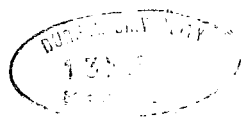
An investigation into reproductive effort in two successional stages using regression techniques

Wilson, A. M.

AN INVESTIGATION INTO REPRODUCTIVE EFFORT IN TWO SUCCESSIONAL STAGES USING REGRESSION TECHNIQUES

A M WILSON

Thesis submitted for
M.Sc. Advanced course
in Ecology.
University of Durham
October 1980



CONTENTS

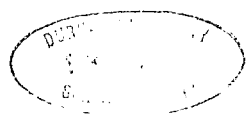
SECTION	PAGE
I. INTRODUCTION	I
2. OUTLINE OF MAIN METHOD	5
3. SITES	7
4. SPECIES	9
5. METHODS	I0
5.I Regression Methods	I0
5.2 Field and Laboratory Methods	I3
6. RESULTS	I5
6.I Regressions	I5
6.2 Plantago lanceolata	I8
i. Vegetative Dry Weight	I8
ii. Reproductive Dry weight	20
iii. Reproductive Effort	2I
iv. Germinability	22
6.3 Leontodon hispidus	23
i. Weights and Reproductive Effort	23
ii. Mechanisms	24
7. DISCUSSION	26
7.I Validity of Techniques Employed	26
7.2 Control of Flowering	3I
7.3 Differences between sites	32
7.4 Succession, Reproductive Effort and r- and K- selection	36
8. SUMMARY	40
ACKNOWLEDGEMENTS	42
REFERENCES	43
APPENDICES	48

1. INTRODUCTION

Life histories are partly the result of selection for the optimal allocation of resources to maintenance, growth and reproduction in a particular environment. The manner in which natural selection acts to partition the available resources has been considered from numerous theoretical viewpoints (e.g. Gadgil and Bossert 1970, Wilbur et al 1974) and has given rise to much recent research (e.g. Gadgil and Solbrig 1972, Harper and Ogden 1970, Stearns 1977). A base tenet of this research work is that there is a 'cost' associated with reproduction (see Stearns 1976).

Harper (1967) suggested that colonising species of plants would have higher reproductive efforts (R.E's) than plants of mature habitats. The theory of r- and K- selection as developed by MacArthur (1962), Cody (1966), MacArthur and Wilson (1967), Gadgil and Bossert (1970) and others predicts that in situations where density-dependent mortality is low r-selection will favour genotypes with a high rate of increase. The degree of environmental uncertainty has also been found to be a significant factor in selection for life history strategies (e.g. Southwood et al 1974, Wilbur et al 1974) Gadgil and Solbrig (1972) correlated highly disturbed or uncertain environments with r- selection and less uncertain environments with K- selection. They suggest that r- selected genotypes may have a greater reproductive effort and shorter life span than K- selected genotypes. Grime (e.g. 1974, 1977) has extended and developed the theory of r- and K- selection to suggest that there may be three main strategies. Plants may be adapted to competition, stress or disturbance with a range of possible options between these extremes.

The majority of previous research on resource allocation has tended to concentrate on one species, either by examining single



species populations from various sites (Gadgil and Solbrig 1972, Bradbury and Hofstra 1975, Hickman 1975, Holler and Abrahamson 1977, Roos and Quinn 1977, Raynal 1979) or by assessing the effect of changing one or more environmental variables on the allocation patterns (Harper and Ogden 1970, Ogden 1974, Hawthorn and Cavers 1978). Other workers have studied allocation patterns in a range of closely related species and attributed variations to differences in life strategy. (Gaines et al 1974, Hickman 1977, Pitelka 1977 Bell et al 1979, Bostock and Benton 1979, Primack 1979).

There has been relatively little work on allocation patterns in a range of species over a succession in the field (Newell and Tramer 1978, Abrahamson 1979, Stewart 1979) ("Succession" has been defined by Connell and Slatyer (1977) as "the changes observed in an ecological community following a perturbation that opens up a relatively large space") Nevertheless these studies have tended to confirm the r- and K- selection theory, the populations in the earlier successional habitats usually having higher reproductive efforts. Stewart (1979) found that higher population R.E's were primarily a result of greater numbers of flowering individuals rather than higher individual R.E. The suggestion that the number of individuals which flower in a population can vary because of changing conditions is supported by Van Andel and Vera (1977). In the perennial Chamaenerion angustifolium the numbers of flowering individuals were decreased by reducing mineral supply.

Stewart's (1979) work left several questions about the mechanism underlying variation in R.E. unanswered. He suggests that the observed variation in R.E. is environmentally rather than genetically controlled but has no empirical evidence. Whilst in some cases variations in resource allocation have been found to be genetically determined e.g. by Gadgil and Solbrig (1972), Abrahamson and Gadgil (1973),

others have shown them to be environmentally cued, plastic responses eg. Hickman (1975), Abrahamson and Hershey (1977), Roos and Quinn (1977).

The variation in the number of flowering individuals in Stewart's work prompted queries concerning the mechanisms which determine the decision to flower. In particular the possibility arose that plant size affects the probability of flowering. The method of analysis which is usually adopted in field resource allocation studies, ie. a random sample of individuals taken from a population at one specified time, makes investigation of this mechanism impossible. A method of following individual plants throughout the season is required. Such a method would not only facilitate investigation of the mechanisms determining the decision to flower, but also render the analysis of changes in reproductive allocation over the growing season statistically more rigorous.

In weight determinations of plants in the field, regression techniques have been used in order to avoid destroying the plants under observation. The method works by setting up relationships linking morphological measurements of the plant and plant weight. Hence the plants can be measured several times as they grow to provide estimates of their weight at intervals of time. Goodall (1945) was one of the first to make use of this method to assess changes in weight of the organs of tomato plants. Whittaker and Woodwell (1968) used regression relationships in their analysis of weight and production of shrubs and trees, advocating parabolic volume as the best Hutchings (1975) used height x diameter^2 to determine weight of Mercurialis perennis but as far as is known only one previous study (Werner 1975) has used the method for a plant with a rosette growth form (Dipsacus fullonum).

In this study it was hoped that by using a regression technique, some of the problems encountered in previous work could be avoided and some of the questions which were raised, answered.

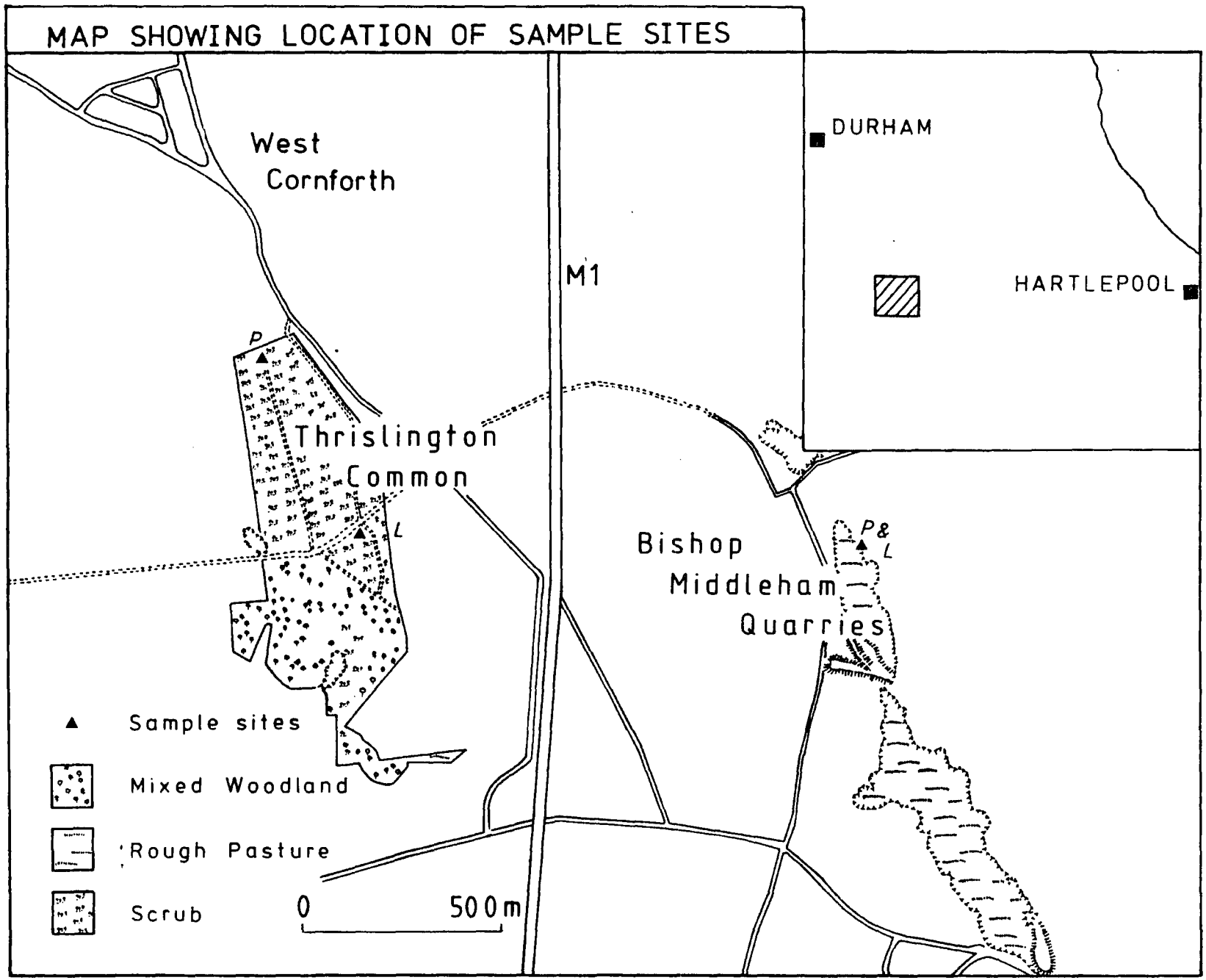
2. OUTLINE OF MAIN METHOD

Since the object of the study was to examine differences in reproductive effort at different successional stages, two sites were selected as being representative of an early and a later successional stage. These were a quarry site and a grassland site respectively. Two species of plant were chosen which were both present at each site and which were considered most suitable for analysis. At each site 40 Plantago lanceolata plants and 40 Leontodon hispidus plants were randomly selected and permanently marked. Another 40 Plantago plants and 40 Plantago seedlings were collected from each site and transplanted into pots in a greenhouse.

All the marked plants in the field and greenhouse plants were measured at two week intervals for a period of ten weeks. For each plant measurements were recorded of plant diameter, number of leaves, flowering scape length and flowering spike length (Flowering spike length was only recorded for Plantago lanceolata. These parameters were selected as being the most suitable predictors of plant vegetative dry weight (plant diameter and number of leaves) and plant reproductive dry weight (flowering scape length and flowering spike length). This assumption was made on consideration of a set of regression analyses relating the vegetative and reproductive dry weights of a set of individuals collected from the field to various measurements of their dimensions.

The regression formula which proved most accurate in predicting the dry weights was then applied to the measurements obtained from the marked plants in the field and greenhouse. Thus an estimate of their dry weight was obtained. The most appropriate regression formula was calculated on three occasions throughout the sampling period to account for any differences in the relationship between

dry weight and the morphological dimensions which might occur over the season. Once the measurements from plants in the field and greenhouse had been converted into dry weights using the most suitable formula a value for their reproductive effort was obtained using Hickmans (1975) formula whereby RE = $\frac{\text{total plant weight}}{\text{weight of reproductive parts}} \times 100$


MAP SHOWING LOCATION OF SAMPLE SITES
West
Cornforth
M1
DURHAM
HARTLEPOOL
P
Thrislington
Common
L
P&
L
Bishop
Middleham
Quarries
Sample sites
Mixed Woodland
Rough Pasture
Scrub
0
500m

3. SITES

The two sample sites chosen were similar to those sampled by Stewart (1979) and were considered to be representative of two seral stages on the magnesian limestone of the Durham escarpment Bishop Middleham quarry (NZ 3332) was chosen as an example of an early successional stage rather than Wingate quarry (used by Stewart 1979) since the latter was being landscaped throughout the sampling period. Bishop Middleham quarry is a Nature Conservancy Council SSS1 and still retains important plant communities which have developed over the past 40 years (Doody 1977). The particular site chosen was typical of much of the area with a large amount of bare ground and a sparse patchy vegetation dominated by Lotus corniculatus associated with Festuca rubra, Plantago lanceolata, and Agrostis stolonifera (see Table 1). In such an environment there are likely to be extremes of temperature, moisture and nutrient availability. In a limestone quarry in New York Raynal (1979) quotes surface temperatures of 48°C during the growing season.

Thrislington Plantation is less than 1 km West of Bishop Middleham quarry (see Map). It is listed as Grade 1 SSS1 (A Nature Conservation Review 1977) and is considered to be the best example of ungrazed magnesian limestone grassland. The vegetation has been identified as a Seslerio-Helictotrichetum association by Shimwell (1968) and supports a number of rare species such as Linum anglicum, Antennaria dioica and Epipactis atrorubens (also found at Bishop Middleham). The area is scheduled for quarrying within the next 50 years (Doody 1977) and attempts are presently being made to determine the feasibility of transplantation as a means of maintaining the genetic stock of individual species and perhaps communities.

TABLE 1. SPECIES LISTS

	QUARRY	LEONTODON GRASSLAND SITE	PLANTAGO GRASSLAND SITE
Achillea millefolium	11	4	2
Agrimonia eupatoria			P
Anthyllis vulneria		9	
Astralagus danicus		11	
Bellis perennis			31
Campanula rotundifolia		8	
Centaurea nigra	32	26	3
Centaurea scabiosa		21	
Centaurium erythraea	3		
Cerastium fontanum			2
Chamaecrion angustifolium			
Chrysanthemum leucanthemum	35		
Cirsium arvense	3		
Cirsium vulgare			P
Conopodium majus		6	
Crataegus monogna	1	7	5
Crepis capillaris			
Dactylorchis fuchsii	P	7	
Epipactis atrorubens		2	
Euphrasia officinalis	20	22	13
Fragaria vesca	11	11	
Galium verum		6	
Gentianella amarella	7	6	1
Gymnadenia conopsea	P	9	P
Helianthemum chamaecistus	2	21	
Hieracium pilosella	4	4	
Hypericum perforatum	7	7	
Hypochoeris radicata			
Hypochoeris autumnalis			11
Lathyrus pratensis			3
Leontodon hispidus	28	28	4
Linum catharticum	31	22	28
Linum anglicum		5	
Listera ovata		7	
Lotus coniculatis	90	13	21

TABLE I (Cont.)

	QUARRY	LEONTODON GRASSLAND SITE	PLANTAGO GRASSLAND SITE
Medicago lupulina	9	7	11
Ononis repens	3		
Plantago lanceolata	50	9	60
Plantago major			4
Plantago media		16	13
Polygala vulgaris	1	9	
Potentilla reptans			15
Potenum sanguisorba	2	10	
Primula veris	1	4	3
Prunella vulgans	29	8	13
Ranunculus bulbosus		5	
Rhinanthus minor		11	3
Ranunculus acris			16
Trifolium repens	1		49
Rosa Canina	P		
Ranunculus repens			6
Rubus fruticosus	2	3	
Scabiosa columbaria	10		
Senecio jacobaea	P	1	P
Senecio vulgaris			P
Silene dioica		P	
Taxaxacum officinale	6		13
Thymus drucei	13	5	
Tragopogon pratensis		3	
Trifolium pratense	15	10	3
Tussilago farfara			
Veronica chamaedrys			P
Viola riviniana		P	
Vicia cracca			5

TABLE I (Cont.) GRASSES, SEDGES AND RUSHES

	QUARRY	LEONTODON GRASSLAND SITE	PLANTAGO GRASSLAND SITE
Agropyron repens			2
Agrostis stolonifera	59	7	72
Agrostis tenuis	1	10	
Anthoxanthum odoratum		13	
Arrhenatherum	P	6	
Brachypodium sylvaticum			1
Briza media		17	6
Bromus crechis	2		
Cynosurus cristatus		13	13
Dactylis glomerata	11	8	22
Deschampsia caespitosa			
Festuca ovina	14		
Festuca rubra	58	34	25
Helictotrichon pratense		2	
Holcus lanatus	6	6	1
Koeleria cristata	4	3	
Lolium perenne		5	6
Phleum pratense			7
Poa pratensis		8	23
Sesleria albicans	2	41	
Carex flacca	12	19	28
Luzula campestris			2
Luzula multiflora			1
P = present but not recorded in quadrat			
Total number of species =	60	54	46

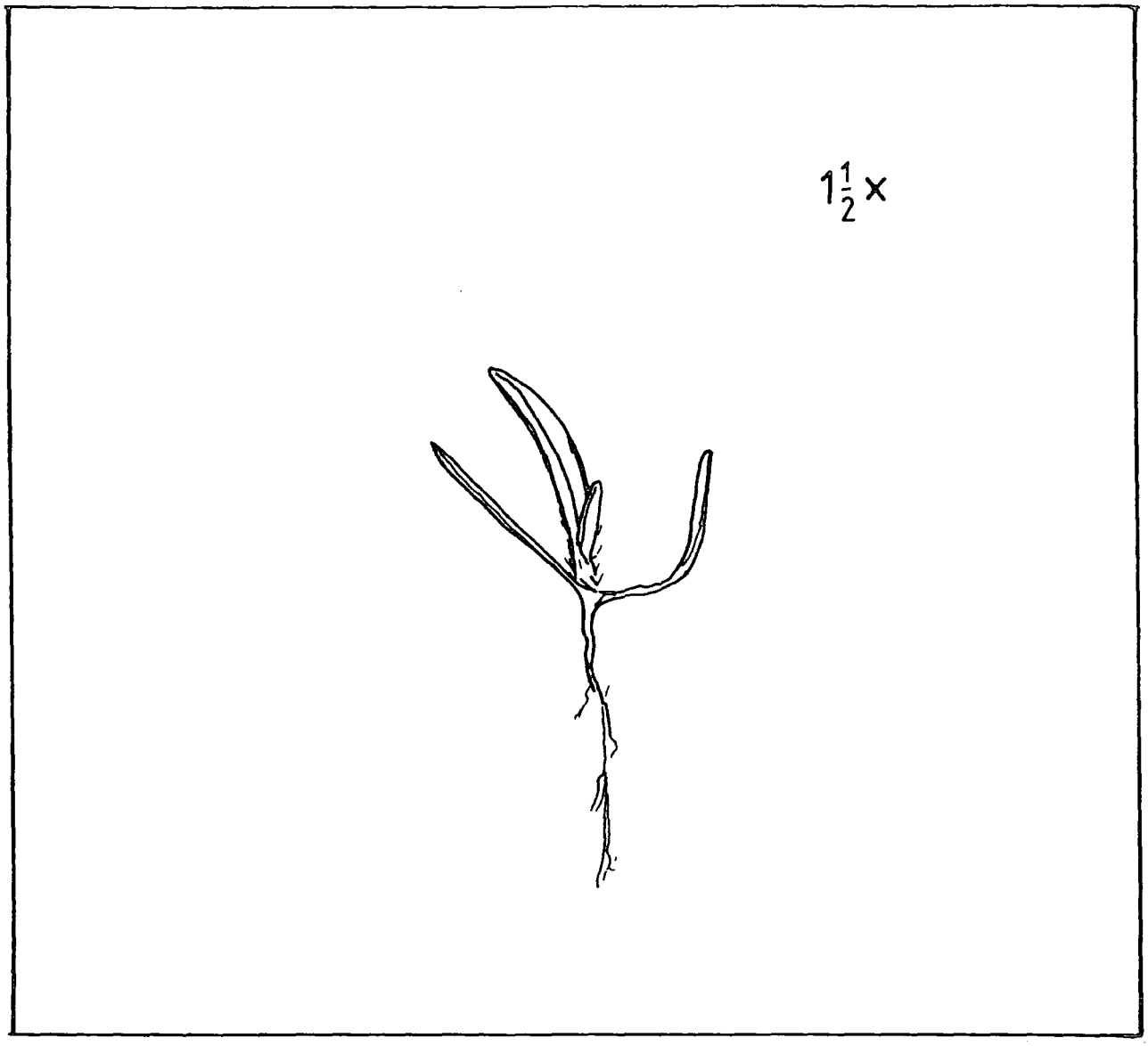
Unfortunately, on examination of the plant communities at Thrislington, it was impossible to find a site which included both of the chosen plant species in sufficient numbers (see later). It was therefore decided to use separate sites of similar size for each species. (see Map). The Leontodon site was on a gentle 6^{o} slope facing N.W and the vegetation was composed of a large number of species dominated by Sesleria albicans and Festuca rubra. The Plantago site was approximately 250m further N. in a level area of slightly inferior grassland dominated by Agrostis stolonifera and Plantago lanceolata.

4. SPECIES

The 2 species studied were selected using criteria which would enable efficient sampling and analysis. Both Plantago lanceolata and Leontodon hispidus are herbaceous perennials and are found at both sites. Stewart (1979) found that in both species individual plants are relatively easily distinguished from each other and in both plants the vegetative structures of the plant (ie leaves, stem etc) could be easily discerned from the reproductive structures (ie scape, inflorescence, seeds etc). In Leontodon the leaves are arranged in a rosette whilst in Plantago the leaves are radical and spirally arranged (Clapham, Tutin and Warburg 1959). These similar features facilitated the choice of parameters for use in the regression analyses.

Characteristically Leontodon hispidus has hispid leaves with forked hairs and this feature was useful in identification of the plant, particularly in the quarry site where there were many similar composites. Moreover P. lanceolata has a very distinctive seed and seedling (see fig 1) which enables it to be distinguished from other seedlings and pertinently, other Plantago species (Muller 1978). The seeds germinate in Spring and Autumn and seedlings could therefore be collected at the commencement of the sampling period in early May.

FIG. I DRAWING AND DESCRIPTION OF PLANTAGO LANCEOLATA SEEDLING (AFTER MULLER 1978)



Hypocotyl 5-20mm., glabrous, herbaceous, slightly woody. Seed leaves 2, sessile, strongly sheathed at ± hairy base, linear 1½-5cm. herb., glabrous, tip rounded-angular. Epicotyl absent. Leaves alternate, petiole 7-20mm. hairy ± strongly sheathed at base, lanceolate-linear with 3 parallel nerves, base curveate, 2½-4cm., herbaceous, with long slender sinuate hairs. Tip rounded -angular, entire.

Germ. autumn-spring.

5. METHODS

The sampling procedure can be subdivided into two sections: methods were employed to derive regressions relating the dry weight of the sample plants to some easily measurable parameter (s) of the plant; the regression obtained from this procedure was then applied to data derived from field measurements collected at regular intervals over the growing season. Thus, the assessment of reproductive effort was possible throughout the season by means of Hickmans (1975) formula (RE = reproductive dry weight/total dry weight as a percentage).

5.1 Regression Methods

The first sample of plants for the regression analyses was taken one week prior to the commencement of regular field sampling. This meant that the parameters which were most suitable for measurement and provided the best estimate of plant dry weight could be determined prior to the recording of plants in the field. At each site 40 *P. lanceolata* and 40 *L. hispidus* plants were collected and put into sealed polythene bags to minimise water loss and consequent reduction in plant size. The plants were washed and stored at 5°C, then measurements were carried out at the earliest opportunity. For each plant vegetative measurements were taken of rosette diameter, number of leaves, total cumulative leaf length, total cumulative leaf breadth and a leaf area index (total leaf length x total leaf breadth). Number of scapes, total cumulative length of flowering spikes were measured, these being possible indicators of reproductive dry weight. The measurement of dimensions was carried out on entire plants since this condition would be obligatory in the field. It was calculated that 40 plants was the least number likely to produce any statistically significant results when the usual flowering percentage of the population was

taken into consideration (Stewart 1979).

The plants were then divided into reproductive matter (scape, flower, fruit seeds etc) and vegetative matter (leaves stem etc), sealed in separate envelopes, labelled and dried at 90°C until a constant dry weight was obtained. The dried plant matter was weighed on a Mettler balance to 4-decimal places. Following Abrahamson and Gadgil (1973) and Gadgil and Solbrig (1972) roots were not included in the dry weight determinations. It is extremely difficult to ensure that the entire root biomass has been obtained (Dittmer 1972) and any attempt to procure the root biomass would have made sampling time impracticable.

Data on individual plant vegetative dry weights and their corresponding dimensions were coded and punched onto computer cards. Similarly data for individual reproductive matter dry weights and the corresponding dimensions were coded. Squared values of diameter were included in these preliminary investigations since Hutchings (1975) concluded that quadratic equations gave a greater predictive accuracy. Scattergrams showing the dry weights plotted against the various measurements together with the relevant regressions and their associated statistics were produced using S.P.S.S. (Nie et al 1975) on the N.U.M.A.C. computer.

The most appropriate index of vegetative plant weight was found to be a combination of plant diameter and number of leaves (see Results). Hence, field data collection of vegetative parameters was restricted to these measurements. Data on both cumulative scape length and cumulative spike length were collected as indicators of reproductive dry weight in Plantago lanceolata. Leontodon hispidus, however, had not begun to flower at the time of the first regression determination.

Any plant species will exhibit changes in the fresh to dry weight ratio during growth ie the relationship between the measured parameters and the dry weights will change. Consequently a series of regressions should always be used to reduce errors (Hutchings 1975). Ideally a regression relationship should be determined frequently enough to eliminate significant differences between successive regressions. However, the regression analyses tended to be very time consuming and it was decided that a total of three separate regression determinations, one camed out at the beginning of the sample period, one in the middle and one at the end would be sufficient to account for any significant deviations which might occur.

In the second and third regressions plants were again taken from the field, measured and separated into their component parts, dried and weighed. Some greenhouse plants (see later) were included in the third regression since these plants tended to be larger than many of the field plants. In the second and third regressions measurements taken were limited to those which had proved most suitable in the first regression (see Table 2). By the time the second set of regressions were determined L. hispidus plants had begun to flower and it was found that total cumulative scape length was the most useful predictor of Leontodon reproductive dry weight. The first regression, therefore was applicable to small plants at the beginning of the season whereas the third regression could be applied to larger plants at the end of the season. This was particularly so in P. lanceolata where the third regression included many of the large greenhouse plants. (See 'Results' for further details of regression applicability).

TABLE 2. CORRELATION COEFFICIENTS FOR FIRST SET OF REGRESSIONS OF WEIGHTS AGAINST VARIOUS PARAMETERS

GRASS

		correlation coefficient	standard error of estimate	probability of significance
Plantago Vegetative Dry Weight with:-	No. of LVES	0.819	89.437	0.00001
	Diameter	0.341	146.6	0.01562
	$Diam^2$	0.315	148.1	0.023
	N x D	0.908	65.2	0.00001
	$N \times D^2$	0.768	99.87	"
	Leaf area index	0.976	33.5	"
	Total leaf length	0.942	51.9	"
	Total leaf width	0.951	47.8	"
Plantago Reproductive Dry Weight with:-	No. of Scapes	0.900	14.95	"
	Total length of Scapes	0.863	17.35	"
	Total length of Spikes	0.960	9.6	"
Leontodon Vegetative Dry Weight with:-	No. of LVES	0.567	9.666	0.00007
	Diameter	0.312	11.15	0.0249
	$Diam^2$	0.294	11.21	0.032
	N x D	0.583	9.52	0.00004
	$N \times D^2$	0.546	9.82	0.00013
	Leaf area index	0.795	7.106	0.00001
	Total leaf length	0.719	8.15	"
	Total leaf width	0.805	6.961	"

TABLE 2. CORRELATION OF COEFFICIENTS FOR FIRST SET OF REGRESSIONS OF WEIGHTS AGAINST VARIOUS PARAMETERS

			QUARRY	
Plantago Vegetative Dry Weight with:-	No. of LVES	0.307	50.9	0.0269
	Diameter	0.689	38.7	0.00001
	$Diam^2$	0.693	38.57	"
	N x D	0.884	25.01	"
	$N \times D^2$	0.835	29.43	"
	Leaf area index	0.965	13.88	"
	Total leaf length	0.909	22.258	"
	Total leaf width	0.904	22.85	"
Plantago Reproductive Dry Weight with:-	No. of Scapes	0.796	10.6	"
	Total length of Scapes	0.880	8.37	"
	Total length of Spikes	0.903	7.577	"
Leontodon Vegetative Dry Weight with:-	No. of LVES	0.652	46.11	"
	Diameter	0.857	31.316	"
	$Diam^2$	0.895	27.07	"
	N x D	0.909	25.36	"
	$N \times D^2$	0.930	22.26	"
	Leaf area index	0.979	12.36	"
	Total leaf length	0.943	19.6	"
	Total leaf width	0.858	31.17	"
		correlation coeffecient	standard error of estimate	probability of significance

TABLE 2. CORRELATION COEFFICIENTS FOR FIRST SET OF REGRESSIONS OF WEIGHTS AGAINST VARIOUS PARAMETERS

			TOTAL	
Plantago Vegetative Dry Weight with:-	No. of LVES	0.801	78.0	0.00001
	Diameter	0.533	110.23	"
	$Diam^2$	0.506	112.39	"
	N x D	0.927	48.76	"
	N x D^2	0.825	73.499	"
	Leaf area index	0.980	25.5	"
	Total leaf length	0.953	39.48	"
	Total leaf width	0.957	37.48	"
Plantago Reproductive Dry Weight with:-	No. of Scapes	0.887	13.07	"
	Total length of Scapes	0.849	15.004	"
	Total length of Spikes	0.952	8.628	"
Leontodon Vegetative Dry Weight with:-	No. of LVES	0.742	34.9	"
	Diameter	0.813	30.3	"
	$Diam^2$	0.861	26.4	"
	N x D	0.921	20.19	"
	N x D^2	0.932	18.76	"
	Leaf area index	0.977	11.078	"
	Total leaf length	0.955	15.4	"
	Total leaf width	0.891	23.6	"
		correlation coefficient	standard error of estimate	probability of significance

5.2 Field and Laboratory Methods

At each sample site a permanent plot 10m by 10m was identified and marked. The vegetation was recorded using randomly located $100mm^2$ quadrats in which the occurrence of species was noted (see Table 1). The specific plants studied (40 Plantago and 40 Leontodon at each site) were identified as those individuals nearest to randomly located points in the 10m grid. The plants were labelled and numbered using a white plastic peg which also facilitated their relocation.

In order to determine whether any observed differences between the plants at the quarry and grassland sites were genetically or environmentally cued it was necessary to remove plants from environmental influences. Since the sampling time involved in this procedure was great it was decided to restrict this experiment to one species ie Plantago lanceolata. Two weeks before commencement of regular sampling 40 plants from each site were carefully excavated and replanted in potting compost in 6" plastic pots. Environmental effects may well be carried over from one season to the next so in order to eliminate these effects seeds or seedlings should be studied, Since seeds were not available 40 young seedlings of uniform cotyledon size were also collected from each site. The seedlings were placed in sealed plastic tubes to minimise water loss and mechanical damage and were transplanted into potting compost in 6" pots (one per pot) as soon as possible. The plants and seedlings were kept in the greenhouse in an environment which simulated external conditions as far as possible.

Measurements of plant diameter, number of leaves, cumulative scape length and cumulative spike length were then taken of all these plants (both field and greenhouse) at 2 week intervals commencing on June 1st. Other studies have used sampling intervals of 3 weeks and more on a variety of plants eg Newell and Tramer (1978) and Bostock and Benton (1979) so 2 weeks was considered an adequate time interval. Sampling was subjectively terminated when the maj-

ority of Plantago had seeded. (Altogether 5 samples were taken).

In the laboratory measurements of Plantago spike length and number of 2 - seeded capsules were noted and a regression relating the two was computed. It was hoped that this would provide an additional measure of reproductive achievement.

In order to assess the relative germinability of Plantago seeds from each site 25 seeds of each type were placed on damp filler paper in Petri dishes and allowed to germinate. In total there were 6 different types of seed:- Field quarry seed, quarry seed from plants grown for one season in greenhouse and quarry seed from seedlings grown in greenhouse; field grassland seed, grassland seed from plants grown for the season in greenhouse and grassland seed from seedlings grown in greenhouse. The experiment was repeated using Petri dishes covered in foil to exclude light. Three replicate experiments were conducted for statistical validity. The numbers of seeds which had germinated after four weeks were noted.

The number of vegetative rosettes produced by each plant grown for one season in the greenhouse at the end of the sampling period was also recorded.

The data from the field and greenhouse sampling were converted to dry weight using the appropriate regression formula. The results were then analysed using various procedures available with S.P.S.S.

6. RESULTS

6.1 Regressions

Scattergrams of the various measured parameters against the dry weights using the first set of regression data were produced and examined. The validity of each parameter as a predictor of plant dry weight was then assessed by means of their correlation coefficients. The data were found to be slightly positively skewed and theoretically a transformation should be applied to such data before any correlation or regression analysis. However, one of the principle objects of the study was to predict absolute values of plant dry weight (particularly in considering the mechanisms involved in the decision to flower) and any transformation of the data at this stage would have made this impossible. It should be noted, however, that the slight shewness may make some difference in the absolute values of the correlation coeffients. Nevertheless their relative relationships will not change.

The correlation coefficient is an index which reflects the degree to which changes in direction and magnitude in one set of data (ie the dry weight values) are associated with comparable changes in the other set (ie the measure parameter). Whittaker and Woodwell (1968) have suggested an alternative method for expression of the relative accuracy of predictions made from regressions. The Standard Error of the Estimate for a Regression.

$$S\,E = \sqrt{(\Sigma d^2/n - 1)}$$

In order to express the relative spread of points from a linear regression the Standard Error was divided by the mean value of the y - observations to produce an estimate of relative error. However, this value is also influenced by skewness and under these circumstances the correlation coefficient was considered to be an adequate index

of the relative accuracy of the predictions.

The correlation coefficients for the various parameters analysed in the first regression sample are shown in Table 2. From this table it is apparent that the best predictors of vegetative dry weight for both Leontodon and Plantago was the leaf area index (R = 0.98 for both plants) (see figs 2 and 1 a and b). Unfortunately this parameter was far too time consuming to collect in the field as were total leaf length and total leaf breadth. Consequently either no. of leaves x diameter (R = 9.3 for Plantago) or no. of leaves x diameter squared (R = 9.3 for Leontodon) (see figs 2iii and iv) were chosen as being most suitable. A composite regression including both the plants from the quarry site and plants from the grassland site was selected because it produced a higher correlation coefficient than either site treated separately.

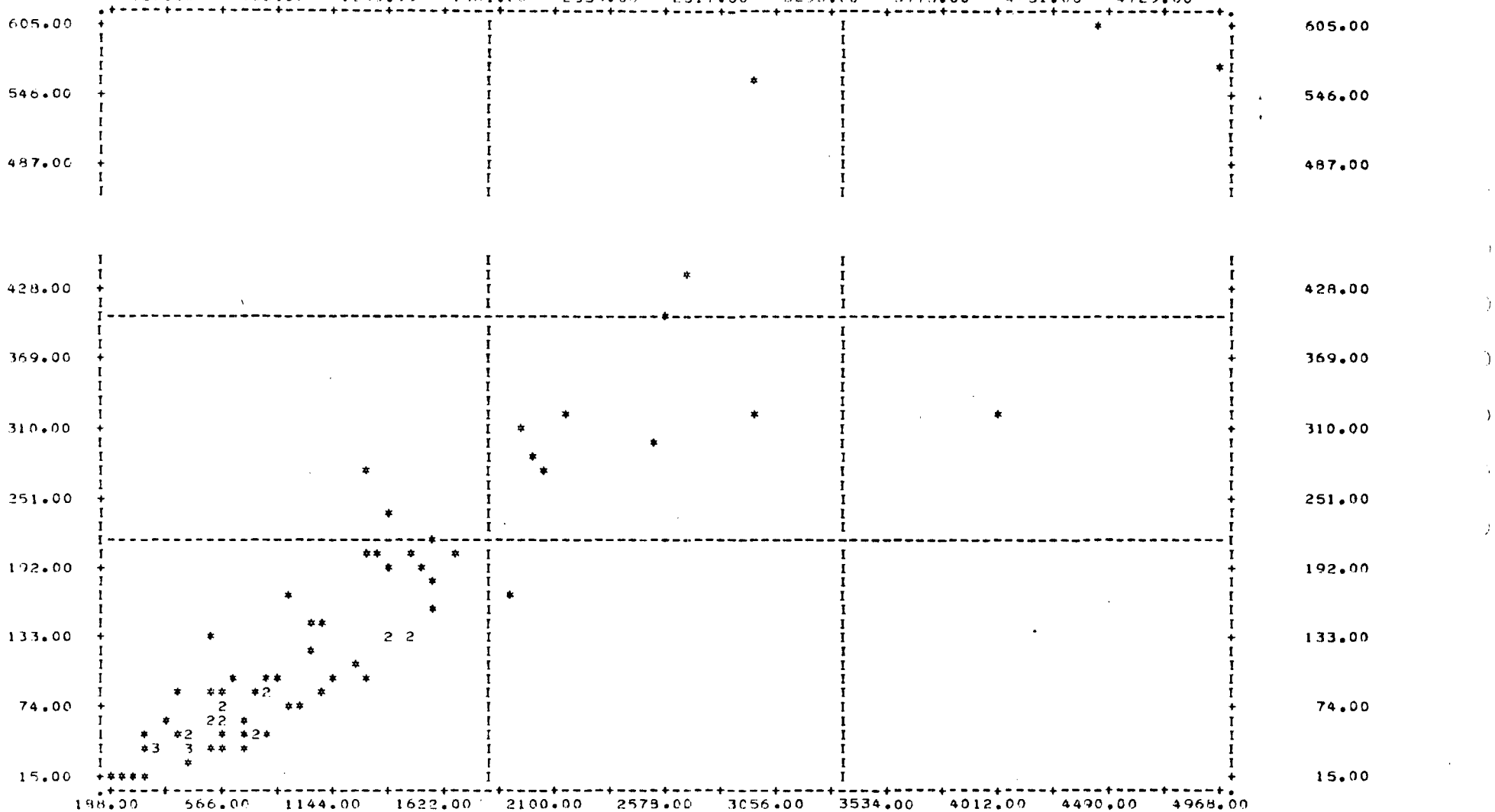
It is also evident from Table 2 that there are some interesting differences in morphology between the two species and furthermore, between similar species at different sites. Leontodon has a much better correlation between vegetative dry weight and diameter (0.81) than Plantago (0.53) suggesting that Leontodon has a more compact form. There is also a striking difference between the Leontodon plants at the quarry site, having a good correlation with diameter (0.85) and the grassland plants having a poor correlation with diameter (0.31). Similarly Plantago plants at the quarry site have a higher correlation with diameter (0.68) than those at the grassland site (0.34).

In the first regression analysis the best indicator of Plantago reproductive weight was the total length of the flowering spike. In subsequent regressions, however the total length of the scape was a more accurate predictor. This was to be expected since as the scape enlarged over the season the relative importance of the

FIG. 2i SCATTERGRAM OF VEGETATIVE DRY WEIGHT WEIGHT WITH NO. OF LEAVES x DIAM.

PLANTAGO LANCEOLATA

FILE NONAME (CREATION DATE = 09/06/79)
SCATTERGRAM OF (DOWN) V13 (ACROSS) V6



STATISTICS..

CORRELATION (R)-	0.92739	R SQUARED -	0.86005	SIGNIFICANCE -	0.00001
STD ERR OF EST -	48.76053	INTERCEPT (A) -	-14.93216	SLOPE (B) -	0.13123

THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 9.73829 ON THE LEFT MARGIN
A VALUE OF 4814.08203 ON THE TOP MARGIN

PLOTTED VALUES -	80	EXCLUDED VALUES-	0	MISSING VALUES -	0

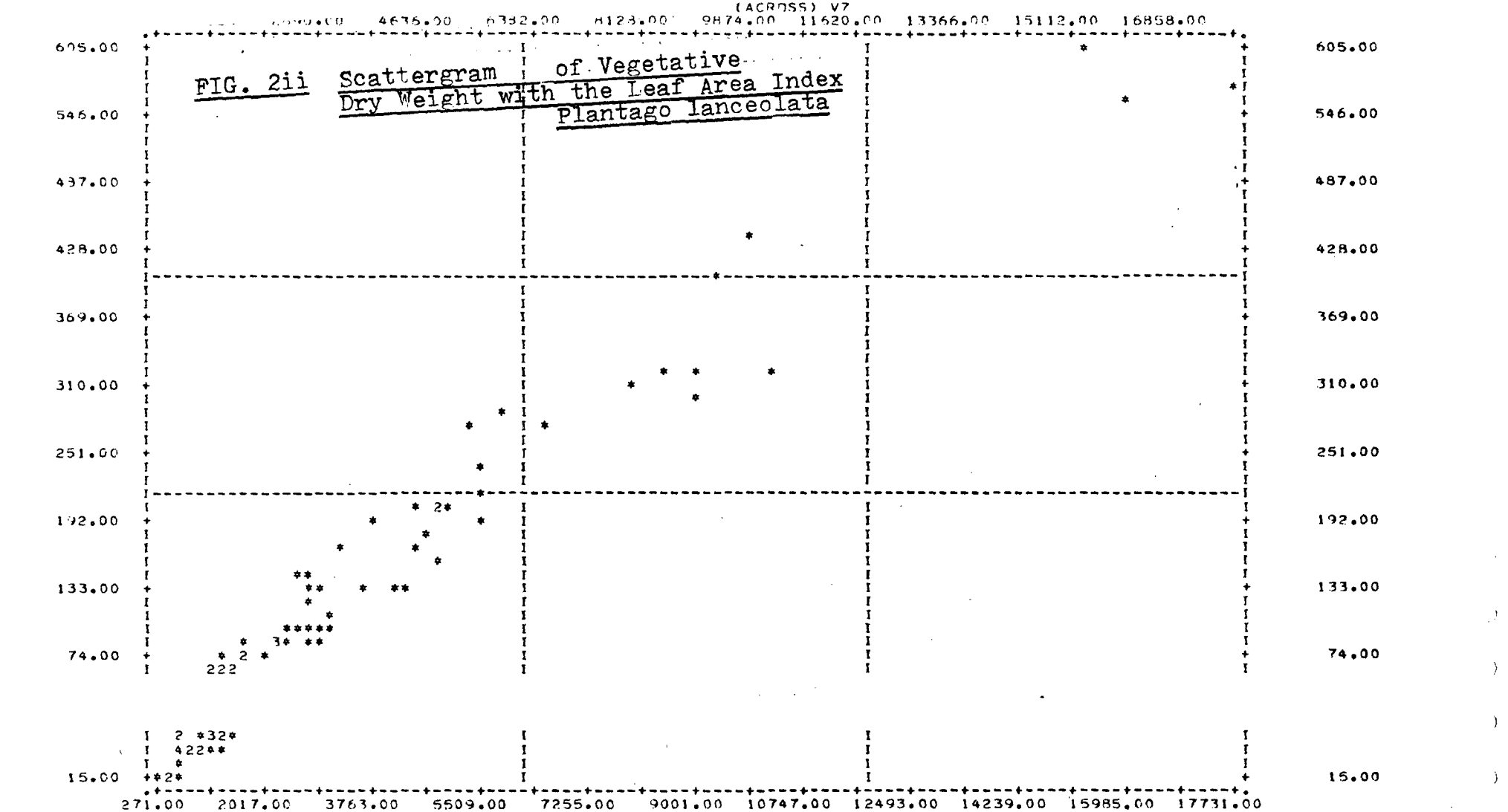


FIG. 2ii Scattergram of Vegetative Dry Weight with the Leaf Area Index Plantago lanceolata

FIRST REGRES SCATTERGRAMS 09/06/79 PAGE 15

STATISTICS..

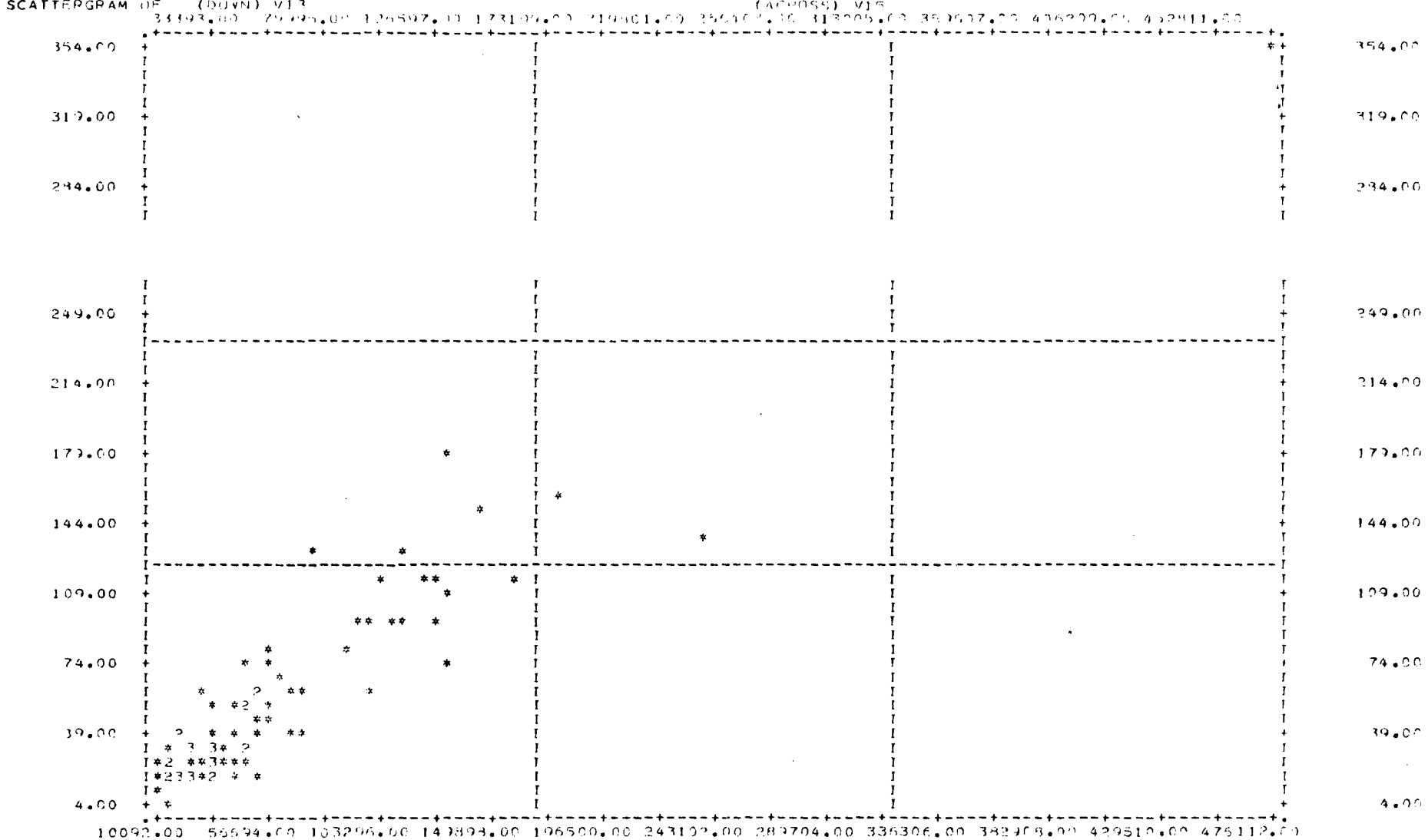
CORRELATION (R)-	0.98062	R SQUARED -	0.96162	SIGNIFICANCE -	0.00001
STD ERR OF EST -	25.53523	INTERCEPT (A) -	14.76862	SLOPE (B) -	0.03586

THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 24.48569 ON THE LEFT MARGIN
A VALUE OF 16790.09375 ON THE TOP MARGIN

PLOTTED VALUES -	60	EXCLUDED VALUES-	0	MISSING VALUES -	0

'*********' IS PRINTED IF A COEFFICIENT CANNOT BE COMPUTED.

Fig. 2iii Scattergram of Vegetative Dry Weight with $No.\ of\ Leaves \times Diameter^2$
Leontodon hispidus



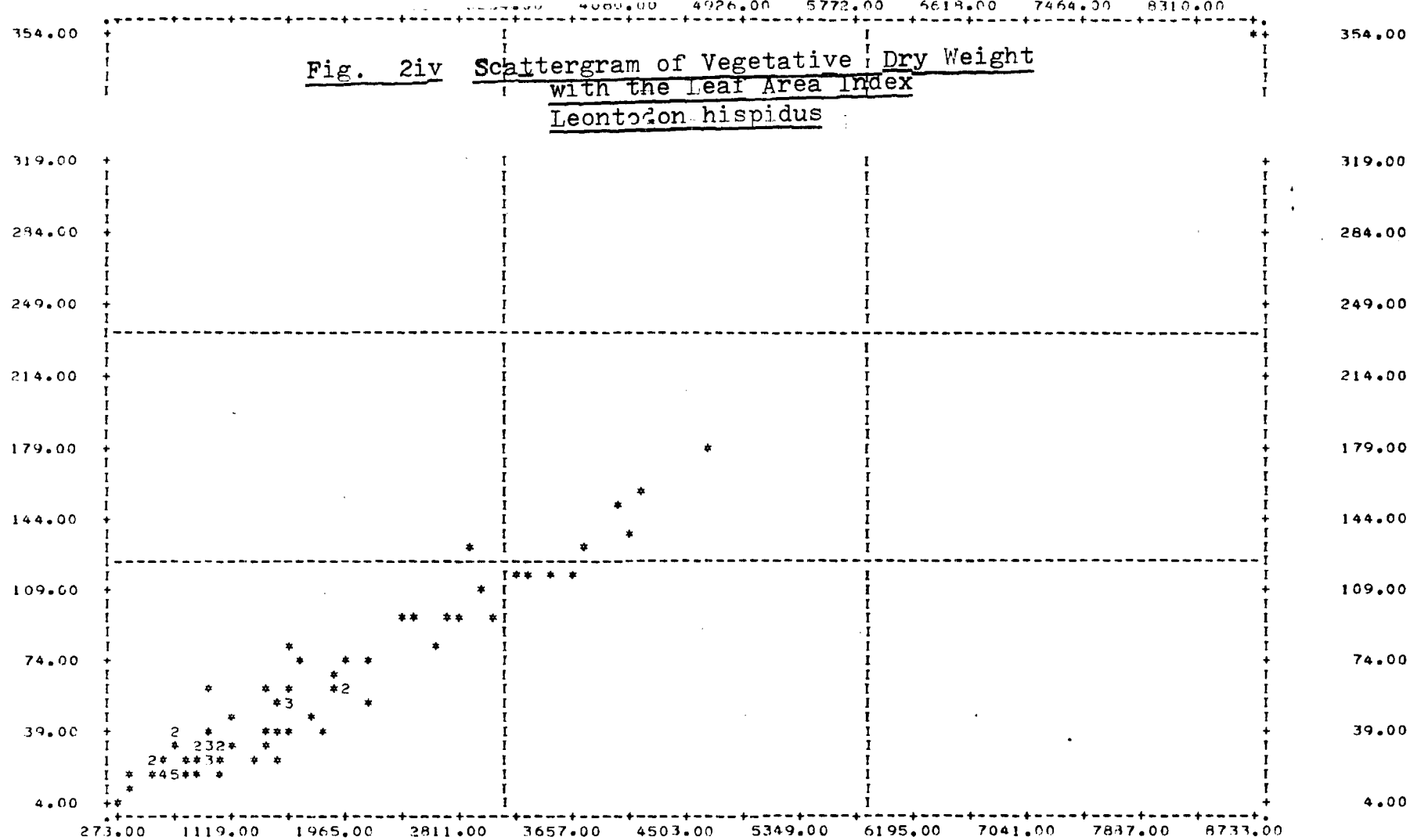
STATISTICS..

CORRELATION (R)-	0.93292	R SQUARED -	0.87033	SIGNIFICANCE -	0.00001
STD ERR OF EST -	18.76306	INTERCEPT (A) -	10.71903	SLOPE (B) -	0.00075

THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 18.25355 ON THE LEFT MARGIN
A VALUE OF 468554.43750 ON THE TOP MARGIN

PLOTTED VALUES -	10	EXCLUDED VALUES-	0	MISSING VALUES -	0

Fig. 2iv Scattergram of Vegetative Dry Weight with the Leaf Area Index Leontodon hispidus



FIRST REGRES SCATTERGRAMS 09/06/79 PAGE 66

STATISTICS..

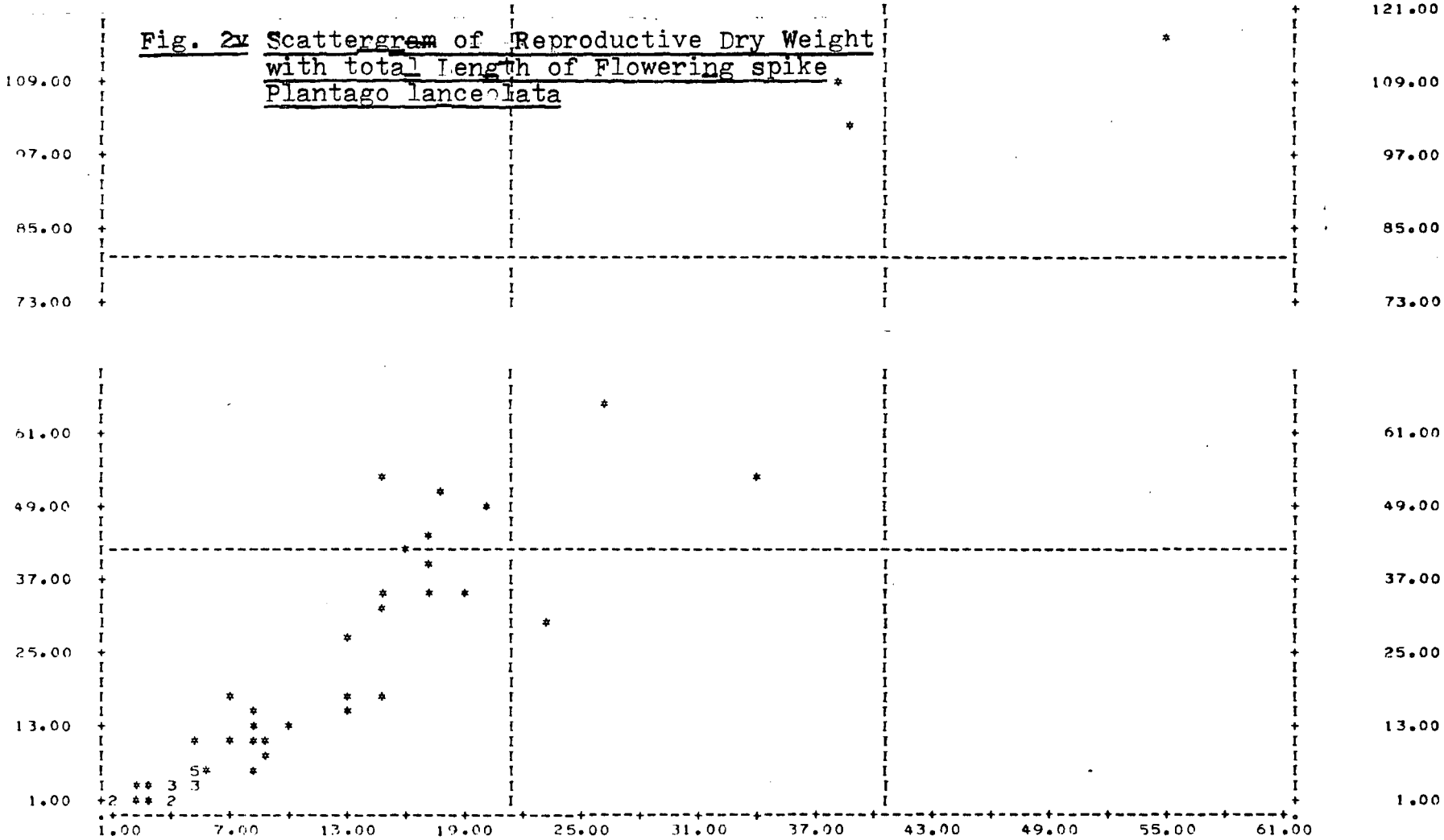
CORRELATION (R)-	0.97714	R SQUARED -	0.95480	SIGNIFICANCE -	0.00001
STD ERR OF EST -	11.07812	INTERCEPT (A) -	-6.56834	SLOPE (B) -	0.03838

THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 3.90982 ON THE LEFT MARGIN
A VALUE OF 328.61768 ON THE RIGHT MARGIN

PLOTTED VALUES -	80	EXCLUDED VALUES-	0	MISSING VALUES -	0

'*********' IS PRINTED IF A COEFFICIENT CANNOT BE COMPUTED.

Fig. 2x Scattergram of Reproductive Dry Weight with total Length of Flowering spike Plantago lanceolata



FIRST REGRES SCATTERGRAMS 09/06/79 PAGE 16

STATISTICS..

CORRELATION (R)-	0.95277	R SQUARED -	0.90777	SIGNIFICANCE -	0.00001
STD ERR OF EST -	8.62837	INTERCEPT (A) -	-5.92718	SLOPE (B) -	2.44766

THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 1.84959 ON THE BOTTOM MARGIN
A VALUE OF 52.83702 ON THE TOP MARGIN

PLOTTED VALUES - 50 EXCLUDED VALUES- 0 MISSING VALUES - 30

'*********' IS PRINTED IF A COEFFICIENT CANNOT BE COMPUTED.

FIRST REGRES SCATTERGRAMS 09/06/79 PAGE 17

terminal flowering spike in the total reproductive weight became less. Total scape length was considered to be the only reliable measure of reproductive dry weight in Leontodon since the flower and fruit altered dimensions throughout the season.

This procedure for selecting regressions was carried out on the 2nd and 3rd samples. The exact parameters which were selected and their associated regression values are given in Table 3. The scattergrams for these regressions are included in the Appendix. The fact that different regressions are necessary over the season indicates that the relationship between the dry weight of the plant and its dimensions does change over the season. All the regression equations were then applied to the field and greenhouse sample data in order to convert these measurements to dry weights. In the case of Plantago the problem of when to apply each regression was resolved subjectively. Since the first regression sample was taken just before commencement of field sampling and growth of the plants at this time was rapid, this regression was only applied to the first field and greenhouse sample. The third Plantago regression included some very large greenhouse plants and when this regression equation was applied to the field data a large number of negative values were obtained (see discussion). The third regression was therefore not applied to field data, only data concerning greenhouse plants.

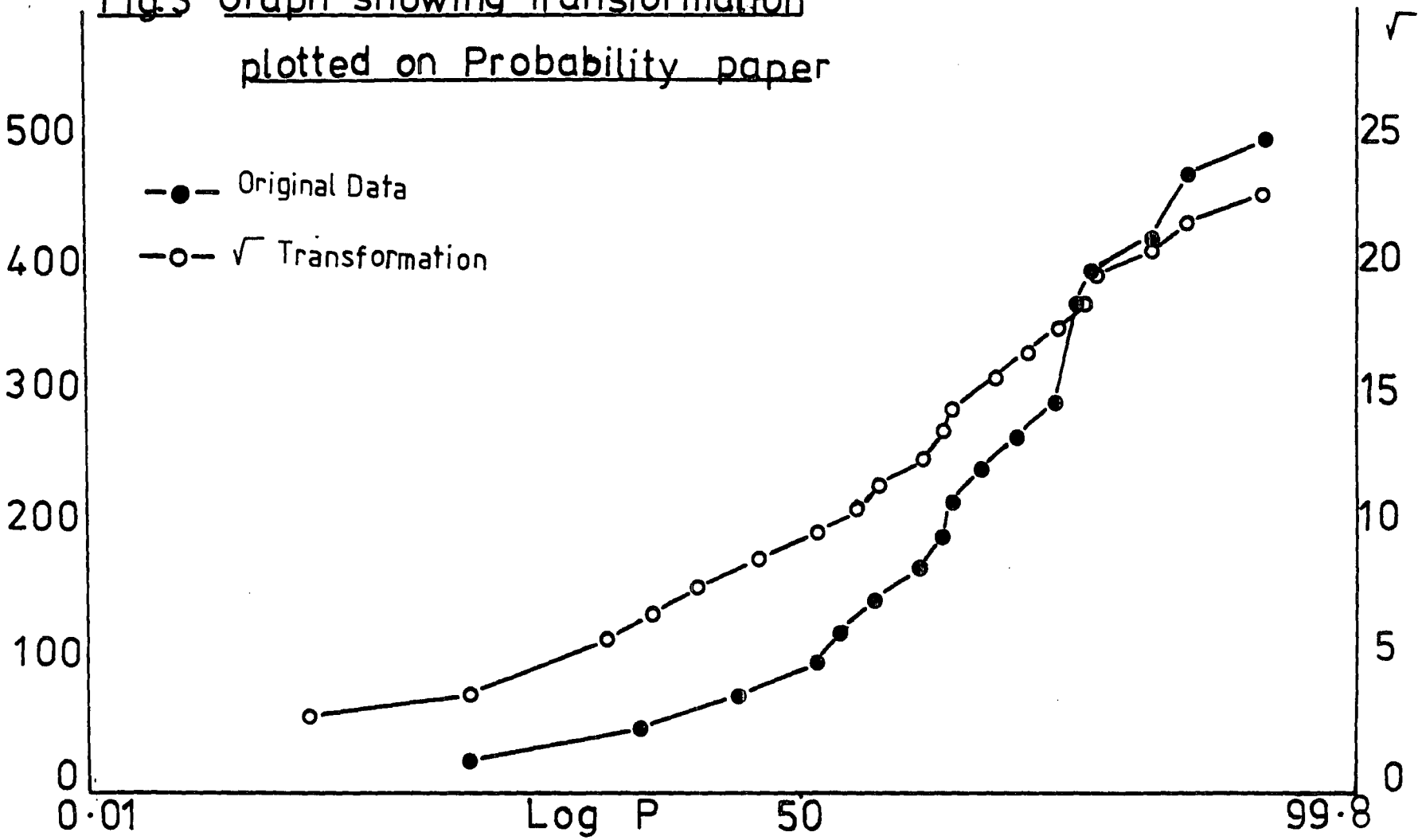
On examination of the dry weight data for Leontodon it was evident that the 1st and 3rd regression equations produced many spurious negative values (see discussion for possible explanations) and it was decided to restrict analysis to the 2nd equation values.

Since some data were again found to be slightly positively skewed a square root transformation was applied before calculation

TABLE 3. REGRESSION EQUATION FIGURES.

REGRESSION	a	b	x
1st. *Plantago* for Vegetative Dry Weight	-14.93216	0.13123	No. of leaves x diameter
2nd. *Plantago* for Vegetative Dry Weight	95.39337	0.00049	No. of leaves x diameter
3rd. *Plantago* for Vegetative Dry Weight	98.76514	0.19403	No. of leaves x diameter
1st. *Leontodon* for Vegetative Dry Weight	10.71903	0.00075	No. of leaves x diameter
2nd. *Leontodon* for Vegetative Dry Weight	-14.47674	0.15567	No. of leaves x diameter
3rd. *Leontodon* Vegetative Dry Weight	58.75476	0.00037	No. of leaves x diameter
1st. *Plantago* for Reproductive Dry Weight	-5.92718	2.44766	Total length of Flowering Spikes
2nd. *Plantago* for Reproductive Dry Weight	-59.82900	0.65728	Total length of Scapes
3rd. *Plantago* for Reproductive Dry Weight	-159.44195	0.99643	Total length of Scapes
2nd. *Leontodon* for Reproductive Dry Weight (Plants were not Flowering at time of First Regression)	1.31637	0.76623	Total length of Scapes
3rd. *Leontodon* for Reproductive Dry Weight	-12.53409	0.68362	Total length of Scapes

Fig.3 Graph showing Transformation plotted on Probability paper



of t - tests to determine significant differences between species and sites. When values from the first set of field data were plotted on probability paper a square root transformation was the most satisfactory in approximating the straight line characteristic of normal data (see fig 3). The transformation was applied to enable the adoption of parametric methods of statistical analysis which are generally considered to be preferable to non-parametric methods (Sokal and Rolf 1969).

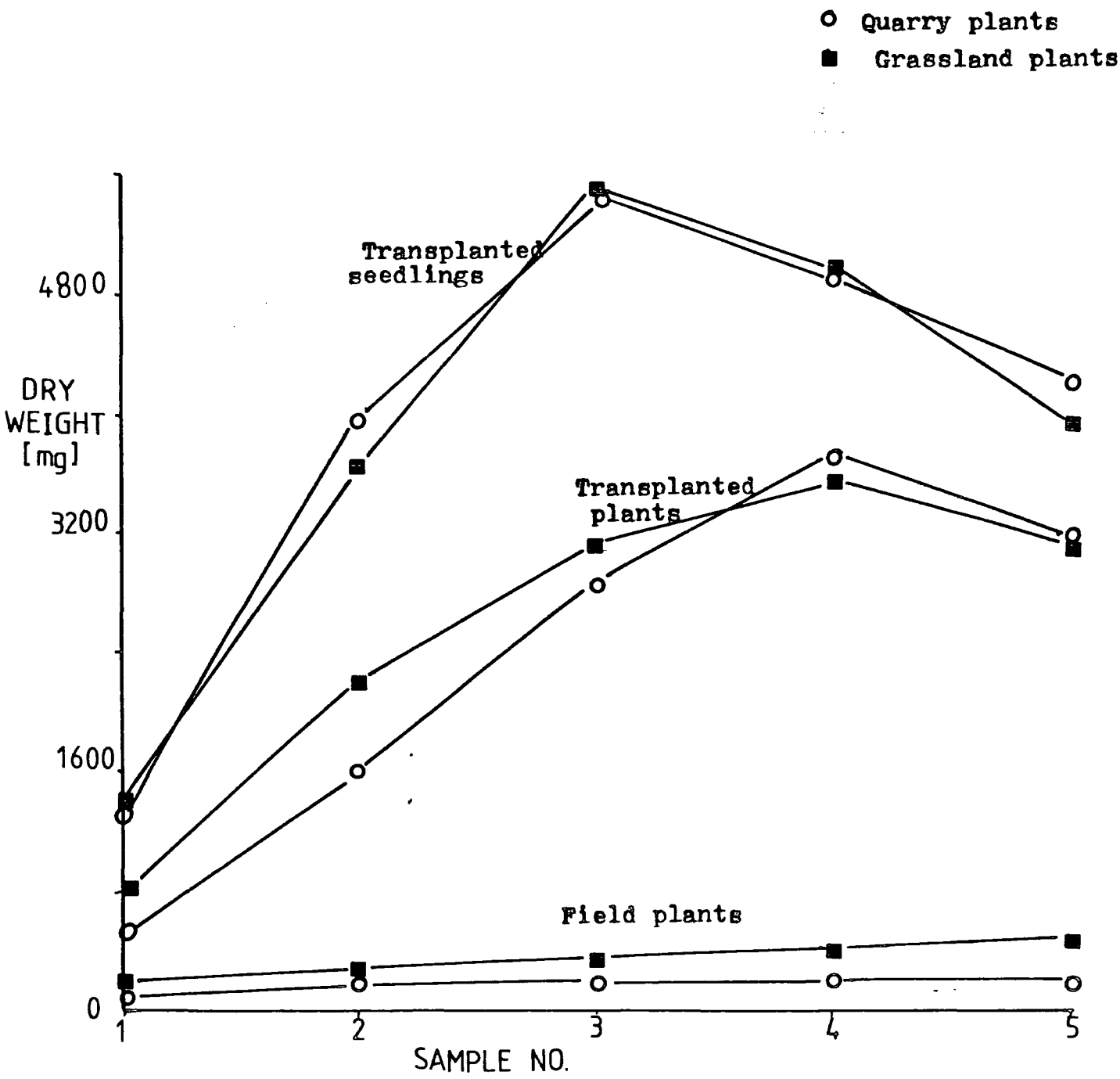
6.2 Plantago Lanceolata

i. Vegetative Dry Weight

The vegetative dry weights of the 3 classes of Plantago are shown in table 4 and fig 4. There is a marked difference in the vegetative weights attained by each class of plant. The greatest weights are achieved by the seedlings which reach an average peak of 5343 mg. in the 3rd sample week, after which they begin to decline. The transplanted greenhouse plants reach an average peak of 3646 mg. in the 4th sample week. Although the seedlings and plants began the sampling period with highly significant differences in vegetative dry weight ($P < 0.001$), this difference becomes less marked over the time period until it becomes unsignificant in the last sample week. The Plantago plants growing in the field have much lower vegetative weights. The Quarry Plantago plants reach a peak of 199.7mg in the 4th week then begin to decline slightly. In the fifth week the grassland Plantago plants have mean vegetative weights of 450.8mg and do not show any evidence of a decline within the sample period. The Plantago plants in the field always have a significantly different mean vegetative dry weight from the transplanted plants in the greenhouse and hence also from the seedlings. ('Seedlings' is used as a distinguishing term meaning those plants

FIG.4 DRY WEIGHT OF VEGETATIVE MATTER

PLANTAGO LANCEOLATA



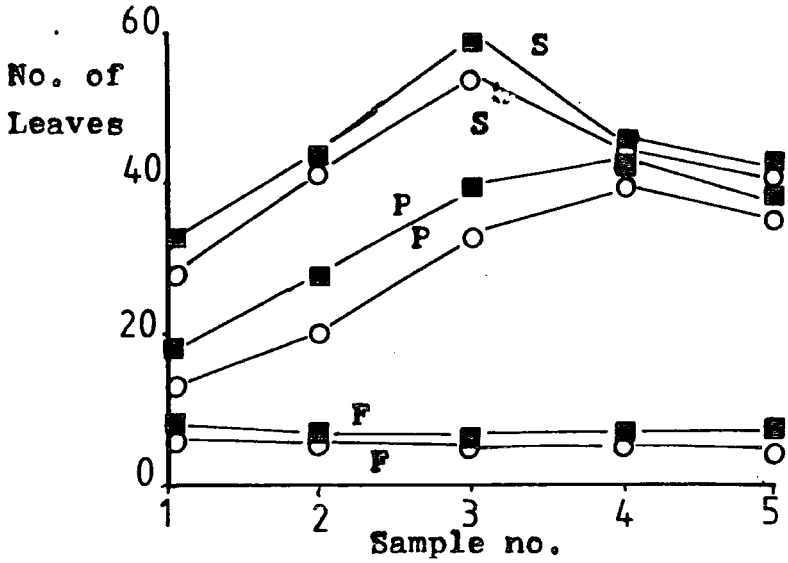
in the greenhouse which were transplanted as seedlings).

In the field Plantago plants, there is always a significant difference in vegetative dry weight between those from the grassland and those from the quarry ($P < 0.001$). The grassland Plantago plants are always larger and this trend becomes more pronounced as the season progresses. In the first two sample weeks there is a difference between the grassland greenhouse plants and quarry greenhouse plants ($P = < 0.01$) but this gradually disappears until in the final week the plants can virtually be regarded as coming from the same population ($P = 0.818$). At no time are the seedlings from the grassland and the seedlings from the quarry significantly different.

These figures for vegetative dry weight are based on the data collected on plant diameter and number of leaves and it is interesting to examine these values separately. The seedlings again have the largest number of leaves with a maximum average/plant of 56.6 in the third week. The greenhouse plants reach a maximum average of 42 leaves /plant in the 4th week whilst the field plants have a maximum number of leaves at the beginning of sampling (7.7/plant for the grassland and 6.6/plant for quarry). Grassland plants consistently have a larger mean number of leaves in all classes but this is only statistically significant at the end of field sampling and beginning of greenhouse plant sampling (see table 5 and fig 5).

The difference in diameter between the various classes of plant is not as pronounced (see table 6 fig 6). Both seedlings and greenhouse plants reach a maximum in the 4th week with mean diameters/plant of 549mm and 442mm respectively. Field Plantago maxima are in the fourth week at the quarry (173mm) and fifth week at the grassland (276mm). The seedlings and greenhouse plants never display any significant difference in diameters at the two sites but in the field populations

FIG. 5 NUMBER OF LEAVES
PLANTAGO LANCEOLATA



S = Transplanted seedlings

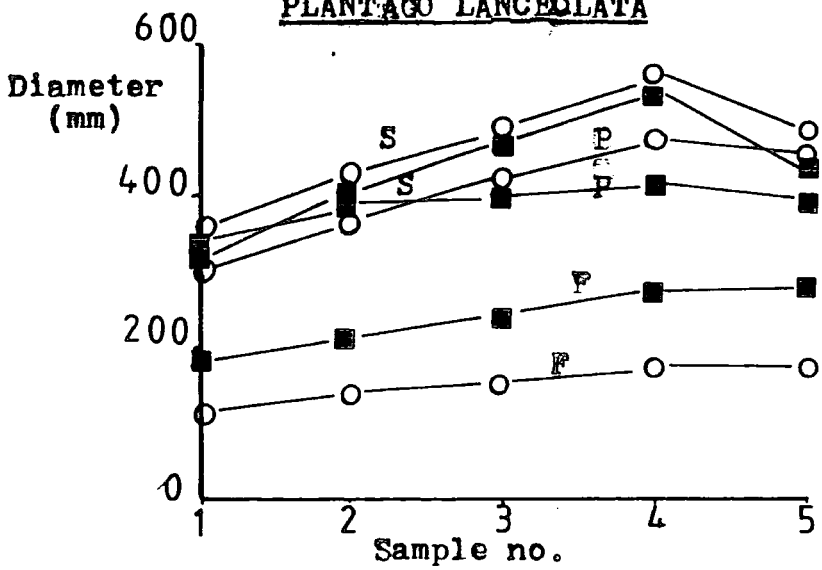
P = Transplanted plants

F = Field plants

○ Quarry plants

■ Grassland plants

FIG.6 DIAMETER OF ROSETTES
PLANTAGO LANCEOLATA



the grassland plants are always larger ($P < 0.001$). The differences in vegetative dry weight between the two populations in the field can be mainly attributed to differences in diameter. However, towards the end of the season differences in the number of leaves per plant contribute towards determining the vegetative dry weight of each plant.

ii Reproductive Dry Weight

The mean reproductive dry weight/plant is shown for the flowering population in fig 7a and for the total population in fig 7b. There is little difference in the general pattern between these two populations, the total population means being slightly lower in value. In all 3 classes the peak reproductive biomass is in the final week and, similarly to the vegetative dry weights, the seedlings have the highest production (5723mg), followed closely by the greenhouse plants (4482mg) then a steep decline to the field plants (300mg). It is interesting to note that in the seedlings the steep rise in reproductive biomass between the second and third week is followed by a decline in vegetative production between the third and fourth weeks. Similarly in the greenhouse plants, the steep rise in reproductive production between the third and fourth weeks is followed by a decline in vegetative production between the fourth and fifth weeks.

The difference between the field plants and greenhouse plants in reproductive dry weight is always significant, particularly towards the end of sampling but any difference between the greenhouse plants and seedlings is less distinct. At the commencement of sampling the difference between the quarry plants is significant ($P = < 0.01$) whilst at the end of sampling the difference between the grassland plants is significant ($P = < 0.001$). Tables 7a and 7b show that although the grassland plants consistently have a greater reproductive production in the field and seedlings this difference is only significant

FIG. 7a MEAN DRY WEIGHT OF REPRODUCTIVE MATTER FOR FLOWERING PLANTS PLANTAGO LANCEOLATA

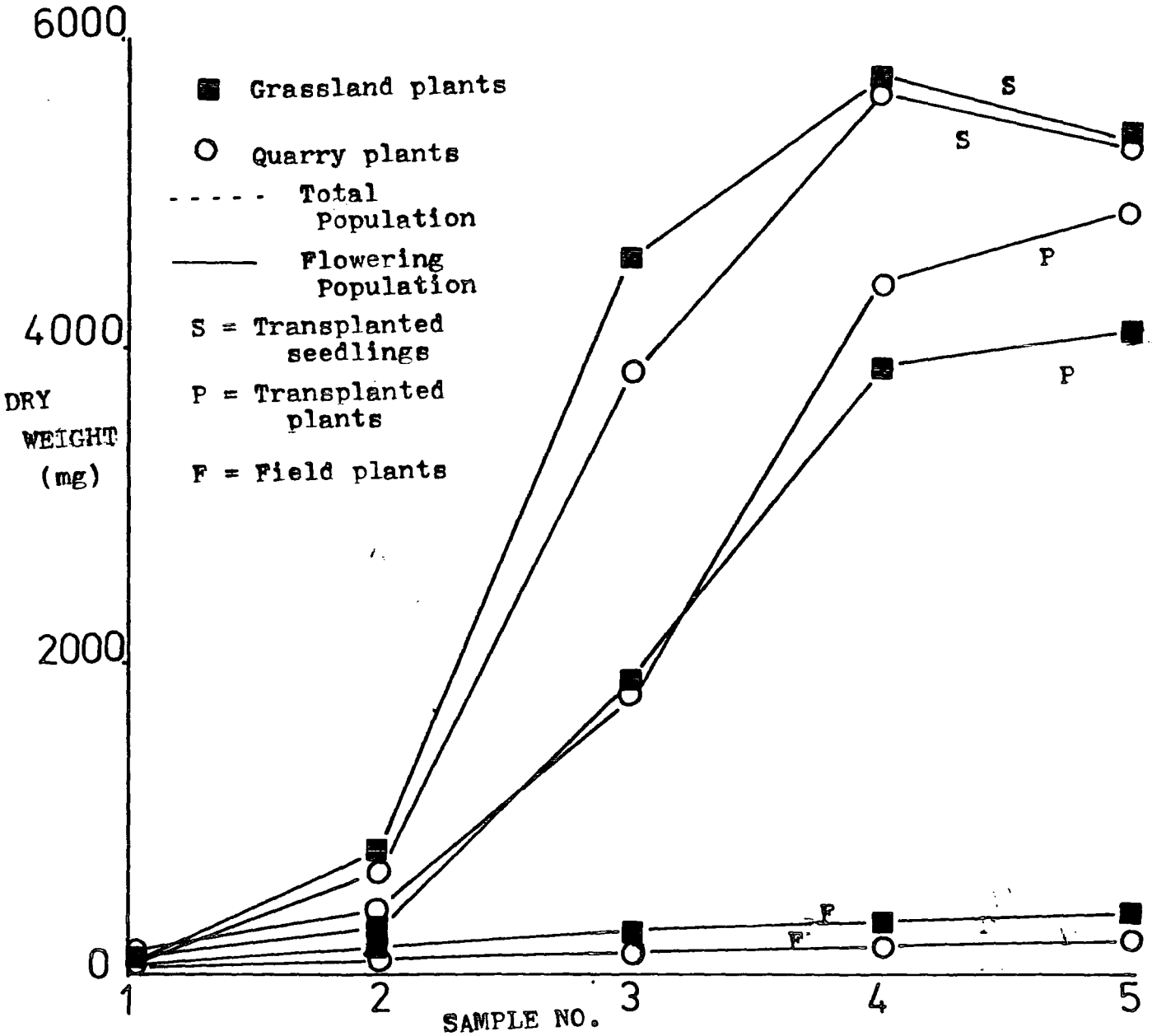
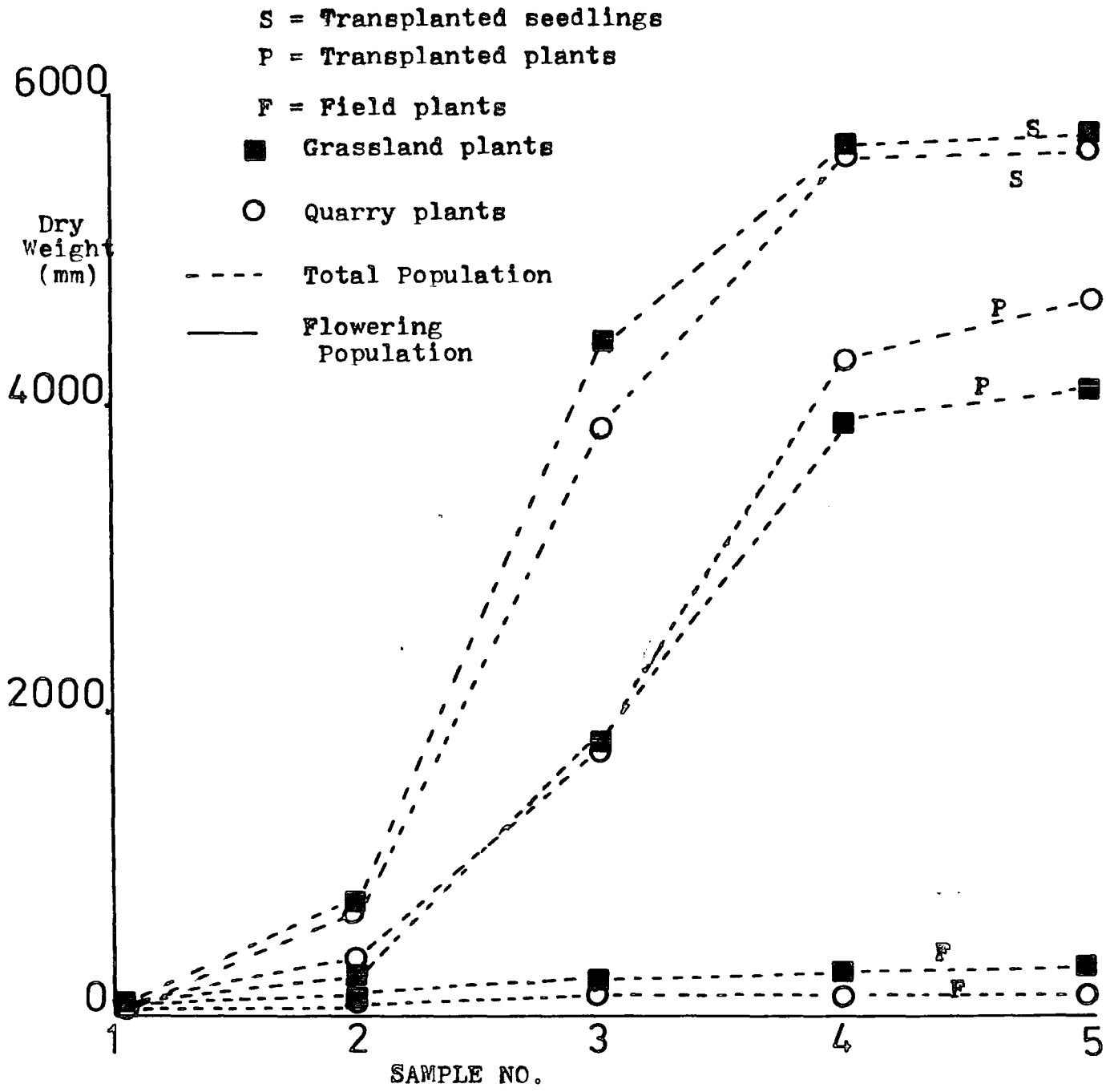


FIG. 7b MEAN DRY WEIGHT OF REPRODUCTIVE MATTER

FOR TOTAL POPULATION

PLANTAGO LANCEOLATA



in the field populations.. The quarry greenhouse plants often have a larger reproductive production but the probability of this difference being significant is never greater than 0.08.

iii Reproductive Effort

The reproductive effort defined as 'the reproductive dry weight as a percentage of the total weight' for all three classes of Plantago is shown in figs 8a and 8b.. The curves taken by the greenhouse plants and seedlings are very similar, reaching a mean maximum per flowering plant in the final week at 58.9% and 58.4% respectively. However the greenhouse plants have a significantly higher mean (10.5% as compared with 3.4%) at the commencement of sampling. The field Plantago plants have a significantly higher mean R.E. at the commencement of sampling (19.25%) but begin to lead off in the third week ending with a significantly lower mean (42.5%). At no time is there any significant difference between quarry and grassland plants either in the field, greenhouse plants or seedlings. Nevertheless it appears that in the field grassland plants commence with a higher R.E. and finish with a lower R.E. whilst in the greenhouse plants grassland plants consistently have a lower R.E. and in the seedlings grassland plants consistently have a higher mean R.E. The mean population R.E. for the greenhouse plants and seedlings closely follows that of the flowering population R.E. shown in fig 8b. This is because virtually all of these plants flowered. The mean population R.E. for the plants in the field, however fluctuates considerably the maxima being at the grassland site - 27.1% in the third week - and at the quarry site - 16.2% in the fourth week.

An alternative method for determining reproductive effort might be to look at the numbers of seeds produced by a plant. It would be difficult to count total numbers of seeds in practise but a regression could be calculated relating a measurable characteristic

FIG. 8a MEAN REPRODUCTIVE EFFORT OF FLOWERING PLANTS

PLANTAGO LANCEOLATA

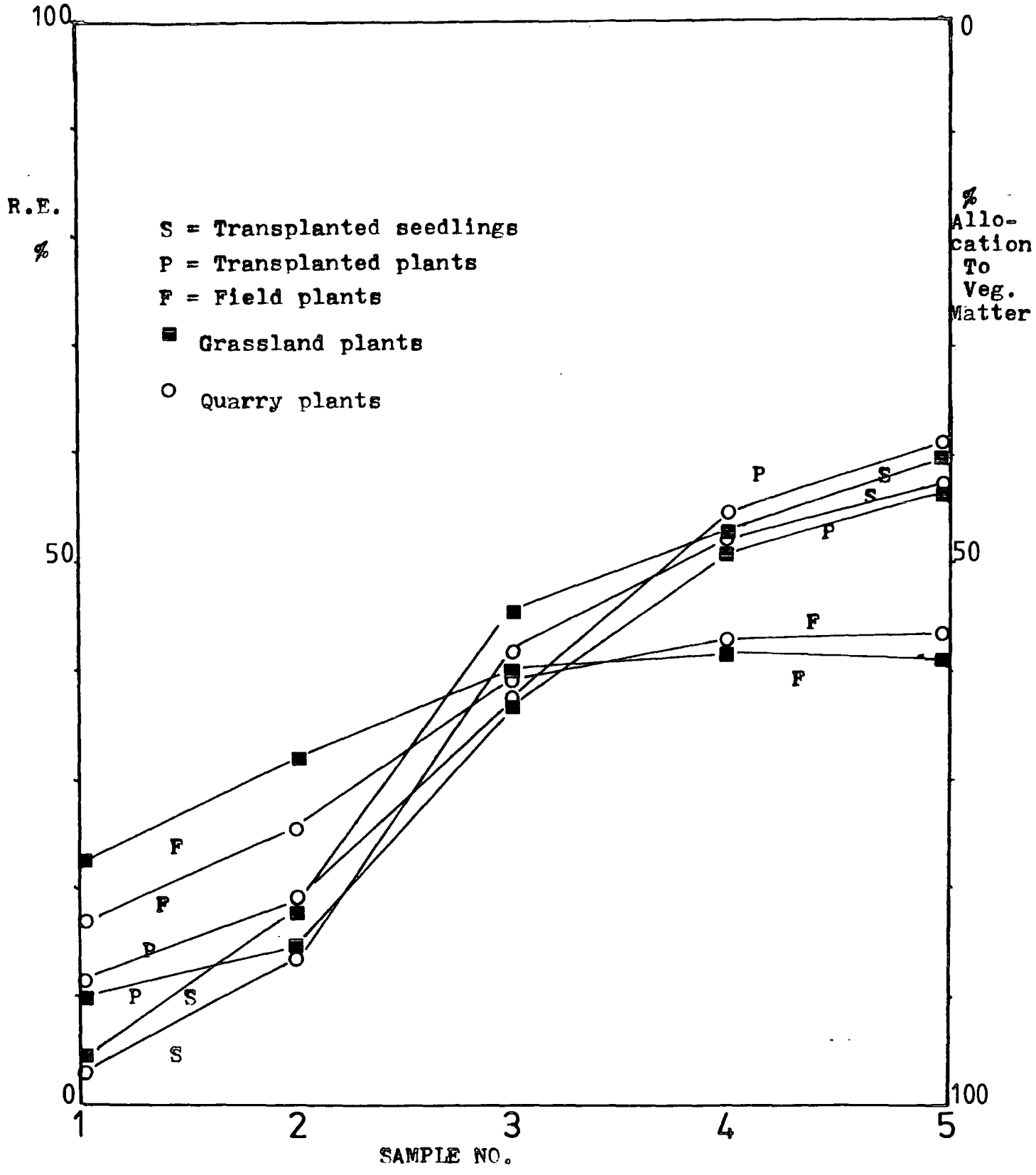
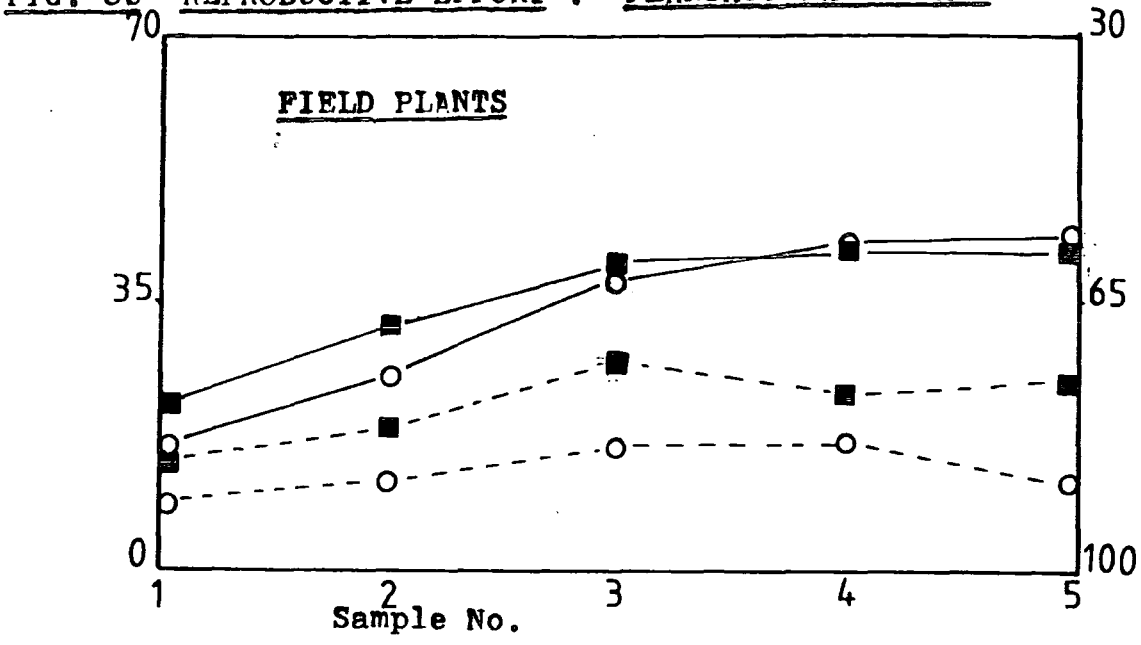
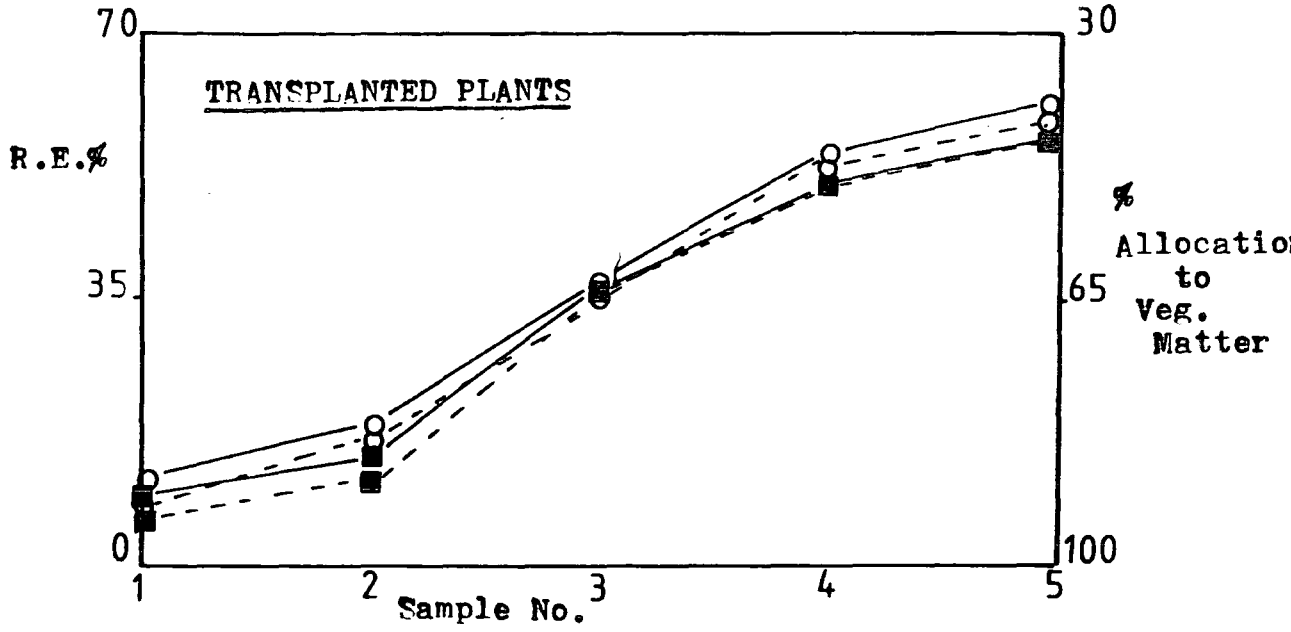
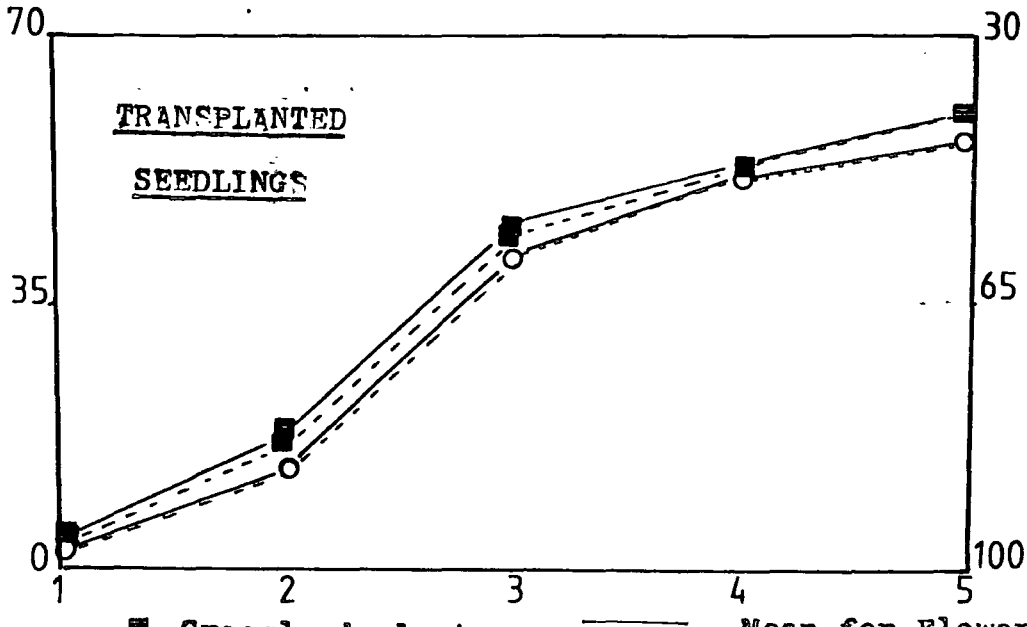


FIG. 8b REPRODUCTIVE EFFORT : PLANTAGO LANCEOLATA







■ Grassland plants
○ Quarry plants
——— Mean for Flowering Pop.
- - - - - Mean for Total Pop.

of the flower or fruit to seed number. The obvious characteristic in Plantago lanceolata is spike length and a very good straight line regression was produced relating this parameter to capsule number (see fig 9). Plantago lanceolata produces a number of 2-seeded fruits or capsules which make-up the spike. Hence the number of capsules produced as a direct indication of the number of seeds. The figures obtained for total spike length/plant in the final week were thus converted to mean capsule numbers per plant using this regression. The results are shown in Fig 10 and Table 9. The seedlings have the largest R.E. with a mean of 877.25 capsules per plant. The greenhouse plants have a mean of 708.3 and the field plants 73.65. In both the field plants and seedlings the grassland plants have a greater R.E. but this is only significant in the field ($P = 0.031$). The quarry greenhouse plants have a significantly higher output than the grassland plants ($P = 0.015$). When these figures were converted to number of capsules produced/gram vegetative dry weight as is done by Primack (1979) some interesting changes in the mean allocations occur. Quarry plants in the field have the largest mean no. of capsules per gram vegetative dry weight (311.8) whereas grassland plants in the field have the smallest allocation (198.66). Greenhouse plants and seedlings from both sites have very similar allocations. (see Table 9 Fig 10)

iv Germinability

The germinability of the seeds could also differ but the results of the germinability experiment are inconclusive (see Table 10). The only significant results were between grassland seedling seeds in the light and dark 12.25 seeds germinating in the light and 7 in the dark ($P < 0.01$) and between grassland and quarry greenhouse plant seeds in the dark, 10.5 grassland seeds germinating in the dark whilst

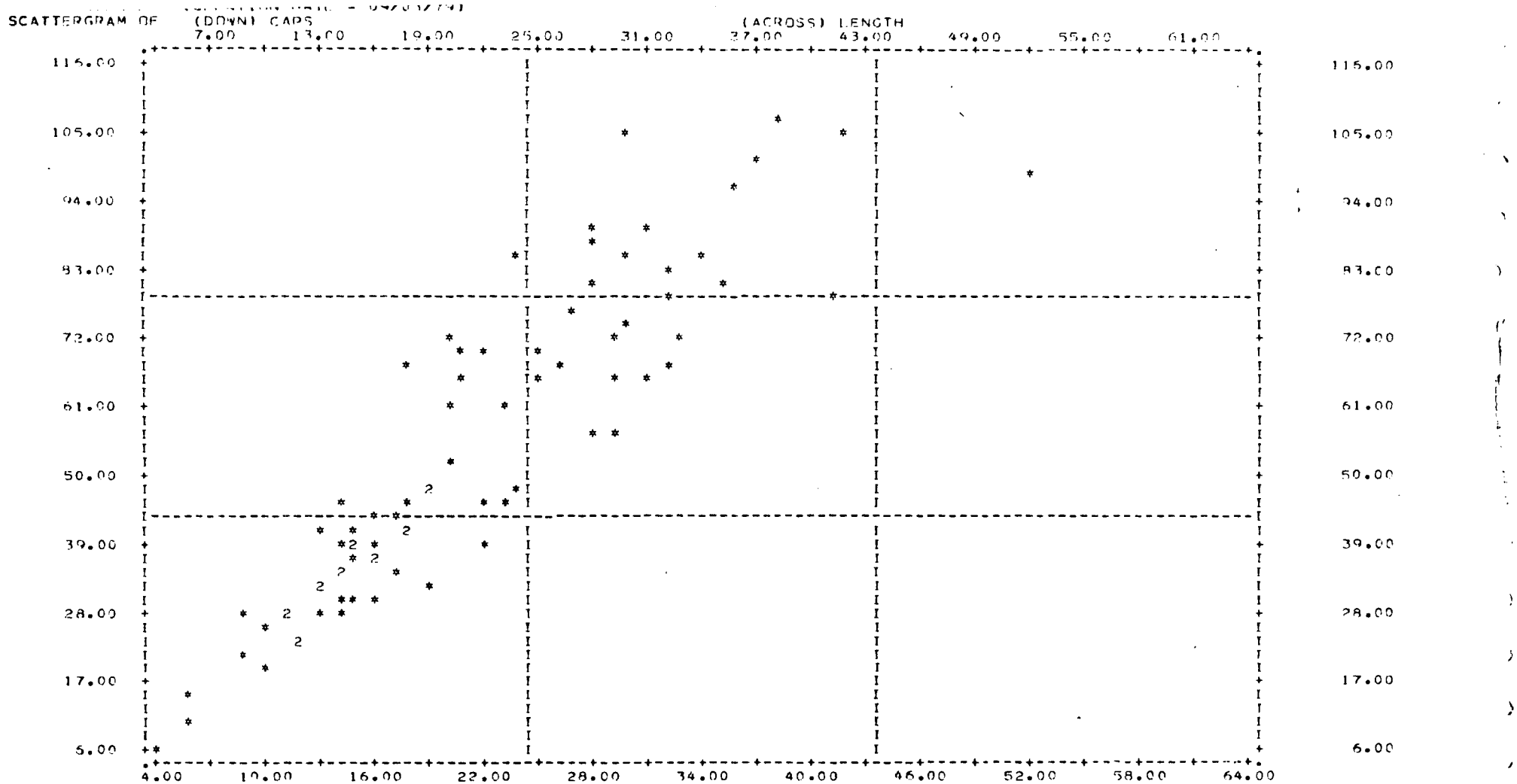


FIG. 9 SCATTERGRAM SHOWING NO. OF SEED CAPSULES PER PLANT WITH LENGTH OF FLOWERING SPIKE : PLANTAGO LANCEOLATA

SCATTERGRAM OF LENGTH/CAPSULES 09/03/79 PAGE 8

STATISTICS..

CORRELATION (R)-	0.90566	R SQUARED -	0.82023	SIGNIFICANCE -	0.00001
STD ERR OF EST -	10.61757	INTERCEPT (A) -	2.61725	SLOPE (B) -	2.40235

THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 12.22663 ON THE LEFT MARGIN
A VALUE OF 48.11246 ON THE TOP MARGIN

PLOTTED VALUES -	80	EXCLUDED VALUES-	0	MISSING VALUES -	0

'*********' IS PRINTED IF A COEFFICIENT CANNOT BE COMPUTED.

FIG. 10a MEAN NO. OF SEED CAPSULES PRODUCED PER PLANT
LEONTODON HISPIDUS

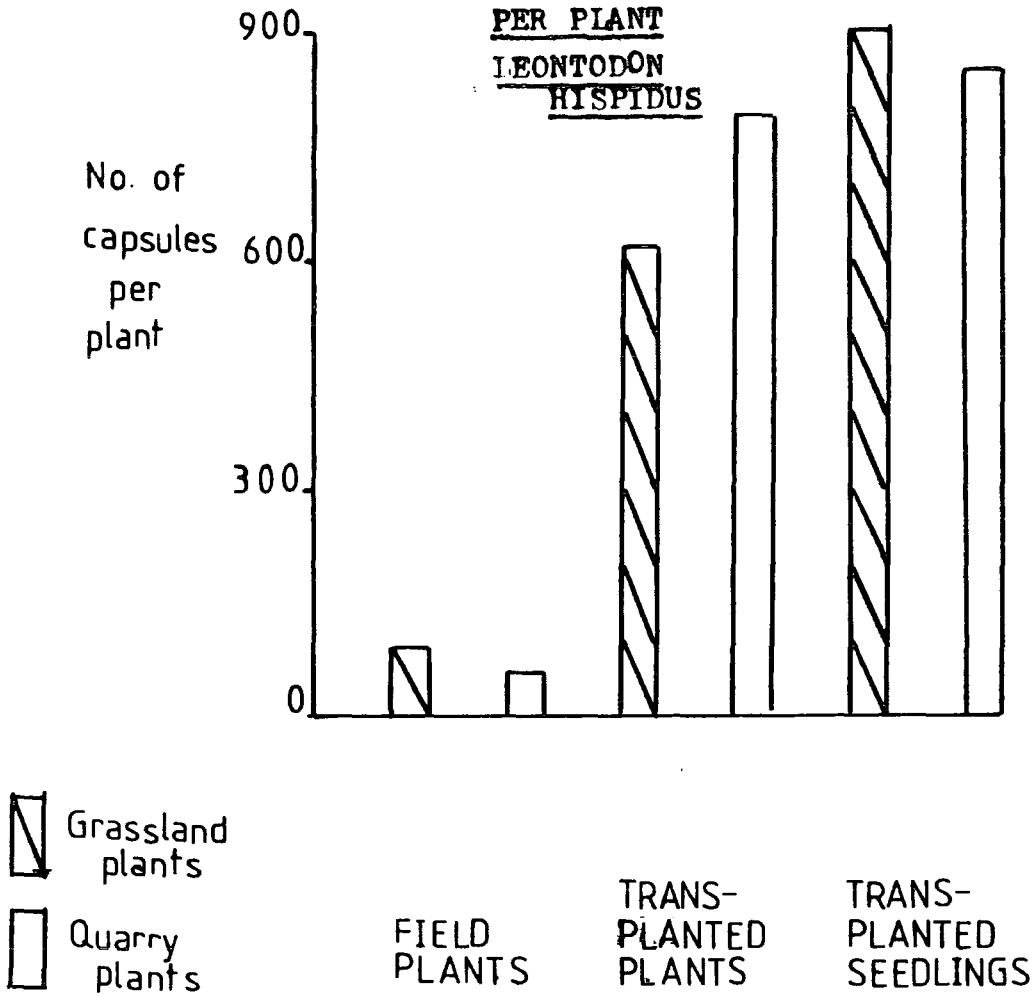
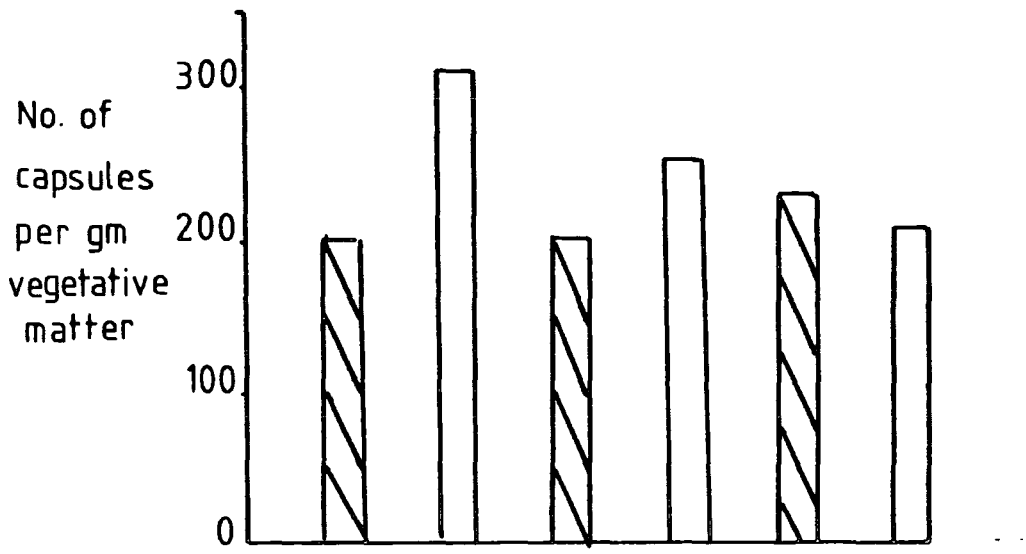


FIG. 10b



only 5.75 quarry seeds germinated in the dark. These results were rather inconclusive.

A comparison of the number of vegetative rosettes produced by greenhouse plants was also inconclusive (see Table 9).

6.3 Leontodon Hispidus

i Weights and Reproductive Effort

The vegetative production of Leontodon hispidus at the 2 sites can be seen in fig 11 and table 11. It is obvious that the quarry plants consistently have a much higher vegetative biomass beginning at 143.2mg plant vegetative dry weight and ending at 202.4mg whilst grassland plants begin at 85.5mg plant vegetative dry weight and end at 140.3mg. The difference between the 2 sites is always significant particularly in the first 3 sample weeks. When this vegetative weight is broken down into its component parts ie number of leaves and diameter (see figs 12 and 13 and Tables 12 and 13) it is immediately evident that this difference is mainly attributable to variations in the number of leaves/plant at each site. At the commencement of sampling each quarry plant has an average of 8.3 leaves whilst grassland plants have 4.9. Even at the end of sampling quarry plants have a mean 8.4 leaves/plant whilst grassland plants have 6.1.

The rate of increase in vegetative biomass over the sampling period is fairly uniform (approx. 15mg/wk.) which contrasts with the rapid increases and fluctuations in reproductive dry weight (see fig 14 and Table 14). At the highest rate of increase quarry plants increase their reproductive dry wt. by 140mg/sample period. Plants were not flowering at either site at the beginning of sampling but quarry plants began in the 2nd week with a mean of 22.9mg/plant and reached 245,8mg/plant in final week. Plants at the grassland site did not begin to devote resources to reproductive production until

FIG. II DRY WEIGHT OF VEGETATIVE MATTER

LEONTODON HISPIDUS

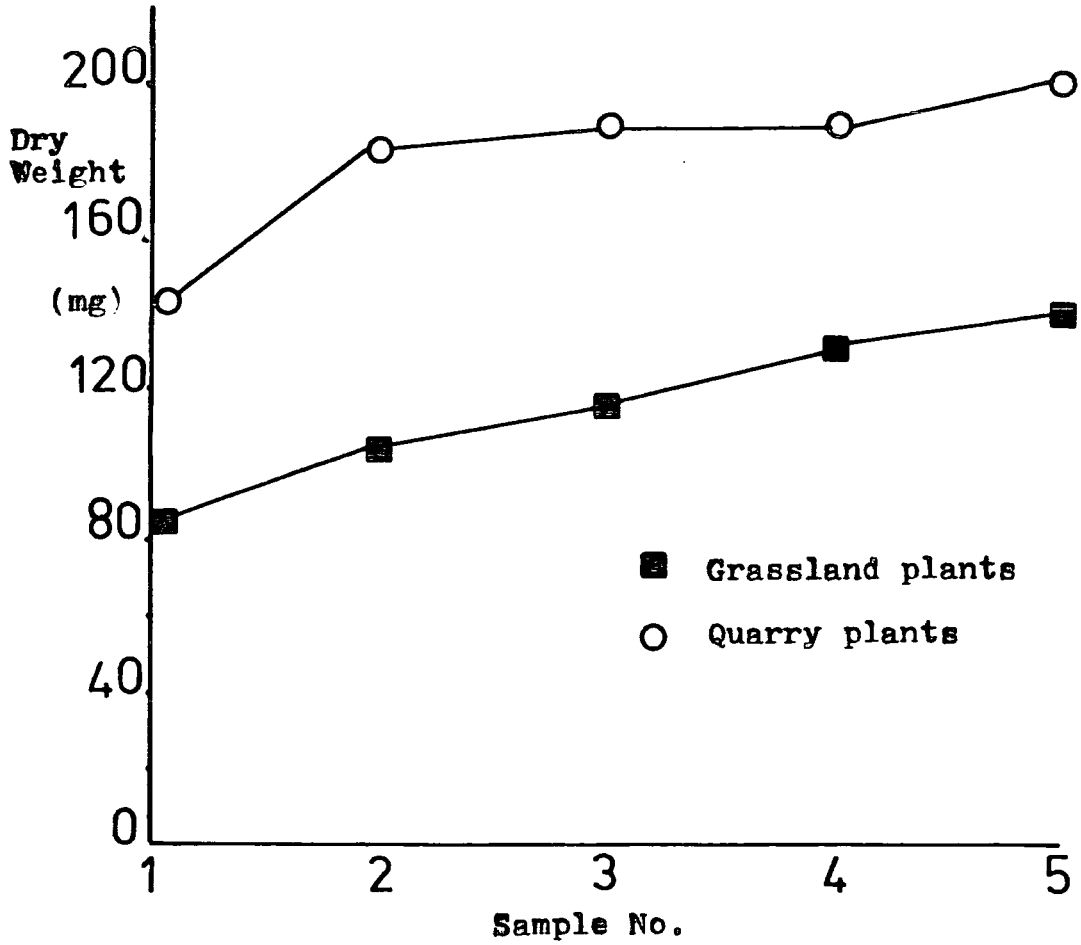


FIG. I2 MEAN NUMBER OF LEAVES PER PLANT

LEONTODON HISPIDUS

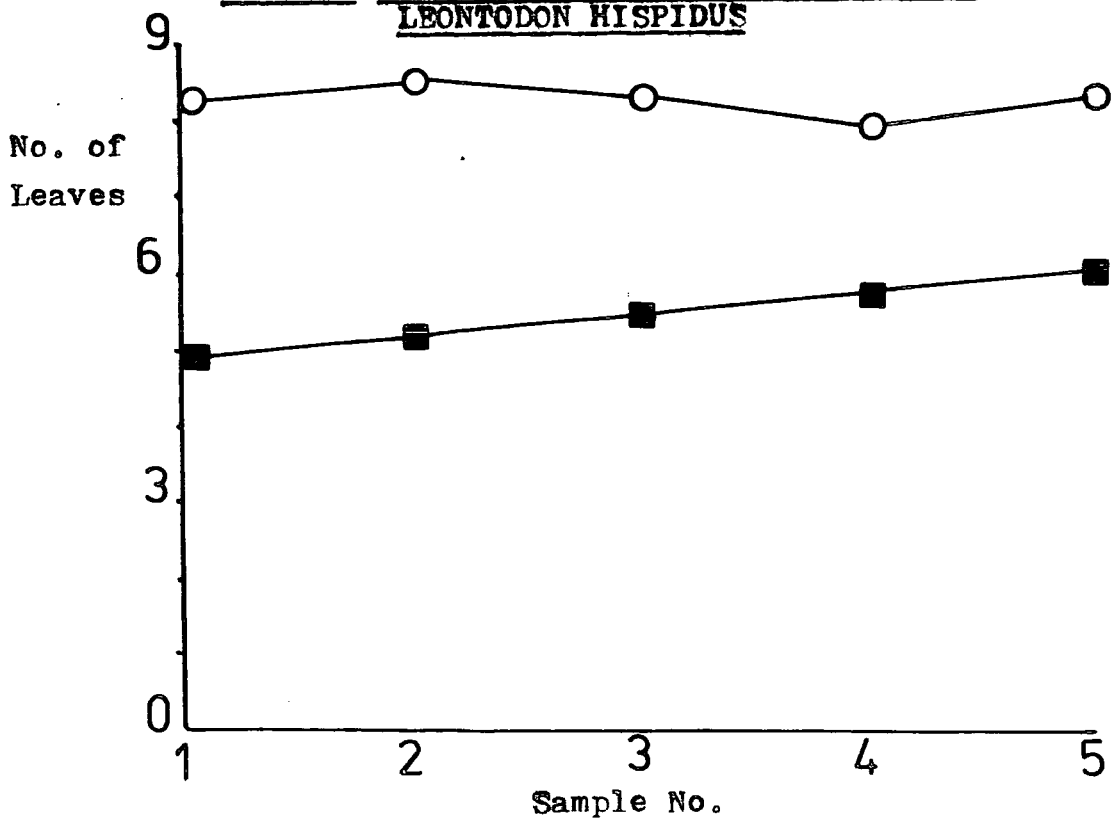


FIG. 13 MEAN DIAMETER OF ROSETTES

LEONTODON HISPIDUS

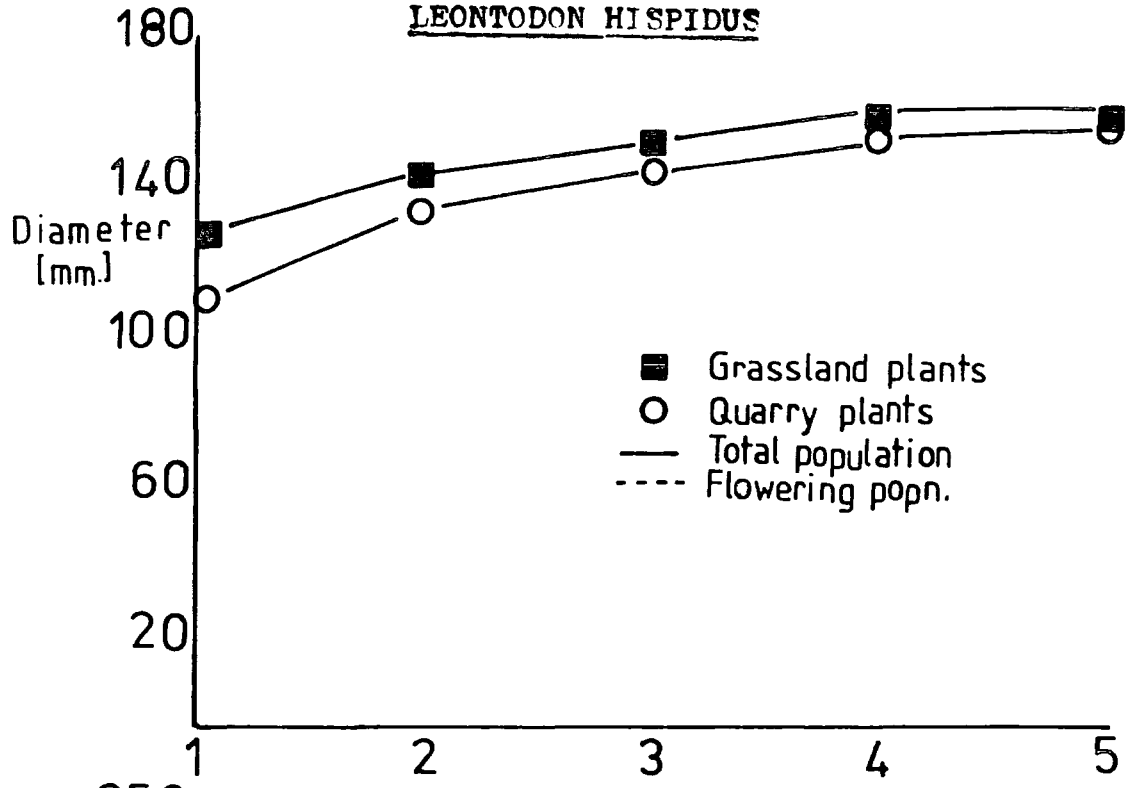
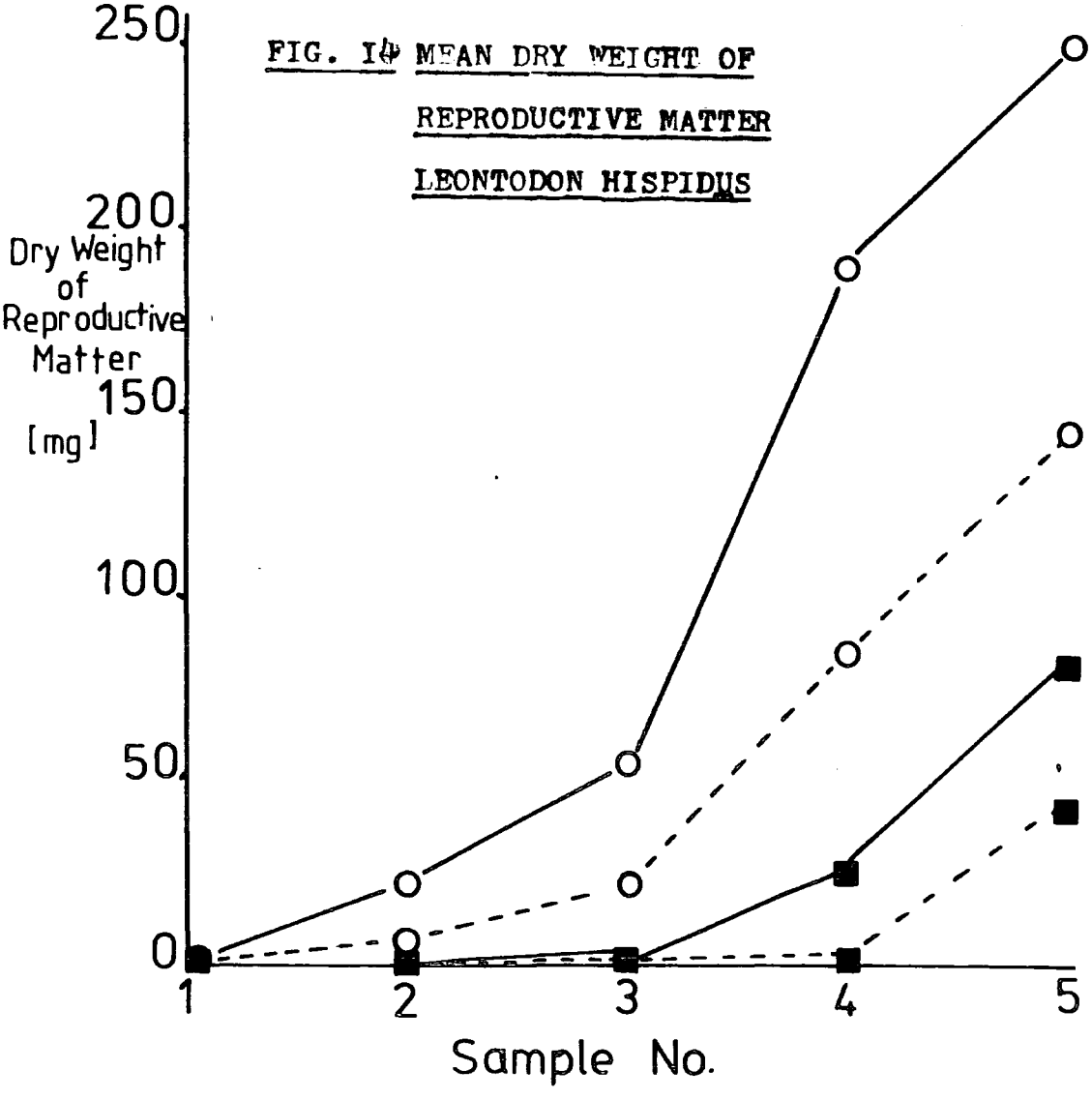


FIG. 14 MEAN DRY WEIGHT OF REPRODUCTIVE MATTER

LEONTODON HISPIDUS



the 4th week, with a mean of 27.8mg/flowering plant and reached 82.1mg in the final week. The differences between the 2 sites were therefore significant in the 3rd, 4th and 5th sample weeks. The population reproductive dry weights generally followed the same pattern, but at a lower level since not every plant flowered. They reached maxima of 146.7mg at the quarry site and 40.5mg at the grassland site.

These figures were converted into reproductive efforts and the results can be seen in Fig 15 and Table 15. Quarry flowering plants attain a maximum reproductive effort/plant of 47.1% whilst grassland plants reach 32.2%. It is interesting that the quarry flowering plants appear to lead off to a plateau in the fourth week and this plateau is not so marked in the total population R.E. Again, there is a significant difference between the two sites in the 3rd, 4th and 5th weeks.

ii Mechanisms

Unfortunately, since so many of the Plantago plants in the field were flowering at the beginning of the sample period it was impossible to obtain sufficient plants for statistically valid tests on the mechanisms which determined flowering. Similarly, virtually all the greenhouse and seedling Plantago plants flowered, which rendered an investigation into the possible mechanisms determining flowering impossible. Tests were consequently only possible on data concerning Leontodon hispidus.

Treating quarry and grassland plants separately the flowering and non-flowering plants were separated into two groups and their weights at the beginning of the sample period tested. The difference between the two groups was significant ($P \leq .001$) at both sites (see Table 16). Non-flowerers at the quarry site had a lower initial

FIG. 15 REPRODUCTIVE EFFORT

LEONTODON HISPIDUS

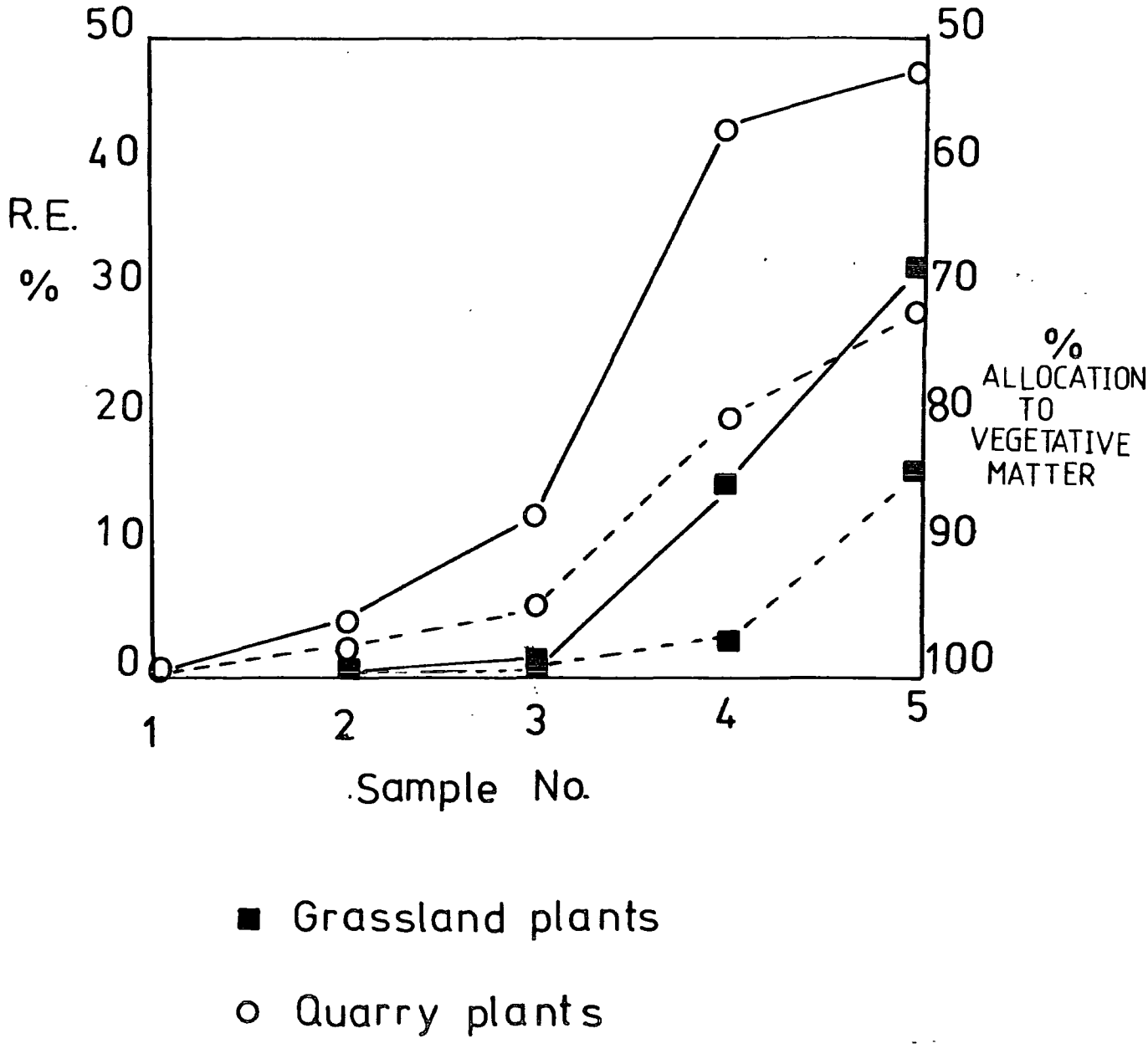
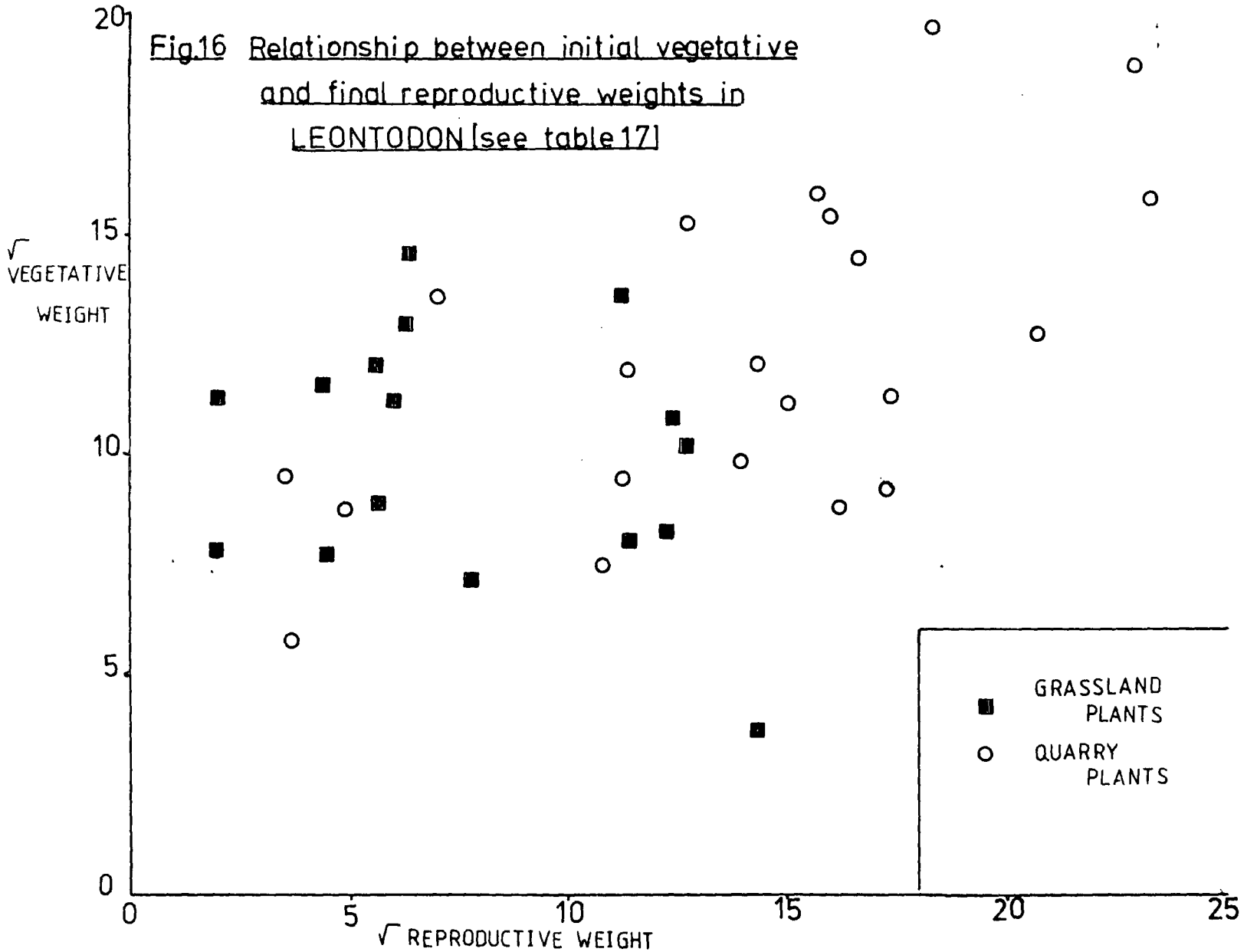


Fig.16 Relationship between initial vegetative and final reproductive weights in LEONTODON [see table 17]



mean vegetative dry weight (7.5^2mg) than flowerers (12.7^2mg). Moreover non-flowerers at the grassland site had a lower initial mean vegetative dry weight (7.63^2mg) than flowerers (10.001mg). The quarry flowerers had a significantly higher initial vegetative weight than the grassland flowerers ($P < 05$) but the difference between the non-flowerers at each site was not significant.

The quarry flowerers were then further subdivided into those which flowered in the 2nd and 3rd sample weeks and those which flowered in the 4th and fifth sample weeks. Although the earlier flowerers had a higher mean vegetative dry weight (13.35^2mg), this was not significantly different from the later flowerers (11.72^2mg). If the grassland plants were included as later flowerers (No grassland plants flowered in the second and third weeks) the difference was significant at the .05 level but it must be remembered that grassland plants were generally smaller than quarry plants (see Table 11).

To test whether initial vegetative dry weight was related to final reproductive dry weight a correlation coefficient was computed (see Table 17 and Fig 16). The correlation between the two was significant at the $P =< 0.001$ level for the quarry plants but not significant for the grassland plants. When the groups were combined the correlation was again significant at the $P =< 0.001$ level.

TABLE 4. PLANTAGO DRY WEIGHT OF VEGATIVE BIOMASS (m.g.)

FIELD PLANTAGO (F)

Week		wk 1	wk 2	wk 3	wk 4	wk 5
GRASS	$\bar{x}$	172.1	273.3	333.9	403.4	450.8
	SD	130.5	162.5	215.8	307.5	430.8
	SE	20.9	27.1	36.5	55.2	77.4
	n	39	36	35	31	31
QUARRY	$\bar{x}$	91.0	173.3	186.1	199.7	185.7
	SD	71.9	94.2	93.9	134.3	116.7
	SE	11.7	15.3	14.9	21.8	18.7
	n	38	38	40	38	39
T-test	T	3.36	3.1	3.93	3.68	3.68
	df	75	72	73	67	68
	P	0.001*	0.003*	0.000*	0.000*	0.000*

GREENHOUSE PLANTS (P)

GRASS	$\bar{x}$	774.2	2211.3	3101.9	3576.2	3102.3
	SD	379	1174.9	1193.6	1446.9	1586.7
	SE	61.6	185.8	188.7	231.7	250.9
	n	38	40	40	39	40
QUARRY	$\bar{x}$	522.8	1624.1	2852.5	3715.5	3183.4
	SD	293.5	956.1	1078.2	1377.1	1507.2
	SE	46.4	151.2	172.6	223.4	244.5
	n	40	40	38	38	38
T-test	T	3.28	2.45	0.97	-0.43	-0.23
	df	76	78	77	75	76
	P	0.002	0.016	0.665	0.665	0.818

GREENHOUSE SEEDLINGS (S)

GRASS	$\bar{x}$	1377.8	3639.5	5514.3	4985.4	3933.1
	SD	653.9	1675.8	1857.8	2223.1	2475.6
	SE	103.4	271.4	301.4	365.5	401.6
	n	40	38	38	37	38
QUARRY	$\bar{x}$	1286.0	3975.7	5171.4	4947.9	4211.4
	SD	557.7	1693.1	1645.9	2043.3	2268.2
	SE	89.3	267.7	260.2	323.1	363.2
	n	39	40	40	40	39
T-test	T	0.67	-0.88	0.86	0.08	-0.51
	df	77	76	76	75	75
	P	0.505	0.381	0.39	0.939	0.6

TABLE 4 (cont.)

* = $P < 0.05$

Difference between F & P in Wk.1	GRASS T =	9.2	$P < 0.001$
	QUARRY T =	9.0	$P < 0.001$
" " P & S in Wk.1	GRASS T =	5.0	$P < 0.001$
	QUARRY T =	7.58	$P < 0.001$
" " P & S in Wk.5	GRASS T =	1.75	N.S.
	QUARRY T =	2.34	$P < 0.05$

TABLE 5. PLANTAGO NUMBER OF LEAVES

FIELD PLANTAGO

Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	7.7	6.8	6.7	6.9	7.2
	SD	3.2	2.2	1.8	2.8	3.6
	SE	0.5	0.4	0.3	0.5	0.6
	n	39	36	35	31	31
QUARRY	$\bar{x}$	6.6	6.6	6.4	5.6	5.1
	SD	2.3	2.0	1.7	1.7	1.7
	SE	0.4	0.3	0.3	0.3	0.2
	n	38	38	40	38	39
T-test	T	1.59	0.30	0.78	2.36	3.32
	df	75	72	73	67	68
	prob	0.116	0.764	0.437	0.021*	0.001*

GREENHOUSE PLANTS

GRASS	$\bar{x}$	17.6	27.8	39.8	443.3	38.9
	SD	6.8	11.2	16.1	17.7	16.1
	SE	1.1	1.8	2.6	2.8	2.6
	n	38	40	40	39	40
QUARRY	$\bar{x}$	13.0	20.6	33.6	39.7	35.1
	SD	5.2	9.0	12.7	14.5	15.2
	SE	0.8	1.4	2.0	2.4	2.5
	n	40	40	39	38	38
T-test	T	3.36	3.15	1.89	1.24	1.08
	df	76	78	77	75	76
	prob	0.81	0.002	0.063	0.218	0.284

GREENHOUSE SEEDLINGS

GRASS	$\bar{x}$	32.1	44.3	58.8	45.9	41.8
	SD	13.0	14.3	17.4	18.2	18.0
	SE	2.1	2.3	2.8	3.0	2.9
	n	40	38	38	37	38
QUARRY	$\bar{x}$	27.7	41.4	54.3	44.7	42.8
	SD	8.6	11.2	14.8	14.7	14.9
	SE	1.4	1.8	2.3	2.3	2.4
	n	39	40	40	40	39
T-test	T	1.77	1.02	1.23	0.32	-0.29
	df	77	76	76	75	75
	prob	0.081	0.311	0.222	0.752	0.774

* = $P<0.05$

TABLE 6. PLANTAGO PLANT DIAMETER (m.m.)

FIELD PLANTAGO						
Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	174.5	212.8	240.9	269.9	275.5
	SD	81.9	84.2	91.2	91.6	93.5
	SE	12.9	13.8	15.4	16.4	16.8
	n	40	37	35	31	31
QUARRY	$\bar{x}$	117.9	141.3	154.6	172.7	169.3
	SD	46.0	59.0	64.4	76.5	80.3
	SE	7.3	9.5	10.1	12.4	12.9
	n	40	39	40	38	39
T-test	T	3.81	4.31	4.77	4.8	5.11
	df	78	74	73	67	68
	prob	0.000*	0.0000*	0.000*	0.000*	0.000*

GREENHOUSE PLANTS						
GRASS	$\bar{x}$	337.4	387.1	397.9	410.9	396.1
	SD	66.7	83.5	70.4	67.9	103.9
	SE	10.5	13.2	11.1	10.7	16.4
	n	40	40	40	40	40
QUARRY	$\bar{x}$	301.3	371.7	425.1	473.1	451.7
	SD	72.2	71.7	61.8	83.3	92.7
	SE	11.4	11.3	9.9	13.5	14.8
	n	40	40	39	38	38
T-test	T	2.33*	0.88	-1.82	-3.62	-2.51
	df	78	78	77	76	77
	prob	0.023	0.38	0.072	0.001*	o.014

GREENHOUSE SEEDLINGS						
GRASS	$\bar{x}$	326.0	397.5	472.9	543.5	448.2
	SD	52.2	52.9	71.0	108.6	115.7
	SE	8.2	8.5	11.5	17.6	18.8
	n	40	39	38	38	38
QUARRY	$\bar{x}$	351.1	429.3	481.8	554.6	478.4
	SD	67.3	54.9	71.5	110.8	141.1
	SE	10.6	8.7	11.3	17.5	22.6
	n	40	40	40	40	39
T-test	T	-1.86	-2.62	-0.55	-0.45	-1.03
	df	78	77	76	76	75
	prob	0.066	0.011*	0.582	0.654	0.939

* = $P < 0.05$

TABLE 7a DRY WEIGHT OF REPRODUCTIVE BIOMASS. PLANTAGO FLOWERING POPULATION

FIELD PLANTAGO (F)

Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	41.3	184.0	288.4	332.4	387.4
	SD	32.6	166.0	222.1	265.0	305.7
	SE	5.6	29.4	40.6	54.1	62.4
	n	34	32	30	24	24
QUARRY	$\bar{x}$	22.7	107.1	177.8	196.2	211.9
	SD	19.7	110.8	149.8	184.8	186.4
	SE	3.5	19.9	26.5	34.3	35.2
	n	31	31	32	29	28
T-test	T	2.75	2.15	2.31	2.2	2.54
	df	63	61	60	51	50
	prob	0.008	0.035*	0.024*	0.032*	0.014*

Difference between F & P: (G)T = 2.33 P<.01; (Q)T = 4.52 P<.001; G. T = 12.29 P<.001; Q. T = 18.18 P<.001

GREENHOUSE PLANTS (P)

GRASS	$\bar{x}$	67.7	334.6	1844.6	3891.8	4133.1
	SD	51.2	308.9	862.5	1807.6	1885.7
	SE	9.8	52.9	138.1	285.8	298.2
	n	27	34	39	40	40
QUARRY	$\bar{x}$	71.5	411.4	1808.7	4419.4	4831.7
	SD	57.6	416.3	1054.2	1474.6	1551.2
	SE	10.2	67.5	171.0	242.4	251.6
	n	32	38	38	37	38
T-test	T	-0.27	-0.88	0.16	-1.40	-1.78
	df	57	70	75	75	76
	prob	0.792	0.382	0.870	0.167	0.079

Difference between P & S: G. T= 1.02 =NS; Q. T= 2.63 =P<.01; G. T = 3.45 = P<.001; Q. T = 1.66 = NS

GREENHOUSE SEEDLINGS (S)

GRASS	$\bar{x}$	56.0	821.6	4554.1	5704.7	5745.7
	SD	34.2	570.4	1671.0	2127.3	2214.9
	SE	5.9	93.8	274.7	345.1	359.3
	n	33	37	37	38	38
QUARRY	$\bar{x}$	40.3	680.0	3866.9	5658.3	5700.5
	SD	935.8	567.2	1990.2	2871.6	2862.3
	SE	6.0	90.8	314.7	454.0	458.3
	n	35	39	40	40	39

P.T.O.

TABLE 7b. DRY WEIGHT OF REPRODUCTIVE BIOMASS PLANTAGO TOTAL POPULATION

FIELD PLANTAGO						
Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	34.2	151.1	238.6	244.0	286.4
	SD	34.5	175.7	239.5	285.8	328.3
	SE	5.5	28.9	40.5	51.3	58.9
	n	40	37	35	31	31
QUARRY	$\bar{x}$	16.2	72.9	130.3	135.6	135.3
	SD	21.1	119.8	164.7	195.0	200.1
	SE	3.3	19.2	26.0	31.6	32.0
	n	40	39	40	38	39
T-test	T	2.81	2.28	2.31	1.87	2.38
	df	78	74	73	67	68
	prob	0.006*	0.026*	0.024*	0.066	0.02*

GREENHOUSE PLANTS						
GRASS	$\bar{x}$	43.8	275.4	1794.5	3891.8	4133.1
	SD	54.4	317.9	908.4	1807.6	1885.7
	SE	8.6	50.3	143.6	285.8	298.2
	n	40	40	40	40	40
QUARRY	$\bar{x}$	56.0	387.8	1758.3	4298.9	4703.7
	SD	60.2	418.6	1086.9	1633.3	1726.7
	SE	9.5	66.2	174.0	264.9	276.5
	n	40	40	39	38	39
T-test	T	-0.95	-1.35	0.16	-1.04	-1.4
	df	78	78	77	76	77
	prob	0.343	0.18	0.872	0.301	0.165

GREENHOUSE SEEDLINGS						
GRASS	$\bar{x}$	45.2	776.4	4430.1	5704.7	5745.7
	SD	39.1	389.1	1817.0	2127.3	2214.9
	SE	6.2	94.3	294.8	345.1	359.3
	n	40	39	38	38	38
QUARRY	$\bar{x}$	34.5	661.5	3866.9	5658.3	5700.5
	SD	36.8	572.0	1990.2	2871.6	2862.3
	SE	5.8	90.4	314.7	454.0	458.3
	n	40	40	40	40	39
T-test	T	1.25	0.88	1.3	0.08	0.08
	df	78	77	76	76	75
	prob	0.214	0.382	0.196	0.936	0.939

* = $P < 0.05$

TABLE 8a. PLANTAGO REPROD. EFFORT. TOTAL POPULATION.

FIELD PLANTAGOS

Week		Wk1.	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	22.1	31.8	39.9	41.5	41.4
	SD	16.1	21.1	19.2	15.5	24.4
	SE	2.8	3.8	3.5	3.2	5.0
	n	33	31	30	24	24
QUARRY	$\bar{x}$	16.4	25.4	39.4	42.6	43.6
	SD	8.4	27.6	21.2	17.0	27.0
	SE	1.6	5.0	3.7	3.2	5.1
	n	29	30	32	29	28
T-test	T	1.74	1.02	0.08	0.24	0.31
	df	60	59	60	51	50
	prob	0.087	0.311	0.936	0.814	0.761

G. T = 4.01 P<0.001* G. T = 2.59 P<0.01*
Q. T = 2.63 P<0.01* Q. T = 3.13 P<0.001*

GREENHOUSE PLANTS

GRASS	$\bar{x}$	9.6	14.9	37.3	50.7	56.5
	SD	6.8	13.9	16.0	16.6	19.0
	SE	1.4	2.4	2.6	2.7	3.0
	n	25	34	39	39	40
QUARRY	$\bar{x}$	11.4	18.7	37.4	54.6	61.3
	SD	6.1	15.4	13.9	12.2	14.8
	SE	1.1	2.5	2.3	2.0	2.4
	n	32	38	38	37	37
T-test	T	-1.05	-1.07	-0.01	-1.18	-.1.24
	df	55	70	75	74	75
	prob	0.03	0.289	0.995	0.243	0.218

G. T = 2.68 P<0.01* G. T = 0.76 = NS
Q. T = 7.6 P<0.001* Q. T = 1.04 = NS

GREENHOUSE SEEDLINGS

GRASS	$\bar{x}$	4.0	18.0	45.5	53.3	60.0
	SD	2.8	11.6	11.8	18.2	20.1
	SE	0.5	1.9	1.9	3.0	3.3
	n	33	36	37	37	38
QUARRY	$\bar{x}$	2.8	13.6	41.8	52.3	56.8
	SD	2.0	8.9	14.1	19.6	22.3
	SE	0.3	1.4	2.2	3.1	3.6
	n	34	39	40	40	39
T-test	T	1.88	1.85	1.26	0.23	0.66
	df	65	73	75	75	75
	prob	0.064	0.068	0.212	0.818	0.512

* = P<0.05

TABLE 8b. PLANTAGO REPRODUCTIVE EFFORT.
FLOWERING POPULATION

FIELD PLANTAGO						
Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	14.7	19.0	27.1	23.2	24.9
	SD	28.6	39.6	38.1	39.2	38.7
	SE	4.6	6.6	6.4	7.0	6.9
	n	39	36	35	31	31
QUARRY	$\bar{x}$	8.9	11.9	15.9	16.2	11.4
	SD	15.9	53.6	52.3	52.3	58.4
	SE	2.6	8.7	8.3	8.5	9.4
	n	38	38	40	38	39
T-test	T	1.1	1.55	1.04	0.62	1.11
	df	75	72	73	67	68
	prob	0.274	0.126	0.304	0.536	0.271

Difference between F & P.
G. T = 1.81 = NS
Q. T = 0.07 = NS
G. T = 4.17 P 0.001
Q. T = 4.92 P 0.001

GREENHOUSE PLANTS						
GRASS	$\bar{x}$	6.1	11.8	36.1	50.7	56.5
	SD	7.4	15.2	17.7	16.6	19.0
	SE	1.2	2.4	2.8	2.6	3.0
	n	38	40	40	39	40
QUARRY	$\bar{x}$	8.7	17.2	36.2	53.1	59.6
	SD	7.7	16.3	15.5	15.2	17.9
	SE	1.2	2.6	2.5	2.5	2.9
	n	40	40	39	38	38
T-test	T	-1.55	-1.53	-0.04	-0.67	-0.76
	df	76	78	77	75	76
	prob	0.125	0.131	0.971	0.506	0.451

GREENHOUSE SEEDLINGS						
GRASS	$\bar{x}$	3.1	16.9	44.3	53.3	60.0
	SD	3.2	12.2	13.9	18.2	20.1
	SE	0.5	2.0	2.3	3.0	3.3
	n	40	38		37	38
QUARRY	$\bar{x}$	2.4	13.2	41.8	52.3	56.8
	SD	2.2	9.1	14.1	19.6	22.3
	SE	0.3	1.4	2.2	3.1	3.6
	n	38	40		40	39
T-test	T	1.15	1.53	0.79	0.23	0.66
	df	77	76	76	75	75
	prob	0.255	0.131	0.432	0.818	0.512

TABLE 9. NO. OF 2-SEEDED CAPSULES/PLANT, lgm. VEGETATIVE WEIGHT AND NO. OF VEGETATIVE ROSETTES/PLANT.

FIELD PLANTAGO

		Total length	Capsules	x caps/gm veg.wt.
GRASS	$\bar{x}$	36.1	89.4	198.66
	SD	25.0	60.1	139.507
	SE	5.1	12.3	28.47
	n	24	24	24
QUARRY	$\bar{x}$	23.0	57.9	311.79
	SD	16.0	38.5	329.9
	SE	3.1	7.6	64.6
	n	26	26	26
T-test	T	2.22	2.22	1.6
	df	48	48	48
	prob	0.031*	0.031*	NS

GREENHOUSE PLANTS

GRASS	$\bar{x}$	257.8	621.9	200.464
	SD	172.0	269.1	169.59
	SE	17.7	42.5	26.8
	n	40	40	40
QUARRY	$\bar{x}$	329.7	794.7	249.638
	SD	139.7	335.6	222.66
	SE	22.9	55.2	36.6
	n	37	37	37
T-test	T	-2.5	-2.5	1.08
	df	75	75	75
	prob	0.015*	0.015*	NS

GREENHOUSE SEEDLINGS

		Total length	Capsules	x caps/gm veg.wt.	No.of vegetative rosettes/plant
GRASS	$\bar{x}$	373.9	900.9	229.055	5.0
	SD	176.6	424.2	171.3	1.6
	SE	27.9	67.1	27.08	0.3
	n	40	40	40	39
QUARRY	$\bar{x}$	354.2	853.6	202.68	4.6
	SD	167.5	402.3	177.38	1.5
	SE	26.5	63.6	28.04	0.2
	n	40	40	40	40
T-test	T	0.51	0.51	0.67	1.22
	df	78	78	78	77
	prob	0.610	0.610	NS	0.225

* = $P < 0.05$

TABLE 10. NUMBERS OF GERMINATING SEEDS IN VARIOUS CONDITIONS.

FIELD PLANTAGO

		Light	Dark	
GRASS	$\bar{x}$	5.25	4.0	
	SD	2.5	1.4	T = 0.87
	SE	1.25	0.707	df = 6
	n	4	4	prob = 0.418
QUARRY	$\bar{x}$	7.25	5.25	
	SD	0.96	2.2	T = 1.66
	SE	0.47	1.109	df = 6
	n	4	4	prob = 0.149
T-test	T	-1.49	-0.95	
	df	6	6	
	prob	0.186	0.379	

GREENHOUSE PLANTS

GRASS	$\bar{x}$	6.25	10.5	
	SD	3.403	1.732	T = 2.23
	SE	1.702	0.866	df = 6
	n	4	4	prob = 0.068
QUARRY	$\bar{x}$	7.5	5.75	
	SD	3.0	3.5	T = 0.76
	SE	1.5	1.75	df = 6
	n	4	4	prob = 0.476
T-test	T	-0.55	2.43	
	df	6	6	
	prob	0.602	0.051	

GREENHOUSE SEEDLINGS

GRASS	$\bar{x}$	12.25	7.0	
	SD	0.957	2.708	T = 3.66
	SE	0.479	1.354	df = 6
	n	4	4	prob = 0.01*
QUARRY	$\bar{x}$	9.75	8.0	
	SD	4.646	1.633	T = 0.71
	SE	2.323	0.816	df = 6
	n	4	4	prob = 0.504
T-test	T	1.05	-0.63	
	df	6	6	
	prob	0.332	0.55	

* = $P < 0.005$

TABLES 11, 12 & 13. LEONTODON HISPIDUS.

TABLE 11: VEGETATIVE BIOMASS (m.g.)

Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	85.5	105.3	117.1	132.6	140.3
	SD	47.3	51.4	49.1	53.5	61.8
	SE	7.5	8.1	7.8	8.8	10.4
	n	40	40	40	40	40
QUARRY	$\bar{x}$	143.2	184.6	190.5	189.9	202.4
	SD	123.1	164.4	152.1	147.0	149.1
	SE	19.5	26.0	24.0	24.2	24.5
	n	40	40	40	37	37
T-test	T	-2.77	-2.91	-2.91	-2.23	-2.28
	df	78	78	78	72	70
	prob	0.007*	0.005*	0.005*	0.029*	0.025*

TABLE 12: NO. OF LVES.

GRASS	$\bar{x}$	4.9	5.2	5.5	5.8	6.1
	SD	1.5	1.4	1.3	1.01	1.4
	SE	0.2	0.2	0.2	0.2	0.2
	n	40	40	40	37	35
QUARRY	$\bar{x}$	8.3	8.6	8.4	8.0	8.4
	SD	3.4	3.5	2.9	2.8	3.3
	SE	0.5	0.6	0.5	0.5	0.5
	n	40	40	40	37	37
T-test	T	-5.89	-5.58	-5.75	-4.64	-3.94
	df	78	78	78	72	70
	prob	0.000*	0.000*	0.000*	0.000*	0.000*

TABLE 13: DIAMETER (m.m.)

GRASS	$\bar{x}$	129.6	146.5	155.6	162.3	161.4
	SD	39.5	40.9	48.8	44.0	44.7
	SE	6.2	6.4	7.7	7.2	7.6
	n	40	40	40	37	35
QUARRY	$\bar{x}$	111.7	135.7	146.2	155.9	159.2
	SD	53.1	64.0	66.4	68.2	68.1
	SE	8.4	10.1	10.5	11.2	11.2
	n	40	40	40	37	37
T-test	T	1.71	0.89	0.72	0.48	0.16
	df	78	78	78	72	70
	prob	0.09	0.374	0.473	0.633	0.874

* = $P < 0.05$

TABLE 14a. LEONTODON HISPIDUS.

REPRODUCTIVE BIOMASS. (FLOWERING POPULATION. m.g.)

Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	0.0	0.0	0.0	27.8	82.1
	SD	0.0	0.0	0.0	24.1	68.6
	SE	0.0	0.0	0.0	12.1	16.6
	n	0	0	0	4	17
QUARRY	$\bar{x}$	0.0	22.9	56.4	185.3	245.8
	SD	0.0	52.0	96.1	134.2	178.4
	SE	0.0	16.4	24.8	32.5	38.1
	n	0	10	15	17	22
T-test	T	0.0	-1.39	-2.27	-2.30	-3.58
	df	0	9	14	19	37
	prob	1.0	0.197	0.039*	0.033*	0.001*

TABLE 14b. LEONTODON HISPIDUS.

REPRODUCTIVE BIOMASS. (TOTAL POPULATION.)

Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	1.3	1.3	1.3	4.2	40.5
	SD	0.0	0.0	0.0	10.8	62.4
	SE	0.0	0.0	0.0	1.8	10.5
	n	40	40	40	37	35
QUARRY	$\bar{x}$	1.3	6.7	21.9	85.9	146.7
	SD	0.0	26.7	63.6	129.0	182.7
	SE	0.0	4.2	10.1	21.2	30.0
	n	40	40	40	37	37
	T	0.0	-1.28	-2.05	-3.84	-3.26
	df	78	78	78	72	70
	prob	1.0	0.205	0.043*	0.000*	0.002*

* = $P < 0.05$

TABLE 15a. LEONTODON HISPIDUS.

REPRODUCTIVE EFFORT. (FLOWERING POPULATION)

Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	0.0	0.0	0.0	15.0	32.2
	SD	0.0	0.0	0.0	12.7	24.8
	SE	0.0	0.0	0.0	6.4	6.0
	n	0	0	0	4	17
QUARRY	$\bar{x}$	0.0	4.6	12.8	43.1	47.1
	SD	0.0	6.9	10.7	20.1	21.7
	SE	0.0	2.2	2.8	4.9	4.6
	n	0	10	15	17	22
	T	0.0	-2.1	-4.67	-2.65	-2.01
	df	0	9	14	19	37
	prob	1.0	0.065	0.000*	0.016*	0.052*

TABLE 15b. LEONTODON HISPIDUS.

REPRODUCTIVE EFFORT. (TOTAL POPULATION)

Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	2.1	1.5	1.4	2.7	16.3
	SD	1.6	0.8	1.0	5.7	23.1
	SE	0.3	0.1	0.2	0.9	3.9
	n	40	40	40	37	35
QUARRY	$\bar{x}$	1.8	2.5	5.7	20.5	28.6
	SD	1.6	3.9	8.5	25.0	28.2
	SE	0.2	0.6	1.3	4.1.	4.6
	n	40	40	40	37	37
T-test	T	1.04	-1.48	-3.21	-4.23	-2.01
	df	78	78	78	72	70
	prob	0.301	0.144	0.002*	0.000	0.048*

* = $P < 0.05$

TABLE 16. COMPARISON OF VEGETATIVE WEIGHTS AT BEGINNING OF SAMPLING FOR THE LEONTODON FLOWERS AND NON-FLOWERS

		√Vegetative Wt. Wk.1 Quarry.	√Veg.Wt. Wk.1 Grass						
Flowers	$\bar{x}$	12.7	10.007	Quarry Flowers	$\bar{x}$	12.7	Quarry Non-Flowers	x	7.5
	SD	4.12	2.73		SD	4.12		SD	2.15
	SE	0.878	0.683		SE	0.878		SE	0.574
	n	22	16		n	22		n	14
Non-Flowers	$\bar{x}$	7.5	7.63	Grass Flowers	$\bar{x}$	10.007	Grass Non-Flowers	x	7.63
	SD	2.15	1.8		SD	2.73		SD	1.8
	SE	0.574	0.436		SE	0.683		SE	0.436
	n	14	17		n	16		n	17
T-test	T	4.68	3.78			2.406			0.1403
	df	34	31			36			29
	P	0.001*	0.001*			0.05*			NS

Comparison of Vegetative Weights of flowers one week before flowering and non-flowers at end of sampling.

		Quarry	Grass
	$\bar{x}$	13.8	12.506
	SD	3.96	2.215
	SE	0.84	0.55
	n	22	16
	$\bar{x}$	11.189	11.02
	SD	3.957	2.325
	SE	1.06	0.563
	n	14	17
T-test	T	1.94	0.79
	df	34	31
	P	NS	NS

Comparison of Vegetative Weights of early and late flowers.

			If Grass Plants are Included
Quarry Flowers Wks. 2 & 3	$\bar{x}$	13.35	
	SD	4.08	
	SE	1.13	
	n	13	
	$\bar{x}$	11.718	10.623
Wks. 4 & 5	SD	3.972	3.33
	SE	1.32	0.66
	n	9	25
	T	0.9	2.707
T-test	df	21	37
P	P	NS	0.05

* = $P < 0.05$

TABLE 17. CORRELATION OF $\sqrt{\ }$ VEGETATIVE WEIGHT FOR LEONTODON AT BEGINNING OF SAMPLE PERIOD AND REPRODUCTIVE WEIGHT AT END OF SAMPLE PERIOD.

QUARRY	r	= .7098
	t	= 4.507
	df	= 21
	P	< .001*
GRASS	r	= .5515
	t	= 1.0913
	df	= 15
		NS
TOGETHER	r	= .559
	t	= 4.045
	df	= 37
	P	< .001*

7 DISCUSSION

7.1 Validity of Techniques Employed

The majority of the regressions employed give an expected error range of between ± 5% and ± 30% (see Appendix) using Whittaker and Woodwell's (1968) estimate of relative error ie.

$$\frac{\sqrt{(\Sigma d^2/n - 1)}}{y}$$ where d = deviation, y = mean observed weight

This is similar to the values obtained by Hutchinson (1975) using data on Mercurialis perennis. He also found that quadratic regressions gave the greatest predictive accuracy. In this study, however, it was found that the use of quadratics with some data (particularly the Leontodon data) can lead to excessive generation of negative values. This difficulty, which occurs when using polynomials has been explained by Mead (1971). In biological situations, polynomials can give ridiculous values of 'y' the dependent variable for particular values of the independent variables. This occurs at the extremes of the possible range and explains why certain regression formulae predict plant dry weights to be negative. Hence quadratics seem to be of limited value in biological situations where the whole range of possible predicted values is not known.

As a result of this problem, the first and last regressions determined for Leontodon hispidus had to be discarded and the second regression was applied to the field data throughout the season. This has probably slightly increased the error in these predictions at the beginning and end of the season since Hutchings (1975) showed that Mercurialis perennis exhibited changes in dimension and weight relations throughout the season. The extent of these changes is debatable and many workers have ignored them. Kuroiwa (1960) states that his regression was made 34 days after sowing but applies it to estimate plant weights from 0-40 days after sowing. Nevertheless,

the fact that different regressions give better estimates over the season for Plantago lanceolata tends to support Hutchings' conclusions. Moreover, this is undoubtedly the case for reproductive dry weight since scape length in Plantago lanceolata is unimportant at the beginning of the season but becomes the major predictor of reproductive dry weight at the end.

Of the plant dimensions which could feasibly be measured in the time available, plant diameter and number of leaves were found to give the best predictive estimates. Not surprisingly diameter is a common parameter utilised in predictive regressions since diameter squared gives some indication of plant area. It has been applied successfully as part of a regression equation by Whittaker and Woodwell (1968) in assessment of tree and shrub production and by Hutchings (1975) to predict the dry weight of Mercurialis perennis. In the majority of previous studies, however, the plants studied have been distinctly three-dimensional in character so the regression provides a factor to convert volume to weight eg Hutchings use hd^2 where h = height and d = diameter. A rosette plant, however can virtually be regarded as two dimensional and empirical measurement of its thickness would be an impractical procedure. Werner (1975) uses a regression based on diameter as an indicator of weight for a rosette plant (Dipsacus follonum). This work on Plantago lanceolata and Leontodon hispidus suggests that a possible parameter to indicate the thickness of a rosette plant might be number of leaves, particularly when the rosette lies close to the ground surface.

For plants such as Leontodon and Plantago where the scape is a major component of their reproductive structures, measurement of its length provides an adequate indication of total reproductive weight. However, this relationship may not be so good at the commencement of reproductive resource allocation as has been shown

for Plantago. It might be argued that when reproductive effort is under consideration this parameter ignores the most vital components ie the fruit and seeds. However, if the previous definition of reproductive effort is accepted (ie RE = dry weight of all reproductive organs as a percentage of the total dry weight), the sole use of this parameter is valid.

In addition to errors caused because of changes in dimension and weight relations throughout the season possibly the largest source of error is that attributable to random variability in the material itself (Sprent 1972). Thus, genotype may effect the relationships between morphological dimensions and mass as will environment e.g. an elongate plant with few leaves, growing in a shady environment may have the same biomass as a stocky plant growing in a light environment. This factor is of particular relevance to this study. Although it was found that plants from the two sites did have slightly different dimension and weight relations, the overall error of the predictions was reduced by combining the two populations in computation of the regression. Moreover this also reduced the number of calculations necessary and differences in morphology of the plants from the two sites could be determined from consideration of the data on rosette diameter and number of leaves.

Other sources of error may have been in weighing and measuring observations and in variations in the amount of water vapour present in each plant. Nevertheless, care was taken at all times to minimise this type of error. Evans (1972) gives examples of evidence for increases in respiration rate and consequent reductions in weight increments caused by disturbance of plant tissues. He indicates that if the time intervals between measurements are long it is unlikely that alterations in respiration rate will persist from one time of measurement to the next. As, similar measurements were taken from

each plant it is unlikely that this phenomenon would differentially effect the plants in one group.

Some difficulty was experienced in delimiting root stock tissue from stem stock tissue in Plantago and this may have been a source of error in the dry weight determinations. Finally, some error may have resulted from the transformation of the data (Hutchings 1975). However it was considered preferable to tolerate this slight error which would enable the use of parametric methods of statistical analysis rather than resort to non-parametric methods which are considered to be less efficient (Sokal and Rolf 1969).

More accurate regressions would undoubtedly have been achieved if several of the more discerning parameters were selected and combined in a complicated multiple regression programme. One of the principle aims of the study, however was to provide a quick simple method of assessing plant weight in the field rather than time-consuming destructive sampling. A laborious field measuring programme would have defeated this object. Taking all of these factors into consideration the regressions provided a useful predictive tool with reasonably accurate estimations. Random variability and the error factors mentioned prevent the possibility of making completely accurate predictions of the values of biological variables. Nevertheless in the subsequent analyses mean plant weights are used, and since individual errors in prediction are normally distributed about the true values, these errors will probably cancel themselves out in the determination of a mean weight based on a large enough sample of individuals.

One of the major assumptions of the study was in the method of assessment of reproductive effort. The limitations of the popular method of R.E. determination by using the weight of reproductive parts as a percentage of total weight (Harper and Ogden 1970) which do not consider the physiological costs of producing such structures have

been pointed out (Hirshfield and Tinkle 1975). Nevertheless, no research technique has proved superior for field studies requiring a large sample size (Primack 1979). The alternative method of assessing final reproduction by determining the number of capsules produced per plant, which was attempted here, shows a similar pattern of allocation to that indicated by the traditional method of R.E. determination. Nevertheless the differences between some sets of plants are more significant and this illustrates the need for caution when interpreting R.E. determinations Hickman (1975) suggests that seed allocation is appropriate for assessing the relative contribution of different plants to the next generation whereas reproductive effort (Harper and Ogden 1970) is a measure of energy cost to the parental generation of making certain seed energy contributions. The difficulty here, is in determining which organs are reproductive e.g. the scapes of P. lanceolata and L. hispidus, being photosynthetic, also have a vegetative function but in this study this is considered as being subsidiary to their reproductive function.

The need for careful examination of possible measures of R.E. is also evident when the data on no. of capsules/unit vegetative weight are examined. The quarry plants in the field have by far the greatest value supporting the r - and K - selection paradigm. Seed output can be used as a measure of the relative fecundity of a species but the germinability of the seeds contributes to this fecundity. The study of germinability of the seeds under different conditions of light and dark was intended as a measure of this factor but the results from this experiment were inconclusive

7.2 Control of Flowering

The decision to flower or not to flower must be a crucial one. In this study it appears that Leontodon is more capable of governing its population RE than Plantago since Leontodon shows a much larger variation in population RE between the two sites. It is probable that this decision is influenced by the size or nutritional status of the plant. Plants must achieve a certain 'ripeness to flowering' before thay are capable ofres,ponding to the environmental factors which induce the formation of flowers (Hillman 1962). Species of Plantago are induced to flowering by long days (Snyder 1948) and Primack (1979) suggests that in annual species of Plantago this threshold of the 'ripeness to flowering' seems to have been lowered enough so that the stimulus to flowering produces a response in every individual regardless of every size and age. He proposes that in perennial species selection may have acted to raise the threshold so that only plants in the 'best condition' flower.

In many studies of reproductive allocation eg Stewart (1979) an examination of plant weight and its relation to flowering is impossible because of the method of sampling. The relationship between plant size and the decision to flower is only valid when the same plants have been followed throughout the season. The use of regression techniques enabled this relationship to be studied. In Leontodon hispidus flowering appears to be controlled by plant size at the beginning of the season supporting Stewarts (1979) theory and Werners (1975) findings for Dipsacus fullonum. Not only is the decision to flower governed by plant size but the level of reproductive biomass is positively correlated with the vegetative weight

at the beginning of the season. Hickman (1975) found a negative correlation between reproductive allocation and dry weight in the annual Polygonum cascadense. Other workers have found that the decision to flower may be influenced by nutrient status (Van Andel and Vera 1977) or the development of a sizeable root biomass (Raynal 1979).

Stewart (1979) found no association between leaf dry weight and flowering when samples were taken simultaneously and suggests that this may be because increase in reproductive biomass is at the expense of growth in vegetative biomass. This response is suggested by the decrease in vegetative weight soon after the onset of flowering shown in the curves for P. lanceolata and L. hispidus. This response is also implied in the percentage allocation diagrams for Senecio vulgaris (Harper and Ogden 1970) and Tussilago farfara (Ogden 1974). The fact that there was no significant difference between the vegetative weights of flowerers one week before flowering and non-flowering at the end of the sampling period whilst there was a difference at the beginning of the season supports this theory (see table 17) Stewart (1979) appears to have been right in saying that weight must be measured before flowering and this might explain why Hickman (1975) found a negative correlation between dry weight and reproductive allocation when he sampled after flowering.

7.3 Differences between Sites

Each of the two species shows a different reaction at each site in terms of its reproductive effort. L. hispidus has a significantly higher RE for three of the four sampling occassions when the plant was flowering. This difference was significant for both mean flowering individual RE and mean population RE ie not only did more of the plants flower at the quarry site but also those which did flower allocated

more of their available resources to flowering than at the grassland site. This decrease in reproductive allocation in a more moderate environment concurs with work by Hickman (1975) on Polygonum cascadense. Reproductive allocation was found to decrease significantly along a moisture gradient so allocation was greatest in the successively harsher and more open habitats. Hickman attributes this environmentally cued response to the short term unpredictability of the environments in which the species grows. Whigham (1974) found the RE of Uvularia perfoliata wassimilarly effected by environmental conditions.

Differences in the level of RE attained by L. hispidus in the earlier sampling periods can be partly attributed to the marked variation in the time of anthesis at the two sites, also noted by Stewart (1979) at Thrislington common and Wingate quarry. Thus the Leontodon plants in the harsher quarry environment where summer drought is likely to be a major mortality factor, flower earlier and devote more resources to sexual reproduction. Law et al (1977) compared populations of Poa annua experiencing either predominantly density-dependent or density-independent regulation. They found that the two populations showed genetically determined life-history differences. 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. These results are similar to those of Abrahamson and Gadgil (1973) who noted that populations of Solidago from successionally less mature sites flowered earlier and had a greater reproductive allocation Roos and Quinn (1977) found significant differences in the mean dates of the first anthesis of Andropogon which were environmentally induced.

In contrast P. lanceolata plants display no significant differences in either mean flowering individual RE or total population RE between the two sites. Despite a considerable and highly significant depression in vegetative and reproductive dry weights at the quarry site the

levels of flowering individual RE remain constant. Hawthorn and Cavers (1978) find a similar response in Plantago major when density was increased and they interpret this as an adaptation to exploitation of frequently disturbed sites by producing seeds 'at all costs'. Constancy in individual sexual RE under differing conditions has been noted by several workers for annuals eg Harper and Ogden (1972) for Senecio vulgaris, Primack (1979) for annual Plantago spp. and perennials eg Bradbury and Hofstra (1976) for Solidago canadensis, Holler and Abrahamson (1977) for Fragaria virginiana, Ogden (1974) for Tussilago farfara and Raynal (1979) for Hieracium florentinum. Some of these studies have indicated changes in vegetative reproduction under different environmental conditions but this factor was not recorded for Plantago and Leontodon in the field. Measurements of the transplanted greenhouse plants indicated that there were no significant changes in vegetative reproduction between plants from the two sites.

Similarly there are no significant differences in population RE between the two sites although there is a consistent trend towards grassland plants having a larger mean population RE (more plants flowered). Stewart (1979) found a variation in the population RE but at his quarry site (Wingate quarry) the population RE was higher than at the grassland site (Thrislington common).

Nevertheless both flowering individual RE and mean population RE vary in the greenhouse plants and seedlings, although again there is no difference between sites. Mean population and mean flowering individual RE reach approximately 59% in the greenhouse seedlings and plants but only 42% per flowering individual and 19% per member of the population in the field samples. This variation in the number of individuals which attempt to flower accords with Van Andel and

Vera's (1977) findings for Chamaenerion angustifolium. More individuals were stimulated to flower under better soil conditions. With P. lanceolata it appears that the difference in environmental conditions between the grassland and quarry sites is not sufficient to stimulate any differences in RE but the difference in conditions between the field Plantago plants and those grown in the greenhouse is sufficient.

The fact that flowering individual RE and mean population RE are very similar in the greenhouse populations whereas these figures vary in the field populations suggests that any field differences in the populations are phenotypic responses to environmental conditions rather than genetically inherited characteristics. Although there are no differences in RE between sites for P. lanceolata the fact that the size differences of plants in the field disappear in the greenhouse suggests these differences are environmental. The significant differences in the vegetative and reproductive dry weights of plants from the quarry and grassland throughout the sampling period is not found in the seedlings from both sites, grown in the greenhouse. For the first two sample weeks transplanted plants in the greenhouse show significant differences but these become less distinct until at the end of the sampling period the two populations can be regarded as being synonymous. Thus, the effect of external conditions is overcome when the plants are grown in a homogeneous environment. Moreover there is a significant difference between transplanted plants grown in the greenhouse for part of their life and seedlings grown there for their entire life, suggesting that environmental factors which have influenced a perennial plant in one season effect the plant's production in the following season. If so, this tends to raise queries concerning the validity of research based on transplanted plants rather than seeds or seedlings.

Hickman (1975), Roos and Quinn (1977) and Raynal (1979) have found differences in RE to be environmental in origin although Roos and Quinn (1977) did find some evidence of genetic differences. Primack (1978) quotes work in which he found differences in P. lanceolata RE to be both genetically and environmentally determined whereas Gadgil and Solbrig (1972) identified two distinct biotypes in Taraxacum officinale.

Unfortunately, no greenhouse experiments were carried out on L. hispidus, which was the species displaying significant differences in RE between the two sites. However the fact that there is no significant difference between the size of the non-flowerers in the quarry and the grassland (see Table 16) suggests that the differences are environmental. Differences in the mean size between the flowerers are to be expected since the quarry plants are larger. This suggests that the quarry and grassland Leontodon plants are similar in the size that must be attained to initiate flowering. Comparison of the actual levels of RE attained by Leontodon at the end of the sampling period must be treated with caution since the level of RE in the grassland was still steeply rising at the end of the study.

7.4 Succession, Reproductive Effort and r - and K - selection

Plantago and Leontodon have very different responses to the variation in environmental conditions occurring in succession. In the field Plantago has a phenotypically lower weight in the early successional stage with a constant RE at both sites. Leontodon, however has a significantly higher plant weight, flowering individual RE and population RE at the earlier successional site. The difference in behaviour of the two species at Thrislington common might be partly because of differences in the sample site used for each species. These effects, however are likely to be negligible since the vegetation

at both sites was the same density and height and was on similar soil.

Succession does not merely involve a change in one or two environmental factors but is a combination of effects which may operate at varying intensities at different stages. Moreover, the type of succession which has been studied in previous work varies. The conditions which operate under a succession from arable fields to deciduous forest as studied by Newell and Tramer (1978) are presumably very different from those operating in a succession from quarry floor to grassland as considered by Raynal (1977) and in this study. The majority of successions which have been studied are of a secondary nature, that is occurring in a gap in an already existing community. The succession studied here has many of the features of a primary succession (that is one which occurs in a pristine unaltered environment), particularly high stress at the beginning of the succession.

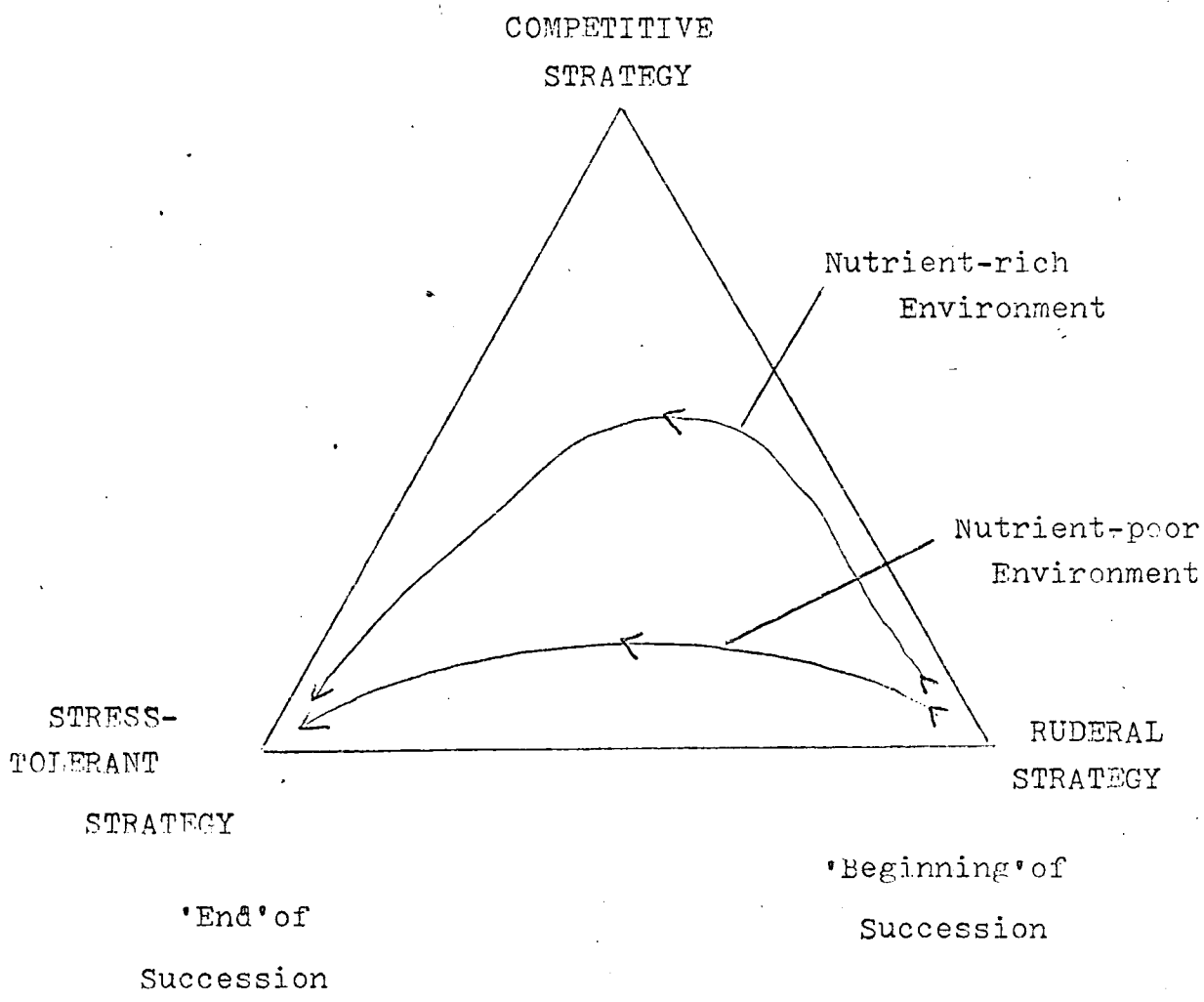
Not only must the variety of different factors involved in succession be taken into account but also the variation in species response. Annuals have been found to have higher RE's than perennials eg Pitelka (1977) and this has been interpreted as an adaptation to their life style and typical habitat. It seems therefore not unreasonable to infer that within each group there may be a range of reproductive strategies. Hence, Leontodon has a strategy adapted to the quarry environment (where it is more common) whereas Plantago is more adapted to the grassland. Each species and in fact biotype may show different responses to changes in the environment and it is inadvisable to infer that other species have similar reactions. Hickman (1977) found a diversity of responses by closely related species along the same environmental gradient and warns against incautious application of proposed general explanations of energy behaviour such as r - and K - selection theory.

Grime (1977) has proposed a model of succession in terms three strategies ie stress tolerant species, competitors and ruderals. Since succession begins with a disturbance ruderals will tend to predominate (ruderals, characteristically have high RE's) As succession proceeds competitive plants will become more successful until in the climax community stress - tolerant individuals will be most prevalent. The exact nature of the succession however, will depend on the nature of the substrate on (see Fig. 17). Thus on a poor substrate such as the quarry floor some ruderals may have to be adapted to resist the adverse conditions. High RE is a good adaption to frequent disturbance but not stress. Vegetative and Reproductive dry weights are lower in the grassland.

Leontodon is a slow growing (^{R}MAX = 0.89 see Grime and Hunt 1975) stress-tolerator and cannot tolerate competition at closed sites such as the grassland. The low RE values obtained for Leontodon here are probably an adaptation related to the high density dependent mortality. At high total vegetation cover more energy will be proportionately allocated to support tissues which maximise a plant's competitive ability for light. Abrahamson and Gadgil (1973) and Gaines et al (1974) found a direct correlation stem allocation and total stand cover. The relative elongation of the grassland Leontodon leaves is shown in table 2. These typical responses to density in the form of the dry weight of plants parts have been well documented eg by Palmblad (1968) as have leaf area responses to shade (Grime 1977). A slow growth rate is typical of stress-tolerators and the plant rosette is well adapted to reduce water loss. Thus Leontodon is physiologically and morphologically better adapted to the quarry site.

Plantago lanceolata is a competitive ruderal (^{R}MAX = 1.7) typically of productive and relatively open sites. It has many

FIG. I7 GRIME'S DIAGRAMMATIC REPRESENTATION OF SUCCESSION AT VARIOUS NUTRIENT LEVELS



features of an annual eg a high growth rate and in particular a tendency to maintain its RE under adverse conditions. This factor accounts for the lack of difference in RE between the two sites although it clearly does better at the grassland site. Reproductive and vegetative dry weights are higher here and it seems unable to attain the same levels of biomass in the stressful quarry site. Hence the different response of each species in terms of their reproductive effort at each site can be explained in terms of the individual species strategy and the nature of the succession under consideration.

8. SUMMARY

1. Regression techniques were found to be useful in predicting mean weights of populations. However, where very accurate results are required the measurement of suitable parameters in the field is too time-consuming and the applicability of such techniques is limited. The relationship between the plant dimensions of Leontodon hispidus and Plantago lanceolata did change throughout the season so more than one regression analysis was necessary.

2. The method of assessing RE was by determining the dry weight of the reproductive parts of the plant as a percentage of its total weight. Two alternative methods of assessing reproductive allocation by determining the number of seed capsules/plant and seed capsules/unit vegetative weight were tried. These methods gave slightly different results and illustrate the need for caution when choosing a suitable method of assessing RE.

3. A greater number of individuals of L. hispidus flowered at the quarry site, that is this site had a larger population RE. The vegetative weight of the plant at the beginning of the season was found to be related to this decision to flower. The larger the plant was at the beginning of the season the more likely it was to flower. Moreover the level of vegetative weight at the beginning of the season was found to be directly related to the level of reproductive dry weight achieved. There was a decline in vegetative weight immediately after flowering in both species.

4. Reproductive effort of P. lanceolata was similar at both sites in the field however, RE of L. hispidus was greatest, (and the date of first anthesis was earlier) at the early successional quarry site. Although the level of RE attained by P. lanceolata in the greenhouse was higher there was again no difference between plants from each site.

5. The two species did differ in biomass and morphology at each site. L. hispidus produced larger plants with longer, wider leaves at the quarry site. P. lanceolata produced larger plants at the grassland site. These morphological differences disappeared when P. lanceolata was grown in a homogeneous environment implying that they were phenotypic responses to environmental variables. Since quarry and grassland L. hispidus plants are similar in the size that must be reached to initiate flowering, this suggests RE and morphological differences in this species are also environmentally cued.

6. The different response of each species at each site in terms of their reproductive allocation is explained in terms of their individual species strategy, the nature of succession, and the special characteristics of the particular succession under consideration.

ACKNOWLEDGEMENTS

My grateful thanks are due to the following people for their help and advice in preparing this thesis.

Dr K Thompson. Lecturer, Dept. of Biological Science, Plymouth Polytechnic who supervised the study.

Mr D Rogers. Dept. of Environmental Science, New University of Ulster who gave much help with computing.

Mr A Stewart who gave advice about research methods.

and many others in the department of Botany at Durham University who offered advice and constructive criticism.

References

Abrahamson, W.G. 1979. Patterns of resource allocation in wildflower populations of fields and woods. Am. J. Bot 66 71 - 79.

Abrahamson, W.G. and D.J. Herchey. 1977. Resource allocation and growth of Impatiens Capensis (Balsaminaceae) in two habitats. Bull. Torrey Bot. Club 104, 160-164.

Abrahamson, W.G. and M. Gadgil. 1973. Growth form and reproductive effort in golden rods (Solidago, Compositae). Am. Nat. 107: 651-661.

Andel, J. van and F. Vera. 1977. Reproductive allocation in Senecio sylvaticus and Chamaenerion angustifolium in relation to mineral nutrition. J. Ecol. 65 747-758.

Bostock, S.J. and R.A. Benton. 1979. The reproductive strategies of five perennial compositae. J. Ecol. 67 91-107.

Bell, K.L. and R.D. Hiatt and W.E. Niles. 1979. Seasonal changes in biomass allocation in eight winter annuals of the Mojave desert. J. Ecol. 67 781-787.

Bradbury, I.K. and G. Hofstra. 1975. The partitioning of net energy resources in two populations of Solidago canadensis during a single developmental cycle in southern Ontario. Can. J. Bot 54 2449-2456.

Clapham, A.R. and T.G. Tutin and E.F. Warburg. 1959. Excursion Flora of the British Isles. Cambridge University Press.

Cody, M.L. 1966. A general theory of clutch size. Evolution 20, 174-84.

Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organisation. Am. Nat. 111. 1119-1144.

Mitmer, E.J. 1972. A method to determine root biomass including uncollected portions. Bull. Torrey Bot. Club 99 146-147

Moody, J.P. 1977. The conservation of the acid-natural vegetation of the magnesian limestone. 1. The Durham Escarpment. Vasculum 62 17-32.

Evans, G.C. 1972. The quantitative analysis of plant growth. Studies in Ecology. Vol.1. Blackwells.

References (cont.)

Gadgil, M. and T.W.H. Bossor. 1970. Life historical consequences of natural selection. Am. Nat. 104 1-24.

Gadgil, M. and O.T. Solbrig. 1972. The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. Am. Nat. 106 14-31.

Gaines, M. and K.J. Vogt, J.L. Hamrick, J. Caldwell. 1974. Reproductive strategies and growth patterns in sunflowers (Helianthus). Am. Nat. 108 889-894.

Goodall, D.W. 1945. The distribution of weight change in the young tomato plant. I. Dry weight changes of the various organs. Ann. Bot. N.S. 9 101.

Grime, J.P. 1974. Vegetation classification by reference to strategies. Nature 250 26-31.

Grime, J.P. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat.

Grime, J.P. and R. Hunt. 1975. Relative growth rate; its range and adaptive significance in a local flora. J. Ecol 63 393-422.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, London.

Harper, J.L. 1967. A Darwinian approach to plant ecology. J. Ecol. 55 247-70.

Harper, J.L. and N.J. Ogden. 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to Sonchus vulgaris L. J. Ecol. 58 681-91.

Hawthorn, W.R. and P.B. Cavers. 1978. Resource allocation in young plants of two perennial species of Plantago. Can. J. Bot. 56 2933-2937.

Hickman, J.C. 1975. Environmental unpredictability and plastic energy allocation strategies in the annual Polygonum cascadense (Polygonaceae). J. Ecol. 63 689-701.

Hickman, J.C. 1977. Energy allocation and niche differentiation in four co-existing annual species of Polygonum in Western North America. J. Ecol. 65 317-326.

References. (cont.)

Hillman, W.S. 1962. The physiology of flowering. Holt, Rinehart and Winston. N.Y.

Hirshfield, M.E. and D.W. Tinkle. 1975. Natural selection and the evolution of reproductive effort. Proc. Nat.l. Acad Sci USA 72 2227-2231.

Holler. L.C. and W.G. Abrahamson. 1977. Seed and vegatative reproduction in relation to density in Eragana virginiana (Rosaceae).

Hutchings, M.J. 1975. Some statistical problems associated with determinations of population paramoters for herbaceous plants in the field. New Phytol. 74 349-363.

Kuroiwa, S. 1960. Intraspecific competition in artificial sunflower communities. Bot. Mag. (Tokyo) 73 300.

Law, R. and A.D. Bradshaw and D.D. Putwain. 1977. Life history variation in Poa annua. Evolution 31 233-246.

MacArthur, R.H. 1962. Some generalised theorems of natural selection. Proc. natn. Acacl. Sci 48 1893-7.

MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press. Princeton, N.J.

Mead, R. 1971. A note on the use and misuse of regression models in ecology. J. Ecol. 59 215.

Nature Conservancy Council. 1977. A nature conservation review. Ed. D. Ratcliffe. Vol.2.

Muller, F.M. 1978. Seedlings of N. Western European Lowland: a flora of seedlings. The Hague. Pub. Junk.

Nie, N.H. and C. Hadlai Hull, J.G. Jenkins, K. Steinbreuner, D.M.Bent. 1975. S.P.S.S. Manual. Pub. McGraw Hill.

Newell, S.J. and E.J. Tramer. 1978. Reproductive strategies in herbaceous plant communities during succession. Ecology 59 228-234.

Ogden, J. 1974. The reproductive strategy of higher plants. II. The reproductive strategy of Tussilago farfara L. J. Ecol. 62 291-324.

References (cont.)

Palmblad, I.G. 1968 Ecology 49 26-34.
Competition in experimental populations of weeds with emphasis on the regulation of population size.

Pitelka, L.F. 1977. Energy allocation in annual and perennial lupines (Lupinus: Leguminosae). Ecology 58 1055-1065.

Primack, R.B. 1979. Reproductive effort in annual and perennial species of Plantago (Plantaginaceae). Am. Nat 114 51-62.

Raynal, D.J. 1979. Population ecology of Hieracium florentinum (Compositae) in a central New York limestone quarry. J. Appl. Ecol. 16 287-298.

Rose, F.H. and J.A. Quinn. 1977. Phenology and Reproductive allocation in Andropogon scoparius (Gramineae) populations in communities of different successional stages. Amer. J. Bot. 64 535-540.

Shimwell, D.W. 1960. The phytosociology of Calcareous Grasslands in the British Isles. PhD. Thesis. Durham University.

Snyder, W.E. 1948. The mechanism of the photoperiodic response of Plantago lanceolata. Am. J. Bot. 35 520-525.

Sokal, R.R. and Rolf, F.J. 1969. Biometry. Freeman and Co., San Francisco. CA.

Southwood, T.R.E. and R.M. May, M.P. Hassell, G.R. Conway. 1974. Ecological strategies and population parameters. Am. Nat. 106 791-804.

Sprent, P. 1972. The mathematics of size and shape. Biometrics 28, 23.

Stearns, S.C. 1976. Life history tactics. A review of the ideas. Q. Rev. Biol. 51 3-47.

Stearns, S.C. 1977. The evolution of life history traits. A critique of the theory and a review of the data. Annu. Rev. Ecol. Syst. 8 145-171.

Stewart, A.J.A. 1979. Reproductive strategies of six perennial plant species in relation to a successional series.

Werner, P.A. 1975. Predictions of fate from rosette size in Teasel (Dipsacus fullonum L.) Oecologia 20 197-201.

References. (cont.)

Whigham, D. 1974. An ecological life history study of Uvularia perfoliata L. Am. Midl. Nat. 91 343-59.

Whittaker, R.H. and G.M. Woodwell. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. J. Ecol. 56 1.

Wilbur, H.M. and D.W. Tinkle and J.P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. Am. Nat 108 805-817.

Appendix I SCAPE LENGTHS FOR LEONTODON HISPIDUS AND PLANTAGO LANCEOLATA

APPENDIX. PLANTAGO TOTAL LENGTH SCAPES. FLOWERING POPULATION

FIELD PLANTAGO

Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	19.3	371.0	529.7	597.1	680.4
	SD	13.3	252.6	337.9	403.2	465.1
	SE	2.3	44.66	61.7	82.3	94.9
	n	34	32	30	24	24
QUARRY	$\bar{x}$	11.6	254.0	361.6	389.6	413.5
	SD	8.1	168.6	227.9	281.1	283.5
	SE	1.4	30.3	40.3	52.2	53.6
	n	31	31	32	29	28
T-test	T	2.75	2.15	2.31	2.2	2.54
	df	63	61	60	51	50
	prob	0.008*	0.035*	0.024*	0.032*	0.014*

GREENHOUSE PLANTS

GRASS	$\bar{x}$	30.1	600.1	2011.3	4065.8	4307.9
	SD	20.9	469.9	865.6	1814.1	1892.5
	SE	4.0	80.6	138.6	286.8	299.2
	n	27	34	39	40	40
QUARRY	$\bar{x}$	31.6	716.9	1975.2	4595.2	5009.0
	SD	23.5	633.3	1057.9	1479.9	1556.7
	SE	4.2	102.7	171.6	243.3	252.5
	n	32	38	38	37	38
T-test	T	-0.27	-0.88	0.16	-1.40	-1.78
	df	57	70	75	75	76
	prob	0.792	0.382	0.870	0.165	0.079

GREENHOUSE SEEDLINGS

GRASS	$\bar{x}$	25.3	1341.1	4730.5	5885.1	5926.3
	SD	13.9	867.9	1677.0	2134.9	2222.8
	SE	2.4	142.7	275.7	346.3	360.6
	n	33	37	37	38	38
QUARRY	$\bar{x}$	18.9	1125.6	4040.8	5838.6	5880.9
	SD	14.6	863.0	1977.3	2881.9	2872.5
	SE	2.5	138.2	315.8	355.7	459.9
	n	35	39	40	40	39
T-test	T	1.85	1.08	1.63	0.08	0.08
	df	66	74	75	76	75
	prob	0.069	0.282	0.106	0.936	0.939

* = $P < 0.05$

Wk.I = Mean spike length per plant

APPENDIX. PLANTAGO TOTAL LENGTH SCAPES.* TOTAL POPULATION

FIELD PLANTAGO

Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	16.4	320.9	454.1	462.3	526.8
	SD	14.1	267.4	364.4	434.8	499.4
	SE	2.2	43.9	61.6	78.1	89.7
	n	40	37	35	31	31
QUARRY	$\bar{x}$	9.1	201.9	289.3	297.3	296.9
	SD	8.6	182.3	250.5	296.6	304.4
	SE	1.4	29.2	39.6	48.1	48.7
	n	40	39	40	38	39
T-test	T	2.81	2.28	2.31	1.87	2.38
	df	78	74	73	67	68
	prob	0.006**	0.026*	0.024*	0.066	0.020*

GREENHOUSE PLANTS

GRASS	$\bar{x}$	20.3	510.1	1960.9	4065.8	4307.9
	SD	22.2	483.7	911.7	1814.1	1892.5
	SE	3.5	76.4	144.2	286.8	299.2
	n	40	40	40	40	40
QUARRY	$\bar{x}$	25.3	681.1	1924.6	4474.3	4880.6
	SD	24.6	636.8	1090.8	1639.1	1732.9
	SE	3.9	100.7	174.7	265.9	277.5
	n	40	40	39	38	39
T-test	T	-0,95	-1.35	0.16	-1.04	-1.4
	df	78	78	77	76	77
	prob	0.343	0.180	0.872	0.301	0.165

GREENHOUSE SEEDLINGS

GRASS	$\bar{x}$	20.9	1272.3	4606.0	5885.1	5926.3
	SD	15.9	896.3	1823.5	2134.9	2222.8
	SE	2.5	143.5	295.8	346.3	360.6
	n	40	39	38	38	38
QUARRY	$\bar{x}$	16.5	1097.5	4040.8	5838.6	5880.9
	SD	15.0	870.3	1997.3	2881.9	2872.5
	SE	2.3	137.6	315.8	455.7	459.9
	n	40	40	40	40	39
T-test	T	1.25	0.88	1.3	0.08	0.08
	df	78	77	76	76	75
	prob	0.214	0.382	0.196	0.936	0.939

* Wk.I= Mean Spike length per plant

APPENDIX. LEONTODON HISPIDUS.

TOTAL LENGTH SCAPES. FLOWERING POPULATION

Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	0	0	0	34.5	105.4
	SD	0	0	0	31.5	89.5
	SE	0	0	0	15.7	21.7
	n	0	0	0	4	17
QUARRY	$\bar{x}$	0	28.2	71.9	240.2	319.1
	SD	0	67.8	125.4	175.1	232.9
	SE	0	21.5	32.4	42.5	49.7
	n	0	10	15	17	22
T-test	T	0	-1.31	-2.22	-2.3	-3.58
	df	0	9	14	19	37
	prob	1.0	0.221	0.0440	0.033*	0.001*

TOTAL LENGTH SCAPES. TOTAL POPULATION

Week		Wk.1	Wk.2	Wk.3	Wk.4	Wk.5
GRASS	$\bar{x}$	0	0.0	0.0	3.7	51.2
	SD	0	0.0	0	14.1	81.4
	SE	0	0.0	0	2.3	13.8
	n	40	40	40	37	35
QUARRY	$\bar{x}$	0	7.1	26.9	110.4	189.8
	SD	0	34.9	83.0	168.4	238.5
	SE	0	5.5	13.1	27.6	39.2
	n	40	40	40	37	37
T-test	T	0	-1.28	-2.05	-3.84	-3.26
	df	78	78	78	72	70
	prob	1.0	0.205	0.043	0.000	0.002

* = $P < 0.05$

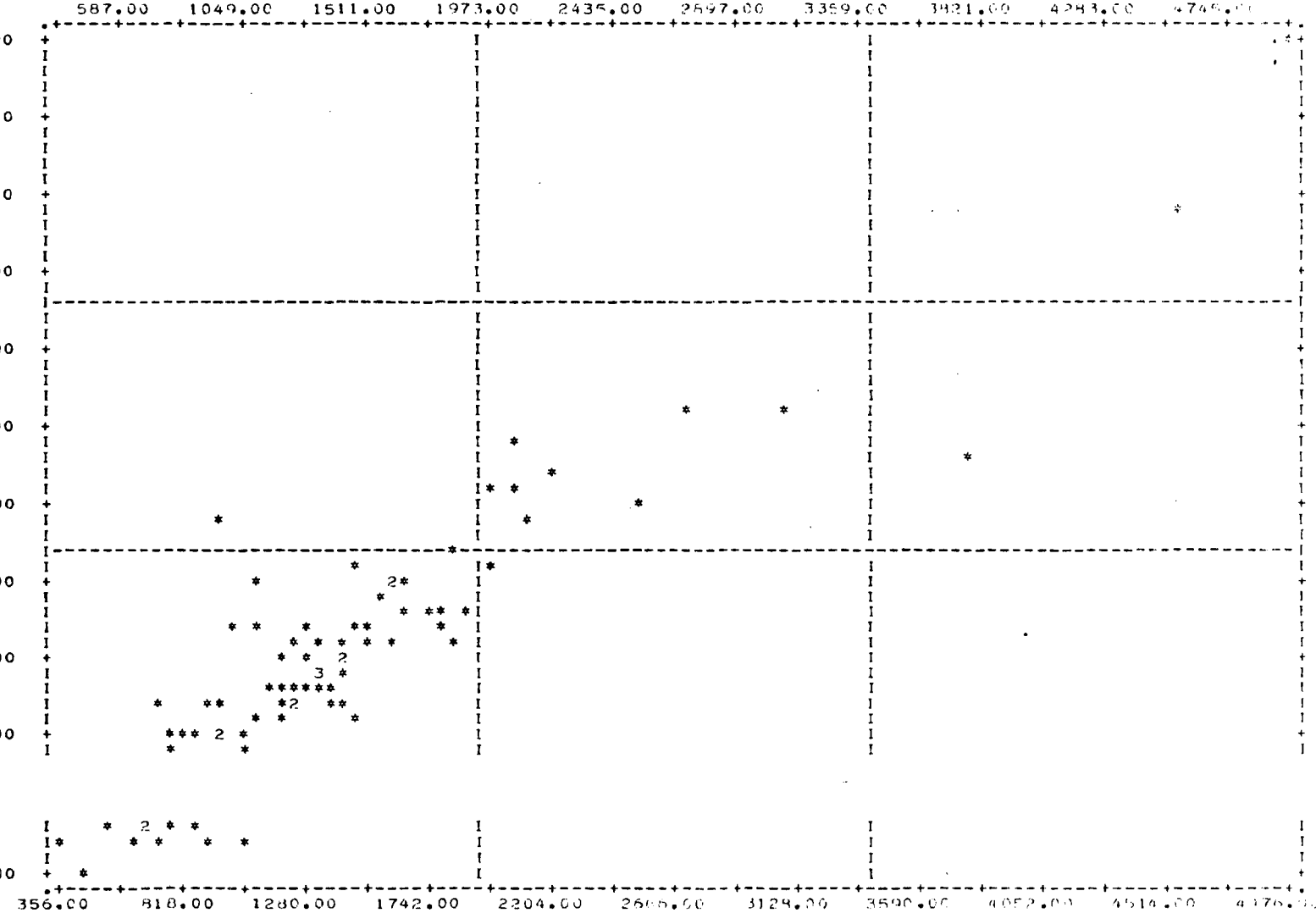
APPENDIX 2 SCATTERGRAMS FOR REGESSIONS

SEC REGRES SCATS

Vegetative Dry Weight with N.x D.
Leontodon hispidus

09/18/79 PAGE 12

FILE NONAME (CREATION DATE = 09/18/79)
SCATTERGRAM OF (DOWN) V9 (ACROSS) V11



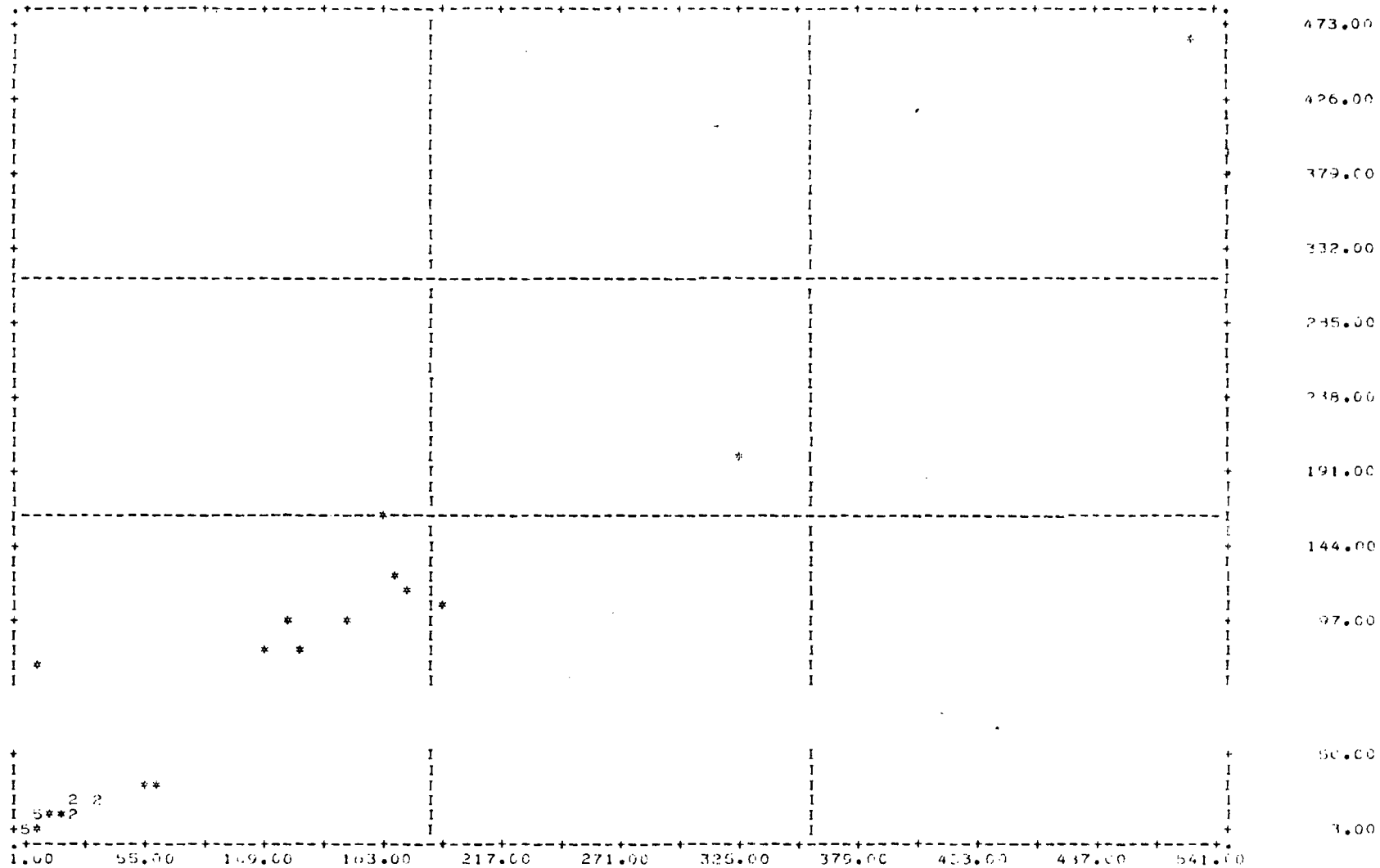
SEC REGRES SCATS 09/18/79 PAGE 13

STATISTICS..

CORRELATION (R)-	0.92219	R SQUARED -	0.85044	SIGNIFICANC -	0.00001
STD ERR OF EST -	51.11822	INTERCEPT (A) -	-14.47574	SLOPE (B) -	0.11757

THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 40.94322 ON THE LEFT MARGIN

FILE NONAME (CREATION DATE = 09/18/79) Reproductive Dry Weight with Total Length of Scapes: Leontodon hispidus
SCATTERGRAM OF (DOWN) V10 (ACROSS) V6



SEC REGRES SCATS 09/18/79 PAGE 27

STATISTICS..

CORRELATION (R)=	0.96991	R SQUARED =	0.94073	SIGNIFICANCE =	0.00001
STD ERR OF EST =	22.34797	INTERCEPT (A) =	1.31637	SLOPE (B) =	0.76023

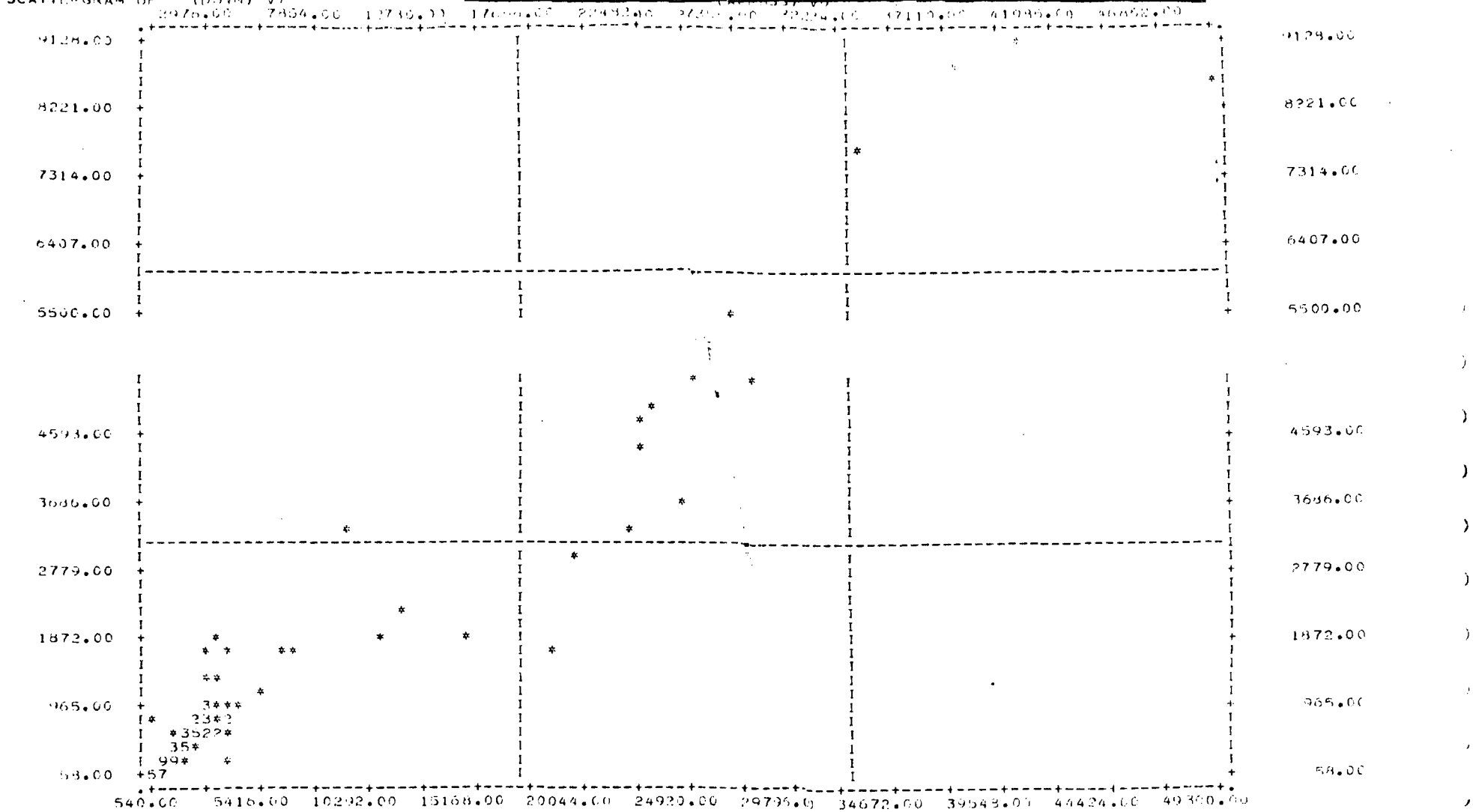
THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 2.08359 ON THE LEFT MARGIN
A VALUE OF 415.04424 ON THE RIGHT MARGIN

PLOTTED VALUES =	32	EXCLUDED VALUES=	0	MISSING VALUES =	48

'********' IS PRINTED IF A COEFFICIENT CANNOT BE COMPUTED.

FILE NONAME (CREATION DATE = 04/19/79)
SCATTERGRAM OF (DOWN) V7

Vegetative Dry Weight with N.D.:Plantago lanceolata



THIRD REGRES SCATS 04/19/79 PAGE 25

STATISTICS..

CORRELATION (R)-	0.97037	R SQUARED -	0.94184	SIGNIFICANCE -	0.00001
STD ERR OF EST -	483.01409	INTERCEPT (A) -	98.76514	SLOPE (B) -	0.19437

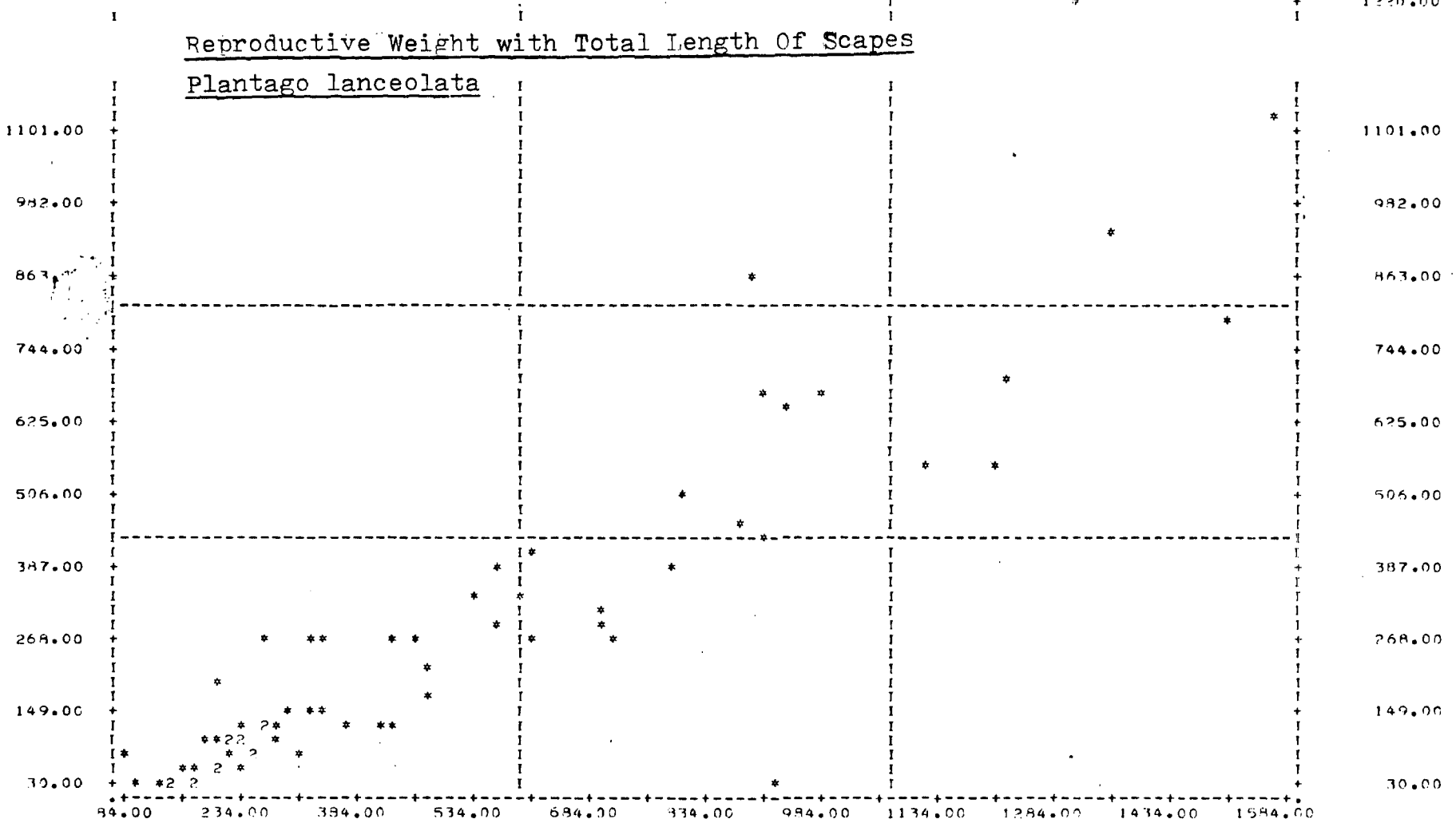
THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 203.54218 ON THE LEFT MARGIN
A VALUE OF 47469.76563 ON THE TOP MARGIN.

PLOTTED VALUES - 131 EXCLUDED VALUES- 0 MISSING VALUES - 2

********* IS PRINTED IF A COEFFICIENT CANNOT BE COMPUTED.

Reproductive Weight with Total Length Of Scapes

Plantago lanceolata



SEC REGRES SCATS 09/12/79 PAGE 46

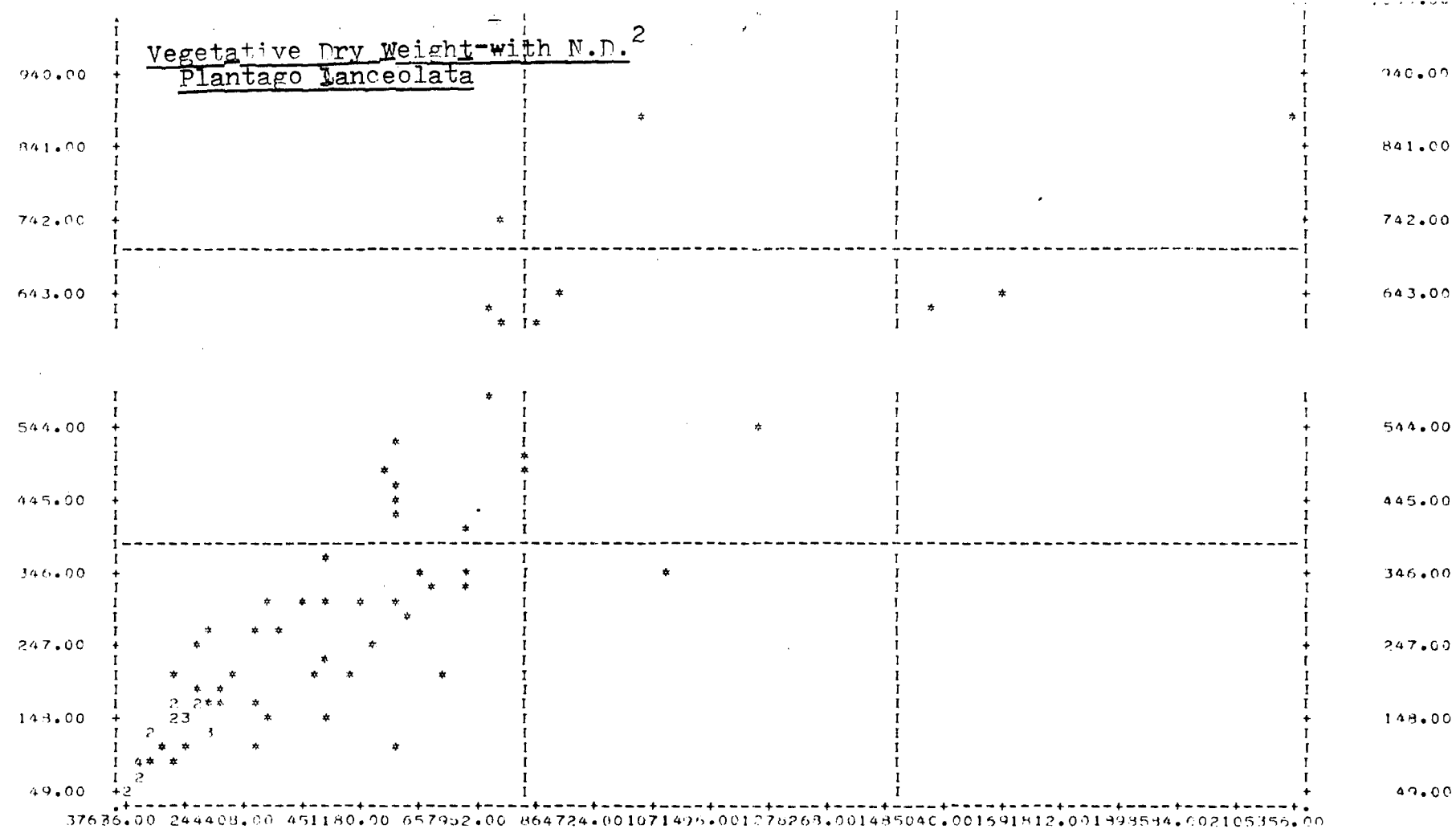
STATISTICS..

CORRELATION (R)-	0.90639	R SQUARED -	0.82154	SIGNIFICANCE -	0.00001
STD ERR OF EST -	116.90988	INTERCEPT (A) -	-59.82000	SLOPE (B) -	0.65728

THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 100.45804 ON THE BOTTOM MARGIN
A VALUE OF 981.30151 ON THE RIGHT MARGIN

PLOTTED VALUES -	66	EXCLUDED VALUES-	0	MISSING VALUES -	14

'*********' IS PRINTED IF A COEFFICIENT CANNOT BE COMPUTED.



SEC REGRES SCATS 09/19/70 PAGE 4

STATISTICS..

CORRELATION (R)-	0.86941	R SQUARED -	0.75588	SIGNIFICANCE -	0.00001
STD ERR OF EST -	119.49769	INTERCEPT (A) -	95.39337	SLOPE (B) -	0.00049

THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 113.76120 ON THE LEFT MARGIN
A VALUE OF 197403.00000 ON THE TOP MARGIN

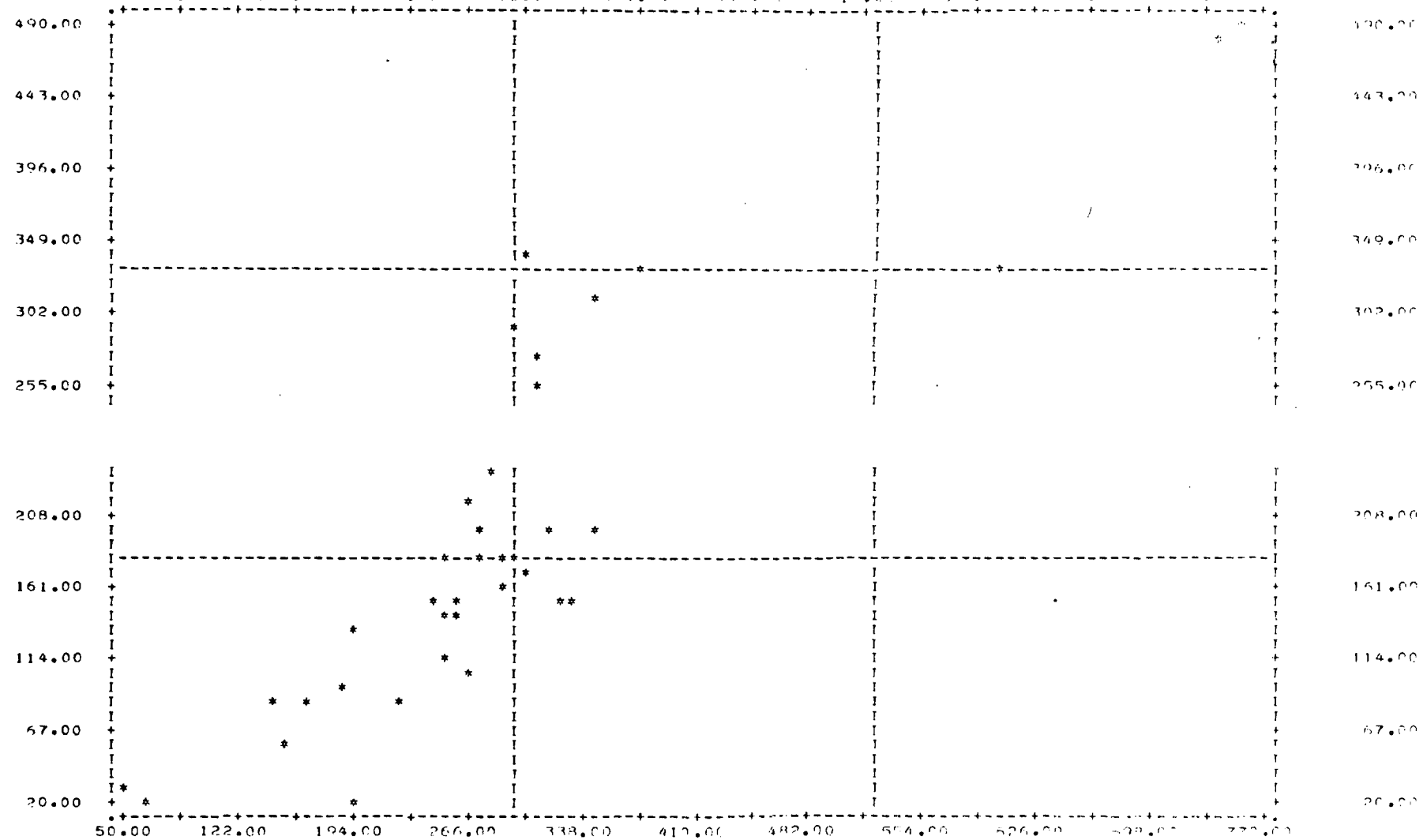
PLOTTED VALUES - 30 EXCLUDED VALUES- 0 MISSING VALUES - 0

'********' IS PRINTED IF A COEFFICIENT CANNOT BE COMPUTED.

SEC REGRES SCATS 09/19/70 PAGE 5

Reproductive Dry Weight with Total Length of Scapes
Leontodon hispidus

FILE NONAME (CREATION DATE = 02/14/79)
SCATTERGRAM OF (DOWN) V8 (ACROSS) V5



STATISTICS..

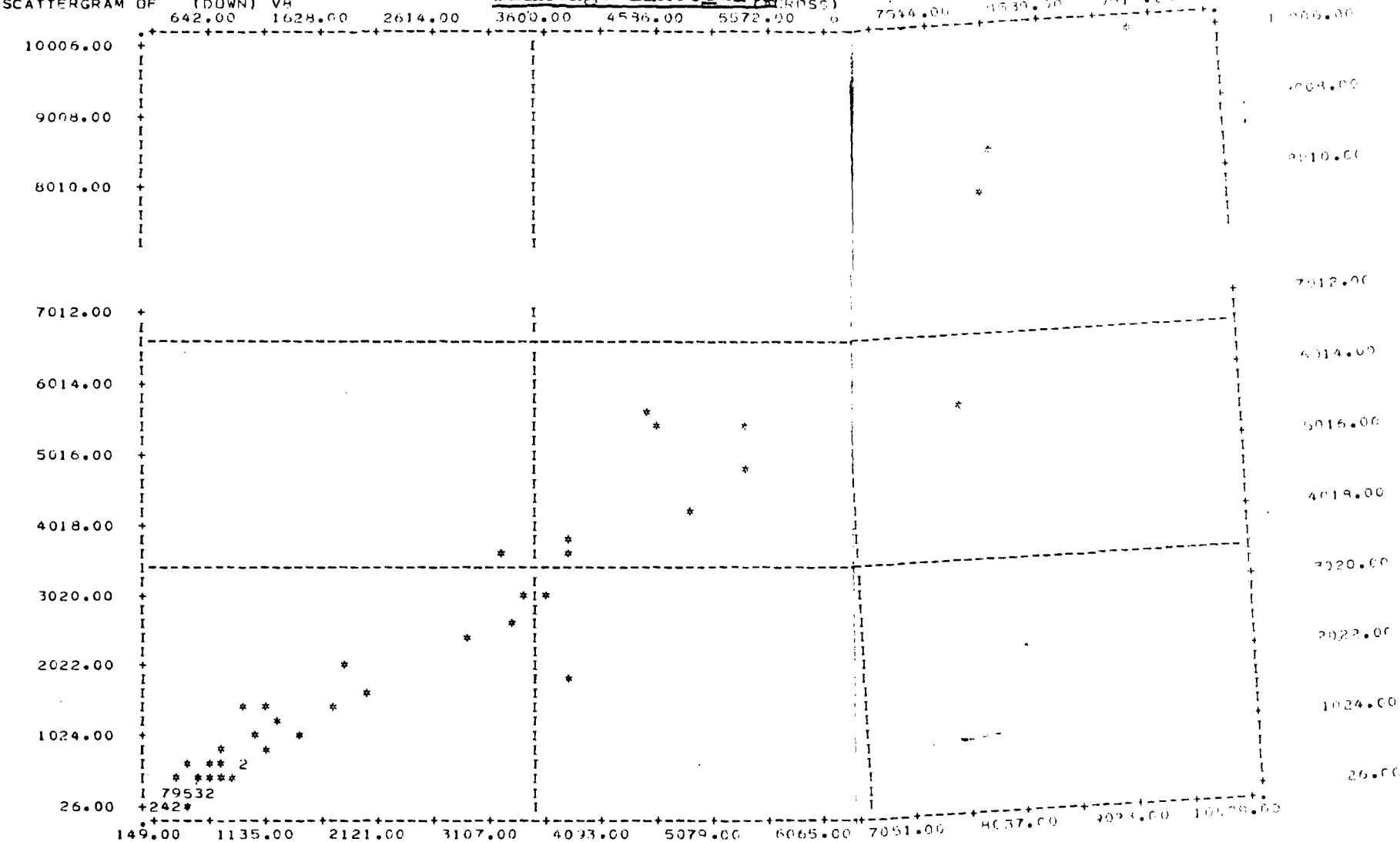
CORRELATION (R)-	0.88265	R SQUARED -	0.77907	SIGNIFICANCE -	0.00001
STD ERR OF EST -	53.08261	INTERCEPT (A) -	-13.52469	SLOPE (B) -	0.63363

THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 21.65698 ON THE LEFT MARGIN
A VALUE OF 748.94082 ON THE TOP MARGIN

PLOTTED VALUES = 37 EXCLUDED VALUES=

THIRD REGRES SCATS **Reproductive Weight with Total Length of Scapes.**

FILE NONAME (CREATION DATE = 09/19/79) **Plantago lanceolata**
SCATTERGRAM OF (DOWN) VS (ACROSS)



STATISTICS..

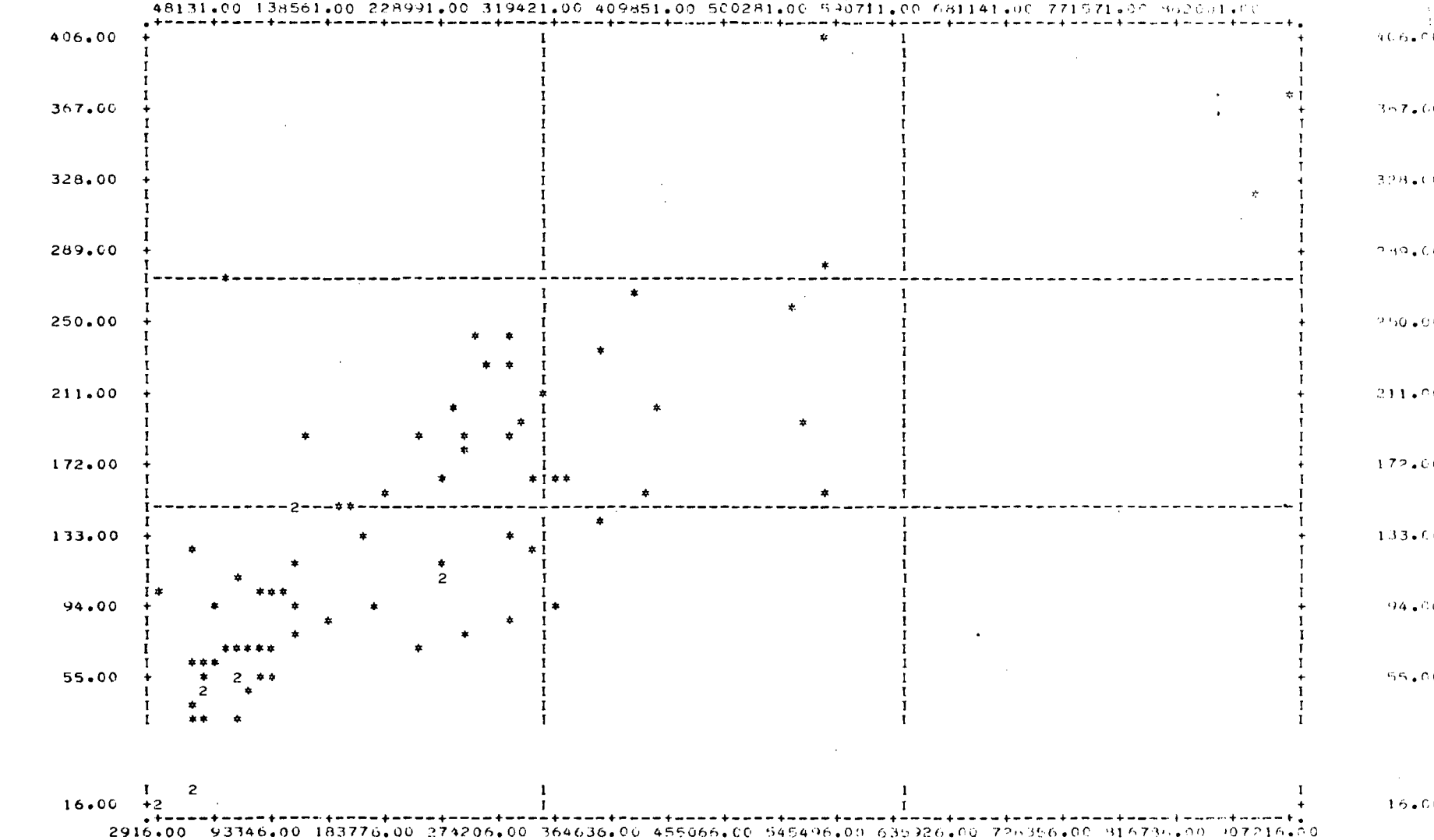
CORRELATION (R)-	0.98205	R SQUARED -	0.96442	SIGNIFICANCE -	0.00001
STD ERR OF EST -	424.97148	INTERCEPT (A) -	-159.44195	SLOPE (B) -	0.99043

THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF -10.97332 ON THE LEFT MARGIN
A VALUE OF 9813.86328 ON THE RIGHT MARGIN

PLOTTED VALUES -	73	EXCLUDED VALUES-	0	MISSING VALUES -	0

THIRD REGRES SCATS Vegetative Weight with N.D.^{2} 09/19/79 PAGE 12

FILE NONAME (CREATION DATE = 09/19/79) Leontodon hispidus
SCATTERGRAM OF (DOWN) V7 (ACROSS) V10



THIRD REGRES SCATS 09/19/79 PAGE 13

STATISTICS..

CORRELATION (R)-	0.79794	R SQUARED -	0.63671	SIGNIFICANCE -	0.00001
STD ERR OF EST -	50.11831	INTERCEPT (A) -	58.75476	SLOPE (B) -	0.00237

THE REGRESSION LINE CUTS THE MARGINS OF THE PLOT AT
A VALUE OF 59.82291 ON THE LEFT MARGIN
A VALUE OF 391.07593 ON THE RIGHT MARGIN

PLOTTED VALUES -	20	EXCLUDED VALUES -	0	MISSING VALUES -	0

APPENDIX 3 ESTIMATES OF RELATIVE ERROR FOR REGRESSIONS USED

Regression	Relative Error %
First Plantago	
Vegetative	5.45
Second Plantago	
Vegetative	I3.35
Third Plantago	
Vegetative	48.06
First Plantago	
Reproductive	I.2I
Second Plantago	
Reproductive	I4.27
Third Plantago	
Reproductive	40.6
Second Leontodon	
Vegetative	5.7
Second Leontodon	
Reproductive	3.9