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Research Letter

A Consideration of the Constancy of Biomass Density in Plant Populations Undergoing Self-Thinning

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The constancy of biomass density was considered in an entire plant population p by combining two adjacent populations p_1 and p_2 for which the self-thinning rule is assumed to be satisfied independently and each biomass density is also assumed to be the same constant value. Under these assumptions, the biomass density d in a population p was formulated as $d = c((km^{-\alpha}+1)(km+1)/(km^{1-\alpha}+1)(k+1))$, where c is biomass density of p_1 and p_2, and k and m are stand area and density ratio of p_1 to p_2, respectively, and α is the self-thinning slope. In the case of $m \neq 1$, the value of d in the above equation is always larger than unity. This fact indicates that the biomass density in a combined population p is not equal to the biomass density c in each population p_1 or p_2 because of systematic error.

1. INTRODUCTION

Biomass density is generally defined as aboveground biomass per unit volume of space occupied by a forest stand. Since the volume of a forest can be approximated as the product of forest height and stand area, the biomass density of a forest has a dimension [weight volume^{-1}] and is an index of the average organic-matter concentration packed in a unit volume of a forest [1, 2]. Since light penetration within a forest stand is affected by the crown or canopy structure [3], the biomass density per unit volume is a key factor in an effective gas exchange and photosynthetic production as well as in a forest stand structure.

Kira and Shidei [2] first demonstrated that the biomass density is approximately constant in fully closed forest stands. Kikuzawa [1] also reported that the biomass density reaches an upper limit of constant value in fully stocked forest stands. On the contrary, Osawa and Allen [4] and Xue et al. [5] pointed out for several forest stands that the constancy of biomass density may not always hold. Thus the constancy assumption of biomass density is still controversial.

In the present paper, we consider, mathematically, the constancy of biomass density from the following viewpoints: in two adjacent populations p_1 and p_2 satisfying the self-thinning rule [6–9] independently, each biomass density is assumed to be the same constant value. If the two populations p_1 and p_2 are combined as a single population under these assumptions, how does the biomass density change? This question is realistic because observed data often corresponds to the case of a combination of two plant populations [10].

2. FORMULATION

Formulation of basic data on two plant populations is given in Table 1. Here, S is the sum of a stand area occupied by two adjacent populations p_1 and p_2, N is the total plant number of populations p_1 and p_2, and X is the total plant mass of p_1 and p_2, respectively, as follows:

$$\begin{aligned} S &= S_1 + S_2, \\ N &= N_1 + N_2 = S_1\rho_1 + S_2\rho_2, \\ X &= X_1 + X_2 = S_1 y_1 + S_2 y_2, \end{aligned} \tag{1}$$

where ρ_1 and ρ_2, and y_1 and y_2 are the stand density and biomass of populations p_1 and p_2, respectively.

Table 1: Formulation data on two plant populations.

	Population p_1	Population p_2	Sum
Stand area	S_1	S_2	$S = S_1 + S_2$
Stand density	ρ_1	ρ_2	—
Mean plant height	H_1	H_2	—
Biomass	y_1	y_2	—
Total plant number	$N_1 = S_1\rho_1$	$N_2 = S_2\rho_2$	$N = N_1 + N_2$
Total plant mass	$X_1 = S_1 y_1$	$X_2 = S_2 y_2$	$X = X_1 + X_2$
Biomass density	$d_1 = y_1/H_1$	$d_2 = y_2/H_2$	—

For convenience sake, the following relationships are taken into consideration:

$$S_1 = kS_2, \quad 0 < k < \infty, \tag{2}$$

$$\rho_1 = m\rho_2, \quad 0 < m < \infty, \tag{3}$$

where k and m are the area and the density ratio between two populations p_1 and p_2, respectively.

The first assumption that two populations p_1 and p_2 satisfy the self-thinning rule independently leads to

$$y_1\rho_1^{\alpha} = K = y_2\rho_2^{\alpha}, \tag{4}$$

where K and α are a constant and a self-thinning exponent, respectively.

Combining (3) and (4) gives the following relationship:

$$\frac{y_1}{y_2} = m^{-\alpha}. \tag{5}$$

The second assumption is that biomass density d_1 in population p_1 is equal to d_2 in population p_2 as follows:

$$d_1 = d_2 = c, \tag{6}$$

where c is a constant. The assumption of (6) indicates that

$$\begin{aligned} y_1 &= cH_1, \\ y_2 &= cH_2. \end{aligned} \tag{7}$$

Considering an entire population of p_1 and p_2, mean plant height H and biomass y are defined as

$$\begin{aligned} H &= \frac{H_1N_1 + H_2N_2}{N_1 + N_2}, \\ y &= \frac{X_1 + X_2}{S_1 + S_2}. \end{aligned} \tag{8}$$

From (5), (7), and (8), biomass density (d) in a combined population of p_1 and p_2, which is defined as y/H, is expressed as

$$d = \frac{y}{H} = c\frac{(km^{-\alpha}+1)(km+1)}{(km^{1-\alpha}+1)(k+1)}. \tag{9}$$

Here, let the (dimensionless) coefficient of c in (9) be as

$$f(k,m) = \frac{(km^{-\alpha}+1)(km+1)}{(km^{1-\alpha}+1)(k+1)}. \tag{10}$$

According to $f(k,m) \gtreqless 1$, biomass density d is determined as $d \gtreqless c$. Therefore, if it is clarified whether $f(k,m)$ is larger, equal to, or smaller than unity, the quantitative relationship between d and c can be assessed.

3. SOLUTION

Case 1 ($m = 1$). Let us consider the simplest case, $m = 1$. In this case, $f(k,m) = 1$ in (10), and then biomass density $d = c$ in (9).

Case 2 ($m \neq 1$). If the denominator and numerator of $f(k,m)$ in (10) are symbolized as f_1 and f_2, the deference Δ between f_1 and f_2 is written as

$$\begin{aligned} \Delta &= f_1 - f_2 \\ &= (km^{-\alpha}+1)(km+1) - (km^{1-\alpha}+1)(k+1) \\ &= k(m^{-\alpha}-1)(1-m). \end{aligned} \tag{11}$$

The value of self-thinning exponent (α) is theoretically considered to be 1/2 from a geometric basis [7, 9] and, recently, to be 1/3 from a resource-allocation basis [6, 8]. Therefore, the present analysis considers the sign of (10) in the cases of $\alpha = 1/2$ and $\alpha = 1/3$ as follows.

Case 2.1 ($\alpha = 1/2$). When $\alpha = 1/2$, (11) is rewritten as

$$\Delta = k\frac{1}{\sqrt{m}}(\sqrt{m}+1)(\sqrt{m}-1)^2 > 0. \tag{12}$$

Case 2.2 ($\alpha = 1/3$). When $\alpha = 1/3$, (11) is represented as

$$\Delta = k\frac{1}{\sqrt{m}}(\sqrt{m}-1)^2(m+\sqrt{m}+1) > 0. \tag{13}$$

In both Cases 2.1 and 2.2, Δ in (11) is positive, or $f_1 > f_2$, so that biomass density d is always

$$d > c. \tag{14}$$

In other words, when we consider an entire population by combining two populations p_1 and p_2, a systematic error occurs, as seen in (14). According to Hozumi [10], a systematic error was detected also in the self-thinning slope (α) in (4) by assuming the 3/2 power law of self-thinning, namely, $\alpha = 1/2$ [7, 9] in a combined population of p_1 and p_2.

4. CALCULATION AND PROPERTIES OF $f = (k,m)$

To examine the degree of deviation from the biomass density c in two populations, the values of $f(k,m)$ in various values of density ratio (m) and area ratio (k) were calculated in the cases of self-thinning slope $\alpha = 1/2$ (Table 2) and $\alpha = 1/3$ (Table 3), respectively. The values of m and k for which the value of $f(k,m)$ is less than 1.05 range from 0.6 to 1.8 and 0.5 to 2.0 in the cases of $\alpha = 1/2$ and $\alpha = 1/3$, respectively. However, controlling the $f(k,m)$ value such that it is less than 1.02, the m values become smaller, ranging from 0.8 to 1.4 and 0.6 to 1.6 in the cases of $\alpha = 1/2$ and $\alpha = 1/3$, respectively.

Since $f(k,m)$ is a coefficient of c in (9), the present numerical analysis may be useful for explaining slight differences in biomass density between populations as observed in, for example, the Chinese pine and larch stands reported by Xue et al. [5].

Table 2: Calculated values of $f(k, m)$ in the case of $\alpha = 1/2$ in (10).

k	m											
	0.2	0.3	0.4	0.5	0.6	0.8	1.0	1.4	1.6	1.8	2.0	3.0
0.1	1.086	1.050	1.030	1.018	1.010	1.002	1.000	1.005	1.010	1.016	1.023	1.066
0.2	1.151	1.087	1.052	1.030	1.017	1.003	1.000	1.008	1.017	1.027	1.038	1.105
0.3	1.201	1.115	1.068	1.039	1.022	1.004	1.000	1.011	1.021	1.034	1.047	1.128
0.4	1.240	1.135	1.080	1.046	1.025	1.005	1.000	1.012	1.024	1.038	1.053	1.143
0.5	1.269	1.151	1.088	1.051	1.028	1.005	1.000	1.013	1.026	1.041	1.057	1.151
0.6	1.292	1.163	1.095	1.055	1.030	1.006	1.000	1.014	1.027	1.042	1.059	1.155
0.7	1.310	1.172	1.100	1.057	1.031	1.006	1.000	1.014	1.027	1.043	1.061	1.157
0.8	1.324	1.179	1.103	1.059	1.032	1.006	1.000	1.014	1.028	1.044	1.061	1.157
0.9	1.334	1.183	1.105	1.060	1.032	1.006	1.000	1.014	1.028	1.044	1.061	1.156
1.0	1.342	1.187	1.107	1.061	1.033	1.006	1.000	1.014	1.028	1.043	1.061	1.155
1.2	1.351	1.190	1.108	1.061	1.033	1.006	1.000	1.014	1.027	1.043	1.059	1.150
1.4	1.355	1.191	1.108	1.061	1.033	1.006	1.000	1.014	1.026	1.041	1.057	1.144
1.6	1.355	1.190	1.107	1.060	1.032	1.006	1.000	1.013	1.026	1.040	1.055	1.138
1.8	1.352	1.187	1.105	1.059	1.031	1.006	1.000	1.013	1.025	1.038	1.053	1.132
2.0	1.348	1.184	1.103	1.057	1.030	1.006	1.000	1.012	1.024	1.037	1.051	1.126

Table 3: Calculated values of $f(k, m)$ in the case of $\alpha = 1/3$ in (10).

k	m											
	0.2	0.3	0.4	0.5	0.6	0.8	1.0	1.4	1.6	1.8	2.0	3.0
0.1	1.050	1.030	1.018	1.011	1.006	1.001	1.000	1.003	1.007	1.011	1.016	1.046
0.2	1.089	1.053	1.032	1.019	1.011	1.002	1.000	1.006	1.011	1.018	1.026	1.072
0.3	1.119	1.070	1.043	1.025	1.014	1.003	1.000	1.007	1.014	1.023	1.032	1.087
0.4	1.143	1.084	1.050	1.030	1.017	1.003	1.000	1.008	1.016	1.026	1.036	1.096
0.5	1.162	1.094	1.056	1.033	1.018	1.004	1.000	1.009	1.017	1.027	1.038	1.100
0.6	1.177	1.102	1.061	1.035	1.020	1.004	1.000	1.009	1.018	1.028	1.040	1.102
0.7	1.189	1.108	1.064	1.037	1.020	1.004	1.000	1.009	1.018	1.029	1.040	1.103
0.8	1.198	1.113	1.066	1.038	1.021	1.004	1.000	1.009	1.018	1.029	1.040	1.102
0.9	1.206	1.117	1.068	1.039	1.021	1.004	1.000	1.009	1.018	1.029	1.040	1.101
1.0	1.212	1.119	1.069	1.040	1.022	1.004	1.000	1.009	1.018	1.029	1.040	1.100
1.2	1.220	1.123	1.071	1.040	1.022	1.004	1.000	1.009	1.018	1.028	1.039	1.096
1.4	1.224	1.124	1.071	1.040	1.022	1.004	1.000	1.009	1.017	1.027	1.037	1.091
1.6	1.226	1.124	1.071	1.040	1.021	1.004	1.000	1.009	1.017	1.026	1.036	1.087
1.8	1.226	1.123	1.070	1.039	1.021	1.004	1.000	1.008	1.016	1.025	1.034	1.083
2.0	1.225	1.122	1.069	1038	1.020	1.004	1.000	1.008	1.016	1.024	1.033	1.079

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