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The self-thinning rule: bibliography revision

Samozřeďovací zákon - revize literatury

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This paper is a general review of the literature published about self-thinning in plant populations and, in particular, about the 3/2 power rule proposed by Yoda and his colleagues in 1963. Methodological aspects of the obtention of the self-thinning line, systematic deviations from the original formulation and the self-thinning of two-species populations are discussed. The importance of the development of size hierarchies for simultaneous mortality and biomass increase to take place in a population is emphasized. It remains clear that the 3/2 power rule is only an approximation to the process of self-thinning which, according to the most common definition of that process, may or may not take place in an overcrowded plant population.

1. Definition

1.1 Original formulation

In overcrowded populations of plants a stage of development can be reached after which some individuals of the population die due to competition while the survivors more than compensate for the loss of biomass due to mortality, so that both the total biomass of the population and the biomass per plant are inversely related to the population density. Yoda et al. (1963) proposed that the size/density relationship (on a log-log scale) followed by an even-aged plant population under such circumstances approaches asymptotically a –1.5 (= –3/2) line, no matter the plant species concerned. The exponential equation proposed for that relationship is known as "3/2 power law" or "self-thinning rule". The size measure originally proposed was the average above-ground weight per plant (W), in which case the function is:

$$\log W = k + a \times \log N,$$

where N is density (plants per unit area), $a = -3/2$ (or -1.5) and k depends on the species studied. Using the total biomass of the population (B) instead of the individual biomass, the function takes the form:

$$\log B = k + (a+1) \times \log N$$

(see section 2.1.2 for discussion about the selection of variables).

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Other approaches to the size/density relationship in crowded plant populations have been published. A linear relationship between log-density and log-average stem diameter was used by Reineke (1933) in order to predict the density of trees stands. The slope of that line was –1.6, irrespective of species, age of the stand or site quality. The equation proposed by Yoda and his colleagues turned out to be very close to Reineke's equation after using known parameters to obtain the biomass of tree boles from their diameter (Yoda et al. 1963). More recently, Yamakura (1989) proposed a similarly simple relationship between number of trees (independent variable) and the average height per tree (dependent variable) for a stratified forest. This model is also closely related to the self-thinning rule.

1.2 Conditions

To what plant populations does the self-thinning rule apply? The original mention of this rule by Yoda et al. (1963) indicates that "[...] the 3/2 law gives the interrelation between the stands of different ages and [/or] on different habitat." The evidence provided by that research group suggests that any monospecific population with even-aged individuals in active growth and suffering density-dependent mortality should follow a trajectory that approaches progressively, but never crosses, this line. This is indeed the interpretation given in most research articles on the subject (Firbank et Watkinson 1990, Weller 1990), although some disagreement exists as to what extent samples taken from

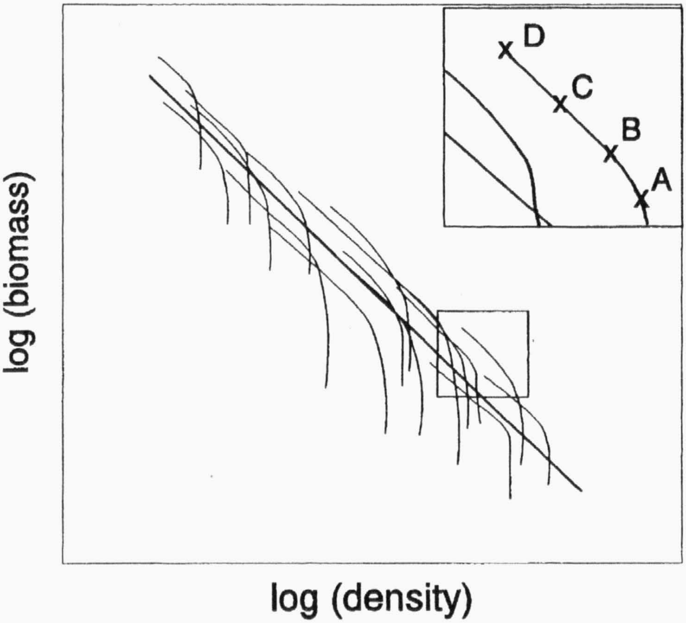

Fig. 1. - Schematic representation of the biomass/density relationship in independent populations of different plants species, including (see detail) a phase of growth with no mortality (up to point A), a phase of growth with little mortality (asymptotic approach to a line; from A to B) and a linear phase, the end of which (point D) indicates the maximum biomass attainable by the population. The thick line indicates the interspecific biomass/density relationship.

more than one population should be used to fit a thinning line (see Osawa et Sugita 1989, Weller 1990). In order to clarify this point the distinction has been made between (Weller 1990): (1) the "dynamic thinning line", which shows the linear phase of the relationship between biomass (or size) and density of one population during the thinning process before constant biomass is reached (Fig. 1, detail), (2) the relationship between biomass and density for non-related plots of one species undergoing density-dependent mortality or about to reach that stage (i.e. plots that do not represent random samples of one population), known as the "intraspecific biomass/density function" and (3) the "interspecific biomass/density function" in which samples of overcrowded or "fully-stocked" populations of different species are connected by a single line (Fig. 1). The researchers that first suggested this rule already distinguished these three relationship (Yoda et al. 1963). Despite recent discussions, the distinction between the dynamic thinning line and the intraspecific biomass/density relationship remains, in practice, unclear (Osawa et Sugita 1989, Weller 1990), depending on whether two populations are considered replicates of the same population or different populations.

The even-aged condition in a population implies that all plants must have emerged at approximately the same time. As far as I am aware, only the study by Cousens et Hutchings (1983) on seaweeds shows evidence of uneven-aged populations departing from the self-thinning line produced by even-aged populations of the same species (in this case the uneven-aged populations followed a line parallel to that of even-aged populations and above it). Mortality during self-thinning is linked to the development of a hierarchy of resource use (dominance and suppression; Harper 1977, Weiner 1990); the factors that determine the dominance of some individuals over others (including age) may vary but size differences appear to have primary importance (but see section 2.2.4). Therefore, it would be expected that a similar trend be followed by a population in which the hierarchy of sizes was determined by time of emergence (as in the case of uneven-aged populations) and a population in which that hierarchy was linked to differences in innate relative growth rate between even-aged individuals. This idea is supported by the results of the studies by Ford (1975) and West et Borough (1983) who showed that the dominant plants within a population follow a self-thinning line with the same slope as the whole population. Significant effects on the self-thinning line could be expected, however, if new individuals have emerged after the onset of self-thinning and such individuals contribute significantly to the biomass and/or to the density of the population.

Although the self-thinning rule was originally proposed for monospecific populations, it has been demonstrated that mixtures of two species with similar growth form behave in the same way (White et Harper 1970, Bazzaz et Harper 1976, Malmberg et Smith 1982, Binkley 1984, see section 3). Unfortunately, the evidence for mixtures of plants with very different growth forms and for combinations of more than two species is almost lacking (but see Marks 1974, White 1985).

Density-dependent mortality implies that, in high-density conditions, some of the plants which would survive in less-crowded populations die. The proximal cause of density-dependent mortality might be either the action of pathogens or pests attacking the least vigorous individuals (Murray 1979, Crooke 1979, Long et Smith 1983) or the lack of resources for the suppressed plants through pre-emption of those resources by the dominants (Harper 1977). In this context, Long et Smith (1983) indicated that "Neither density nor competition kills trees.[...] severe competition makes individual trees [...] more susceptible to direct agents of mortality." The effect that different density-dependent causes of mortality may have on the self-thinning of a population is unknown. That effect would depend on the extent to which the vigour of those individuals that survive is preserved. Little effort has been devoted to the study of the actual process of plant death in overcrowded conditions.

The extent of mortality in a population seems to be more relevant than the causes of mortality for studies dealing with the testing of Yoda's law. As indicated in section 2.1.1, the degree of mortality is concerned with the selection of points for fitting the thinning line. In the wake of some studies (Jacobs 1979, Weller 1987a), Lonsdale (1990) proposed that the mortality within the population should be at least half an order of magnitude relative to the original density for the population to be considered to be following the self-thinning line. Knox et al. (1989) considered that 20% mortality of the population was a convenient limit to start referring to a population as being self-thinning, whereas West et Borough (1983) included populations with 10% mortality within that category.

Initially, the self-thinning rule was proposed for populations with clearly identifiable individuals (seedlings, annual species and a number of tree species). Some studies have shown that clonal species can follow a similar trajectory (Kays et Harper 1974, Hutchings 1979, Hutchings et Budd 1981). On the other hand, it has been shown that some clonal species, however dense their shoot populations, either never reach the theoretical self-thinning line or they reach the line at a stage when shoot growth is hardly taking place, so that no shoot mortality has to compensate for that growth (Hutchings et Barkham 1976, Hutchings 1979). In those species that develop dense populations of shoots which could invade without being invaded („phalanx" strategy of growth; Lovett Doust 1981), the production of shoots would be delicately balanced in order to avoid mortality due to overcrowding and, at the same time, restrict to a minimum the chances of establishment of other species (Pitelka 1984). The persistence of physiological connections between sister shoots or ramets is thought to contribute to such an equilibrium (Pitelka 1984, Harper 1985).

1.3 Evidence

Data sets on self-thinning can be classified into three groups according to the kind of data provided and how these data were obtained. (1) Populations which are randomly sampled and from which direct measures of number and biomass of plants are obtained (either by weighing every single individual or by measuring the total biomass and then dividing it by the number of individuals); most of the studies on herb species are included in this category (e.g. Yoda et al. 1963, White et Harper 1970, Bazzaz et Harper 1976, Schmitt et al. 1987, Weiner et Whigham 1988). (2) Populations in which the biomass (or volume) of a sample of individuals is estimated over time from linear dimensions using either *ad hoc* or generalized equations; this is the case for most experimental studies on the self-thinning of tree species (e.g. West et Borough 1983, Gardner 1990); the study by Hutchings et Budd (1981) on *Mercurialis perennis*, a perennial herb, is also included in this group. (3) Populations for which measures of growth and mortality are taken and used to estimate future growth and mortality; forestry yield tables represent this group (e.g. Borough et al. 1978, Boudoux 1978). All of these sources can be considered valid evidence for the dynamic self-thinning relationship; a fourth group of data sets, derived from plant populations for which only the maximum biomass (or an estimation of it from linear measurements) and the density at which this is achieved are available (e.g. data sets compiled by Cannell (1982)) connects "snapshots" of a number of clearly unrelated populations and may be considered useful, in this context, only to show the generality of the interspecific size/density relationship.

The errors involved in gathering biomass/density relationships vary from one kind of study to another. In the case of tree populations estimations of either volume or bole weight per tree have been used in place of the total aboveground weight. Therefore, the error of the estimated mean volume or mean bole weight would involve the addition of the errors of the individual estimations. In the case of yield tables, the sequence of biomass/density data over time is derived from known parameters, so that there is also an estimation error for each point on the thinning line. The agreement, at least qualitative, of data sources (1), (2) and (3) with the 3/2 power law of self- thinning has been relatively satisfactory considering the very different sampling and measurement errors involved and the range of conditions under which the populations involved were growing.

1.4 Interpretations of the self-thinning rule

Yoda et al. (1963) accompanied their 3/2 power law with a simple dimensional argument to justify its generality. A brief description of that argument follows: (1) the biomass (or volume) per plant is proportional to the third exponent of a linear dimension of the plants; (2) the area occupied by each plant is proportional to the square of the same linear dimension; (3) the area occupied by each plant is inversely proportional to the density of the population when the cover of the population reaches 100%. The 3/2 power law can be derived combining these three assumptions and would then represent the maximum packing of plants that could be possibly achieved on a surface at specific densities. This dimensional argument was criticized by White (1981) on the grounds that no linear dimension to the third power was found to be proportional to the volume or biomass of the plants. Givnish (1986), on the contrary, indicated that height could be considered such a linear measure. Several other models have addressed either directly or indirectly the self-thinning process. The model by Aikman et Watkinson (1980) took the –3/2 exponent as a pre-requisite, whereas other models arrived to the conclusion that the –3/2 exponent was highly likely given the plant growth parameters found in nature (Ford et Diggle 1981, Pickard 1983, Hara 1984a, b, Slatkin et Anderson 1984, Clark 1990, 1992). Some studies related the self-thinning exponent to geometrical measures of the plants and assumed that its actual value changed for different species and conditions (Weller 1987b, 1989, Norberg 1988, Osawa 1992). The influence of the interference by neighbours on the light interception and photosynthesis of individual plants and consequently their growth and mortality were taken into account in several models (Lonsdale et Watkinson 1983, Charles-Edwards 1984, Morris et Myerscough 1983, Perry 1984, Hara 1986, Prentice et Leemans 1990). Little attention has been paid to the role of the shortages of resources other than light in the self-thinning process (but see Hardwick 1987, Morris et Myerscough 1987).

Although no definite answer has been found, the apparently narrow range of self-thinning slopes ($-1 > a > -2.5$) for the whole range of plant species studied seems to be linked to the equally restricted capacity of plants to pack biomass in each unit of volume available (Weller 1989, Norberg 1988). In other words, the self-tolerance of plants (the tolerance of individuals to the interference by others of the same species, as expressed by Zeide (1985)) is, apparently, independent of the size and density plants can achieve. Differences between species tend to be reduced when they grow at high densities, the characteristic growth patterns, for instance, being suppressed to some extent. The increase in apical dominance with shading level is one of the growth features that seems to be common to most plant species (see Björkman 1981, Morgan et Smith 1981, Smith 1982, Corre 1983, Warrington et al. 1988). It is also possible that the responses of plants in terms of biomass production and photosynthate distribution are restricted by competition. The degree to which the growth rate of an individual can be increased as a result of the death of a neighbour plant is limited by its size and the number of meristems of that plant that are able to become active (Waller 1986). Since nutrients are constantly being "lost" to persistent (support) tissues, the degree of activity a meristem can display is negatively related to size. Despite the diversity of plant growth forms, the same general design and environmental constraints appear to have restricted the possible outcomes of overcrowding in plant populations.

2. Critical factors affecting the slope of the self-thinning line

The generality of the self-thinning rule as originally proposed and, in particular, that of its slope have been criticized in the last few years from several points of view (but see Barreto 1989). On the one hand, the methodology followed to find the self-thinning equation of a population has been recently questioned (see Westoby 1984, Weller 1987a, Zeide 1987, Lonsdale 1990). On the other hand, clear evidence against the generality of the thinning parameters has been gathered (see Weller 1987a, Zeide 1987).

2.1 Methodological factors

2.1.1 Selection of populations

The decision of whether to include a given population within the set of data to which the thinning line is to be fitted has paramount importance for the slope of that line (see Westoby 1984, Weller 1987a, Osawa et Sugita 1989, Lonsdale 1990). As mentioned in section 2.2.1 (see references therein) the trend followed by the biomass/density relationship of a population during self-thinning is curvilinear rather than linear (approaching a line asymptotically). Therefore, the self-thinning slope of a population as it goes from stage A to stage B (i.e. just entering the phase of simultaneous growth and mortality; Fig. 1 detail) may be substantially different from that of a population going from stage B to stage C. Unfortunately, there is no way of statistically assessing the slope of the asymptote that the population is approaching just by knowing the curve followed (Lonsdale 1990). That line can be identified by following the time trend of a dense population from its early stages of growth up to the point of its ceiling biomass ($a = -1$), something that has been done only in a few studies (see Zeide 1987 for examples). Consequently, it is usually difficult to decide at what point the population has actually reached the thinning line (Firbank et Watkinson 1990). For the sake of the objectivity of this kind of study, it would be convenient to sample the population at clearly identifiable stages of development (i.e. avoiding overlapping of either biomass or density values between samples) and to judge the suitability of the sample as a whole, without making decisions about the suitability of each single replicate within each sample. One way of objectively deciding which samples to include in the line-fitting process, would be statistically assessing the curvilinearity of the trajectory and omitting those samples that, either from one end of the trajectory or from the other, significantly contribute to alter the linear trend sought (as in Morris et Myerscough 1991). The variance and subjectivity added by the process of selection might also be reduced by changing the self-thinning model to a curvilinear one, which would be considerably more complex (see Smith et Hann 1984).

The difficulties imposed by the curvilinearity of the size/density trajectory when approaching the self-thinning line, led some researchers to consider that a minimum mortality should occur in a population for it to be included when testing the self-thinning rule (see section 1.2). However, this prerequisite would imply restricting, from start, the possibilities of finding a steep-sloped thinning line.

2.1.2 Selection of data sets and variables

The use of the total above-ground biomass (B) of the population instead of the average plant biomass (W) in self-thinning studies has gained support in the last decade (Westoby 1984, Weller 1987a, Lonsdale 1990, among others). The main argument against the use of the average biomass has been the fact that the density (N) is used to obtain that value (W = B/N) and consequently both variables are "spuriously" correlated, making the relationship between them "uninterpretable" (Weller 1987a). However, statisticians consider such relationships valid as long as the variables represent intelligible concepts (Prairie et Bird 1989). In any case, the value of the mean weight per plant would obviously be the same (without considering differences in measurement error) whether we calculate it by measuring the weight of every plant or obtain it by dividing B by N.

Another point argued in favour of the use of the total biomass instead of the mean individual biomass is that the individual biomass can be significantly correlated with the density of survivors even when the total biomass is not (Weller 1987a). In other words, the average weight per plant may increase due to the decrease in number of plants even if none of the survivors grows. This problem can be restricted to one of definition; if self-thinning is defined as the process by which the density of a population decreases due to competition whereas its total biomass increases, then any cases in which the growth of the survivors does not "over-compensate" for the death of some individuals (and the consequent loss of biomass) should not be considered a self-thinning population (even if the survivors did actually grow). Consequently, only data sets in which there is a negative correlation between total biomass and density should be included in self-thinning studies. Although this is a good way of setting the "lower limit" for the data sets to be analyzed, it does not invalidate the use of the average plant biomass for fitting the self-thinning line.

2.1.3 Line-fitting method

The standardization of the method used for line fitting is crucial for the self-thinning rule. *Least squares regression* (LSR) was the most common fitting method used by the early workers on this subject (see Yoda et al. 1963, White et Harper 1970, Bazzaz et Harper 1976). The inadequacy of LSR was first pointed out by Mohler et al. (1978) on the grounds of the impossibility of determining which variable (density or size) should be considered the independent variable, since both change concomitantly and are measured with error. There is a more severe drawback in using LSR: its sensitivity to outliers, particularly those with extreme values for any of the two variables (see Neave et Worthington 1988). This problem must be taken into account when fitting a thinning line because of the higher probability of outliers occurring in some areas of the size/density plot than in others (due to the nature of the data and the logarithmic transformation of the variables). Mohler et al. (1978) suggested the use of the *major axis* (the first axis of principal components analysis, PCA) as a more adequate procedure. Nowadays the PCA is the most commonly used line in self-thinning studies, although LSR has been used recently (Gibson et Good 1986, Buford 1989, Felker et al. 1990, Dunn et Sharitz 1990).

Since the slope obtained by PCA is always steeper than that obtained by least squares regression for the same data set, Lonsdale (1990) suggested that the theoretical self-thinning slope must be slightly more negative than –3/2. The use of PCA for this kind of analysis has been criticized because the dependence of the slope on the scale used, a problem not solved by the logarithmic transformation of the variables as previously thought (Leduc 1987). The sensitivity of PCA to outliers is also high. An alternative technique, the *reduced major axis* or *geometric mean regression* (GMR) (Ricker 1984, Leduc 1987), was used by Gorham (1979) in dealing with the interspecific size/density relationship (closely related to the self-thinning rule or "part of it", as mentioned above). This is considered a valid line-fitting technique when both variables are subject to error (Ricker 1984, Leduc 1987, Dunn et Sharitz 1990), which is the case in self-thinning populations. Zeide (1987) recommended the use of GMR but did not use it himself in two papers on self-thinning (Zeide 1985, 1987). Leduc (1987), in a study comparing several line-fitting techniques (including those already mentioned), concluded that GMR was the most suitable whenever the comparison of slopes with a theoretical value was the main objective, whereas the use of least squares regression would be more convenient when predictive power was sought. GMR has received, however, some criticism (Sprent et Dolby 1980). In cases like self-thinning, where the data are usually grouped into samples according to time or age, and the number of replicates and samples is relatively low, median-based fitting techniques such as *Theil's incomplete regression* (TIR) (see Neave et Worthington 1988) may be preferred. In this technique the data set is divided into sub-sets (each of which would correspond to the replicates of one sample of the population under scrutiny) and the median of the gradients linking these subsamples is obtained. In a recent study on field populations of seedlings dominated by *Galium aparine*, the self-thinning slopes obtained differed significantly from –3/2 in three out of five populations when TIR was used but only in one of them when PCA was used (Puntieri 1991). It would be necessary to assess the validity of these line-fitting techniques in other data sets on self-thinning in order to assess their suitability. Special effort should be devoted to reducing the variance between repetition plots in self-thinning experiments, so as to reduce, at least in practice, the importance of the decision about which line-fitting technique to use.

2.1.4 Statistics

The importance of the statistical comparisons between slopes and intercepts of thinning lines has been emphasized by Weller (1987a). Although this author supported the use of PCA for the estimation of the self-thinning line equation, he recommended the use of Pearson's correlation coefficient between biomass and density as a means of determining whether a population is self-thinning or not. Disagreements may thus be found between the slope's confidence limits found for a set of data using a line-fitting technique other than LSR and the significance of Pearson's correlation coefficient.

White (1985) pointed out that the intercept to be compared between lines should be one corresponding to a reasonable density for the species, preferably one within the range of densities found in the study. Comparing intercepts for "N = 0" means extrapolating the thinning line to unreal values and can lead to uninterpretable results (see Weller 1987a).

2.2 Systematic deviations from the self-thinning rule

The results of studies carried out after the self-thinning rule was proposed supported the constancy of the slope b of Yoda's equation for most plant populations (see Harper et

White 1974, White et Harper 1970, Kays et Harper 1974). However, it was soon recognized that the value of b could differ from –3/2, with the concomitant change in the intercept, in some cases even when simultaneous increase in total biomass and decrease in density occurred.

2.2.1 Time trend

As mentioned above, it has been shown in several studies that the slope of the self-thinning line is far from constant over time: the slope is very steep during the first stages and becomes progressively less negative, approaching asymptotically the –3/2 line (Drew et Flewelling 1977, 1979, Long et Smith 1983, Weller 1987a, Zeide 1987). One study on natural populations reported a sigmoid thinning trajectory (Carleton et Wannamaker 1987) which seems to be an exception possibly due to the effect of some degree of density-independent mortality (see section 4). Considering the discrete character of mortality, the approach of a population to the – 3/2 asymptote would be a stepwise process, more so if the distribution of the individuals is random. In the latter case some individuals could suffer a premature death (for the total biomass of the population) due to the effects of local overcrowding.

2.2.2 Plant morphology

Some attempts have been made to explain part of the variation of the self-thinning slope in terms of morphology and large taxonomic groups of plants (Harper 1977:185-187, White 1980, Lonsdale et Watkinson 1983, Weller 1987a, Lonsdale 1990). The results have been rather controversial and depended much on the data sets included or excluded from the computations (see Lonsdale 1990). Using data from forestry yield tables of eight species, White et Harper (1970) found, in general terms, a gradient of decreasing intercept from species with more pyramidal crowns (conifers) to round-crown species (angiosperms). The self-thinning slopes were, however, similar between species. Weller (1987a) summarized a number of data sets on self-thinning and found the mean thinning intercept higher (and the slope steeper) for populations of coniferous trees than for populations of angiosperm trees, and higher for dicot than for monocot herbs. This last conclusion was at odds with Lonsdale et Watkinson's (1983) results who suggested that species with needle-like leaves, like grasses, follow thinning slopes with higher intercept because of their higher capacity to packing biomass within a volume. Tables of growth (either measured or simulated) of several species of *Eucalyptus* published in two studies on this genus (Borough et al. 1978, Jacobs 1979) suggest that the self-thinning slope for this genus is steeper than for any other group of species (see Weller 1987a). The considerably high growth rate of eucalypt trees might account for such steep thinning slopes (some of the data sets analyzed, however, did not seem to have reached the linear phase of the thinning trend). Unfortunately the data available do not allow us to distinguish between the effect of the physiological features associated with the taxonomy of plants and the effect of their morphological characteristics.

Several of the models proposed to explain the self-thinning rule used morphological features such as the relationship between height and diameter (Weller 1987b, Norberg 1988), the leaf area development (Perry 1984), or the crown area development (Clark 1992). The empirical support for these theoretical developments, however, is scarce (but see Blake et al. 1991). The results obtained by Ellison (1989) working on three species of *Chenopodiaceae* with contrasting leaf development suggest that the pattern of arrangement of the photosynthetic surface is important for the self-thinning slope: the species with scale leaves (*Salicornia europaea*) had no self-thinning; the species with broad leaves (*Atriplex triangularis*) had a thinning slope not significantly different from the proposed –1.5 and the species with intermediate leaf development (*Suaeda maritima*) had a slightly steeper thinning slope. This result could also have been a consequence of the differences between these species in their rates of self-thinning and the population density they need in order to reach the self-thinning line. Because of the curvilinear trajectory of the log-weight/log-density relationship, the population (though thinning) might not be able to reach the linear part of that relationship if the initial density is not high enough. This problem can be difficult to tackle when the species used for the study has particularly plastic growth, enabling the plants to survive under relatively „gentle" glasshouse conditions. In another experiment, Westoby (1976) tested the difference between the thinning lines of populations of "leaved" and "leafless" pea plants and found no significant differences.

2.2.3 Physiology

Physiological differences between species may determine their capacity to grow and their tolerance to environmental constraints (including the interference from neighbours). Zeide (1985) proposed that, for a stand of individuals of the same species, the degree of self-tolerance of the stand is given by the ratio, growth rate/mortality rate, and that the slope of the thinning line is a measure of the self-tolerance of the stand. In fact, he found that some tree species tolerant to shade have steeper thinning lines than species intolerant to shade. A similar comparison was carried out by Weller (1987a) using 46 data sets for angiosperm trees and 267 for gymnosperm trees from several studies. He found that shade-tolerant angiosperm tree species self-thinned along steeper slopes than shade-intolerant angiosperm tree species. The comparison between shade-tolerant and shade-intolerant conifers gave the opposite result (steeper thinning slope for the latter group). Lonsdale (1990) re-analyzed Weller's data sets after considering that the results were affected by pseudoreplication (several data sets for each species were included in the computations). The number of data sets that remained after that re-selection was considerably lower (14 conifers and 8 angiosperm tree species). Taking all trees as a group, a significant positive correlation was found between shade-tolerance and the intercept of the thinning line (the slope was not significantly affected by that character). These kinds of comparison have not been attempted for herb species or shrubs.

2.2.4 Resource availability

The effect of soil fertility and shading on the self-thinning trend of a species have been tested in several studies. The more relevant results are mentioned separately for soil nutrients and light and discussed under a common heading.

Nutrients. Contrasting results have been found in different studies on the effects of nutrient level on the self-thinning trajectory. In some of these studies the initial differences created by the nutrient level in the biomass/density relationship (which suggest parallel thinning trends) disappeared later on, i.e. the trends of populations at different fertility levels converged to a common trend (Yoda et al. 1963 (see Fig. 2a), White et Harper 1970, White (cited by Westoby 1984), Smith et Hann 1984). This means that the populations at higher fertility level moved faster along the self-thinning line (they had higher growth rates and mortality rates than those at lower fertility), but the populations at lower fertility had a somewhat steeper thinning slope (the growth rate of the average plant was relatively

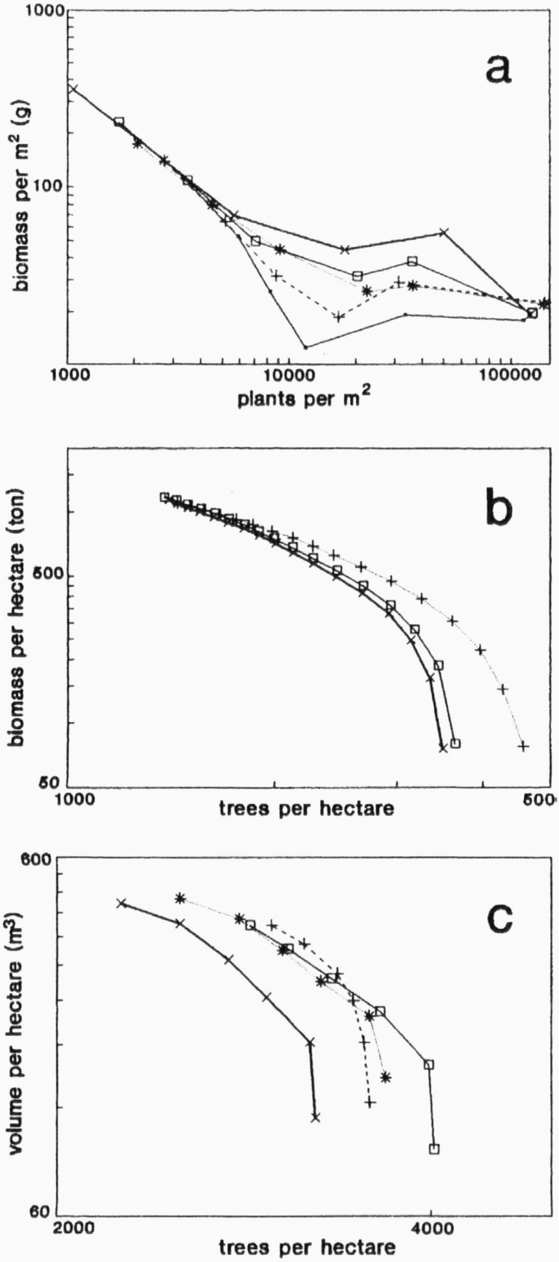

Fig. 2. - Effect of the level of nutrients on the self-thinning trajectory of plant populations. Results obtained by (a) Yoda et al. (1963) on *Erigeron canadensis*, (b) Duke et al. (1989) using a model which utilizes real data on growth and mortality of trees, and (c) Gardner (1990) on *Pseudotsuga menziesii*. In all three graphs the level of nutrients can be ranked as follows (from highest to lowest level): —×—, —□—, —✱—, —+— and —·—.

higher than the mortality rate compared with the populations at higher fertility level). The higher rate of self-thinning at high fertility level means that both growth and mortality are hastened when the resource availability increases. Increased self-thinning rates and a steeper self-thinning slope at higher fertility levels were reported by Gibson et Good (1986). Morris (1980), Furnas (1981) and Zeide (1987) also found that the self-thinning trend in low-quality conditions followed a lower (less negative) slope. Westoby (1984) questioned Morris' and Furnas' conclusions on the grounds that a different result could be obtained by omitting a few extreme points of their data sets: populations at different fertility levels would tend to follow parallel thinning lines, i.e. lower for low fertility populations. The same could be said of some of the evidence shown by Zeide (1987). The results obtained by Morris et Myerscough (1985) working on *Trifolium subterraneum* supported Westoby's view. However, in a detailed study on *Ocimum basilicum*, Morris et Myerscough (1991) found a reduction in the steepness of the self-thinning line at lower nutrient levels. The results obtained by Duke et al. (1989) using a model based on actual data on tree growth and mortality (Fig. 2b), on the other hand, show a similar effect of fertility: the self-thinning slope becomes steeper as fertilization increases. Data on Douglas-fir stands provided by Gardner (1990) indicate that increased fertility accelerates the self-thinning process but show, opposite to previous studies, that populations in more fertilized soils can follow a thinning line with lower intercept (Fig. 2c). This interpretation, however, has to be taken carefully, though, since the populations studied by Gardner started growing at different densities and may have not reached the linear phase of their thinning trajectories.

Light. The results of different studies on the effects of shading on the self-thinning trend differed, though less dramatically than in the case of soil-nutrient levels. Some authors reported a slope closer to –1 for deeply shaded populations (White et Harper 1970, Kays et Harper 1974, Lonsdale et Watkinson 1982), whereas others found that shading lowered the level of the thinning line without changing its slope (Westoby et Howell 1981, 1982, Hutchings et Budd 1981). However, the source of the disagreement tends to disappear when extreme-shade treatments are excluded from the computations (see Lonsdale et Watkinson 1982). Moderate levels of shading seem to lower the level of the self-thinning line without affecting its slope.

Resource levels and size variation. Self-thinning is the result of the unequal access of the individuals of a population to the limiting resource. Mortality is supposed to take place amongst those individuals with lower ability to utilize that resource (White et Harper 1970). Competition for light between individuals is inherently asymmetric, i.e. bigger plants intercept a higher proportion of light than the proportion of the total biomass of the population contained in these plants (Weiner 1990). Competition for other resources is bound to be two-sided (Newman 1983, Weiner 1990). According to this view, the size variation that drives self-thinning would be more likely to develop whenever light is the limiting resource. This is supported by those studies in which soil resource shortages decreased the mortality rate of the population (Yoda et al. 1963, White et Harper 1970). This has enabled some authors to conclude that self-thinning is a direct result of competition for light (Weiner et Thomas 1986, Weiner et Whigham 1988, Thompson et al. 1990, Weiner 1990). However, there is currently evidence that this may not be the case, at least at low nutrient levels (Schlesinger et Gill 1980, Morris et Myerscough 1991).

Morris et Myerscough (1991) found that despite packing more biomass per unit of volume occupied (judged by the height of the canopy and the lateral extension of the

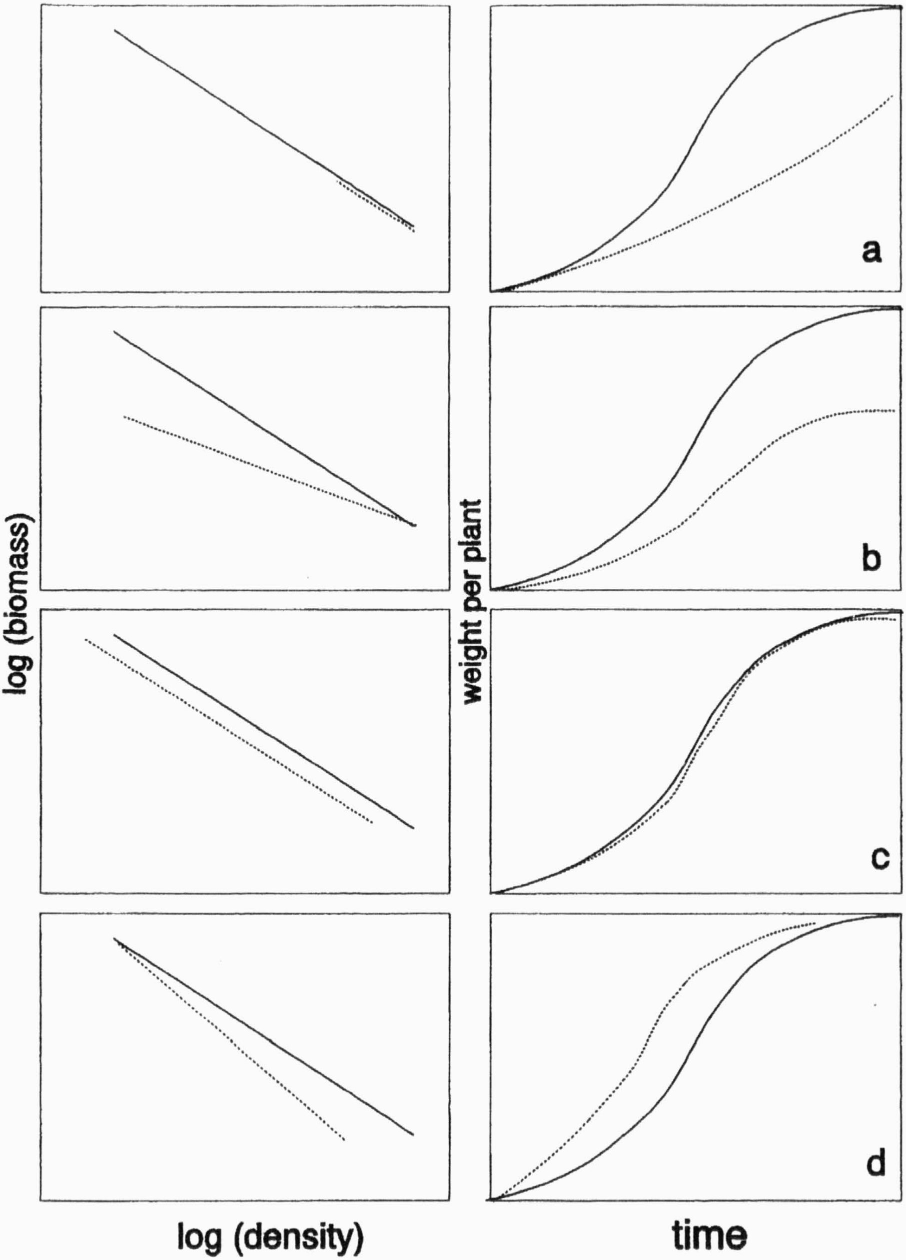

Fig. 3. - Four possible outcomes of the level of soil nutrients on the self-thinning trajectory of a population (left column) and the average growth curve of the survivors (right column). Solid line: high level of nutrients; dashed line: low level of nutrients. See description in the text.

leaves) at lower levels of nutrients, the self-thinning trend of these stands was less steep at low-nutrient than at high-nutrient level rather than steeper, as predicted by models based on light limitation and biomass packing (Lonsdale et Watkinson 1983, Givnish 1986, Norberg 1988). These authors suggested that the increase in the allocation of biomass to roots at low-nutrient levels could have increased the degree of overlap between the depletion zones of neighbour plants below-ground. In that case the self-thinning trajectory would be driven by below-ground competition. However, they recognized that low-nutrient levels can also slow-down the rate of self-thinning, so that the low-nutrient populations would follow the same thinning line as high-nutrient populations of the same species but at a lower pace. Different species and different soils could, as they suggested, cause nutrient level to result in either of these two responses.

The self-thinning process can be interpreted as the result of intraspecific competition, which determines a hierarchy of use of the limiting resource among neighbour plants. The way in which different levels of a resource will affect the self-thinning trajectory of a population would depend on the extent to which the hierarchy of resource use is modified. This, in turn, may be the result of the effect of different resource levels on the growth curve of individual plants. Four likely outcomes of changing the level of nutrients for a population may be described under this perspective. (a) The level of mortality is the same at low- and high-nutrient levels for a given increase in biomass, but the rate of self-thinning is higher at high-nutrient level (Fig. 3a). This corresponds with the "altered-speed competition" of Morris et Myerscough (1985). In this case the hierarchy of use of the limiting resource is not changed by the restriction in the availability of nutrients; the rate of growth of the survivors would be reduced, but their growth geometry would be unaltered. (b) The level of mortality is increased for a given increase in biomass at lower nutrient levels (Fig. 3b). In this case, which corresponds to Morris et Myerscough's (1991) "altered-form competition", the hierarchy of resource use would vary at different nutrient levels; the growth curve of the survivors would have different parameters at low- than at high-nutrient levels (their geometry of growth would be affected), which could result from a more symmetric competition in the first case. This could be the outcome if light were the limiting resource at high-nutrient level and one of the nutrients in short supply became the limiting factor at low-nutrient level. (c) The relative rates of mortality and biomass production are similar at both nutrient levels but the low nutrient stand moves along a lower-biomass line (Fig. 3c). Both the hierarchy of resource use and the capacity of the survivors to produce biomass are similar at different nutrient levels, but the number of survivors for a given population biomass is lower when nutrients are in short supply. In this case either light would remain as the limiting resource or soil nutrients are limiting but the hierarchy for their use is similar to that for light. (d) For a given decrease in density the rate of biomass production is relatively higher (although the biomass should be lower) at lower nutrient levels (Fig. 3d). Nutrient deficiency would increase the development of a hierarchy of resource use, which could take place if competition for the limiting resource at low-nutrient level were more asymmetric than that for the limiting resource at high-nutrient level. The latter seems the most unlikely outcome according to our current knowledge on competition for nutrients.

Morris et Myerscough (1991) assumed that competition would be more intense whenever the mortality rate of a population is high relative to its biomass production. They concluded, accordingly, that competition is more intense at lower nutrient levels in a population following model (b) but not in a population following model (a). However,

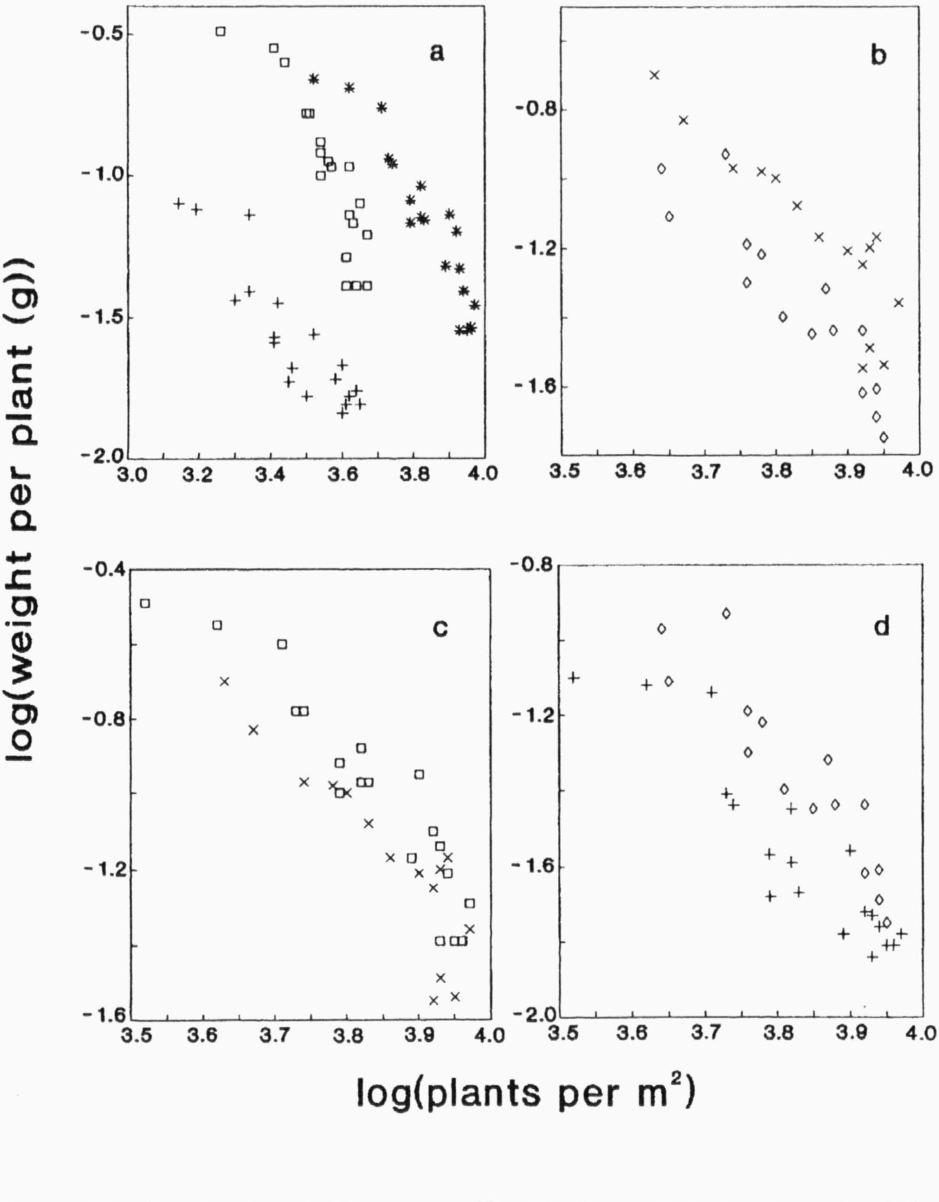

Fig. 4. - a. Thinning trajectories of *Trifolium pratense* (□) and *Medicago sativa* (+) in mixture when plotting mean weight per plant vs. partial density of each species, and self-thinning of the mixture considering weight and density of both species (✳). b. Self-thinning of monocultures of *T. pratense* (x) and *M. sativa* (◇). c. Thinning of *T. pratense* in mixture using the total density of the mixture (□) and self-thinning of that species in monoculture (x). d. Thinning of *M. sativa* in mixture using the total density of the mixture (+) and self-thinning of that species in monoculture (◇). Data source: Malmberg & Smith 1982.

it could be argued that competition intensity ought to be measured not in terms of mortality but in terms of biomass loss relative to that produced by non-competing plants. There is evidence that mortality may not take place in dense populations even when competition is intense, due to the lack of hierarchy development (see Eversole 1955, Oliver 1967, Burschel et Huss 1987:220, Oliver et Larson 1990:83).

3. Self-thinning in mixtures of species

The self-thinning law was originally proposed for monospecific populations. However, there is clear evidence that mixtures of species follow a similar pattern (White et Harper 1970, Bazzaz et Harper 1976, Malmberg et Smith 1982, Binkley 1984, White 1985). In the few studies where this problem was tackled, both the weight per plant considering all components of the mixture against the total density and the weight per plant for each component species against the species density were plotted and their thinning relationships obtained. In this context, the former relationship can be called "self-thinning of the mixture" and the latter "thinning of the component species". In order to compare the thinning trend followed by a species in mixture with that of the same species in monoculture, the use of the average weight per plant is more convenient than that of the total biomass of that species since the total biomass would depend on the proportion of each species in the mixture. None of the published studies on the self-thinning of mixtures of species accounted for here compared the trajectory followed by each of the components of the mixture with that of the monoculture of the same species. Nevertheless, Malmberg et Smith (1982) provided a graphical comparison (Fig. 4a, b). These authors concluded that the behaviour of the component species in the mixtures was similar to that of the species in monoculture and that both mixtures and monocultures followed typical –3/2-slope lines. In addition, the data provided by Black (1960) for mixtures and monocultures of the same species (*Trifolium pratense* and *Medicago sativa*) show a similar result after the selection of the appropriate points (i.e. omitting those which made the thinning trajectory significantly curvilinear): the monocultures self-thin following the same trend as the component species of the mixtures.

Some advantages can be gained by plotting the weight per plant of each component species against the total density of the mixture: (1) the real density at which plants are growing is considered, (2) the thinning trend of each component species becomes more comparable with that of a monoculture of that species at a density similar to that of the mixture, and (3) the trends of the components can be compared with each other despite their differences in relative density. The association between the self-thinning trend of a species in monoculture as compared with that followed by the same species in a mixture with another species using the total density of the mixture in the x-axis, may indicate the degree of (realized) niche overlap between both species and their relative competitive abilities during that period of time. A hypothetical example will be used to describe the possible outcomes of such a comparison. Figure 5a shows the self-thinning lines obtained for species A and B in monoculture. If both species have identical competitive abilities and realized niche for the conditions of the experiment, the thinning trajectory of each of them in the mixture would be similar to that of the respective monoculture. If, on the other hand, species A and B have low or no overlap in their niche requirements, and consequently interspecific competition would be lower than intraspecific competition, the individuals of each species would behave as if the level of crowding were lower than that

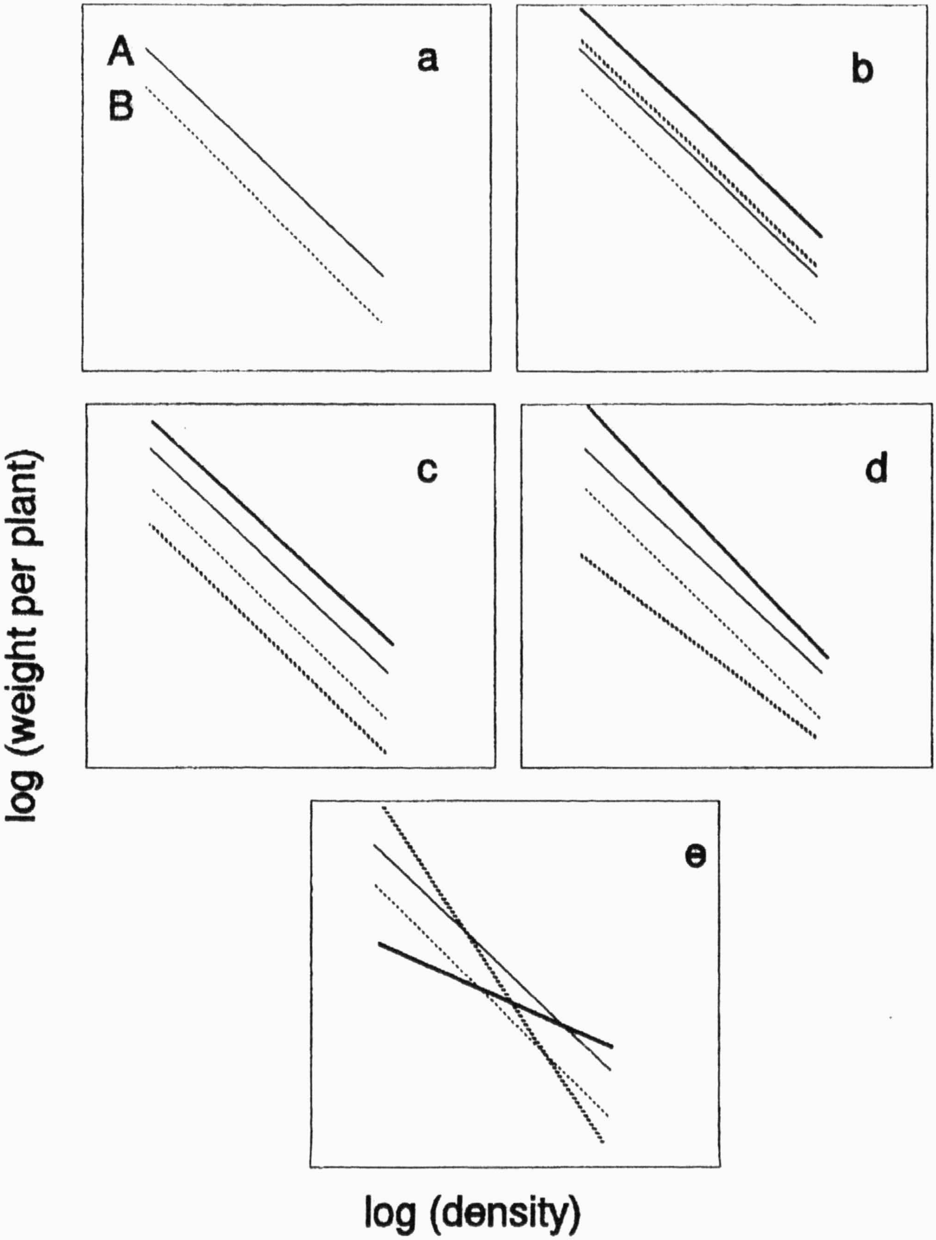

Fig. 4. - Thinning of species A (solid line) and B (dashed line) in monoculture (graphic a and thin lines of graphs b-e) and in mixtures (thick lines of graphs b-e) assuming different levels of resource-use overlap and competitive ability (see text for description).

Table 1. - Major axis slope, intercept and 95% confidence limits for both parameters of the thinning lines (expressed as log (mean wt/plant) vs log (total N)) of *Trifolium pratense* and *Medicago sativa* in monoculture (mon.) and mixture with each other (mix.) and for both species in mixture (total mix.) obtained for Malmberg & Smith's (1982) data.

	Slope			Intercept		
	Mean	Lim 1	Lim 2	Mean	Lim 1	Lim 2
Trifolium mon.	-2.56	-3.41	-2.02	8.68	11.97	6.60
Medicago mon.	-2.56	-3.28	-2.08	8.44	11.18	6.59
Trifolium mix.	-2.35	-2.83	-2.00	8.01	10.15	6.67
Medicago mix.	-2.05	-2.45	-1.74	6.25	7.79	5.08
total mix.	-2.36	-2.84	-2.00	7.87	9.71	6.50

indicated by the density of both species; therefore the thinning line of each species in the mixture would have a higher intercept than the self-thinning line of the respective monoculture (Fig. 5b). In those cases in which A and B have some degree of niche overlap and one of the species, let us say A, has some initial competitive advantage over the other in exploiting the limiting resource, there could be at least three possible outcomes: (1) the competitive advantage of A over B is constant during the thinning period, the thinning line of A has a higher intercept and that of B a lower intercept than their respective self-thinning lines but their slopes remain the same (Fig. 5c). (2) The competitive advantage of A increases over time, so that the thinning line of A has a steeper slope and that of B a less steep slope than their respective self-thinning lines (Fig. 5d). (3) The initial advantage of A for resource capture decreases over time and therefore the thinning slope of A is less steep and that of B is more steep than in the respective self-thinning line (Fig. 5e).

A re-analysis of Malmberg et Smith's (1982) published data in the wake of this discussion was carried out. After omitting two values corresponding to the lowest weight per plant for each data set (obviously previous to the period of self-thinning, as pointed out in that paper), the major axis lines (instead of the least squares regression lines used in the original study) fitted were significantly ($P<0.05$) steeper (more negative) and higher (with higher intercept) for *M. sativa* in monoculture than in mixture with *T. pratense*, indicating that: (1) the competitive ability of *T. pratense* plants is higher than that of *M. sativa* plants and (2) that the difference between the performance of individuals of *M. sativa* in monoculture and in mixture increases as self-thinning goes on (Table 1, Fig. 4c, d).

The potential value of the self-thinning rule for mixtures of species was also pointed out by Binkley (1984), who studied the behaviour of populations of Douglas-fir trees in mixtures with alder. In this case the niche difference between both species is given by the nitrogen-fixing capability of the alder. Unfortunately, only mixtures of these two species, and not single-species stands, were studied. Despite the efforts made in selecting species with known morphological differences for self-thinning studies of mixtures (e.g. White et Harper 1970, Bazzaz et Harper 1976), in none of them has the ecological niche difference between the component species been considered.

4. Generalities of the self-thinning process and needs for further research

Despite the proven inconstancy of the self-thinning equation proposed by Yoda et al. (1963) for different plant populations, the range of values within which its slope varies is still remarkably limited considering the variability of plant morphologies, growing conditions, and measurement errors involved. Even populations of sessile sea animals appear to follow a pattern of growth and mortality similar to that predicted by the 3/2 power law (Hughes et Griffiths 1988, Ardisson et Bourget 1991). A number of models on competition have shown that the parameters of growth found in plants make it very likely that the value of the self-thinning slope be close to the theoretical -3/2 (Pickard 1983, Hara 1984a, b, Slatkin et Anderson 1984, Weller 1987b, Yamakura 1989, Prentice et Leemans 1990). The empirical evidence agrees with this: only a few studies have found slopes steeper than -3 and for most of them it is arguable whether the population under scrutiny had reached the linear phase of the size/density relationship (e.g. Jacobs 1979 Table A3.5, Ellison 1989).

The self-thinning slope can be interpreted as the ratio between the relative growth rate (RGR) of the average plant and the relative mortality rate (RMR) of the population (Zeide 1985). The constancy of the ratio RGR/RMR during self-thinning is indicating that the processes of growth and mortality within the population are closely compensating each other. The restricted variation of the slope of that line, on the other hand, evidences that, at some stage of growth, the way in which the surviving plants respond to competition and the mortality of their neighbour plants is similar for most plant populations. The fact that all plants are units of volume growing on a surface means that whichever plant population is considered, the mortality of some individuals will, in a sense, release an amount of resources proportional to an exponential function of the number of dead plants (Whittington 1984). In very dense populations that amount of resources newly available to the survivors will result in a proportional increase in the biomass of the survivors. The RGR of plants is the outcome of the interaction between physiological (photosynthetic rate) and morphological (allocation of resources to stem, leaves and root) growth parameters which would tend to compensate each other so that the oscillations of the RGR are minimized (Květ et al. 1971, Evans 1972). As a consequence, the response of plants to newly available resources can be precise and smooth in terms of dry weight increment. This view poses a question to be taken into account in future research: does the RGR of the survivors of a self-thinning population depend on the resources already captured by their suppressed (and eventually dead) neighbours?, or does it depend just on those resources available in the substrate? Radioactive labelling of resources in self-thinning populations could give us the answer.

The fact that most populations of plants with high density follow, at some stage a trajectory similar to that predicted by the 3/2 power law, indicates the relevance of the development of size hierarchies in such populations; in most cases, dominant individuals (which are only slightly affected by competition) could be identified from very early stages of growth. There are, however, deviations from this general pattern: some crowded plant populations have been found not to develop a size hierarchy. In these populations all individuals are equally affected by competition (there are no dominant or suppressed individuals). This can lead to the stagnation of the population (sensu Oliver et Larson 1990), a condition of no biomass increase or mortality but in which each individual keeps for some time its capacity to resume growth if an autogenic or allogenic factor determines that a size hierarchy be developed (e.g. Eversole 1955, Oliver 1967, Mitchell et Goudie 1980, Burshel et Huss 1987:220, McFadden et Oliver 1988). Stagnation seems to occur

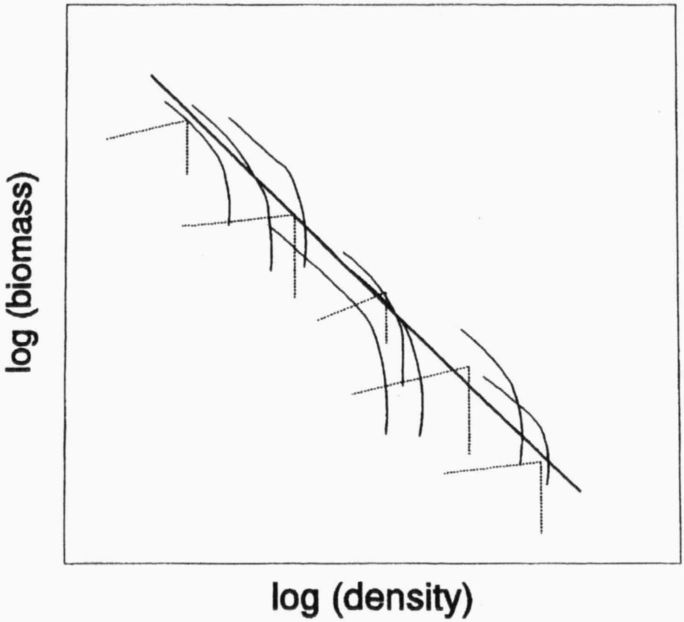

Fig. 6. - The biomass/density relationship of plant populations with (solid curves) and without (dashed curves) size hierarchy development.

more often in trees than in herb species, but a similar condition (then termed "inanition") was reported by Chippindale (1948) and Cooper (1948) for populations of grasses under low nutrient supply. Other grass seedlings are known to be able to virtually stop growing but remain alive under such conditions (Fenner 1978, Howe et Snaydon 1986, Aguilera et Lauenroth 1993). Similarly, crowded roadside populations of *Galium aparine* seedlings were found to reach a condition similar to that of stagnation (Puntieri 1991). In the case of herb species, stagnation may facilitate the action of pathogens which could cause irreversible damage to all or most individuals of the population in the mid- to long-term. Two distinctive patterns of response of plant populations to high density could then be identified (Fig. 6): (a) with early size hierarchy development in which the population approaches gradually a self-thinning line and (b) without size hierarchy development in which the population reaches the maximum biomass for that population density (tangential to the expected self- thinning line) and then, after a period of stagnation, suffers high mortality with decreasing (or constant) total biomass; the further development of the population in the second pattern would depend on the capacity of the survivors to resume growth after stagnation.

The occurrence of stagnation may have important evolutionary consequences for a population. Some studies have shown that the genotype of a plant can be related to its probability of surviving the self-thinning process (Bazzaz et al. 1982, Govindaraju 1989), so that this process can be one of the determinants of the genetic makeup of the population, and consequently be of great importance for the process of natural selection (Harper 1977, Antonovics et Levin 1980). In view of the evidence cited in the previous paragraph, it could then be suggested that ecologists looked more at the conditions and species more likely to affect the chances of a population to reach stagnation, which could radically change the trend that would be expected if competition drove natural selection. Unfortunately, the search for generalities about the self-thinning process has concentrated on a reduced number of species under a reduced number of conditions. Systematic studies on the development of size hierarchies and self-thinning following the fate of individual plants of a number of species are lacking.

In conclusion, self-thinning may take place following an approximately similar trajectory in very different but always overcrowded plant populations. Yet, it may not occur at all, both in clonal and unitary plant species. Further research needs to be concentrated upon the causes, either intrinsic or extrinsic, of such an important qualitative difference between species in the outcome of competition.

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Souhrn

Článek přináší přehled dosud publikované literatury o samozřeďování v rostlinných populacích; zvláštní pozornost je věnována 3/2 zákonu, navrženému Yodou a jeho spolupracovníky v roce 1963. V práci jsou diskutovány metodologické aspekty prokládání samozřeďovací přímky, dosud zjištěné odchylky od původní formulace zákona a samozřeďovací procesy ve směsích dvou druhů. Je zdůrazněn význam vývoje velikostní hierarchie populace pro uskutečnění dvou souběžně probíhajících procesů - nárůstu biomasy a mortality. Samozřeďování - přidržíme-li se jeho obvykle používané definice - může probíhat podle obdobné trajektorie ve velmi odlišných, vždy však přehuštěných populacích. Nemusí však k němu docházet vždy, což platí jak pro unitární, tak i pro klonální rostliny.

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