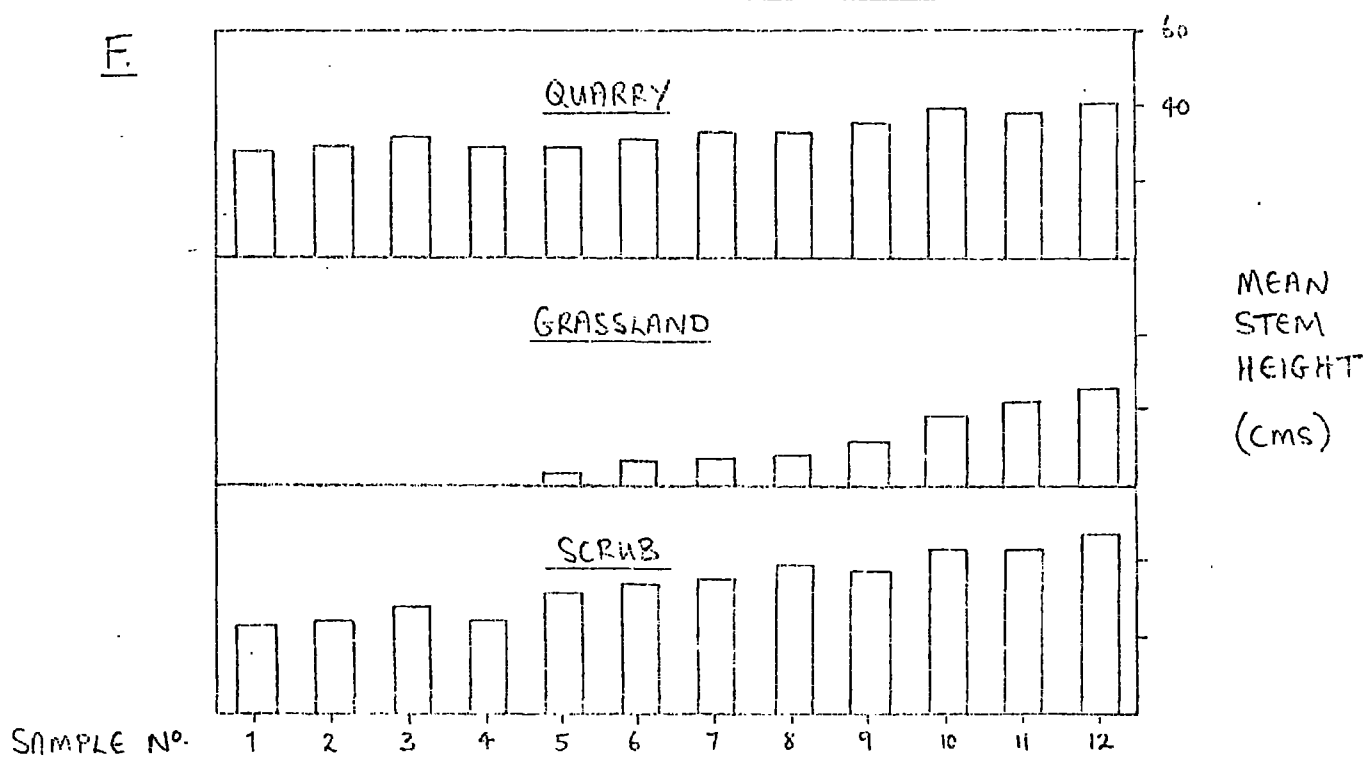
FIGURE 31 (CONT.)

PHENOLOGY OF MEAN STEM HEIGHT.

PLANTAGO MEDIA.



POTERIUM SANGUISORBA.



D. Palatability experiments

The results for the experimental feeding of Cepaea nemoralis on Leontadon hispidus are given below:-

<u>Site from which leaves</u> <u>were collected</u>	<u>Mean consumption (dry</u> <u>weight) per 24 hours, in</u> <u>choice experiments</u>
Quarry	24.1 mg
Grassland	23.8 mg
Scrub	27.3 mg

The differences between the three means (averaged from all replicates) were tested using Student's "t" - test. The 't' values for comparisons of quarry with grassland leaves, grassland with scrub leaves and scrub with quarry leaves were 1.08, 1.62 and 1.47 respectively. None of these results were significant at an acceptable level of probability. It was therefore shown that the individual Cepaea did not discriminate between leaves taken from different parts of the succession.

9.

DISCUSSION

The results of this study are best considered at two levels; reproductive allocation at an individual and population level. Intra-specific differences in the proportion of resources that plants allocate to reproductive structures, though not evident at the individual level, are quite distinct at the population level.

The data presented here show no differences between individuals taken from opposite ends of a succession, in terms of reproductive effort. This accords with previous work by Harper and Ogden (1970) who found that percentage seed allocation in Senecio vulgaris remained within fairly narrow limits (18-24%) despite several-fold increases in total dry weight and subjection to a range of soil conditions. Only very extreme stress altered this pattern, when individuals failed to flower at all.

These findings suggest that percentage reproductive allocation in many species is fairly fixed. In adverse conditions, such as nutrient stress or drought, perennial individuals may simply not attempt to flower at all. This "all-or-nothing" policy would be tactically sensible for the plant, since an attempt to flower, despite sub-optimal conditions, would run the double risk of reduced seed viability and a reduced chance of survival for the parent plant.

The differences in reproductive effort between sites at the population level are clearly directly correlated with the number of individuals that actually flower. The most inherently unstable habitat, the quarry, shows (for four species at least) the highest joint (i.e. population) allocation to reproductive structures. This is entirely in accordance with the MacArthur and Wilson (1967) concept of r-selection being the dominant force in unstable or ephemeral environments.

Conventional theory would suggest that the influence of K-selection would increase with successional status, since the environment becomes increasingly stable and predictable. The scrub site however appears to contain some populations that have a higher collective reproductive effort than corresponding populations in the grassland site, the latter being successional less advanced.

The explanation lies in viewing the three different habitats in terms of the level of both inter- and intra-specific competition. The quarry site represents a relatively open environment where the plant cover is less dense. As such, the site presents a greater freedom from competition and therefore a greater availability of resources to each plant. This means firstly that plants can attain a size that is compatible with viable seed-production and secondly that the seedling offspring have a greater chance of establishment and survival in the future as seeds rather than vegetative propagules.

The grassland habitat represents the opposite end of the spectrum, where, with a much higher plant density, competition for available resources is very fierce. Many individuals will be crowded out before getting a chance to flower and will therefore rarely experience conditions of sufficiently abundant resources to trigger off the mechanism that initiates the production of flowering stems. In addition, for those individuals that do manage to flower, the chances of offspring seedling establishment are severely reduced by the dense herbaceous cover. Tamm (1972) found, in permanent plots of perennial herbs under competitive conditions, that the seedling population, though reasonably large, had a very low chance of survival. Grime (1977) lists low seed production as part of the general competitive strategy in highly competitive habitats. Thus the population as a whole devotes a greater proportion

of the available energy to the growth of persistent vegetative organs, thus conferring advantages in a crowded, competitive environment (Harper and White, 1971).

The patterns observed in the scrub site are less easily explained. The biotic limiting factors make this habitat a reasonably stressed one for herbaceous perennials. The occurrence of Crataegus monogyna introduces shade, and possibly also drought (through competition for water), as potentially severe stress factors. Stress-tolerant plants however are usually shy flowerers (Grime 1977). It seems more likely that the slightly lower level of competition, aids more frequent flowering.

The reduced competition in the scrub community may be due to several factors. Table 1 shows a decline in the number of grass species and a reduced abundance of the two dominants, Seeleria albicans and Festuca rubra. This may well be due to the differential adaptiveness of grasses (as opposed to forbs) to increased levels of shade and leaf litter deposition by C. monogyna. Sydes (1978) has shown very convincingly that Poa trivialis and many other grass species are adversely affected by the amount of accumulated tree litter. Total surface area of litter was shown to be more important than weight, which suggests that the inhibitory effect operates through shading. Competition from grasses may be more important to the perennial forbs than competition from species of similar morphology, through the effects of shading at the field layer level. In short, shading and litter deposition from the Crataegus bushes may affect the relative abundance of grass species, which in turn have the greatest shading effect on the forbs.

Thus it appears that populations from the quarry behave more like annuals, attempting to produce seed fairly frequently. The grassland

populations however behave more as true perennials, with less frequent flowering and, possibly longer individual life.

It is clear therefore that the decision whether to flower or not is crucial to the ultimate reproductive effort of the population. It has been shown that total weight of leaves (Figure 24) does not bear any obvious relation to whether individuals flower. This is presumably therefore also true for leaf area. It is possible however that this result overlooks the fact that different component parts may compete for the same fixed supply of resources. Thus, growth in one compartment or module (such as inflorescence stems) may be at the expense of others (such as leaves). This is clearly shown in the percentage allocation diagrams for Senecio vulgaris given by Harper and Ogden (1970) for Tussilago farfara (Ogden 1974) and for Chrysanthemum segetum (Howarth and Williams 1972), where the start of allocation to flowers and receptacles coincides with a dramatic reduction in the percentage dry weight of leaves. Leaf area, number and dry weight may therefore actually decrease to allow for growth of reproductive organs. The overlap of leaf dry weight for flowering and non-flowering individuals (Figure 24) may therefore not be altogether surprising. It seems likely that the critical turning point between flowering and non-flowering is induced by the competitive effects of other plants. There may be a particular nutrient which controls this, which is in short supply in the grassland, but which becomes abundant (relative to the number of individuals) in the less competitive site.

The hypothesis is therefore that competition suppresses flowering, since dense vegetation causes a greatly reduced chance of seedling establishment and success. The removal of competition in more open habitats allows a greater total size to be attained as well as more

frequent attempts to flower and produce seed.

The clear demonstration of inter-site differences in time of anthesis beg the question whether this is genetic or merely a plastic response to environmental conditions. Clearly the answer to this can only be established by growing seed, collected from different sites, under constant environmental conditions and observing what differences persist.

The likelihood of these differences being genetically fixed is small, due to both the physical and temporal proximity of the three sites. The grassland and scrub sites are adjacent to one another so that there is probably significant gene flow and total mixing of genotypes. Similarly, the quarry site is not sufficiently long established to contain a significantly different gene population from the original grassland that existed before the quarry was created.

Time of anthesis therefore seems to be in response to environmental conditions. In the quarry, the relevant limiting factor is probably summer drought, which forces individuals to complete as much of their flowering cycle as possible before the full impact is made. In the grassland population, the main limiting factor is not environmental but biotic - namely the effect of competition from other individuals. These two limiting factors can be regarded as operating in density-independent and density-dependant ways respectively, the former operating at an earlier stage in the flowering season.

This accords with the findings of Law et al., (1977) who compared populations of Poa annua experiencing predominantly density-dependant and density-independent regulation. They found that the two showed characteristic life-history differences that were genetic. Selection under density-independent regulation produced individuals that had a

shorter pre-productive period, a higher seed output earlier in life and shorter lives in general.

The time of anthesis for the scrub site can be viewed as a mid-stage between these two. The density-dependant competitive effect is not as pronounced as in the grassland population. It is possible that the slightly earlier flowering is also due to the effects of shade later on in the season, with the gradual extension of the Crataegus canopy and the increased density of the field layer.

The variation in total plant weight, stem height, leaf area and the leaf length : breadth ratio between sites are all environmentally induced. The first three would be in response to available nutrient and water resources, the fourth a response to shading in the scrub. The elongation of leaves serves to enable the plant's photosynthetic apparatus to attain a greater height and therefore compete more effectively for light.

Responses to density in the form of dry weight of plant parts has been well documented in the literature (Palmbiad 1968; Harper 1977), as have leaf area responses to shade (Grime, 1977). In this case, all are most probably plastic rather than genetic responses.

The conclusions to be drawn from the data on palatability of Leontodon leaves to Cepaea nemoralis are necessarily very tentative. Two arguments can be distinguished. The first takes the data at face value and concludes that plants from different parts of a succession do not differ in their allocation of resources to herbivore avoidance (or repulsion). The second argument notes that Cepaea nemoralis is a very generalised herbivore, having been reported to accept a wide variety of food-plant species (Grime et al., 1968; Williamson 1976). It is thus possible that relatively small differences in palatability between

leaves taken from different sites may be ignored by Cepaea, while being quite significant for other more important herbivores, such as the Lepidoptera and Hemiptera.

There are several stumbling blocks in drawing conclusions from a study of this kind. Firstly the range of the succession may be regarded as too narrow. The environmental conditions are all fairly similar -- climate, soil series, geology. The only differences are in the percentage ground cover, the species density and composition and the degree of shade and drought. Arguably these differences are not sufficiently great to induce significant changes in plant response. The studies by Abrahamson and Gadgil (1973) included sites from a very wide range of environmental conditions, from a dry, disturbed site to a hardwood community. It is possible that a greater range of environmental conditions for this study, as well as greater geographical separation (to eliminate gene flow) would provide some differentiation in terms of individual reproductive effort.

It is generally accepted that perennials, having the choice between seed production or vegetative (clonal) reproduction, will use the former in unstable habitats that experience density-independent population regulation and the latter in crowded environments, where competitive ability and size are crucial (Harper 1977). Tamm (1972) found that Primula veris individuals in a crowded environment were very long lived, flowered very rarely and resorted to the replacement of the few dead individuals by vegetative propagation. It is quite possible that the grassland perennial populations studied have a higher rate of clonal growth than their counterparts in the unstable quarry site, where individuals behave more like annuals, producing seed every year.

A further difficulty concerns the consideration of root biomass.

The practical difficulties involved in accurately measuring this component would have been formidable. In common with other workers (Abrahamson and Gadgil, 1973; Gadgil and Solbrig, 1972) it was therefore decided to neglect all underground plant tissues.

Much controversy has centred around the choice of plant variables to use as measures of "allocation". The whole concept of allocation is rather vague since it has connotations involving a range of resources: energy, major nutrients and time. Harper and Ogden (1970) have argued that dry weights of component parts are not sufficient since they give no indication of the energetic value of each component (i.e. the production cost to the plant). They have therefore determined the average calorific content of each component and used this to correct subsequent measurements of dry weight. This still begs the question as to whether energy allocation is relevant, since in some cases the content of certain critical elements may be of paramount importance.

Hickman and Pitelka (1975) argue that time-consuming calorimetry is not necessary to determine energy allocation patterns in plants, since, for four ecologically diverse species, there was no significant difference between the patterns of energy allocation based on calories and those based on dry weight measurements. It would appear therefore that the findings of this study are legitimate indications of energy allocation.

The final point concerns the measurement of reproductive effort. Certain workers have used seed as the measure of allocation to reproduction (Harper and Ogden, 1970; Ogden, 1974). This study has used the dry weight of all reproductive organs: inflorescences, receptacles, buds and seeds. This accords with the methods used by Abrahamson and Gadgil (1973) and Gadgil and Solbrig (1972).

Two arguments are presented in favour of this approach. Firstly, it is the simplest and quickest method for an extensive study such as this. Secondly, it is a more realistic measure of the reproductive potential of a species in a particular site. Seed weight measures the final reproductive achievement after the effects of stress (shade, density etc.) and disturbance (grazing, seed predation etc.) have modified the patterns of allocation. Dry weight of the whole reproductive structure is a more accurate estimate of reproductive "intent" or true effort, before this has been modified by external conditions.

The results of this study appear to indicate that individuals within a species adopt fairly fixed strategies towards reproductive effort, in terms of the proportion of resources devoted to flowering and seed production. This is strategically sound for perennial species that can delay reproduction and wait for a season that provides the necessary conditions for seed production. Any other strategy might jeopardise the viability of seed produced and/or the survival of the parent plant.

The differences between populations in terms of the numbers of individuals flowering is clearly a plastic response to environmental conditions, such as shade and drought, and to the density-dependant effects of competition.

10.

SUMMARY

1. The phenology of dry weight allocation of plant tissue to major component parts was studied, over a twelve week period in six common herbaceous perennial species. Samples were taken from three field populations, representing a successional sequence from open quarry, through ungrazed grassland, to Crataegus scrub.
2. Reproductive effort, defined as the percentage allocation of dry weight plant tissue to reproductive structures (buds, inflorescences, receptacles and seeds) was calculated for each population, arranged to include all individuals, for each of the sampling periods. The different phenologies showed distinct intra-specific differences in peak reproductive effort, for four of the six species studied. In those four species, greatest population reproductive effort was shown in the disturbed quarry site, while the grassland populations showed the lowest values. The scrub site was intermediate between the other two.
3. Data on the relative percentages of flowering (i.e. showing some sort of reproductive structure) and non-flowering individuals in each population showed that the non-flowering percentage was very high in the grassland populations and correspondingly low in the quarry populations. This suggested that most of the intra-specific variation in population reproductive effort was explained by the proportion of individuals that actually flower.
4. Treating the flowering part of the population as a separate subsample, it was shown that average individual reproductive effort was very constant for all three sites, even though there were marked differences in mean total plant dry weight.

5. The data for mean total plant dry weight for the flowering sub-sample showed, for most species, lowest values in the grassland, increasing, via the scrub site, to highest values in the quarry population.
6. Data on the dry weight of leaves in relation to reproductive effort, for individual plants, showed that there was no precise dividing line between those individuals that flowered and those that did not.
7. Data on time of anthesis showed that quarry populations, for five species, was advanced in relation to the other two sites, sometimes very markedly. Generally, the grassland populations were the last to flower.
8. The intra-specific differences in leaf-area and stem height generally followed the same order ; smallest in grassland populations and largest in quarry populations. Leaf length : breadth ratios were found to be greater in the scrub populations of three species.
9. Leaf palatability experiments using Cepaea nemoralis showed that the snails did not discriminate between leaves (of the same plant species) taken from different parts of the succession.
10. It is hypothesised that individual perennial plants maintain their reproductive effort in any one year (if they flower) fairly constant, despite changes in the successional status of the habitat. The variation between sites in the number of individuals that flower, the time of anthesis and the various plant physical dimensions is seen as a plastic response to environmental conditions and the degree of competition.

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I would also like to thank Mrs Christina Webb for patiently typing the final script.

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APPENDIXSAMPLING DATES

<u>Sample Number</u>	<u>Date when sample was collected</u>
1	24.5.78
2	31.5.78
3	7.6.78
4	14.6.78
5	21.6.78
6	28.6.78
7	5.7.78
8	12.7.78
9	19.7.78
10	26.7.78
11	3.8.78
12	9.8.78

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