

# PLANT POPULATION STRUCTURE AND PRODUCTIVITY

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**SUMMARY:** In many animal populations age distribution has been studied as a basic component of population structure. In plants, developmental plasticity and vegetative reproduction may mean that age distribution is less significant than size distribution, particularly in production processes occurring within populations. Changes in size distribution with time and at different densities are discussed, with particular reference to herbaceous monocultures. The relationship between size distribution and 'productive structure' (layering) is considered and examples of the vertical profile of chlorophyll content have been taken from three herb communities. The effects of these population attributes on rates of mortality and turnover, gross production, net production and biomass are discussed and a graphic model is presented which relates aspects of production to density.

## INTRODUCTION

In the population ecology of animals 'population structure' refers to the age distribution of individuals of each sex within the population. Knowledge of the relative proportions of young and old or males and females, often summarised diagrammatically as a 'pyramid of numbers', is regarded as a preliminary step in the quantitative description of that population. This knowledge is an essential prerequisite if reliable predictions of future population trends are to be attempted.

The concept of 'structure' in this sense has not been generally applied to plant populations. The study of plant population dynamics has suffered particularly from emphasis given to plasticity and vegetative reproduction, characteristics which render plants awkward as demographic units (Harper, 1967). Vegetative reproduction presents us with problems of definition, both of the true genetic individual and of the unit to be regarded as an individual for the purpose of counting. Plasticity may cause individuals of the same absolute age to differ 100-fold or more in size, allowing them to play very different roles within the population. The ecologist may, understandably, be reluctant to give such individuals equal weight in a population census. Finally, it is often difficult or impossible to ascertain the absolute age of a plant growing in the field, although careful observation may sometimes make this possible, as when scars are left by annually-produced inflorescences (Tamm, 1948). Many temperate-forest trees provide notable exceptions to these difficulties. Most trees lack vegetative reproduction and form discrete countable individuals whose age can be estimated without too much difficulty. Moreover,

particularly in New Zealand, many species have distinct sexes, so that for these species it seems feasible to construct pyramids of numbers directly comparable with those obtained for animal populations.

## THE FREQUENCY DISTRIBUTION OF PLANT WEIGHTS

In most herbaceous plants age and size are not synonymous, so that the concept of population structure must be expanded to include the weight and height distributions of the individuals within the population. Japanese workers associated with Kira in the 1950s (Hozumi *et al.*, 1955, Koyama and Kira, 1956) found that populations in which weights were initially normally distributed developed a positive skew as the population aged. This skewing was exaggerated at high population densities and led eventually to the appearance of L-shaped frequency distribution curves. Koyama and Kira argued that these distributions are often log-normal, i.e. a histogram of the log of the weights follows a normal curve. This log-normality they interpreted as arising from the exponential nature of the growth processes. They argued that skewing was exaggerated by intraspecific competition, but that it would develop even in non-competing, widely spaced populations. Obeid *et al.* (1967), studying the European fibre flax (*Linum usitatissimum* L.), have confirmed the Japanese work and, as suggested by Donald (1963), have examined the influence of density on the frequency distributions of certain yield components.

Log-normal frequency distributions are not restricted to plants growing in monocultures. In 1966 I investigated the frequency distributions of

weight in mixed annual herb communities colonising an arable field in Wales (Appendix 1). The distributions of the community as a whole, and of the individual species populations, were all markedly skewed in favour of small individuals (Fig. 1). In four of the seven cases examined there was no significant departure from log-normality (Fig. 2). It may be a fair generalisation to con-

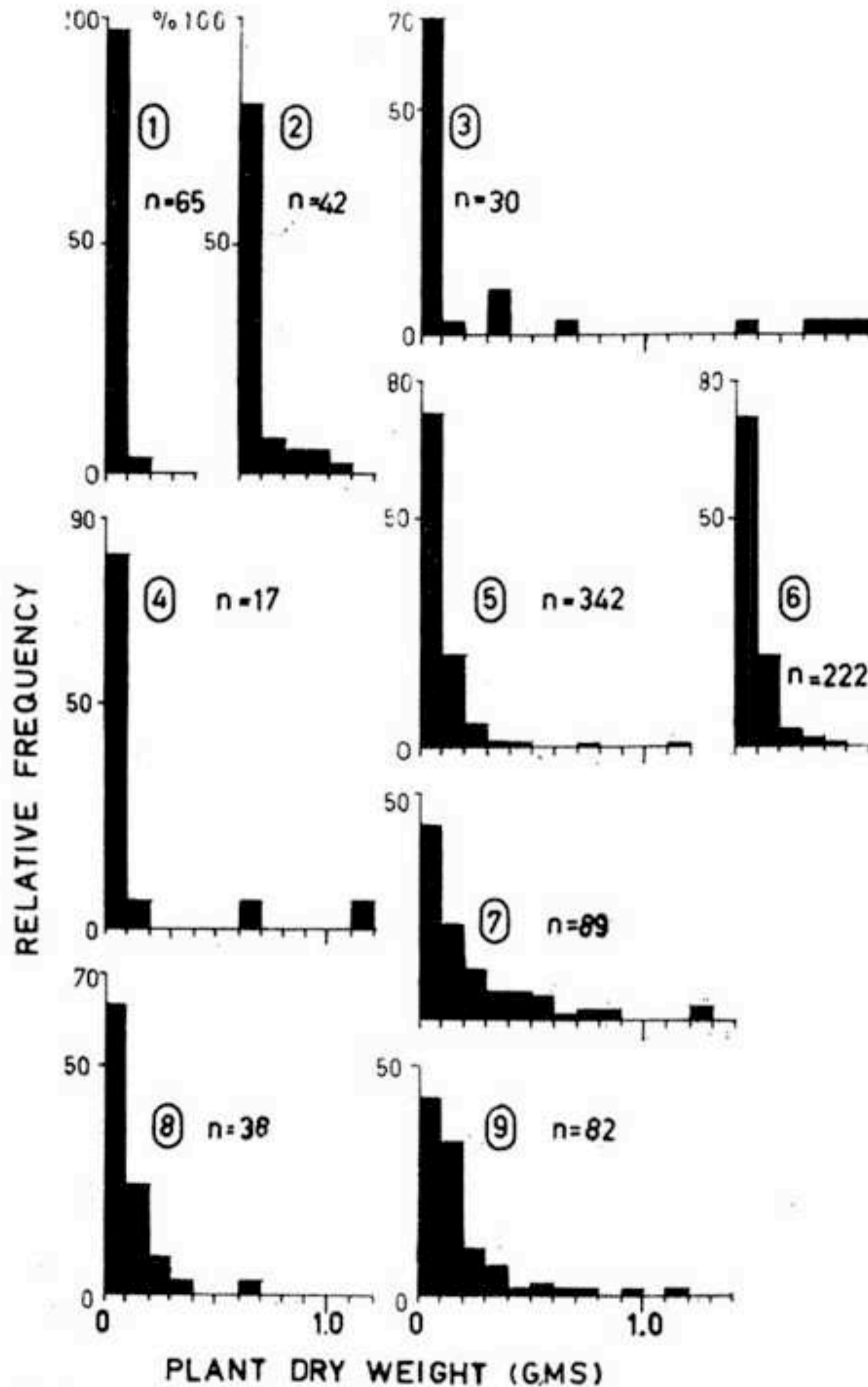


FIGURE 1. Frequency distributions of individual plant dry weight in mixed annual weed populations colonising an arable field in N. Wales.

*n* is the density of individuals per 6 square feet and the sample size. The ringed numbers refer to the species as follows: 1, Graminae, mostly *Poa annua* L. 2, *Atriplex patula* L. 3, *Polygonum aviculare* agg. 4, All other species (see Table 3, Appendix 1). 5, *Stachys arvensis* L. 6, *Stellaria media* (L.) Vill. 7, *Spergula arvensis* L. 8, *Senecio vulgaris* L. 9, *Polygonum persicaria* L. and *P. lapathifolium* L.

clude that annual (and perennial?) plant populations usually consist of a few large individuals and a relatively large number of small ones, and that this skewing increases with increasing density and the passage of time.

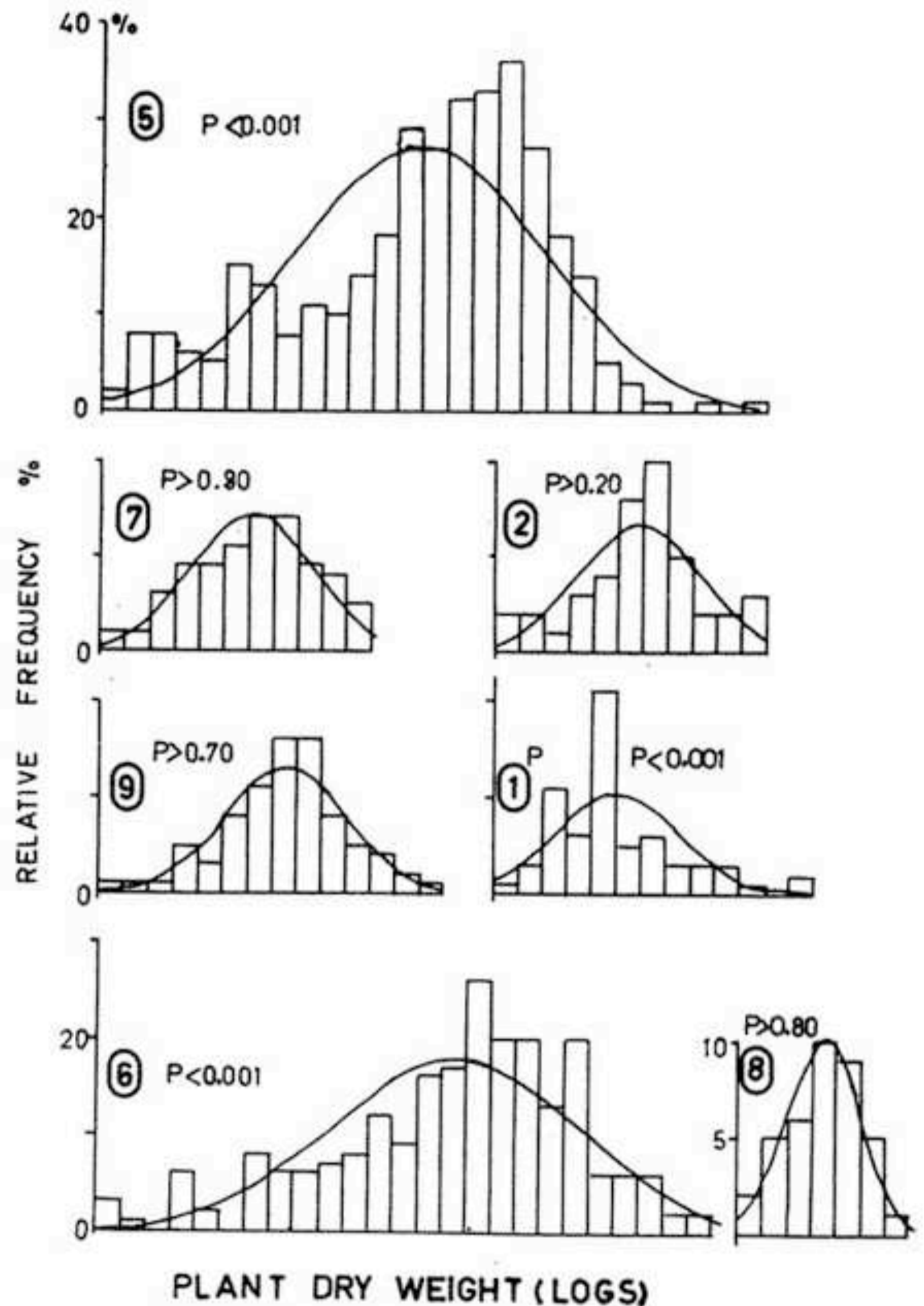


FIGURE 2. Frequency distributions of the logarithms of individual plant dry weight in mixed annual weed populations colonising an arable field in N. Wales

For details of derivation of class intervals see Appendix 1. For key to species see Figure 1. Goodness of fit to normal curve tested by chi-square. P values greater than 0.05 indicate no significant departure from normality.

#### THE FREQUENCY DISTRIBUTION OF PLANT HEIGHTS (THE HEIGHT PROFILE)

Several sets of data for annual plants growing in pure cultures (Koyama and Kira, 1956; Kuroiwa, 1960a) indicate that generally the height frequency curve is either more-or-less normal at all densities or negatively skewed (i.e. it is skewed

in the direction opposite to the weight frequency curve). Similarly, in perennial herbaceous monocultures highly skewed weight distributions may be associated with approximately normal height distributions (Fig. 3). This situation suggests that at least some of the abundant low weight individuals in dense populations tend to maintain their height, struggling to reach a canopy provided primarily by a few large plants. In *Helianthus annuus* L. (Kuroiwa, 1960a; Hiroi and Monsi, 1964) these suppressed plants are lank and etiolated, with a relatively increased proportion of non-photosynthetic to photosynthetic tissue (stem to leaves). Tezuka (1960) has demonstrated the same effect in high density stands of *Fagopyrum esculentum*.

In more complex vegetation the height frequency distribution, or profile, of the community as a whole may show several distinct modes; for example, those corresponding with the upper limits of herb, shrub and tree strata in a forest community. However, if we consider all the individuals present rather than individual species, these strata may not always be as distinct as is frequently supposed. Grubb *et al.* (1963) have pointed out that, in tropical rain forest, the frequency distribution of individual tree heights frequently approximates a hollow curve, with many small trees and few large ones in any limited area.

If seedlings are considered this skewing is even more marked. Similarly, highly skewed girth frequency distributions have been recorded for all individuals in 25 plots in rain forest in Guyana, although girth distributions for individual species often deviated from this pattern (Ogden, 1966).

Plant communities are so varied in composition and structure that no general statement concerning their height frequency distributions is possible. In herbaceous monocultures, however, the changes in the distribution of weight and height frequencies with the passage of time indicate that an initial situation in which all or most of the individuals reach the canopy develops into one in which a much smaller proportion of individuals do so.

PRODUCTIVE STRUCTURE (THE BIOMASS PROFILE)

As suggested above, the concept of stratification, or layering, has generally been applied to forest communities. Japanese workers associated with Saeki (Monsi and Saeki, 1953; Saeki and Kuroiwa, 1959) using the 'stratified clip' technique, have studied the vertical profile of biomass of leaves and stems within herbaceous monocultures. This profile they have called the 'productive structure' of the population (Fig. 4). 'Productive structure' is an important aspect of Odum's 'organic structure' (Odum, 1966); although the former term has been applied mainly to populations and the latter to ecosystems.

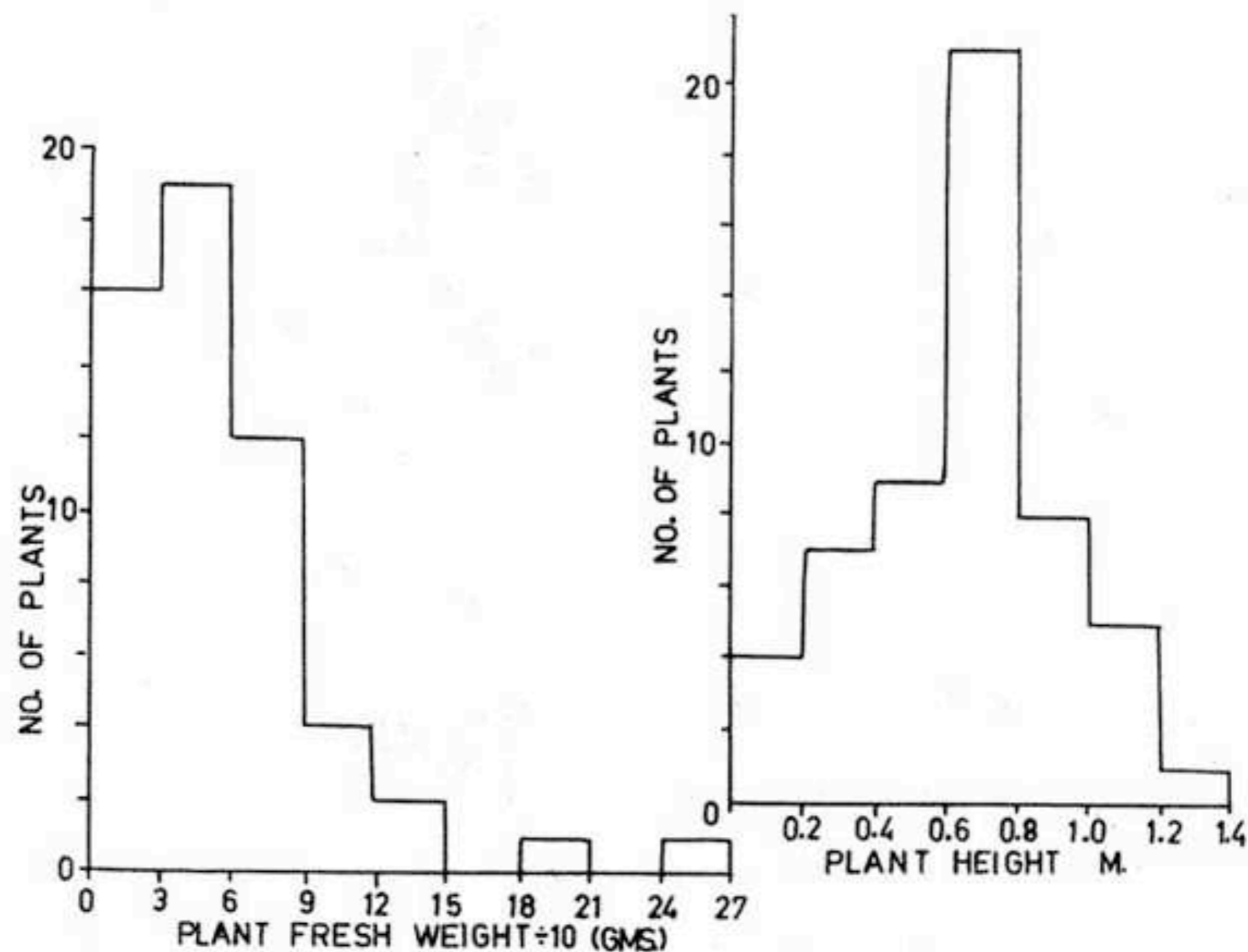


FIGURE 3. Frequency distributions of weight and height in a natural stand of *Elatostema rugosum*.

Although the vertical distribution of leaves and the relative proportions of leaves and stems are certainly of great importance in controlling population productivity, we must not forget that large quantities of chlorophyll may be present in stems (Ovington and Lawrence, 1967). This suggests that the vertical profile of chlorophyll content might be more important than that of leaf distribution. The results of some preliminary examinations of productive structure in perennial herbs are given in Figures 4, 5 and 6, and further details given in Appendix 2.

Pigment stratification in natural communities of *Elatostema rugosum* A. Cunn. Precur. (a large forest herb spreading by horizontal stolons) was similar to that shown by natural 'swards' of *Tradescantia fluminensis* Vell. (Fig. 5). In both, chlorophyll concentration (optical density/g. measured at  $665m\mu$ ) was greatest in the upper 40 per cent of the 'sward', and the total quantity of pigment per unit area was greatest in two distinct layers. The uppermost of these layers was the region of vertical leafy stems, where chlorophyll was present at a high concentration. The lower layer was composed by horizontal creeping stems, where pigments were at a low concentration, but in which most of the biomass

occurred. In other herbaceous species such accumulation layers ('sinks') frequently lack chlorophyll and are located underground, for example in bulbs, tubers and rhizomes. Note that the stolon layer of a *Tradescantia* sward harbours

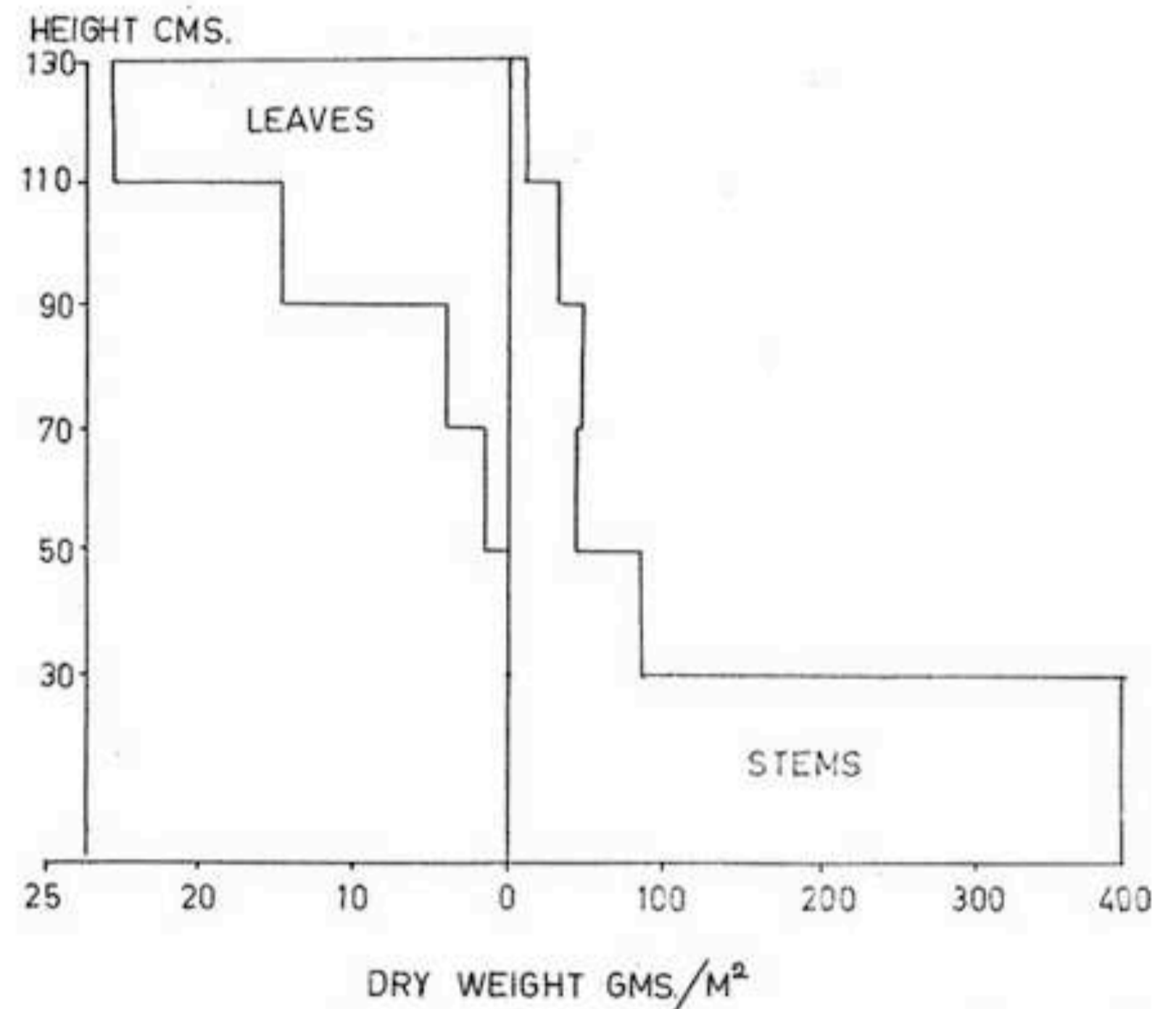


FIGURE 4. Productive structure in a natural stand of *Elatostema rugosum*.

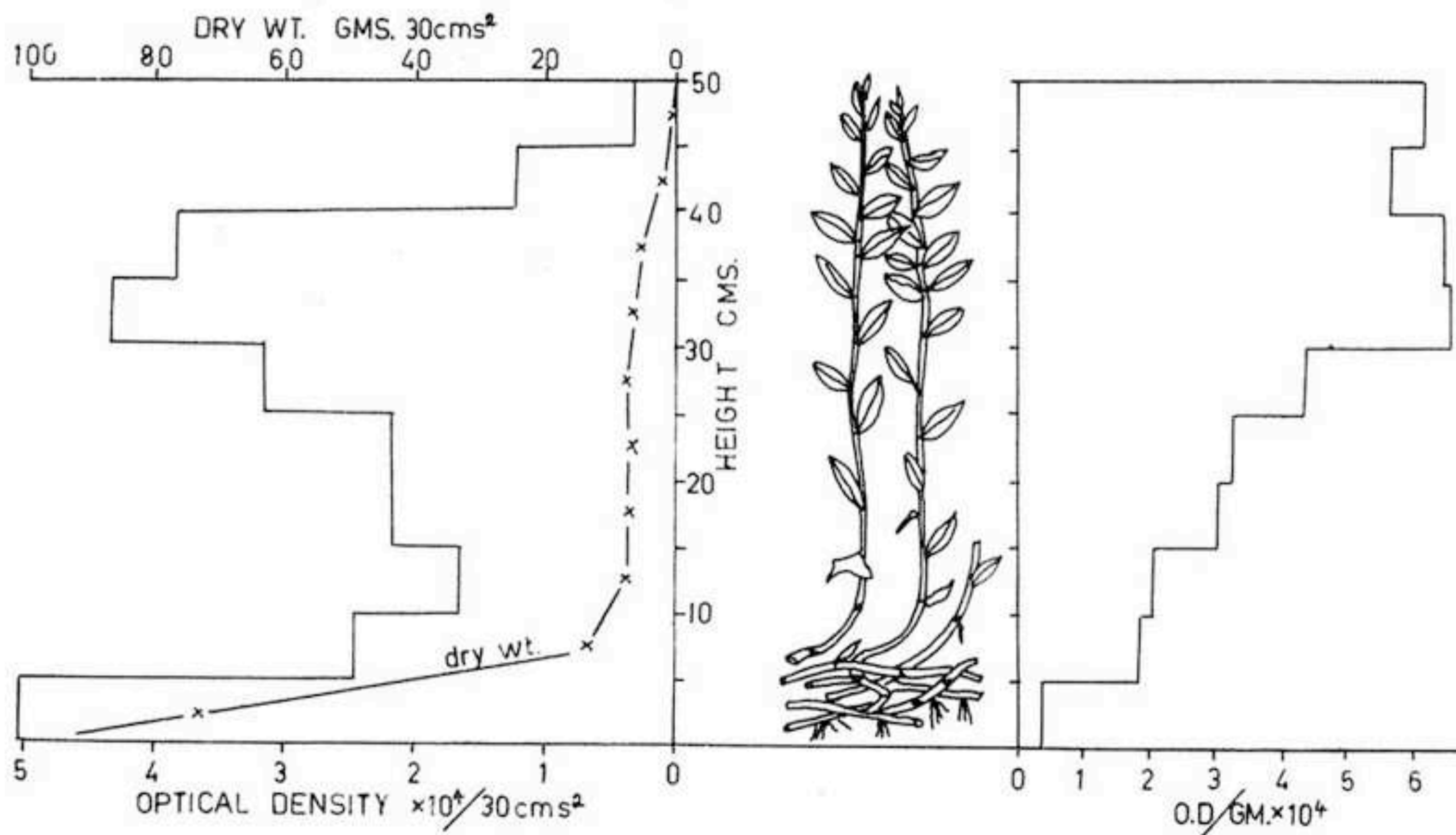


FIGURE 5. Vertical distribution of pigment and dry matter in a natural stand of *Tradescantia fluminensis*.

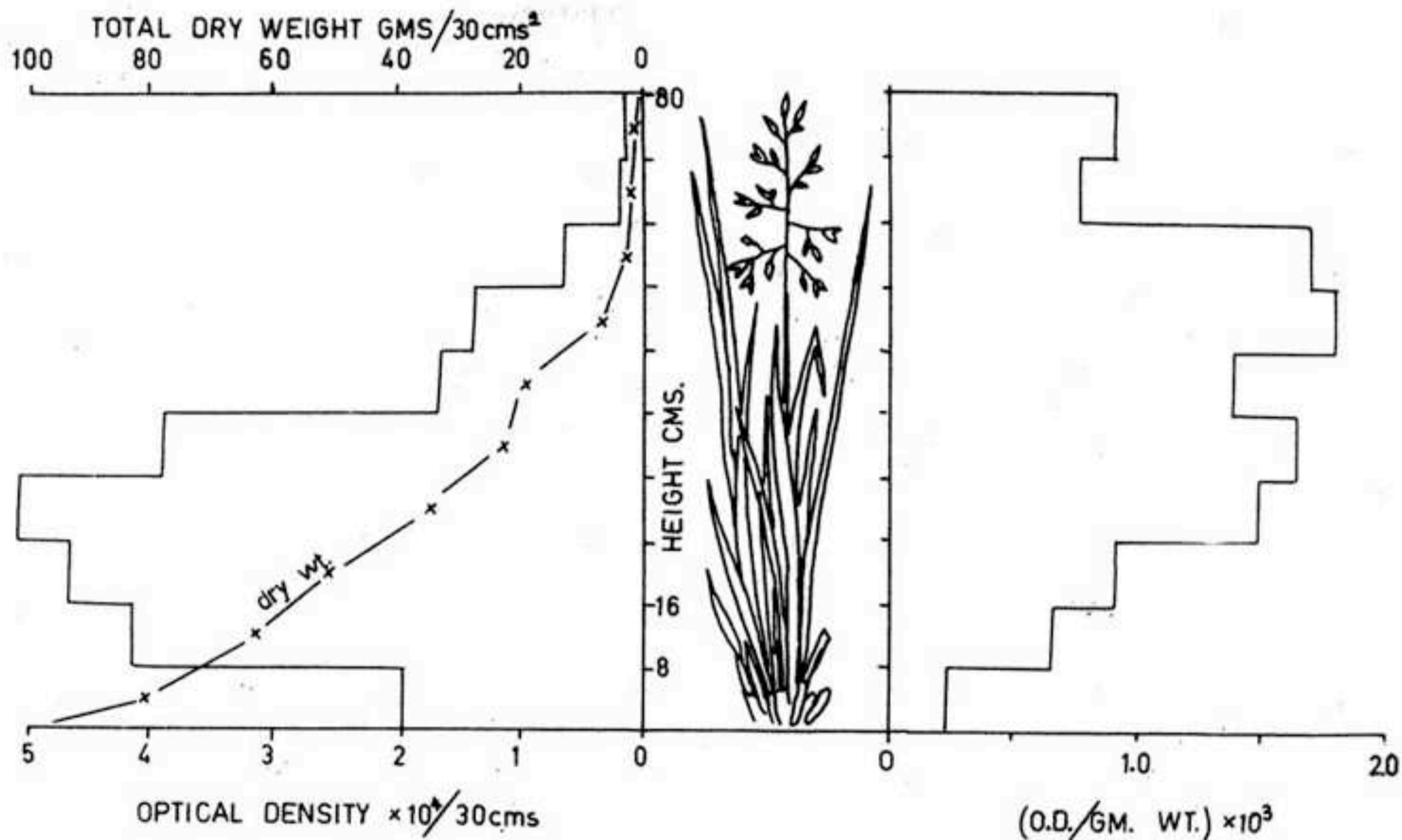


FIGURE 6. Vertical distribution of pigment and dry matter in a natural stand of *Bromus catharticus*.

a large and diverse invertebrate fauna, so that the community as a whole possesses an upper producer zone and a lower heterotrophic zone in which matter accumulates in plant structures and is eaten by invertebrates.

In tall *Bromus catharticus* Vahl. grassland, three intergrading layers can be recognised: (1) an upper in which chlorophyll is at a high concentration, but in which there is little dry matter; (2) a middle with the greatest absolute quantity of chlorophyll and (3) a lower containing little chlorophyll but most of the dry matter.

#### THE INFLUENCE OF THE FREQUENCY DISTRIBUTIONS AND PROFILES OF HEIGHT AND WEIGHT ON POPULATION PRODUCTIVITY AND MORTALITY

Watson (1947) showed that with the growth of a sward, leaf area index (L.A.I.) increases so that the lower leaves gradually become shaded by those above and contribute less and less to growth. Eventually a point is reached when further increase in leaf area will not increase the growth rate of the population, because as one new leaf comes into function above, an old leaf passes out of function in the shade below. When this point is reached, assuming no changes in the gross morphology of the plants, the photosynthetic system has reached its maximum extent and further

growth will be restricted to the non-photosynthetic parts. The consequence of this is a gradual decrease in the photosynthesis/respiration ratio towards a value of one, at which the plants are at compensation point and no further growth is possible.

It is clear that similar processes operate on individuals within dense stands. Kuroiwa (1960a) classified individuals in a dense experimental stand of *Helianthus annuus* into five classes ranging from dominant to suppressed. He examined how these different classes shared the total leaf area at different levels in the population profile and how this influenced their energy budgets. His

TABLE 1. Productivity of high density stands of *Helianthus annuus*. (From Kuroiwa, 1960a.)

Plant classification	Plants/m. <sup>2</sup>	Biomass g./m. <sup>2</sup>	g./m. <sup>2</sup> /day		
			Gross prodn.	Respiration	Net production
Dominant	16	105	11.2	6.4	4.8
Large intermediate	32	80	8.7	5.5	3.2
Intermediate	58	60	6.6	4.6	2.0
Small intermediate	64	35	3.0	2.6	0.4
Suppressed	30	8	0.6	0.7	-0.1
Totals	200	288	30.1	19.8	10.3

results (Table 1) indicate that the suppressed plants suffer a progressive decrease in gross production/respiration ratio, so that the quantity of net production ( $P_g - R$ ) gradually declines. Suppression may progress beyond compensation point whereupon the plants respire reserves presumably accumulated before the development of excessive skewness. Long (1936) demonstrated that suppressed plants of this species possess lower cal./g. values than dominants; so it is certain that these suppressed plants have very little food store. Unless they can correct their negative energy balance they must perish.

It seems likely that when suppressed plants are at, or near, compensation point they will be particularly vulnerable. Any reduction in gross production caused by increased shading by growth of dominants, shortening of days, attack by herbivorous insects or saprophytic fungi may cause rapid death. However, Tamm's (1948) observations on perennial herbs showed that small suppressed individuals in pastures may survive for many years. Furthermore, internode measurements and leaf scars on tree seedlings in forest shade suggest that these may remain close to compensation point for long periods. Only an increase in light through opening up of the canopy is likely to allow the further development of such suppressed offspring. In dense populations the skewed frequency distribution of plant weights indicates that a large proportion of the population falls into the suppressed class, so that a high rate of mortality is to be expected. Less dense populations gradually develop skewness so that individuals are being constantly recruited to the suppressed class and passing from this class by mortality. It seems possible that such a process could explain the steady death rate of some perennial plants in natural populations. (See Harper (1967) for an analysis of the data in Tamm (1956)).

TABLE 2. Productivity and population dynamics of experimental *Prunus persica* (L.) populations over 186 days. (Data from Mathews and Westlake, 1969.)

Initial density (No./m. <sup>2</sup> )	Term. b'mass (g. dry wt/m. <sup>2</sup> )	Net prodn. (g. dry wt/m. <sup>2</sup> )	Mortality (% Initial density)
6.25	512	530	0
25.0	1011	1015	0
44.4	979	1145	16.0
100.0	775	1410	50.0
400.0	690	1775	66.7

Mathews and Westlake (1969) have recalculated some of Hirano and Kira's (1965) data on productivity of dense seedling stands of *Prunus persica* (L.) (Table 2) and make the important point that yield at final harvest (terminal biomass) may give little indication of the amount of matter which has been lost in the form of dead leaves and dying individuals prior to harvest. Total net production may be as much as two or three times as great as biomass in high density populations. I reached the same conclusion in experiments with the rhizomatous perennial *Tussilago farfara* (Ogden, 1968). In low density populations of this species the maximum biomass achieved in a two-year period was over 65 percent of the total net production. In high density stands, however, maximum biomass was only between 55 and 60 percent of the total net production. This difference was caused primarily by increased individual and leaf mortality at high density.

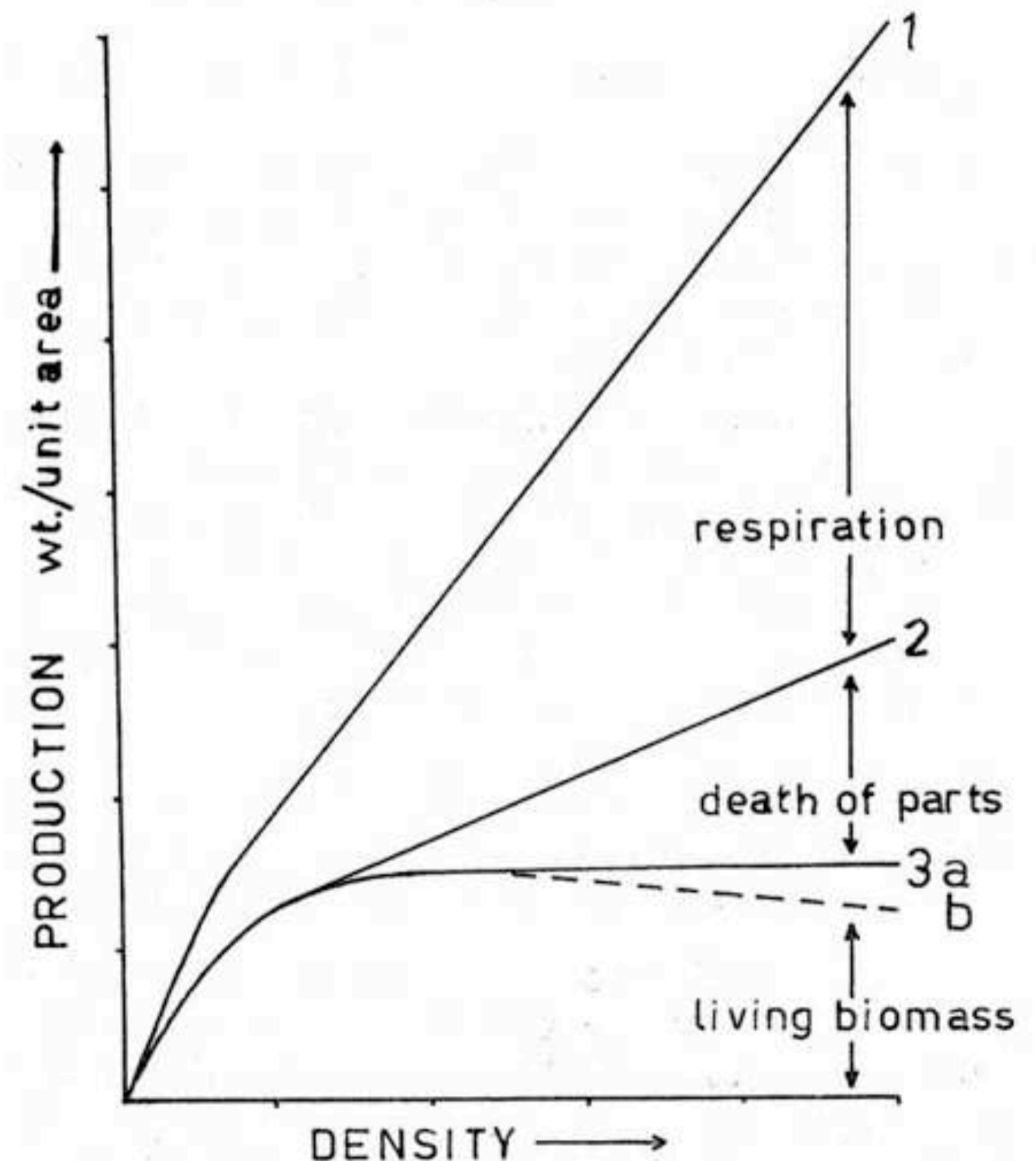


FIGURE 7. General diagrammatic model showing suggested relationships between biomass, net production, gross production and density in annual monocultures.

Both scales in arbitrary units. Curve 1, total gross production up to time of harvest. Curve 2, total net production up to time of harvest. Curve 3, a or b, biomass at harvest.

Kuroiwa's data for *Helianthus* (Table 1, from Kuroiwa, 1960a) and *Abies* sp. (Kuroiwa, 1960b) indicate that a dense population containing many suppressed individuals loses a proportionally greater quantity of its gross production through respiration than does a less dense stand. The evidence given above suggests, also, that more of the net production of such dense stands is lost by the death of parts of the population. An asymptotic curve is usually found when average yields, in terms of biomass weights per unit area, are plotted against density. The homeostatic mechanisms implied by this curve operate through the skewing of the weight frequency distribution. This, in turn, is controlled by the vertical pattern of leaf (or chlorophyll) distribution which develops as the individual plants compete together for light. Homeostasis of final yield is achieved only by adjustments of the energy balances of the individuals within the population. If account is taken of net production and, even more so, of gross production, then it appears that high density stands will outstrip those at lower density as productive, though wasteful, systems (Fig. 7).

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APPENDIX 1

AN ANALYSIS OF THE FREQUENCY DISTRIBUTIONS OF INDIVIDUAL PLANT WEIGHTS IN A MIXED ANNUAL WEED COMMUNITY COLONISING AN ARABLE FIELD IN NORTH WALES

1. Description of site

The area investigated was a 6x6 foot plot in mixed but apparently homogeneous annual vegetation growing on an arable field at the experimental station of the School of Plant Biology at the University College of North Wales, Bangor, Caernarvonshire, in August 1966. At this time the plant cover was composed of 17 species,

mostly annuals (see Table 3) and was about 6 in. high. Most of the plants possessed some ripe seed, so that the sward as a whole might be considered mature. Although the density was high, about 150 individuals per square foot, some bare soil was visible because of the general paucity of leaves at this time.

## 2. Methods

An area of 6 sq. ft was marked out within the plot and all individuals within it were removed with their roots, and individually bagged. They were dried at 70°C for three days before weighing. The species' data were classified into a variety of weight-class groups using a computer programme which defined the number of weight classes as  $\frac{max.-min.}{n}$  where *max.* and *min.* were the heaviest and lightest plants respectively and *n* was any specified integer. In practice, the size of *n* is dependent on the total population size (see Koyama and Kira, 1956). This method of classification is arbitrary, but there seems to be no justification for using a class interval related to the standard deviation when the population is not normally distributed (Fig. 1). Subsequently, the data were logged and reclassified using a class interval determined by  $4s/n$  where *s* is the standard deviation and *n*

is any specified integer (Fig. 2). This formula gives for each species, different class intervals and a different number of classes.

## 3. Results

Density and biomass data for the whole community sample are presented in Table 3. The weight-frequency distributions of the most numerous species are presented in Figures 1 and 2. All the species had approximately log-normal weight-frequency distributions. In four of the seven instances in which the logged data were tested for departure from normality using the chi-square test, no significant ( $P < .05$ ) departure from normality was found (Fig. 2).

## APPENDIX 2

### STUDIES OF PIGMENT STRATIFICATION IN NATURAL COMMUNITIES OF *TRADESCANTIA FLUMINENSIS* VELL., *ELATOSTEMA RUGOSUM* A. CUNN. PRECUR. AND *BROMUS CATHARTICUS* VAHL.

#### 1. Description of sampling sites and size of samples

See Table 4 (below). The sampling was done during December 1968.

TABLE 3. Density and biomass of all species per 6 sq. ft. in an annual weed community.

Species	Density	% Density	Total biomass (g.)	% Biomass	Mean biomass/plant (g.)
<i>Stachys arvensis</i> L.	342	36.9	31.2	27.2	0.09
<i>Stellaria media</i> (L.) Vill.	222	23.9	21.5	18.7	0.10
<i>Spergula arvensis</i> L.	89	9.6	23.5	20.5	0.26
<i>Polygonum persicaria</i> L.	82	8.8	16.5	14.4	0.20
<i>Polygonum lapathifolium</i> L.					
Graminae*	65	7.0	0.9	0.8	0.01
<i>Atriplex patula</i> L.	42	4.5	3.6	3.1	0.09
<i>Senecio vulgaris</i> L.	38	4.1	4.6	4.0	0.12
<i>Polygonum aviculare</i> agg.	30	3.2	10.6	9.2	0.35
Other spp.**	17	1.8	2.4	2.1	0.14
TOTALS	927	99.8	114.8	100.0	0.15

\* Mostly *Poa annua* L.

\*\* *Matricaria matricarioides* (Less.) Porter. *Capsella bursapastoris* (L.) Medic. *Fumaria muralis* ssp. *boraei* (Jord.) Pugsl. *Anagalis arvensis* L. *Veronica officinalis* L. *Geranium molle* L. *Sonchus oleraceus* L. *Ranunculus repens* L. *Taraxacum officinale* agg.

TABLE 4. Description of sampling sites and sample sizes.

Sample	<i>Tradescantia</i>	<i>Elatostema</i>	<i>Bromus</i>
Locality	Bledisloe Park Palmerston North, N.Z.	Kahuterawa valley. Tararua Range, N.Z.	Massey University campus, Palmerston North, N.Z.
Description of site	Lowland forest remnant on flat by stream	Montane forest on steep stony bank	Open grassland on waste ground
Sample size	0.5×0.5 m.	1.0×1.0 m.	0.5×0.5 m.
Number of samples	1	2	1
Ht. veg. sampled (cm.)	50	130	72
No. stratified clips	10	6	10
Width of strata (cm.)	5	20	8



2. *Methods*

The area to be sampled was marked out with tall pegs and the surrounding vegetation removed. Working from the top downwards the vegetation in the sample area was clipped to successive heights using hand shears. The material from each stratum was kept separate and weighed. Sub-samples were taken from each stratum for determination of dry weight and chlorophyll. With *Elatostema* separate determinations were made for leaves and stems and a second m.<sup>2</sup> sample was taken for height and weight frequency distributions (Fig. 3). For chlorophyll estimation sub-samples (0.5–1.0 g.) were ground with pestle and mortar in about 20 ml. of 2:1 methanol:petroleum ether mixture and the mixture was then filtered into a large separation funnel. Extraction was repeated three times, the extracts being added to the separation funnel each time. The contents of the funnel were then shaken with c. 40 ml. of saturated sodium chloride solution and the aqueous methanol separated off and re-extracted with petroleum ether four times. The resulting petroleum ether extract containing the chlorophyll was

dried with anhydrous sodium sulphate, and its optical density at 665 m $\mu$  read in an Eel 'Spectra' spectrophotometer.

3. *Results*

Chlorophyll and dry matter profiles for the *Tradescantia* and *Bromus* communities are presented in Figures 5 and 6. The results for *Elatostema* were similar to those for *Tradescantia*, but difficulty arose because the extraction process removed suspended substances and pigments other than chlorophyll. Therefore the large total optical density per unit area in the layer of creeping horizontal stems might not arise entirely from chlorophyll. Total biomass weights/m.<sup>2</sup> are given in Table 5. With *Bromus* a considerable quantity of dead leaf bases, culms, etc., was present in the lower layers of the sward and in *Tradescantia* the sample included dead leaves and small twigs fallen from the trees above.

It is unwise to draw any generalisations from such few data, but the remarkable contrast in succulence between the *Elatostema* and *Bromus* stands should be noted.

TABLE 5. *Biomass per sq.m.*

SAMPLE	<i>Tradescantia</i>	<i>Elatostema</i>	<i>Bromus</i>
Total fresh weight (g./m. <sup>2</sup> )	7135	10713	5426
Total biomass dry wt. (g./m. <sup>2</sup> )	815 (528*)	645	1155
% dry matter	11.4	6.1	21.3

\* excluding dead matter and surface rootlets.