

Growth and mortality of individual plants as a function of „available area“

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Summary. We looked at the relationship between “available area”, as defined by Thiessen polygons around individual plants, and plant size and mortality in even-aged greenhouse populations of *Lapsana communis* L. Polygon area was a good predictor of plant weight in these populations. After nine weeks growth, just prior to the onset of self-thinning, the dry weight of plants was directly proportional to the square root of polygon area. After the onset of self-thinning, plant weight appeared to be directly related to polygon area to the 3/2 power. Plants in small polygons were much more likely to die than those in larger areas. Thinning changed the frequency distribution of polygon sizes from highly skewed and unequal to normal and more equal, while inequality in surviving plant sizes did not appear to be affected by thinning.

Introduction

Most studies on plant interference or competition have looked at total population yield and mean yield per individual as a function of plant density or other independent variables (Harper 1961). Mean values obscure plant to plant variation which may be very great (Obeid et al. 1967) and this variation is probably a reflection of differences in individual fitness (Solbrig 1981; Sohn and Policansky 1977). Density is an abstraction which is necessary when individual organisms are motile and keep changing their relationship with neighbours. With higher plants and other fixed organisms, it becomes possible to relate some part of the performance of individual plants to the position and nature of their neighbours (Mack and Harper 1977; Hickman 1979, Weiner 1982).

One way to look at the proximity of a plant to its neighbours is through the use of Thiessen or Voronoi polygons (Mead 1966; Rhynsburger 1973; Liddle et al. 1982). To construct Thiessen polygons from a map of plant locations represented by points, lines are drawn between a point and all nearby points. Polygons are formed by the perpendicular bisectors of these lines (Fig. 1). The polygon around a plant includes all points in the plane which are closer to that plant than to any other. The polygon also defines the immediate neighbours of an individual. Overall density is the reciprocal of mean polygon area per plant. The local area of an individual can be thought of as the inverse of the local density of its neighbours.

Thiessen polygons have proven to be poor predictors of plant size in some experimental studies (Mead 1966; Liddle et al. 1982), in part because neighbour proximity and number may be less important than differences in time of germination (Ross and Harper 1972, Watkinson et al. 1983), spatial heterogeneity or genetic variation. The reductionist programme entails studying these factors individually and in combination. Thiessen polygons are a reasonable measure of two-dimensional area available to comparable individuals and may provide useful independent variables for predicting plant weight in even-aged monospecific populations.

Methods

A flat 116 cm × 116 cm and 15 cm deep was constructed in a heated glasshouse at Pen-y-Ffridd Field station, Bangor. The flat was filled with 10 cm of John Innes compost No. 1 followed by 4 cm of the same compost passed through a 3 mm sieve. The soil was levelled, soaked with de-ionized water and re-levelled. Seeds were sprinkled onto the surface at a density of 2×10^4 seeds m^{-2} . The seeds were covered with 0.5 cm of sifted compost and watered with de-ionized water. Watering was only done when necessary, using a fine spray.

Three days after the emergence of the first seedling the positions of the seedlings within a 96 × 52 cm area were mapped on a sheet of glass suspended just above the seedlings. The map was then traced onto graph paper and Thiessen polygons drawn around each. Any seedlings emerging after the first three days were removed. Polygons were constructed manually and areas were measured either directly using graph paper, or by cutting out the polygons, weighing them and calculating the area from the weight of a known area of paper.

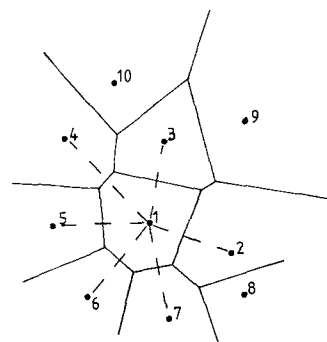


Fig. 1. The construction of Thiessen polygons. The perpendicular bisectors of the lines joining adjacent seedlings (dashed) form the polygon and define which plants are neighbours. Thus, plants 8–10 are not neighbours

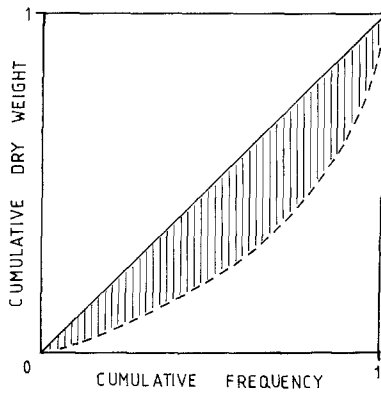


Fig. 2. A measure of the degree of inequality within a population. The y axis is the variable whose concentration or inequality is to be measured, which is plant dry weight in this case (see text). The ratio of the area between the Lorenz curve and the diagonal to the area under the diagonal is a measure of inequality (Weiner and Solbrig 1984).

After nine weeks growth, just prior to the onset of self thinning, plants from part of the mapped area (plot 1) were harvested (harvest 1). Plants were cut at soil level, put into individual paper bags, dried in an oven at 50 degrees C for 48 h and then weighed. Great care was taken throughout harvesting to record the precise position of each plant so that the polygon area that it had occupied was known. After fifteen weeks, plants in a second plot (41 × 26 cm) of the mapped area were harvested and dried (harvest 2). Their positions were also accurately recorded.

The degree of hierarchy or inequality in the polygon areas and the dry weights was measured using methods from economic income distribution theory (Lorenz 1905; Gini 1912; Sen 1973) which have been applied to plant population hierarchies by Weiner and Solbrig (1984). Individuals are ranked by size and the cumulative frequency is plotted against the cumulative fraction of the total dry weight (for example) on a scale of 0–1 (Fig. 2). For a population of perfectly equal individuals the resulting line would be the diagonal from the origin to the top right corner. If there is any inequality within the population, the result will be a curve beneath the diagonal. The ratio of area between the curve and the diagonal to the area under the diagonal is called the Gini Coefficient (G) and is a measure of the degree of concentration or inequality. It varies between 0 – complete equality and a theoretical maximum of 1.0 – “perfect” inequality.

Results

The frequency distribution of the areas of polygons in plot 1 is shown in Fig. 3. It is very skewed and unequal with many small polygons. The frequency distribution of the dry weights of the plants occupying complete polygons is shown in Fig. 4: this distribution shows less inequality than that of the polygon areas.

Fig. 5 shows the relationship between log polygon area and log plant dry weight at harvest 1: the regression accounts for 60% of the variation. The distribution of residuals is in accord with the assumptions of regression analysis.

At the time of harvest, the plants with the largest polygons (> 10,000 mm²) still had green cotyledons, indicating that no leaves had died. Plants with smaller polygons had only a few live leaves and had shed many dead ones.

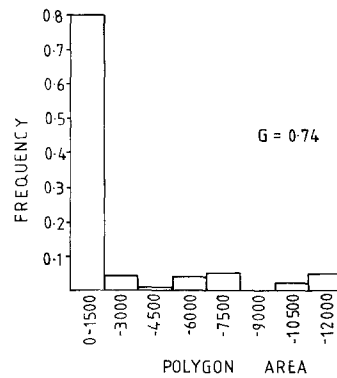


Fig. 3. The frequency distribution of the polygon areas occupied by plants harvested after nine weeks (harvest 1)

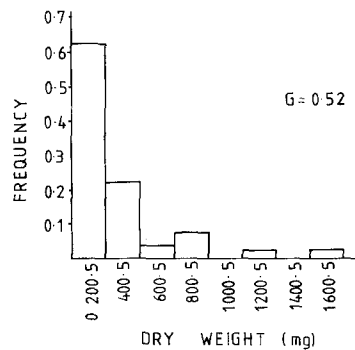


Fig. 4. Frequency distribution of the dry weights of the plants harvested after nine weeks (harvest 1)

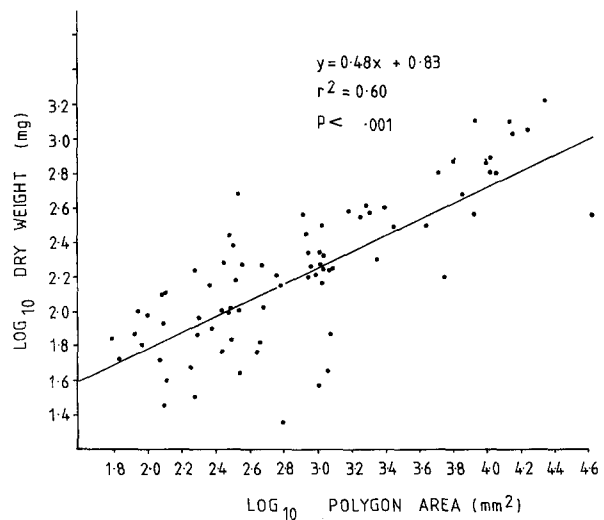
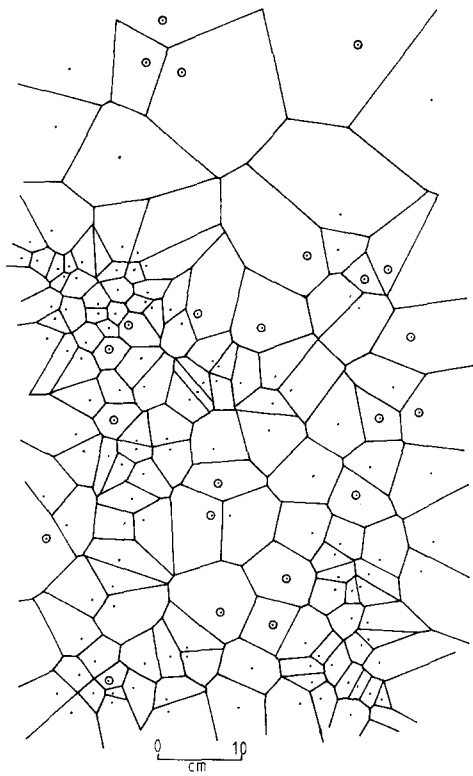
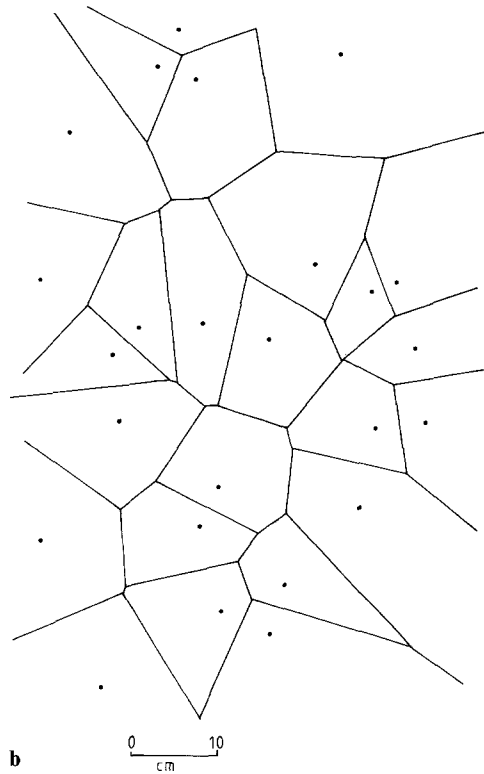


Fig. 5. Relationship between the dry weight of individual plants of *Lapsana cummunis* and the polygon area the plants occupied (harvest 1)

The polygon map of the seedlings in plot 2 is shown in Fig. 6a. Edge plants (not occupying complete polygons) are omitted. The ringed points indicate plants which survived for 15 weeks. The surviving plants are drawn on Fig. 6b with their new polygons (constructed from the neighbours that survived until the time of harvest). The frequency distributions of the polygons areas at the seedling stage and at harvest are shown in Fig. 7. Before self thinning the distribution of polygon areas was very skewed and unequal as in the earlier harvest (Fig. 3). After thinning the distribution appeared normal with much less inequality.



a ○ PLANTS PRESENT AT HARVEST



b

Fig. 6. a Map of the seedlings within the area harvested after fifteen weeks. The points which are ringed represent plants which were alive at harvest (harvest 2). b Map of the plants which were alive after 15 weeks. Polygons are based upon survivors only

Only 21% of the seedlings were still present at harvest. Table 1 shows the fraction of seedlings which survived for 15 weeks in relation to the area the seedlings occupied.

The frequency distribution of the dry weights of the

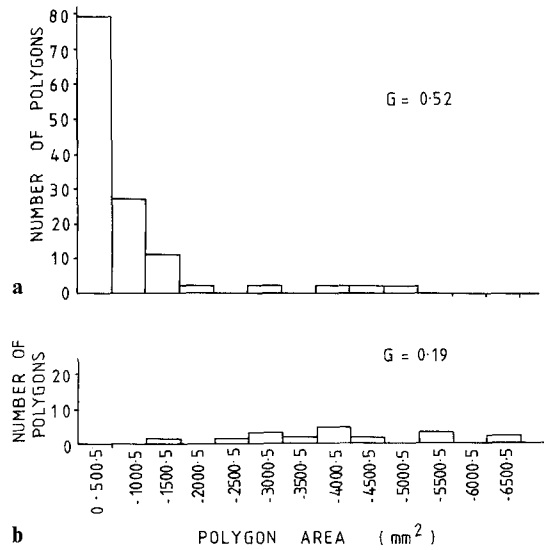


Fig. 7. Frequency distributions and inequality measurements of polygon areas occupied by plants in the second area harvested a) when seedling (Fig. 6a) and b) at harvest (Fig. 6b)

Table 1. Fraction of individuals of *Lapsana communis* surviving for 15 weeks in relation to the polygon area the plants occupied when seedlings

Area occupied when a seedling (mm ²)	n	Fraction surviving until week 15
< 500.5	79	0.065
500.5–1,000.5	26	0.12
1,000.5–1,500.5	14	0.36
1,500.5–2,000.5	2	1.0
2,000.5–3,000.5	2	0.5
> 3,000.5	6	1.0

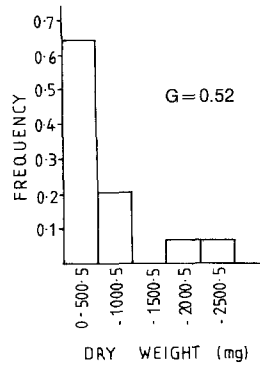


Fig. 8. Frequency distribution of dry weights of surviving plants harvested at 15 weeks

plants at harvest 2 is shown in Fig. 8. This distribution is heavily skewed with a strongly developed hierarchy similar to that found in the plants in the other area before thinning (Fig. 4).

The relationship between log dry weight at harvest 2 and log polygon area occupied when a seedling is shown in Fig. 9a. The relationship between log dry weight at harvest 2 and log polygon area occupied at harvest 2 is shown in Fig. 9b. The polygon area of a plant at the seedling stage gives a better fit in a regression with dry weight at harvest than does its polygon area at the time of harvest. Although the sample size is small, the slope of the log harvest polygon area vs. log plant weight is 3/2, which is what

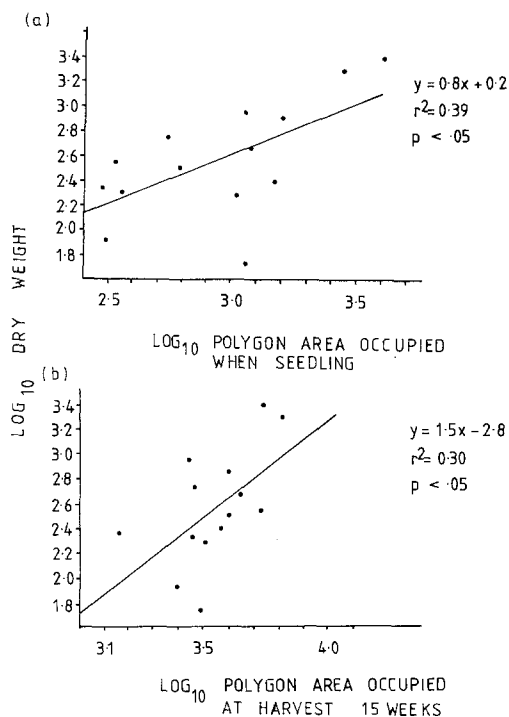


Fig. 9a, b. Relationship between dry weight of individual plants of *L. communis* and polygon areas occupied a when seedlings and b at harvest

would be expected from the application of the 3/2 thinning law (Yoda et al. 1963; White and Harper 1970) at the individual plant level.

Discussion

The relationship between available area and plant weight (Figs. 5, 9) cannot be linear over the entire range of possible polygon areas since plant weight cannot continue to increase in polygon areas above which interference does not occur. Thus, the curve must level off above a certain polygon area. But the relationship between log polygon area and log plant weight may be linear within the range of polygon areas in which interference is important, just as the relationship between log mean plant weight and log density is linear after plant size and density reach the limits imposed by the $-3/2$ law.

From these data we begin to see a coherent picture of the development of an even-aged stand as a predictable process of growth and death of individuals in space and time. As plants grow, a size hierarchy develops within the population. One of the factors determining an individual's size and position in the hierarchy is the proximity of its neighbours. Thiessen polygon areas appear to be a useful way of describing neighbourhoods in these monospecific stands of upright plants with simultaneous germination.

As mean plant size approaches the limits described by the 3/2 thinning law, mortality starts to occur. Plants with close neighbours (occupying smaller polygons) are more likely to die and their areas become available to the survivors (or they die because their areas are taken over by larger individuals). Before self-thinning begins, a plant's weight is proportional to its polygon area to a power less than one (approximately one half in this case): at this stage

the size hierarchy of polygon areas is greater than the hierarchy of plant weights. After thinning the weight of survivors is proportional to polygon size to the 3/2 power and the hierarchy of polygon area is less than the hierarchy of plant weights. Polygon size at the seedling stage is a better predictor of plant performance than polygon size after self-thinning. This implies that some of the reduction in growth of survivors due to interference at an earlier stage has an effect which persists after those neighbours have died. Although the post-thinning polygons appear to be normally distributed and the degree of inequality in polygon sizes is reduced, the degree of inequality of weights of surviving plants is similar to that before mortality began. Thus, a hierarchy develops before self-thinning begins and is maintained as thinning occurs. As the smallest individuals die, differences in growth rates due, in part, to interference exaggerate differences in size between the largest and smallest survivors. The hierarchy is continually being generated by growth and interference and reduced by mortality of the smallest individuals.

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