

OLM 9.4 Regulation of plant populations by self-thinning

The size of plant individuals – unlike those of most animals – are very much dependent on their actual environment, therefore it is strongly influenced by the densities of their populations as well.

The relation between population density and the average size of plant individuals can be studied in two different ways. One is the comparison of populations sown at different densities at the same stage of population growth (constant final yield), the other is following the size of individuals and number of survivors during the growth (self-thinning). Both types of study result in a plot of average individual sizes or total biomass as functions of population density, but they lead to different conclusions.

By comparing stands of different densities of the same plant species we find that increasing density does not yield a proportional increase in biomass per unit area – the plot saturates at high densities (Figure 9.4.1). This relation is called the „constant final yield” pattern (Weiner and Freckleton 2010). „Final” means the far end of the density scale, not that of the vegetation period; „yield” is the total biomass above ground. The reason for saturating dynamics is at high densities total biomass production per unit area is constrained by the concentration of available nutrients and light, not by the number of individuals. The average size of competing individuals is the ratio of biomass per unit area and population density, so that plotting the logarithm of average individual size against the logarithm of density results in a line of slope -1.0 in the saturation segment of the diagram (Figure 9.4.1).

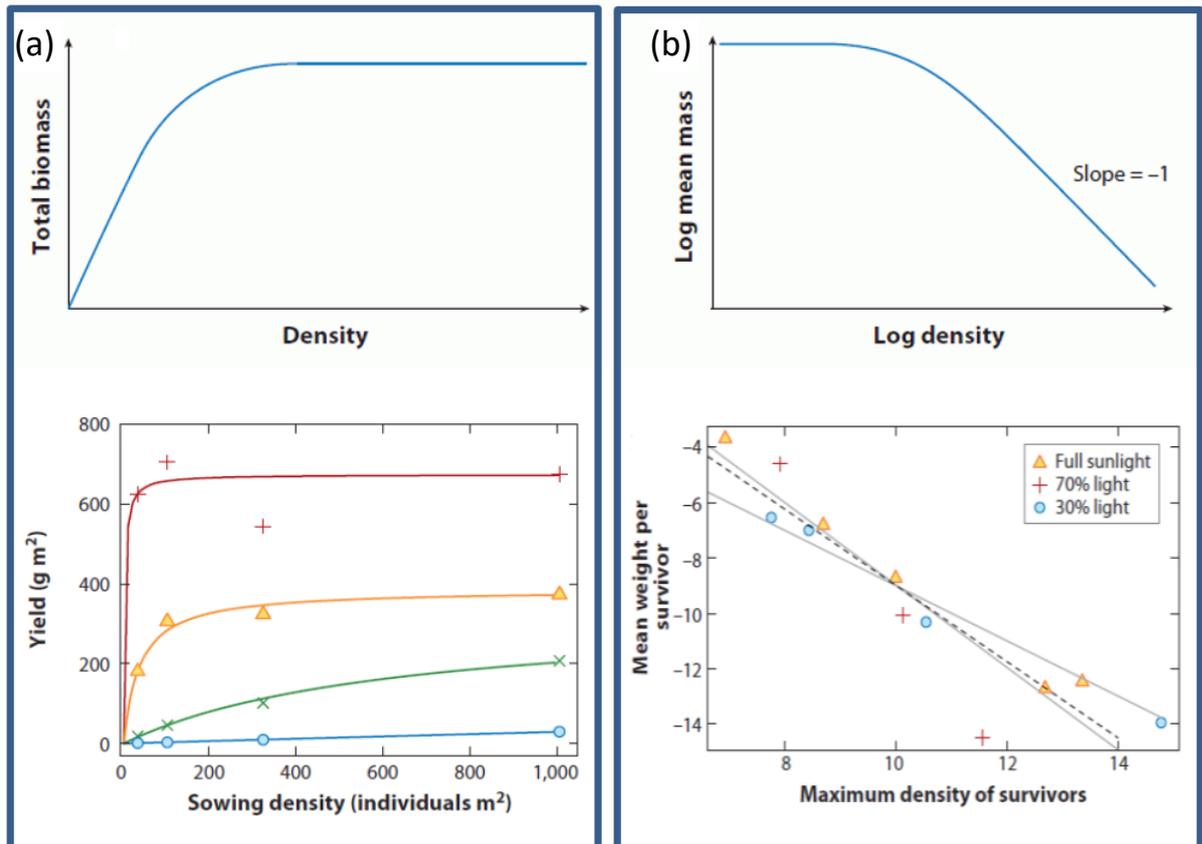


Figure 9.4.1: Comparison of stands of different plant densities at the same stage of development.

panel b): If the amount of resources available to an individual does not depend on population density (i.e., in sparse populations), panel b): the size of individuals is also independent of density and panel a): the biomass per unit area increases with density in a linear fashion. At high densities the biomass per unit area is limited by available resource, and a) it saturates as a function of actual density in consequence and b) decrease in the average biomass of individuals compensates for higher density leading to a -1 slope of $\log \text{density} - \log \text{size (mass)}$ of individual relationship (after Weiner and Freckleton 2010). The same relations are revealed in the experiments with *Lolium perenne* by Kays & Harper (1974) shown in the lower parts of the two panels. The different symbols on the left panel belong to ever later harvesting times after sowing: seed was sown on 12 February 1972 and harvests made on 3 and 24 March, 14 April, 2 June and 21 July. The dashed line in the right panel is the line fitted to the data, the grey line represents the theoretical line of slope -1.

When the size of individuals in populations sown at different densities is followed it can be seen that a fraction of the individuals die during the growth phase at high sowing densities. This process happening on the time-scale of individual life is called *self-thinning*. Due to the asymmetric nature of competition for light it is mainly the shorter individuals which die (Figure 9.4.2).

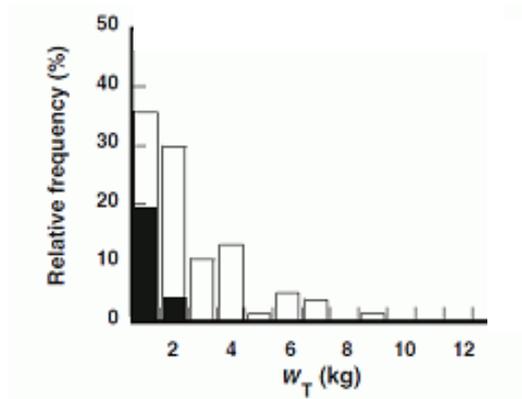


Figure 9.4.2: Example for the temporal change in the phytomass frequency distribution of the mangrove species *Kandelia obovata* on Okinawa island (Japan).

White bars are survivors, black bars represent individuals which died next year. Average phytomass $\bar{w}_T = 1.98 \text{ kg}$, density = $84/25 \text{ m}^2$ (Analuddin, Suwa and Hagihara 2009).

Following the growth of individuals in very densely sown populations (along trajectories of Figure 9.4.3) we find that at first the size of the individuals increases without density change; then self-thinning sets in and density starts to decrease while the size of survivors further increases. Plotting average individual mass against density on logarithmic scales in this growth phase we find that the trajectories started at different sowing densities converge to the same straight line, the self-thinning line (

Figure 9.4.3). Yoda et al (1963) assumed proportional growth of individuals in all three dimensions during the growth phase and they predicted that, upon this assumption, the slope of the self-thinning line should be $-3/2$. Their argument was based on the fact that the area occupied by an individual increases with the square of its linear size, whereas its mass increases in a cubic fashion with linear size. The average area occupied by an individual is the reciprocal of the actual population density (i.e., the size of survivors increases with the death of individuals thinned out during this phase, due to the increased area that the survivors can occupy). These geometric relations are sufficient for the prediction of the $-3/2$ slope. However, the assumption of a constant allometry might well be false in many cases, since both the size and the shape of plant individuals may be very plastic due to their modular construction, and the space capture of an individual might be different during its growth, depending on sowing density and external factors. More densely sown individuals might be very thin compared to their height, for example. It is not only the size distribution but also the spatial structure of the population that is affected by self-thinning. In nature monospecific, even-aged stands develop by renewal of forests after catastrophes (e.g. development of pioneer pine forests after fire). In such stands the spatial pattern of seedlings is usually close to random, which is an irregular mosaic of more and less dense patches. The survival of the individuals depends on the local density therefore self-thinning sets in mostly at the dense patches, which shifts the pattern towards regular (Kenkel 1988).

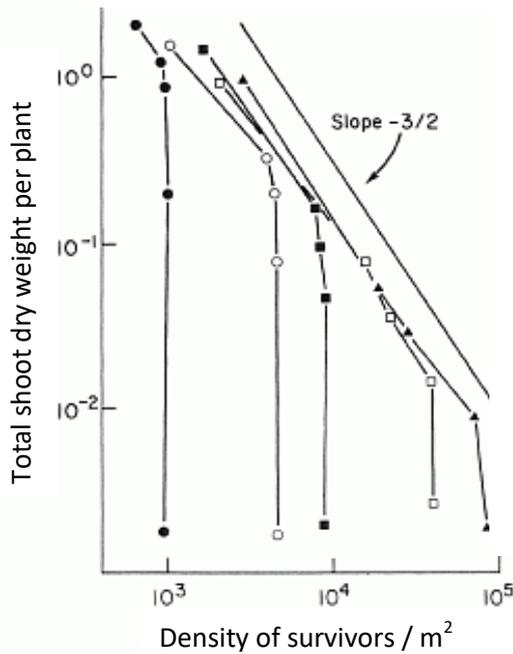


Figure 9.4.3: Self-thinning processes in *Lolium perenne* stands

The five different sowing densities: 1000 (●), 5000 (○), 10000 (■), 50000 (□) and 100000 (▲) seeds/m². Lines connect the states of the same stand at five different time points so that they represent the temporal trajectories of the stands, spanning from the lower right (earliest) to the upper left (latest) region of the plot (Lonsdale and Watkinson 1982).

Both the „constant final yield” pattern and self-thinning are the results of population regulation due to the same principles as in unitary organisms, the only difference being that the size plasticity of plants necessitates the choice of a population abundance variable different from individual density applicable to unitary organisms. Proper measures of plant abundance include biomass density or „cover”, which can be adequately related to regulating variables like nutrient concentration in the soil, or light availability.

The -3/2 power law

Let us approximate plant individuals with a cuboid on a square base of side length d and height h (Figure 9.4.4.).

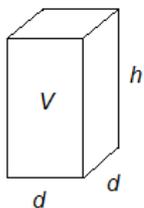


Figure 9.4.4: A schematic representation of a plant individual.

The density (N) of individuals is the reciprocal of the area ($A=d^2$) captured by an individual:

$$N = \frac{1}{d^2} \tag{9.4.1}$$

The mass (M) of an individual is the product of its volume ($V=d^2h$) and its density (ρ):

$$M = V\rho = d^2h\rho \tag{9.4.2}$$

The relations of different linear extensions of plant individuals are usually characterised by (so-called „allometric”) power functions:

$$h = ad^b \quad (9.4.3)$$

in which a and b are constants. We may assume that the density of plant individuals does not change with their size. Substituting h from Eq. (5.17) into Eq. (5.16) we get

$$M = ad^{2+b} \rho \quad (9.4.4)$$

for the relation of the horizontal size d and the mass M of the individuals. Substituting d^2 from Eq. (5.15) we find that the mass of an individual is proportional to a power function of population density N :

$$M \propto N^{-\frac{2+b}{2}} \rho \quad (9.4.5)$$

where the exponent depends on the allometric parameter b . If ρ is constant, and the height of a plant is a linear function of its horizontal extension d (i.e., $b = 1.0$), then the exponent of N turns out to be $-3/2$.

References

- Analuddin, K., R. Suwa, et al. (2009). The self-thinning process in mangrove *Kandelia obovata* stands. *Journal of Plant Research* 122(1): 53-59.
- Kays S, Harper JL. 1974. The regulation of plant and tiller density in a grass sward. *Journal of Ecology* 62:97–105.
- Kenkel, N. C. (1988). Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology* 69(4): 1017-1024.
- Lonsdale, W. M. and A. R. Watkinson (1982). Light and self-thinning. *New Phytologist* 90(3): 431-445.
- Weiner, J. and R. P. Freckleton (2010). Constant Final Yield. *Annual Review of Ecology, Evolution, and Systematics* 41(1): 173-192.
- Yoda, K., T. Kira, et al. (1963). Self thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University* 14: 106-129.