THEIL'S INEQUALITY INDEX APPLIED TO QUANTIFY POPULATION VARIATION OF PLANTS WITH REGARD TO DRY MATTER ALLOCATION

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SUMMARY

The inequality index of THEIL (1967) was initially developed to calculate income inequality in human populations. It is applied here to determine the per organ dry weight variation in plant populations and integrated to an index of population variation (IPV). The weight fractions used to calculate the IPV are further used to calculate an allocation index (AI) for each plant member of a population. The method implicates the possibility to reconstruct the relative contribution of each organ (or individual) to the overall indices of the population, thus smoothing the way for a further interaction between population ecology on the one hand and ecophysiology and ecogenetics on the other. Some applications of the method are given and discussed with regard to the need to evaluate and improve various concepts of evolutionary strategies.

1. INTRODUCTION

Various concepts of plant and animal strategies have been developed by evolutionary ecologists. In the concept of r- and K-strategies (MacArthur & Wilson 1967) reproductive allocation is one of the major parameters to determine the position of a species in the r-K spectrum (Gadgil & Solbrig 1972; Harper & Ogden 1970). Growth characteristics such as relative growth rate and a morphology index have been used as the main parameters to determine the position of species in the spectrum of C-S-R-strategies (Grime 1974, 1979). Both reproductive and growth strategies seem to be concerned mainly with the rate of production and the allocation of biomass (cf. King & Roughgarden 1982, 1983; Pacala & Roughgarden 1982). In addition to the biomass allocation, attention has been paid to the allocation of nutrients (Van Andel & Vera 1977; Raper et al. 1978; Van Andel & Jager 1981; Abrahamson & Caswell 1982; Ernst 1983a, 1983b), because nutrients might be the important currency for plants rather than energy (Harper 1977).

Evolutionary interpretations of actual ecological patterns of adaptation require insight into the variability of the parameters used rather than into the mean values for different species. Ernst (1983b) suggested that the frequency distribution of total dry matter of plants and the relationship between dry matter

and nutrient concentration indicate whether or not a population suffers from stress. With regard to allocation of dry matter, plastic energy allocation patterns were established in *Sedum lanceolatum* (JOLLS 1980) and in *Plantago coronopus* (WAITE & HUTCHINGS 1982), and the phenotypic and genotypic components of growth and reproductive patterns were analysed in *Typha latifolia* (GRACE & WETZEL 1981). Ecotypic differentiation in allocation patterns of *Sonchus arvensis* was shown by PEGTEL (1976). ROZIJN & VAN DER WERF (1984) have studied the pattern of growth, reproduction and dry matter allocation in two congeners, *Aira praecox* and *Aira caryophyllea,* from which they have been able to discriminate between drought avoidance and drought tolerance strategies. Theories based on the study of whole growth cycles have been rare considering the number of theories already presented to determine evolutionary strategies. It must be kept in mind, though, that interest in manipulating the distribution of dry matter of plants for applied purposes has long been present in agricultural and horticultural endeavours (e.g. VAN DOBBEN 1962; VAN DOBBEN et al. 1981; HERZOG 1982; SANO & MORISHIMA 1982).

In the majority of studies on allocation, the analysis is performed by comparing sets of two variables (e.g. reproductive effort, root-shoot ratio, leaf-root ratio). A recurrent problem is how to manage mathematically allocation patterns when more than two variables are involved (e.g. roots, stems, leaves, flowers, seeds). ABRAHAMSON (1979) and ABRAHAMSON & CASWELL (1982) applied multivariate statistics to establish differences in plant allocation patterns between groupings of species or between populations. This method enables us to arrange populations or species in a spectrum of strategies by comparing mean values, variances and covariances. It does not make it possible to categorize each individual member of a population within such a spectrum. Thus, further analysis of results from both population ecology and ecophysiology and population genetics to determine evolutionary strategies is limited by this method.

In the present paper emphasis is placed on measuring the variability within populations on the basis of dry matter allocation. The method described enables us to calculate an overall 'index of population variation' and an 'allocation index', and in addition to determine the contribution of each individual member to both these indices. Furthermore, ontogenetic drift of the pattern of allocation is taken into account. This means that processing zero values must be permitted (e.g. for plants which do not yet flower). As the indices are calculated from relative dry weight values, comparison between different species will also be possible to a certain extent. Examples are given to elucidate the method.

2. METHOD

2.1. Index of population variation (IPV)
Suppose we have N plants with root dry weight values X_{11}, X_{21}, ..., X_{N1}, and shoot dry weight values X_{12}, X_{22}, ..., X_{N2}. In this case the number of variables n = 2.

We calculate the root fraction x_{i1} and the shoot fraction x_{i2} for each individual plant $i = 1, 2, ...N$ as follows:

$$x_{i1} = \frac{X_{i1}}{\sum\limits_{i=1}^{N} X_{i1}} \quad \text{and} \quad x_{i2} = \frac{X_{i2}}{\sum\limits_{i=1}^{N} X_{i2}}$$

Note that the sum of the fractions $\sum\limits_{i=1}^{N} x_{i1} = \sum\limits_{i=1}^{N} x_{i2} = 1$, which means that the root fractions are comparable with the shoot fractions. We apply the inequality index of THEIL (1967) to calculate the IPV_{root} and the IPV_{shoot}:

$$IPV_r = \ln N + \sum\limits_{i=1}^{N} x_{i1} \ln x_{i1} = \sum\limits_{i=1}^{N} x_{i1} \ln Nx_{i1}$$

$$IPV_s = \ln N + \sum\limits_{i=1}^{N} x_{i2} \ln x_{i2} = \sum\limits_{i=1}^{N} x_{i2} \ln Nx_{i2}$$

Finally we put the index of population variation $IPV = (IPV_r + IPV_s)/2$. In general:

$$IPV = \frac{1}{n} \sum\limits_{j=1}^{n} \sum\limits_{i=1}^{N} x_{ij} \ln Nx_{ij} \quad (i = 1, 2, ..., N \text{ individuals and}$$
$$j = 1, 2, ..., n \text{ variables})$$

The $IPV = 0$ if all fractions are equal $(x_i = \frac{1}{N})$, while at maximum inequality (one x_i-value equals 1 and all other x_i-values are zero) the $IPV = \ln N$. These limits hold for the IPV as the sum of the values $x_i \ln Nx_i$, but due to the logarithmic function any individual term $x_i \ln Nx_i$ may get a negative value. To prevent this we prefer to calculate the contribution of each individual to the overall IPV_r and IPV_s respectively as follows:

$$x_{i1} \ln Nx_{i1} - x_{i1} + \frac{1}{N}$$
$$x_{i2} \ln Nx_{i2} - x_{i2} + \frac{1}{N}$$

Note that after summation the latter two terms cancel each other $(-1 + 1)$.

2.2. The allocation index (AI)
Suppose again N plants with root dry weight values $X_{11}, X_{21}, ..., X_{N1}$, and shoot dry weight values $X_{12}, X_{22}, ..., X_{N2}$. Similar to the procedure in section 2.1. we calculate the root fractions x_{i1} and the shoot fractions x_{i2} $(i = 1, 2, ..., N)$. We prefer to calculate the allocation index on the basis of these fractions, rather than on the basis of the dry weight values, for two main reasons:

a. The individual plants are considered as members of a population, which means that the root weight of an individual plant is not only dependent on the growth of that particular individual, but also on the growth of other members

of the population (e.g. neighbours).

b. The allocation index is independent of the height of the dry weight values, because $\sum\limits_{i=1}^{N} x_i = 1$ for each variable. In this way the allocation index can be generalised for two or more variables. Moreover, the indices for different stages of the life cycle can be compared one with another.

Again we apply the inequality index of THEIL (1967) to calculate the AI of the population:

$$AI = \frac{1}{N} \sum_{i=1}^{N} \sum_{j=1}^{n} y_{ij} \ln ny_{ij} \quad (i = 1, 2, ..., N \text{ individuals},$$

$$j = 1, 2, ..., n \text{ variables})$$

in which

$$y_{1j} = \frac{x_{1j}}{\sum\limits_{j=1}^{n} x_{1j}}, ..., y_{Nj} = \frac{x_{Nj}}{\sum\limits_{j=1}^{n} x_{Nj}}$$

Note again that $\sum\limits_{j=1}^{n} x_{1j} = \sum\limits_{j=1}^{n} x_{2j} = ... = \sum\limits_{j=1}^{n} x_{Nj} = 1$

Similar to the procedure presented in section 2.1. we calculate the allocation index of each individual as a contribution to the overall allocation index of the population as follows:

$$y_{1j} \ln ny_{1j} - y_{1j} + \frac{1}{n}$$

until

$$y_{Nj} \ln ny_{Nj} - y_{Nj} + \frac{1}{n}$$

The lower limit of the overall AI is zero (maximal equality), the upper limit is $\ln n$ (maximal inequality).

2.3. Graphical presentation

Although not strictly necessary for interpreting the results of the calculations, a graphical presentation will be given in some cases to elucidate what is happening.

In the case of two variables, the fraction values x_{i1} can be plotted against x_{i2} (see *fig. 1a*). The 45 degree line represents the points where the allocation index equals zero. The more a point deviates perpendicularly from this line, the higher the allocation index is. Note, however, that deviations of points close to the origin (relatively small plants) result in a higher index than similar deviations of points far from the origin (big plants).

In the case of IPV = 0, all points are located at the mean value for the two variables. The more a point deviates from this mean point, on or along the 45
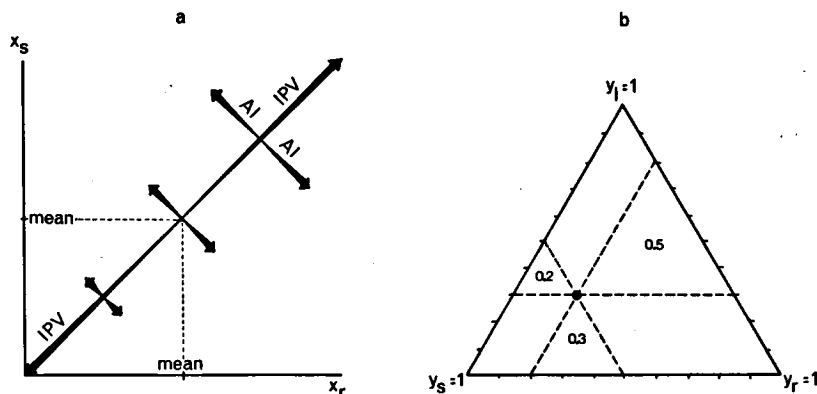
Fig. 1. Graphical presentation and interpretation of fraction values.
a) Root fraction (x_r) plotted against shoot fraction (x_s). In this case

$$\sum_{i=1}^{N} x_{ir} = \sum_{i=1}^{N} x_{is} = 1.$$

b) Allocation fractions of root (y_r), stem (y_s) and leaves (y_l). In this case $y_{ir} + y_{is} + y_{il} = 1$ for each individual $i = 1, 2, ..., N$. An example is given for which $y_{ir} = 0.2$, $y_{is} = 0.5$ and $y_{il} = 0.3$.

degree line, either upwards or downwards, the higher the index of population variation is.

In the case of three variables, it is useful to arrange the points representing the three allocation fractions y_{ij} of the plants within a triangle (*fig. 1b*), comparable to the well-known soil triangle. In the centre of the triangle the AI equals zero.

2.4. Advantages of Theil's inequality index
Suppose we have three plants, A, B and C, with total weights of 9, 9, and 18 g respectively (*table 1*). For each plant give three subunit weight values, say for roots, leaves and reproductive organs (plants B and C do not yet flower, resulting in zero values). The advantages of Theil's index as compared to the

Table 1. Comparison between different measures of variation. Cases A, B, and C can be considered plants or treatment (see text). After LISMAN (1974).

Case	A			B			C		
Total	9			9			18		
Subunits	2	6	1	5	4	0	10	8	0
Fractions	0.22	0.67	0.11	0.56	0.44	0	0.56	0.44	0
Mean deviation		2			2			2	
Standard deviation		$\sqrt{14/3}$			$\sqrt{14/3}$			$2\sqrt{14/3}$	
Coefficient of variation	$1/3\sqrt{14/3}$			$1/3\sqrt{14/3}$			$1/3\sqrt{14/3}$		
Variance log-transform.		0.103			∞			∞	
Theil's index		0.250			0.412			0.412	

other measures of variation mentioned in *table 1* can be summarized as follows:
a. Theil's index remains unchanged if all subunit values are multiplied with a certain factor, resulting in similar fraction values (compare B with C).
b. Theil's index declines if one subunit fraction is enlarged at the expense of the other fractions (compare A with B).
c. If we only encounter small deviations from the mean value during a computation of Theil's index, then the index is strongly correlated with the variance in the logarithmic transformation of the original data. However, Theil's index has the advantage over the variance of the logarithmic transformed data that it still gives a useful value when one of the input variables is zero, whereas the variance of the logarithmic transformation is infinite in that case.
d. The contribution of each subunit fraction to the overall index for the population can be calculated (see sections 2.1. and 2.2.), which does not hold for all other measures.

With regard to the index of population variation the situation is completely analogous. In this case, the symbols A, B, and C in *table 1* represent three treatments or three stages of the life cycle and the subunits represent three replicates

Table 2. Mean dry weight (mg), IPV and AI of populations of 12 species grown under uniform conditions, at 2 harvests (N = 10, n = 2).

Species	Harvest	Mean dry wt.			IPV ($\times 10^3$)			AI ($\times 10^5$)
		root	shoot	total	root	shoot	mean	
Lolium perenne	1	85.7	105.6	191.3	118	64	91	872
	2	273.5	229.1	502.6	40	40	40	296
Poa pratensis	1	20.7	60.7	81.4	115	49	82	628
	2	143.5	263.0	406.5	72	32	52	753
Poa trivialis	1	50.9	92.4	143.3	63	47	55	623
	2	235.9	282.2	518.1	12	35	24	368
Agrostis stolonifera	1	12.4	32.6	45.0	313	228	271	1863
	2	150.1	199.8	349.9	37	15	26	475
Festuca pratensis	1	110.9	129.9	240.8	23	14	19	156
	2	275.1	269.0	544.1	79	66	72	· 518
Holcus lanatus	1	92.8	157.3	250.1	76	18	47	1263
	2	305.8	312.0	617.8	26	9	18	229
Anthoxanthum odoratum	1	52.2	112.4	164.6	121	32	77	2029
	2	289.7	307.5	597.2	26	15	21	373
Trifolium repens	1	16.3	47.6	63.9	124	123	124	699
	2	106.3	458.6	564.9	14	25	19	493
Taraxacum spec.	1	137.6	132.3	269.9	18	34	26	236
	2	438.3	192.2	603.5	19	16	18	206
Rumex obtusifolius	1	170.4	182.3	352.7	54	11	32	1709
	2	685.3	294.6	979.9	27	19	23	1232
Rumex acetosa	1	83.2	112.3	195.5	42	38	40	1168
°	2	424.5	220.3	644.8	37	27	32	279
Lychnis flos-cuculi	1	36.9	111.0	147.9	128	77	102	1129
	2	212.0	339.9	551.9	22	24	23	436

(zero values indicate died plants).

3. APPLICATIONS

3.1. Two variables, two harvests

Seedlings grown from seeds of 12 grassland species from moderately fertile to fertile soil were grown in a glasshouse, one plant per pot. All the pots contained an equal amount of moderately fertile soil. Ten plants per species were harvested after five weeks of growth, and again ten plants after eight weeks. The mean dry weights and the IPV and AI values are presented in *table 2*. For four of these species a correlation diagram of log-transformed root and shoot dry weight and a graph representing the corresponding fraction values are presented (*fig. 2*). The IPV and the AI of *Taraxacum* spec. are relatively small for both harvests, as could be expected for this apomictic species. The IPV and the AI of *Poa pratensis* are somewhat higher. In *Anthoxanthum odoratum* the IPV and the AI appear to be subject to ontogenetic drift; at harvest 1 the values are high, whereas they are low at harvest 2. Note that the high IPV at harvest 1 is mainly due to a high degree of variation of the root weights (the slope of the regression line is less steep than the 45 degree line). *Rumex obtusifolius* revealed a low IPV and a high AI for both harvests.

A comparison between the species can only reveal preliminary indications on variability, because two harvests were made at certain moments during a species specific growth cycle. Therefore, three species were selected to compare the indices for the whole growth period.

3.2. Two variables, ten harvests

Seedlings grown from seeds of three grass species were grown in a glasshouse, one plant per pot, each containing an equal amount of fertile soil. One group of plants was grown under the light conditions in the glasshouse, another group of plants in shadow (c. 40 percent of the normal daylight conditions). From the fourth week of growth onwards, five plants per treatment were harvested each week, for ten weeks (frequent small harvests; cf. HUGHES & FREEMAN 1967). *Table 3* gives the equations for the growth curves of the log-transformed total dry weights, approximated by a second degree polynomial (cf. VAN ANDEL & JAGER 1981), the RGR-equation, the final dry weight values (harvest 10), and the mean IPV and AI values for all ten harvests together. Note that the overall IPV and AI values for the whole growth curve are based on the fraction values determined separately for each harvest. Although the growth curves differ significantly between the species and between the treatments, the two treatments effectuated only slight differentiations in the IPV and AI. Only in *Holcus lanatus* the IPV is twice as low in the light group compared with the shadow group of plants. The scatter diagram for *Holcus lanatus* is presented in *fig. 3*.

3.3. Effects of density; two and three variables

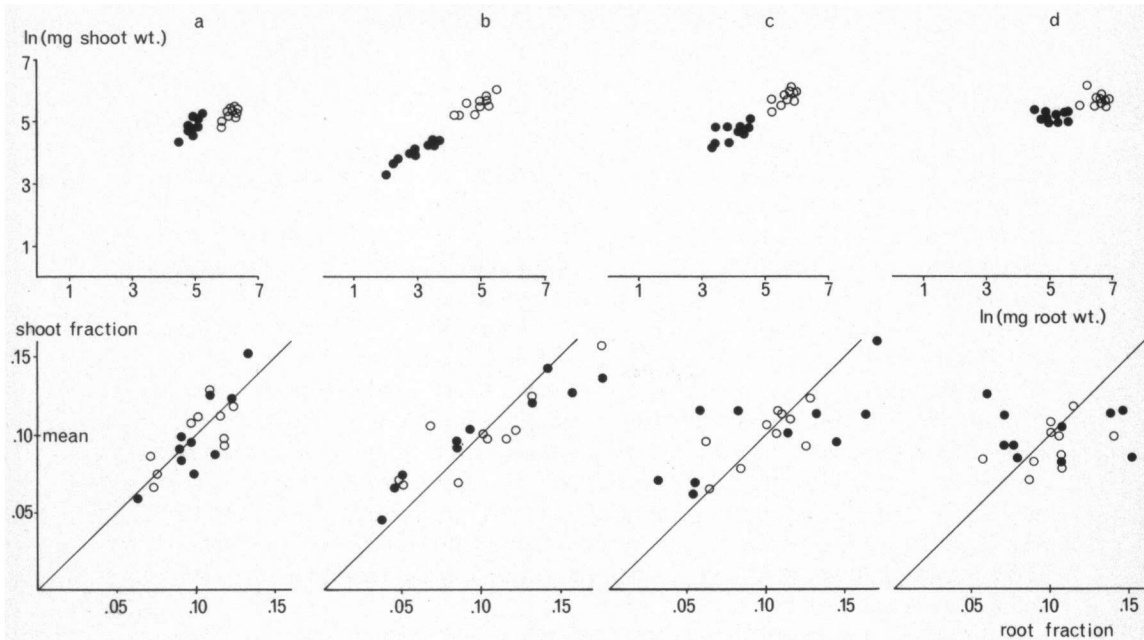Seedlings of *Lychnis flos-cuculi* were grown in two densities, 10 plants and 100

Fig. 2. Scatter diagrams for *Taraxacum* spec. (a), *Poa pratensis* (b), *Anthoxanthum odoratum* (c) and *Rumex obtusifolius* (d).

Upper diagrams: ln (root wt) plotted against ln (shoot wt).

Lower diagrams: root fraction (x_{ir}) plotted against shoot fraction (x_{is}). ● first harvest, N = 10; 0 second harvest, N = 10.

plants per 10 dm². For each density a 2 × 2 factorial design was arranged: two soil fertility levels and two soil moisture levels, all in triplicate. All the plants which survived (90 to 100 percent) were harvested after 8 weeks of growth. *Table 4* presents the mean root and shoot weight per plant, the mean IPV and the mean AI. The major effects result from density; the high density effectuates a lower mean dry weight and a higher IPV and AI.

In this case we encountered the problem that ln N as a maximum value for the IPV was different for the two densities. This effect appeared to be insignificant, because the values of the IPV are much closer to zero than to ln N. When we calculated the mean IPV of some random selections of 10 plants out of the 100 per pot, the result was similar to the IPV calculated for all 100 plants together. In the design presented after this, the problem has been avoided.

Seedlings of *Urtica dioica* were grown on fertile soil in a glasshouse under three different regimes:

a. Without interference (one plant per pot, each containing 250 g soil).

b. With above ground interference (similar to treatment a, but groups of 9 pots were put 3 × 3 adjacently).

c. With above and below ground interference (groups of 9 plants per pot contai-

Table 3. Some results of *Lolium perenne, Holcus lanatus* and *Anthoxanthum odoratum,* harvested 10 times ($N = 5, n = 2$).
a. Polynomial fit of the growth curve, and RGR (W = mg total dry wt.; $1 < x < 10$).
b. Mean final dry weight W_{10} (in mg).
c. Mean IPV ($\times 10^3$) and AI ($\times 10^5$) of all 10 harvests.

Species	Treatment						
	Light (100% daylight)				Shadow (40% daylight)		
a. L. perenne	$\log W = -0.585 + 0.593 \, x - 0.018 x^2$				$\log W = -0.412 + 0.446 \, x - 0.014 \, x^2$		
	$\text{RGR} = 0.593 - 0.018 \, x$				$\text{RGR} = 0.446 \, x - 0.014 \, x$		
H. lanatus	$\log W = -0.918 + 0.683 \, x - 0.022 \, x^3$				$\log W = -0.546 + 0.401 \, x - 0.005 \, x^2$		
	$\text{RGR} = 0.683 - 0.022 \, x$				$\text{RGR} = 0.401 - 0.005 \, x$		
A. odoratum	$\log W = -0.690 + 0.539 \, x - 0.014 \, x^2$				$\log W = -0.510 + 0.336 \, x - 0.007 \, x^2$		
	$\text{RGR} = 0.539 + 0.014 \, x$				$\text{RGR} = 0.336 - 0.007 \, x$		
b.	W_{10}	root	shoot	total	root	shoot	total
L. perenne		895	3351	4246	71	551	662
H. lanatus		1306	4644	5950	228	1588	1816
A. odoratum		563	2303	2866	77	398	475
c.		root	shoot	mean	root	shoot	mean
L. perenne	IPV	51	37	44	63	27	47
	AI			286			398
H. lanatus	IPV	28	15	22	54	36	45
	AI			260			189
A. odoratum	IPV	49	32	40	48	27	38
	AI	.		171			263

ning 9 × 250 g soil; the soil surface was 9 times that of a single pot in treatments a and b).

Harvests were made in triplicate (3 × 9 plants per treatment), after 5, 7, 9, 11, 13 weeks of growth. Each plant was subdivided into roots, stems and leaves.

The mean dry weight values per plant and the mean percentages of dry matter allocation are shown in *fig. 4.* The IPV and the AI are given in *table 5.* An example of a graphical presentation of the allocation fractions is to be found in *fig. 5.* The single plants (treatment a) grew continuously and did not reach peak amount of production within 13 weeks. With above ground interference growth reduction occurred from the 9th week onwards, as compared to the single plants. With full interference some acceleration of growth rate took place after an initially similar growth reduction, and at the end of the experimental period the plants started dying off.

The allocation index fluctuates with time, independent of the treatments as could be expected on the basis of the percentages dry matter allocation (*fig. 4*). Corresponding to the development of the plant, initially the leaf fraction contributes for the greater part to the allocation index (stem and root fractions are equally low), while during later growth stages the highest contribution is due to the root fraction (stem and leaf fraction are equally high).

The index of population variation changes significantly in the course of time,
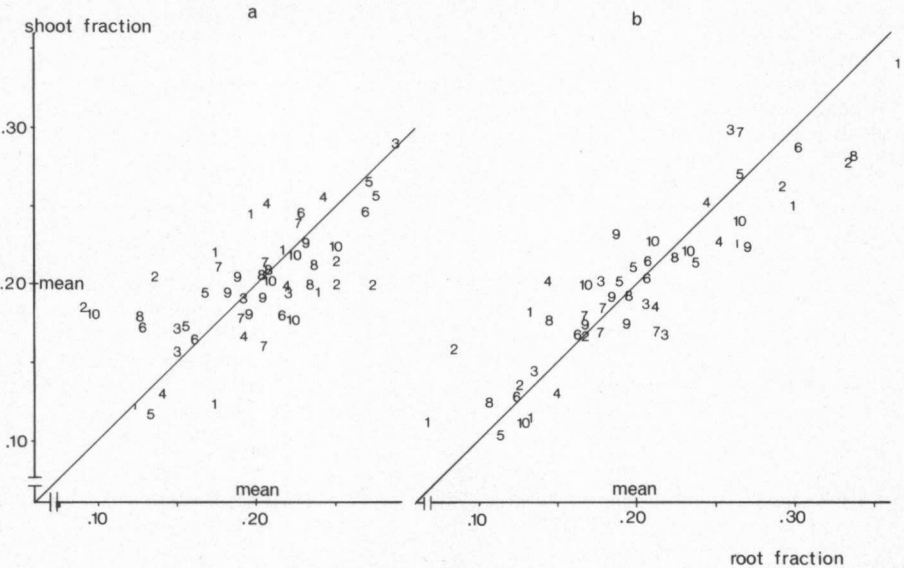
Fig. 3. Scatter diagrams for *Holcus lanatus*, grown in light (a) and in shadow (b). The figures indicate harvests 1, 2, ..., 10 (N = 5 per harvest).

Table 4. Some results of *Lychnis flos-cuculi*, grown in two densities (N = 10, N = 100), at two soil fertilities and two soil moisture levels. Mean values of 3 replicates.

Fertility level	Moisture level (% field capacity) wet (80%)		moist (40%)	
	high	moderate	high	moderate
10 plants / 10 dm^2				
mg dry wt./plant				
root	35.2	30.5	48.4	38.3
shoot	341.7	313.8	374.7	355.4
total	376.9	344.3	423.1	393.7
IPV* ($\times 10^3$)	156	89	58	75
AI ($\times 10^5$)	778	352	351	406
100 plants / 10 dm^2				
mg dry wt./plant				
root	8.5	9.7	9.1	7.4
shoot	145.1	107.0	131.7	113.1
total	153.6	116.7	140.8	120.5
IPV* ($\times 10^3$)	299	252	242	266
AI ($\times 10^5$)	1581	1966	1354	1968

*IPV$_r$ and IPV$_s$ did not differ significantly.

and depends on treatment (*table 5*). Without interference it decreases from the 7th week onwards, with above ground interference it fluctuates, and with full interference it increases up to the 9th week. After five weeks, when there is still no difference between the treatments with regard to the mean dry weight or dry weight allocation, there is already a marked effect on the population variation. The plants grown separately show a high degree of variation at the beginning, then the variation is smoothed out with time. Under full interference on the contrary, variation is initially low but reaches expression in time. This effect could not be ascribed to one of the three organs in particular, because a similar variation exists for each organ.

4. DISCUSSION

Although the examples presented here concern the allocation of dry matter to only two or three organs per plant, it is clear that the technique is applicable to all number of variables (1, 2, 3, ..., n). Moreover, it is not only applicable to dry matter allocation, but to all types of resource allocation. Due to calculating the indices from relative values (fractions), comparisons are permitted between different stages of the growth cycle, between different populations (treatments), and to a certain extent also between different species. It is even possible to determine the contribution of each individual (or organ) to the overall indices. The method provides a basis for further evaluation and reformation of various concepts of strategy (see Introduction). A few aspects will be discussed here.

Growth analysis should be supported by measurements of dry matter distribution, and subsequent calculation of the allocation index. The contribution of each of the organ dry weights to the AI can be determined easily, which makes it possible to utilize results from ecophysiological studies concerning internal distribution and transport of carbohydrates and nutrients (e.g. RYLE 1970; DINA & KLIKOFF 1974; OTZEN 1977; CALLAGHAN 1980; TIETEMA 1981; LAMBERS et al. 1982; SCHULZE 1982; SIMPSON et al. 1983; ROBINSON & RORISON 1983). Allocation patterns might indicate whether the relative growth rate is determined mainly by the water balance or/and the efficiency of uptake and transport of nutrients

Table 5. Mean IPV and AI of *Urtica dioica* grown under 3 different treatments: a) without interference, b) aboveground interference, c) full interference. (N = 3 × 9, n = 3).

Harvest time		5 weeks	7 weeks	9 weeks	11 weeks	13 weeks	mean
IPV* (× 10^3)	Treatment						
	a	208	223	135	63	25	110.8
	b	146	98	223	191	332	198.0
	c	84	142	263	261	226	195.2
AI (× 10^3)	a	16	9	9	15	7	11.1
	b	16	10	17	10	24	15.6
	c	8	8	25	19	10	14.0

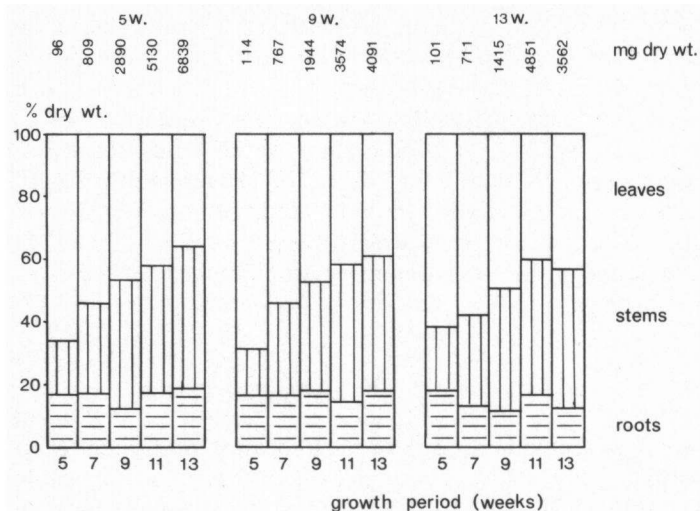*IPV$_r$, IPV$_s$ and IPV$_1$ did not differ significantly.

Fig. 4. Mean dry weight allocation (%) and mean total dry weight (mg per plant) of *Urtica dioica*, grown without interference (a), with aboveground interference (b), and with above and belowground interference (c). N = 3 × 9 plants per harvest.

(cf. RAPER et al. 1978), or by the photosynthetic capacity (cf. VAN DOBBEN 1962), of by a combination of the two (cf. LUCKWILL 1959; BROUWER 1962; THORNLEY 1972; DREW 1982). ASTON & BRADSHAW (1966) showed genetic differences in stolon length of *Agrostis stolonifera*, depending on the degree of salt stress. In *Elytrigia repens* similar phenomena were observed in plants from arable fields and grasslands (NEUTEBOOM 1980). MARSDEN-JONES & TURRILL (1957) and BAKER & DALBY (1980) showed genetically fixed morphological differences between populations of *Silene cucubalus* and *Silene maritima*, which appeared to be related to solar radiation, temperature, nutrition and water balance as also suggested for populations with adaptations to a surplus of heavy metals by BRÖKER
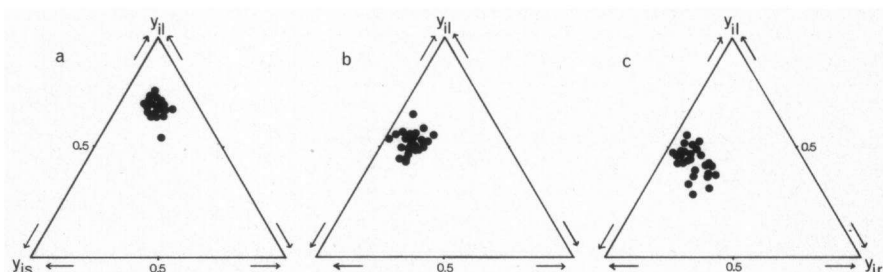

Fig. 5. Allocation diagram for *Urtica dioica*, grown with full interference (treatment a), harvested after 5 weeks, 9 weeks and 13 weeks.

(1963). The allocation index might be used as a marker in these cases. As long as the mechanisms underlying the relative growth rate are still unknown, it seems premature to suggest a genetic basis for variation in RGR as has been done by GOTTLIEB (1978), BURDON & HARPER (1980), and BREWSTER & BARNES (1981).

Another advantage of the present method of quantifying allocation data is the possibility to process zero values. Seed production can be introduced as zero value in computation of the allocation index as long as the vegetative phase of growth lasts, and then given as real seed weight as soon as appropriate. It then becomes possible to bring growth and reproductive strategies under one heading, and to integrate the results from both these approaches which are usually given separately. The technique presented here is more realistic than the rather unnatural model of VINCENT & PULLIAM (1980), who assumed annuals to be asexual.

As a technique is now available to quantify variation within populations, and to determine the contribution of individual plants and organs to the index of variation, it is opportune to investigate the ecological significance of population variation, and to relate the results to ecophysiology and population genetics. This interrelationship is a prerequisite for interpreting ecological adaptation in terms of evolutionary strategies.

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