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A POPULATION DYNAMICAL DESCRIPTION OF THE SELF-THINNING LAW

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Abstract. There is a simple allometric relation between average plant mass and the maximum number of plants in a given area as plants become older and bigger. This relaton, named self-thinning law, is valid when the canopy is totally closed. I neglect this very strict assumption, and regard canopy closure as a dynamically variable quantity. Assuming that intra- and interpopulation competition is determined by canopy closure, I studied a population dynamical model to describe self-thinning of even-aged plants. The parameters of the equations are measurable in the field. I extend the model to multi-species assemblages. Emergence of interpopulation interaction could modify the outcome of the self-thinning relation depending on the result of competition.

Introduction

Although there are many laws in plant ecology, relatively few have been precisely described. A law or relation is well-defined if we are able to give the range of its validity. The best known such law is perhaps the self-thinning law, if there is any regularity at all (see *e.g.* Lonsdale 1990). The mathematical form of the relation is: $W=kN^{-3/2}$, where W is the plant's mean biomass, N is the number of plants in a given area, and k is a constant. The power -3/2 is an universal constant independent of the species, habitat and the age of the stage. One can obtain this equation easily from two basic assumptions (Yoda et al. 1963):

1. Growth and self-thinning maintain the total canopy closure.

2. Plants which belong to the same species are geometrically similar independently of growth stage and habitat conditions.

From the first assumption we can write

$$R^2 N^{-1} = \text{constant}, \qquad (1)$$

where R is the mean radius of a plant. Using the second assumption we have

$$h/R = \text{constant}, \qquad (2)$$

where h is the mean height of a plant. From (1) and (2) we get

$$W \propto R^3 = kN^{-3/2}. \ (3)$$

After Reineke's (1933) classical paper, the existence of this robust law has been confirmed by many authors. Many of them, e.g., Gorham (1979) and White (1981) consider it as a particularly well-fitted relation. Others (Binkley 1984, Westoby 1984) emphasize that the law works well when the community stand contains many species. There is, however, no agreement as to the universality of the -3/2 power constant (Zeide 1987, Weller 1987, 1989, Norberg 1988).

Canopy closure as a dynamical process

Three different states can be distinguished in a self-thinning process (Fig. 1). When there are many small plants in an area, competition is weak, and so the curve is very steep. The next state is the well-known self-thinning state, when competition maintains a dynamical equlibrium. The third different state is distinguished when plants become so old and big that the physiological constraints act meaningfully. The first phenomenon which was mentioned above emerges before the canopy closure is complete, the last one when the canopy closure starts decreasing because of gaining the physiological effects, *e.g.*, plants almost attain their maximum heights.

Thus, Yoda's first assumption is true in a limited range of the self-thinning. Generally, canopy closure varies with time! It first increases, then maintains a constant value for a long time, and finally it slowly starts to decrease. In my population dynamical model canopy closure is a variable quantity, as in reality.

The population dynamical description

In the frame of my model the self-thinning law emerges as an asymptotic state of a dynamical process. The model describes the complete curve (see Fig. 1), not only the "self-thinning" range of it. We could measure the parameters which will be introduced into the model with two independent measurements (one of them is the self-thinning measurement). In the light

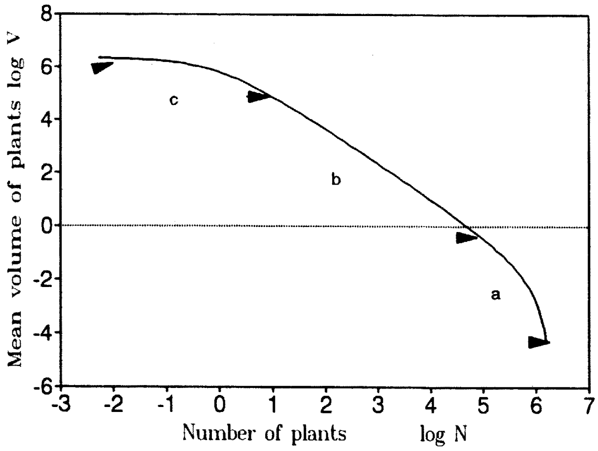

Figure 1. A typical self-thinning curve with three distinct states. Many seedlings, weak competition (a). Straight line - the self-thinning range (b). Superannuated stand (c).

of experimental data we could verify or reject the assumptions. The model is extended when there are many even-aged species in the field. In particular, the case of two species is studied. It is shown how competition modifies the self thinning curves.

There are earlier dynamical models approaching this problem. In Aikman and Watkinson's (1980) computer simulation model the growth rate is modified by the density, and when growth rate becomes negative the plant dies immediately. This model studies the transformation of the inner variability of the stage under the influence of self-thinning. The strength of competition is defined by the nearest neighbour interaction in Slatkin and Anderson's model (Slatkin & Anderson 1984). They simulated even-aged plants belonging to the same species.

The growth of an individual plant is related to the rates of photosynthesis and respiration. Starting from these facts, Perry (1984) used a generalized von Bertalanffy equation to describe biomass growth of an individual plant. He assumed an independent simple relation between density and mortality, and used a well-known function which connects the efficiency of photosynthesis with density. The model works with many parameters, and the steepness of the self-thinning curve depends strongly on them. Burrows (1991) studied the dynamics and structural deformation of monocultures. He distinguished growth phases, and treated plants with different canopy shapes and two kinds of uniform packing arrangement. He also used the generalized von Bertalanffy equation and converted the original equations into a dimensionless form.

The model

Equation (1), which is the mathematical form of Yoda's first assumption, means that the average two-dimensional characteristic lengths of plants multiplied by the number of plants is a constant. This quantity may be named as the two dimensional density.

My assumption is as follows: the growth of plants is modified by intra- and interpopulation competition, and this competition depends on the two-dimensional densities.

We are interested in average behaviour, so we neglect the within-population variance, and count only with the average quantities. Let $V(t)$ be the average volume of the plants at time t, and $N(t)$ the number of plants at the same time. Let $p(t)$ indicate the two dimensional density. If we accept Yoda's assumptions, then $p(t)=V(t)^{2/3}N(t)$. Many authors (*e.g.* McMachon & Kronauer 1976, Nornberg 1988) state that the elastic similarity assumption is more precise for tree-like structures. In this case $p(t)=V(t)^{3/4}N(t)$. Mohler et al. (1978) have shown that $N \propto R^{-a}$, where a takes real values between 1.24 and 1.42, significantly less than 2 as in Yoda's first assumption. We assume only that $p(t)=V(t)^{l} N(t)$, where $l > 0$ depends on the geometric relations.

Assume further, as the simplest case, that there is only one even-aged species. The self-thinning process is described by a difference or by a differential-equation system:

$$dV(t)/dt = A(p(t),V(t))\,V(t) \qquad (4)$$

$$dN(t)/dt = -F(p(t))\,N(t), \qquad (5)$$

where $A(p(t),V(t))$ is the growth function which depends on $p(t)$, because of competition, and $V(t)$ because of physiological constraints. $F(p(t))$ is the mortality rate. If we use difference equations, which are very natural in even-aged systems, then we change $dV(t)/dt$, $dN(t)/dt$ to $V(t+1)-V(t)$ and $N(t+1)- N(t)$, respectively. This description is more convenient in computer simulations, but analytical methods are more suited to differential equation systems.

First, we prove that the self-thinning law is asymptotically true in this system, if some further and obvious assumptions are introduced. We study the range where physiological effects can be neglected, e.g. we regard a not too old stage. Then $A(p(t),V(t)) = A(p(t))$. It is clear that $A(0) > 0$; $F(0) \geq 0$ ($F(0) > 0$ means that there is spontaneous extinction), and $A(p)$ decreases; $F(p)$ increases if $p(t)$ increases. Assume further, that there is a p^* where $A(p^*)=0$. Then we are able to prove that the system has a positive stable fixed point, $p^{\sim}$. There is a similar assertion in the case of difference equation system. The precise statements and the proofs are in the Appendix. This result means that $p(t)=p^{\sim}$ =*constant* is true asymptotically, or in other form: $V(t)^{l}\,N(t) = p^{\sim}$, which is equivalent to the self-thinning law;

$$V(t)=p^{\sim\,1/l}\,N(t)^{-1/l}. \qquad (6)$$

The introduced two functions $A(p(t))$ and $F(p(t))$ are very general differentiable monotone functions. A method widely used in population biology is to take the Taylor series of the growth function (Hallam & Levin 1986 p. 247), neglecting the second and every higher order parts in the expansion. A typical example is the Lotka-Volterra system. So we approximate our functions with their Taylor series around $p^{\sim}$, and we take into consideration only the zero and first order parts, as it is done in the Lotka-Volterra situation. Then:

$$A(p(t)) = A_0 - p(t), \tag{7a}$$

where

$$A_0 = A(p^{\sim}) - p^{\sim} dA(p^{\sim})/dp > 0, \quad \alpha = -dA(p^{\sim})/dp.$$

$$F(p(t)) = -\mu\, p(t), \tag{7b}$$

where we assume that $F(p^{\sim}) - p^{\sim} dF(p^{\sim})/dp = 0$, because in a crowded stage mortality comes from the density dependent part (Lonsdale 1990), $\mu = dF(p^{\sim})/dp$. This approach is good when p is near enough to $p^{\sim}$. Then we get the following equations from (4) and (5):

$$dV/dt = (A_0 - \alpha V^l N)\, V \tag{8}$$

$$dN/dt = -\mu V^l N^2 \tag{9}$$

Dividing (8) by (9) and converting the right hand side we obtain an ordinary differential equation, which connects V with N directly:

$$dV/dN = -A_0/\mu\, V^{-l+1} N^{-2} + \alpha/\mu\, V N^{-1}. \tag{10}$$

This is a so called Bernoulli-type equation, which can be transformed into an exactly solvable linear differential equation. After integrations one obtains

$$V^l = 1/N_0 \,[p^{\sim} (N/N_0)^{-1} - (p^{\sim} - p_0)(N/N_0)^{\alpha l/\mu}], \tag{11}$$

where $p^{\sim} = A_0 l/(\alpha l + \mu)$, N_0, p_0 mark the initial values. Multiplying (11) by N, it will be transformed into the following equation

$$p = p^{\sim} - (p^{\sim} - p_0)(N/N_0)^{\alpha l/\mu + 1}. \tag{12}$$

We can see not only the asymptotic behaviour of the model (e.g. $p \rightarrow p^{\sim}$ if $N \text{-->} 0$), but also the complete process of canopy closure as N decreases.

Estimating parameters incorprorated into the model

There are two constants in (3), one of them is the exponent, here -3/2, and the other is k, another measurable parameter in field studies. Comparing (6) or (12) with (3) we can see that in our model $k = p^{\sim 1/l}$ (13) and the exponent is equal to -1/l. So if we have a correct self- thinning measure we could estimate l and $p^{\sim}$ from it. The correct self-thinning measure means that the process is measured before the canopy closure. Then, using (12), the exponent $1 + \alpha l/\mu$ may be estimated. (Transform (12) into $\log(p^{\sim} - p) = (p^{\sim} - p_0) + (1 + \alpha l/\mu)\log(N/N_0)$, then the slope of the line is equal $1 + \alpha l/\mu$). To estimate the parameter A_0, we have to measure the plants's average biomass production in a crowded stage (p is very close to the maximal density, $p^{\sim}$), and its first derivative times with this two-dimensional density (see 7a). It is clear whether A_0 varies with time. Not knowing its exact form, we use merely its average quanity. So every introduced constant is measurable, because we have four variables A_0, l, α, μ and four independent equations.

Computer solutions

Consider again the difference equation form of our model, as an easily computable version of the self-thinning process. We are interested in the full process, including the effects of physiological constraints. Thus (7a) is extended by a new part, and (7b) is modified in accordance with the property of this description:

$$V(t+1) = [A_0 - V^l(t)N(t) - \beta V(t)]\, V(t)$$

$$N(t+1) = [1 - \mu V^l(t) N(t)]\, N(t),$$

where $A_0 > 1$, α, β, $\mu > 0$.

As it is expected, on the log-log plot we do not get a straight line, but a curve (Fig. 2a). Representing the two dimensional density, it becomes clear that density is nearly constant only in a limited range (Fig. 2b).

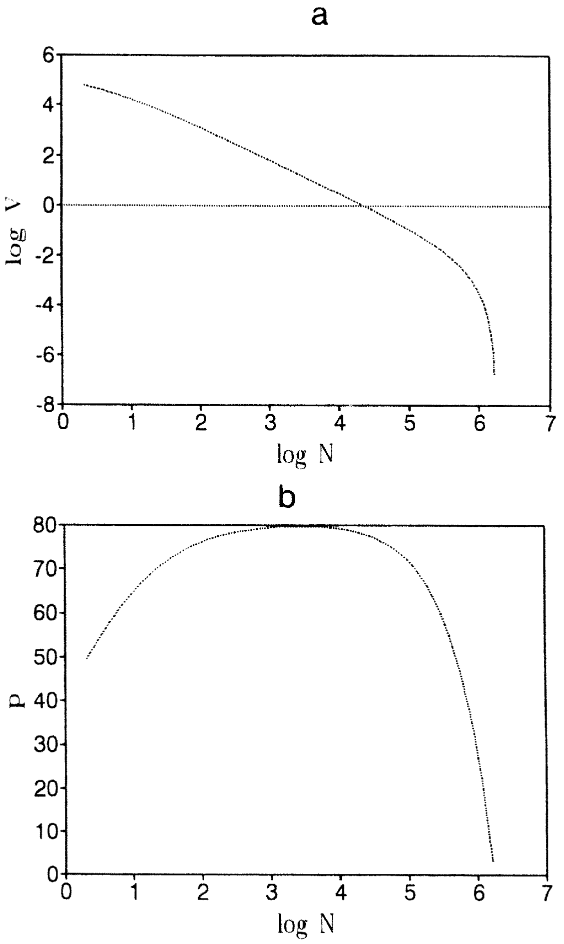

Figure 2. Complete self-thinning process simulated by the model. a, Slope increases from -1.48 to -1.03 as number of individuals decreases ($r^2 > 0.99$ everywhere). b, Physiological constraints cause that two dimensional density starts to decrease if plants attain a critical size. $A_0 = 1.2$, $\alpha = 0.001$, $\beta = 0.001$, $\mu = 0.001$, l = 3/4 (elastic similarity), $V_0 = 0.001$, $N_0 = 500$.

Where p varies only a little bit, there the slope is defined merely by the parameter l. If p is out of this part of the curve we could compute very different slopes.

These facts lead us to the conclusion: an authentic self-thinning estimation demands the measurement of canopy closure at the same time, and this auxiliary estimation shows the range where the classical self-thinning law is valid.

"Syn-thinning"

Monocultures are very rare in nature (apart from the man-made agricultural and forestry systems). In a forest, for example, thinnings are the results of intra- and interpopulation competition. This process will be termed here the 'syn-thinning', following Juhász-Nagy (1986)

The model is extendable to study syn-thinning of many even-aged stages. It is assumed, like in the case of the one species model, that the interpopulation competition is connected with the two-dimensional density. Generally we could say that:

$dV^{(i)}/dt = A^{(i)}(p^{(1)}, p^{(2)}, .. p^{(n)}, V^{(i)})\, V^{(i)}$

$dN^{(i)}/dt = F^{(i)}(p^{(1)}, p^{(2)}, .. p^{(n)})\, N^{(i)}$,

where these equations describe the i-th species, and i goes from 1 to n. Following the procedure described earlier, we consider the first term assumption of this equation system:

$$dV^{(i)}/dt = (A_0^{(i)} - \sum_{j=1}^{n} \alpha_{ij}\, p^{(j)})V^{(i)} \tag{14}$$

$$dN^{(i)}/dt = - \sum_{j=1}^{n} \alpha_{ij}\, p^{(j)}\, N^{(i)}. \tag{15}$$

Multiplying (14) with $l^{(i)} V^{l^{(i)}-1} N$ and (15) with $V^{l^{(i)}}$, and summing these equations we get:

$$dp^{(i)}/dt = (a_0^{(i)} - \sum_{j=1}^{n} b_{ij}\, p^{(j)})p^{(i)}, \tag{16}$$

where $a_0^{(i)} = l^{(i)} A_0^{(i)} > 0$, $b_{ij} = l^{(i)} \alpha_{ij} + \mu_{ij} > 0$. This equation is identical to an n dimensional competitive Lotka-Volterra equation. It is very convenient because the properties of these systems are well-known.

Consider the particular case when $n=2$. $P^{(1)}$ and $p^{(2)}$ are greater than zero (coexistence) if $b_{11}\, b_{22} > b_{12}\, b_{21}$ (see *e.g.* Roughgarden 1979). Thus, there are positive stable fixed points $p^{\sim(1)}$ and $p^{\sim(2)}$ of the system. Then, as I have shown above, the self-thinning law is asymptotically true for both species. If this inequality does not hold, then one of the species will become extinct. How is the self- thinning law modified then? This question leads us to the next section.

Computer studies

As mentioned above, in computer simulations we use difference equations. The stability properties of this system are not the same as for the differential equation system, but similar. For example, in a Lotka-Volterra differential equation system the fixed point is defined by the intersection of two straight lines; in a difference equation system by the intersection of two hyperbolas (these are the isoclines in this case). Otherwise we do not utilize these differences, but only the existence and absence of coexistence. As I have shown in the previous section, power-like (self-thinning) relations are valid asymptotically in the case of coexistence. If there is no coexistence, the self-thinning curves are modified essentially (Fig. 3). The species which goes extinct is thinned more slowly than expected (Fig. 3a), and the winner has a steeper thinning line (Fig. 3b). These phenomena are understandable if we examine the canopy closure curves (Fig. 3 c, d). Figure 3c shows that after a maximal value the density starts to decrease rapidly, which means that the actual point of intersection ($p^{1/l}$) decreases as N decreases in the self-thinning curve (Fig. 3a). The better competitor, however, could not reach its equal density (Fig. 3d) (unless the other species is totally killed), thus the slope is steeper than expected.

Summary and outlook

My population dynamical description takes into consideration the average properties of populations. We assume that the mortality and the volume or biomass production is led by the two dimensional density $V^l N$, where l may vary with respect of species, as it is verified earlier.

The very general one-species model system is obedient to the classical self-thinning law asymptotically, and the power equals $-1/l$. We took assumptions of the general functions, and were able to prove that this procedure is right if the actual canopy closure is not too far from the maximum canopy closure. The parameters introduced in the system are estimated from field experiments. The slope of the self-thinning line depends on the state of the stand if physiological constraints are built into the model, as demonstrated in computer simulations.

Assumptions were redefined in such a way that I was able to extend the model to the case of many even-aged species. This system can be transformed to a differential equation system identical to an n-dimensional Lotka-Volterra model.

In a real case (with many species) one could get very different self-thinning curves in function of competitive event. An acceptable field experiment studying self-thinning of many species would have to take into account the competitive properties of the community as well. As it was demonstrated, if species are in stable coexistence, there is a range where the classical self-thinning description is valid.

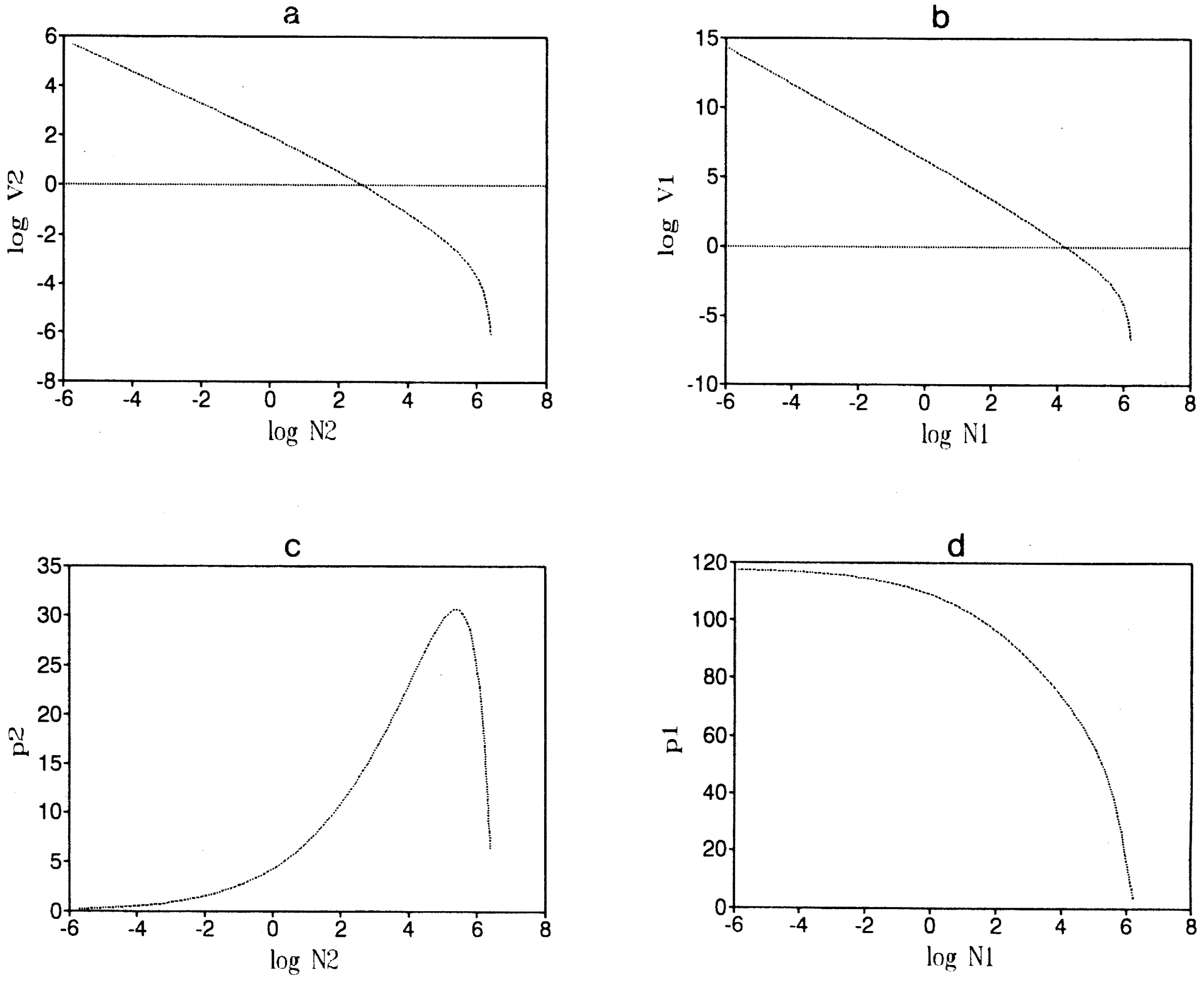

Figure 3. Self-thinning graphs, when there is competitive exclusion. a. Self-thinning curve of the species tending to extinct. Slope of thinning (e.g., -0.78 in the middle of the line) differs significantly from - 1.33 as it is in the case of coexistence. b. The winner of the competition is thinned more slowly (slope = -1.46 in the noted region). Standard errors are less than 5x 10^{-3}. c . After the transient state the two-dimensional density (or canopy closure) begins to decrease, and tends to zero. d. Species one could not reach the equilibrium density, unless species two is totally neglected. Figures c, d explain the deviations in the thinning curves. (For detailed interpretation, see text). $A_0(1) = 1.2$, $A_0(2) = 1.2$, $\alpha_{11} = \alpha_{12} = \alpha_{21} = \alpha_{22} = 0.001$, $\mu_{11} = \mu_{22} = \mu_{21} = 0.001$, $\mu_{12} = 0.002$, $l = 3/4$, $V_0(1) = V_0(2) = 0.001$, $N_0(1) = N_0(2) = 500$.

The transformation of the population's inner structure is a very interesting question (Ford 1975, Slatkin & Anderson 1984, Westoby & Howel 1986). A more complicated stochastic or computer simulation model could consider this question. In the light of relations between competitive and self-thinning properties, I suspect that a connection could be found between the nature of syn-thinning and the process of succession.

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APPENDIX

Consider the following differential equation system:

$$dV/dt = A(p(t))\,V(t) \qquad (a1)$$

$$dN/dt = -F(p(t))\,N(t) \qquad (a2),$$

where $p(t)= V^{l}(t)\,N(t)$, $l > 0$.

Furthemore, assume that $dA/dp < 0$, $dF/dp > 0$ (a3), (*e.g.* if density increases biomass production decreases and mortality increases), $lA(0) - F(0) > 0$ (a4). This latter inequality is identical to the next practical state: when density approaches zero, then it increases. At low density one expects $A(p)$ to be greater than zero ($A(0) > 0$ (a5)), and $F(p)$ to be positive ($F(0) \geq$ (a5)). Further there is an overcrowded state p^*, where $A(p^*)=0$ (a6). Then there is a $p^{\sim} > 0$ stable fixed point of the system.

Proof:

Multiply (a1) with NlV^{l-1}, (a2) with V^l and sum these new equations to get

$$V^l dN/dt + NlV^{l-1} dV/dt = [lA(p) - F(p)]V^l N, \qquad (a7)$$

and considering that $p = V^l N$ this can be transformed into

$$dp/dt = [lA(p) - F(p)]\, p. \qquad (a8)$$

$P^{\sim}$ is a fixed point, if $lA(p^{\sim}) - F(p^{\sim}) = 0$. Since we assumed that (a4), (a5), and (a6) are true, it is clear that this kind of point exists. Using (a3) one can show that $d/dp[lA(p) - F(p)] < 0$, e.g. this fixed point is stable.

The analogous state in the case of the difference equation system is

$$V_{t+1} = A(p_t)\, V_t \qquad (b1)$$

$$N_{t+1} = F(p_t)\, N_t \qquad (b2),$$

where $A^l(p_t)$, $F(p_t)$ are monotone decreasing functions (b3).

$$A^l(0) > 1, F(0) \geq 1. \qquad (b4)$$

Then there is a $p^{\sim}$ fixed point of the system (b1,2).

The proof is very similar to the method explained above, but the stability properties could be very complicated (see, for example, the logistic difference equation). We can attain to a chaotic range from a stable fixed point along bifurcations (*e.g.* Lauwerier 1986). Roughly we can say that if density does not increase very fast, then we remain in a stable region.

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