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SIZE DISTRIBUTION DYNAMICS OF PLANTS WITH INTERACTION BY SHADING

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ABSTRACT

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The time development of the frequency distribution of individual weights in a plant population is analyzed theoretically by using the von Foerster equation. It is shown that the shading caused by large individuals leads to a positively skewed (L-shaped) pattern of stationary distribution, which is often observed in the field. The basic assumptions are: (a) the growth rate of a plant is reduced due to shading by surrounding higher individuals; and (b) the growth rate function of a plant has a logistic form. As the shade-effect is enhanced the model predicts that: the L-shaped pattern of the steady-state weight distribution becomes more pronounced; and the L-shaped pattern appears at an earlier stage.

INTRODUCTION

The relationship between plant density and plant weight distribution has been extensively studied by many investigators (Koyama and Kira, 1956; Stern, 1965; Obeid et al., 1967; Ogden, 1970; Jack, 1971; Ford, 1975). They analyzed the size distribution of plant populations which began to grow synchronously, and observed the following characteristic properties for various herbaceous plants and trees:

(1) In the early stage of growth, the individual's weight showed a nearly normal distribution.

(2) As plants grew, the weight frequency distribution skewed towards smaller sizes until an L-shaped distribution with the mode located at the

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left-end class was reached. Namely, the population was dominated by small plants with a few large individuals.

(3) The higher the plant density, the earlier the L-shaped distribution appeared.

Koyama and Kira (1956) explained that the observed L-shaped distribution could be regarded as a log-normal size distribution, resulting from random variation in the initial size and growth rate of plants. However, Harper (1967) and Ford (1975) emphasized the importance of interplant competition in the process of plant growth. In fact, Mead (1966) explained the variation in plant weight by the difference in the area which each individual could utilize. Yoda et al. (1957) showed that neighboring plants affected each other's growth. They observed that there was a negative correlation between the weight of an individual and its nearest neighbors. In the light of these observations, the density dependence stated above suggests the possibility that the L-shaped distribution is caused by intraspecific competition.

Plant growth is affected by a number of environmental factors. Among such factors, light has a decisive influence in many cases (Hiroi and Monsi, 1960; Stern, 1965; Ford, 1975). If a plant is surrounded by taller individuals the availability of light is limited owing to shading by neighboring plants, hence its growth rate is reduced. Since only larger plants cause this shade-effect, the light environment for each plant depends on the size distribution of plants, and competition for light between plants is one-sided.

In this paper, we will formulate a mathematical model which describes the dynamics of plant growth including the shading effect, and examine the density dependence of the time-change of size distribution. On the basis of the analysis, the findings on size distribution mentioned above will be explained.

MODELLING

Consider a plant population which grows in a homogeneous field. We assume that the plants have the same size distribution per unit area at any place in the field. The number of individuals is denoted by $n(W, t)\,dW$, with weights ranging between W and $W + dW$, per unit area at time t. Further, growth rate and mortality of individuals are denoted by v and M, respectively. The basic equation governing the dynamics of $n(W, t)$ is given by the von Foerster equation (Trucco, 1965; Oldfield, 1966; Shinko and Streifer, 1967; Levin and Paine, 1974; Nagano, 1978; Paine and Levin, 1981; Iwasa, 1981; Kirkpatrick, 1984):

$$\frac{\partial n}{\partial t} = -\frac{\partial}{\partial W}(v \cdot n) - M \cdot n \tag{1}$$

The functional forms of v and M are determined by specifying interactions between individuals including the shade-effect.

We assume that each plant in the population is shaded by larger plants which grow in its neighborhood area S. The total number of neighboring plants larger than W in the area is given by:

$$N(W, t) = S\int_{W}^{\infty} n(W', t)\, \mathrm{d}W' \tag{2}$$

$N(W, t)$ is the 'size rank', since $N(W, t)$ represents the cumulative number of individuals ranking from the largest to the one of size W. Note that from the definition of N in equation (2) the size distribution $n(W, t)$ is given by differentiating N with respect to W:

$$n(W, t) = -\frac{1}{S}\frac{\partial N}{\partial W} \tag{3}$$

Because of shading by the larger plants, the growth rate of a plant with size W decreases with increasing size rank N:

$$\frac{\partial v}{\partial N}(W, N) < 0 \tag{4}$$

Based on the experimental studies of Shinozaki and Kira (1956), we assume that the growth rate v is given by a logistic-type growth function as

$$\begin{aligned} v(W, N) = \frac{\mathrm{d}W}{\mathrm{d}t} &= rW\left(1 - \frac{W}{K(N)}\right) \quad &&\text{for } W < K(N) \\ &= 0 &&\text{for } W \geq K(N) \end{aligned} \tag{5}$$

where r is the growth coefficient. It follows from equation (4) that $\mathrm{d}K(N)/\mathrm{d}N$ is negative. Among the candidates of K satisfying $\mathrm{d}K/\mathrm{d}N < 0$ and $K > 0$, we adopt the rather simple function:

$$K(N) = \frac{K_0}{1 + AN} \quad \text{for } K_0,\ A > 0 \tag{6}$$

K_0 is the maximum size of plants growing in the unshaded condition ($N = 0$). We refer to A as 'susceptibility' because the shade-effect is intensified with increasing A. To summarize, the following set of equations constitutes the basis of our model:

$$\frac{\partial n}{\partial t} = -\frac{\partial}{\partial W}(v \cdot n) - M \cdot n \tag{7-1}$$

$$v(W, N) = rW\left\{1 - \frac{(1 + AN)}{K_0} W\right\} \tag{7-2}$$

$$N(W, t) = S\int_{W}^{K_0} n(W', t)\, \mathrm{d}W' \tag{7-3}$$

with the non-negative initial condition $n(W, 0) = q(W)$ distributing between $W = 0$ and $W = K_0$.

It can be seen from equation (5) that $v(W, N) = 0$ for $W \geq K_0$. Thus W starting from $W_0 < K_0$ will never grow beyond K_0: the range of integration in equation (7-3) is restricted from W to K_0.

ANALYSIS

(1) Case of no mortality

Here we analyze the case when the mortality is so low that we can assume $M = 0$. Let us first consider the steady state at which the growth rate $v(W, N)$ has reached zero. By setting $v(W, N) = 0$ in equation (5) we obtain the size rank at the steady state:

$$N(W, \infty) = \frac{K_0}{AW} - \frac{1}{A} \tag{8}$$

For convenience of the later discussion, we introduce a size frequency distribution defined as:

$$f(W, t) = n(W, t) \Big/ \int_0^{K_0} n(W, t)\, \mathrm{d}W$$

Using equation (3) we obtain the steady state distribution:

$$\begin{aligned} f(W, \infty) &= n(W, \infty) \Big/ \int_0^{K_0} n(W, \infty)\, \mathrm{d}W \\ &= -\frac{1}{SD}\frac{\partial N}{\partial W} = \frac{K_0}{ASDW^2} \quad \text{for } \frac{K_0}{1 + ASD} < W < K_0 \end{aligned} \tag{9}$$

where

$$D = \int_0^{K_0} q(W)\, \mathrm{d}W$$

D is the total plant number in a unit area, which is kept constant at the initial value because the mortality is equal to zero. This steady state function has a truncated form as shown by the solid line in Fig. 1. Since the top individual is completely free from shading, it can reach the maximum weight value $W_{max} = K_0$. On the other hand, the bottom individual with the rank $N = D$ attains the minimum weight $W_{min} = K_0/(1 + ASD)$. The value of the minimum weight, W_{min}, is obtained from the condition that (see appendix):

$$\int_0^{K_0} f(W, \infty)\, \mathrm{d}W = \int_{W_{min}}^{K_0} \frac{K_0}{ASDW^2}\, \mathrm{d}W = 1$$

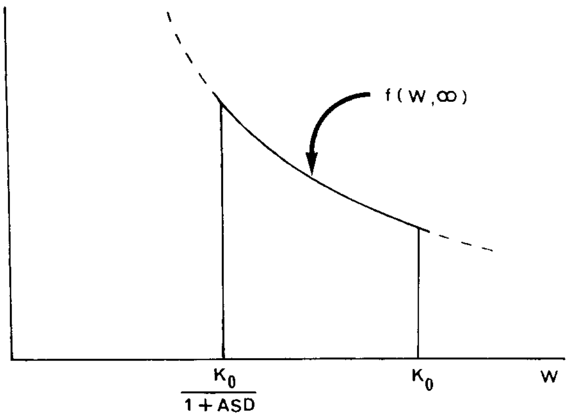


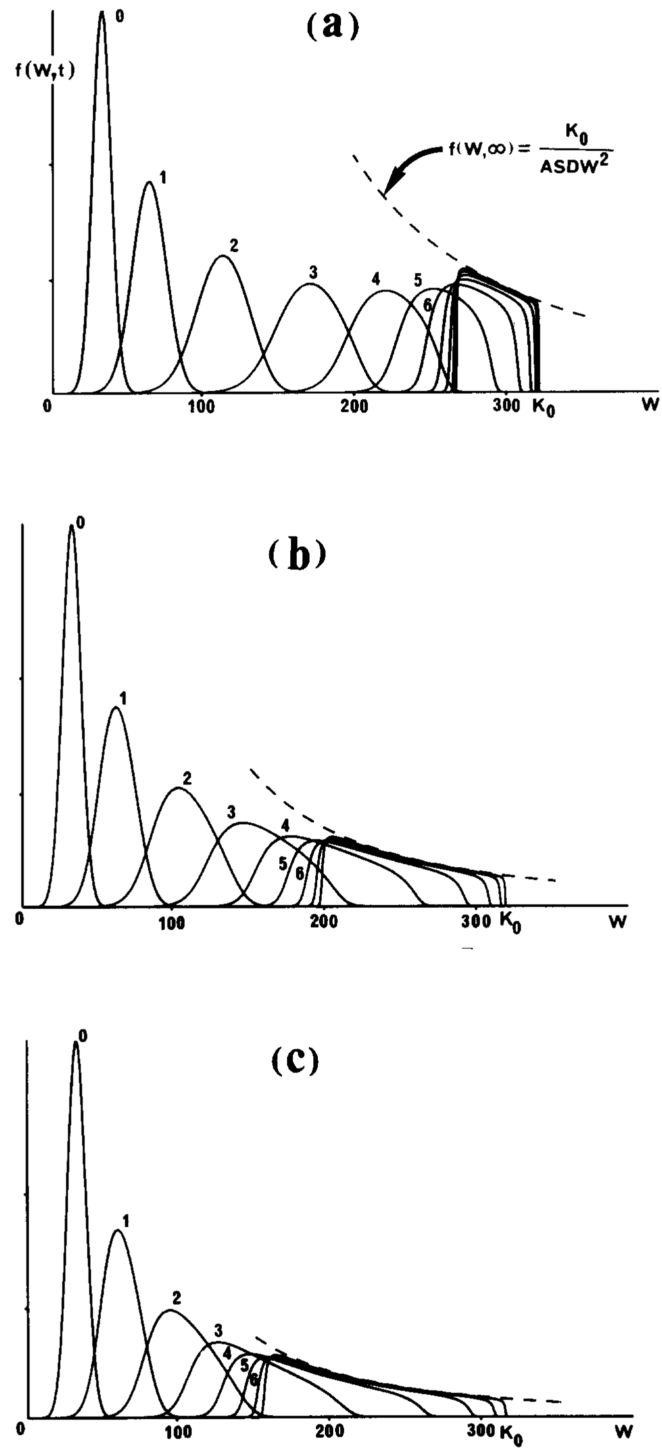
Fig. 1. Steady state frequency distribution, $f(W, \infty)$. It has a truncated form distributing between $W_{max} = K_0$ and $W_{min} = K_0/(1 + ASD)$. As the product ASD becomes larger, the distribution becomes more skewed.

From Fig. 1 we can see that as the product ASD becomes larger, the left edge of the distribution shifts towards the origin and that the steady state frequency distribution becomes more positively skewed.

We have also solved equation (7) analytically as a function of time for the transient state of plant growth. The details and results of the mathematical analysis are summarised in the appendix. The time development of the size frequency distributions $f(W, t)$ given by equation (A-9) are shown in Fig. 2 for ASD values of 0.2, 0.6 and 1.0. From Figs. 2a–c, it can be seen that the frequency distribution of individual weights $f(W, t)$, which was originally a normal distribution, gradually changes its pattern and finally establishes a steady state characterized by a truncated L-shaped distribution. The asymmetry of the distribution becomes more obvious as the value of ASD increases, namely as the susceptibility A or the plant density D increases. If we compare the distribution patterns at any time step in Figs. 2a–c, it can also be concluded that the L-shaped pattern appears earlier with increasing population density. These results give a reasonable explanation for the characteristic growth pattern of plant populations observed in the field. When there is no shade-effect, $ASD = 0$ (see Fig. 2d), the population shows a normal size distribution, the mode of which moves to the right with time, tending to a delta function at $W = K_0$, i.e. all the plants can reach the maximum size K_0.

(2) The case $M \neq 0$

In case (1) we assumed that the effect of mortality on the weight distribution is zero. Actually in many cases of experimental fields (Ford,


(a)
f(W,t)
$f(W,\infty) = \frac{K_0}{ASDW^2}$
0
1
2
3
4
5
6
0
100
200
300
K_0
W
(b)
0
1
2
3
4
5
6
0
100
200
300
K_0
W
(c)
0
1
2
3
4
5
6
0
100
200
300
K_0
W

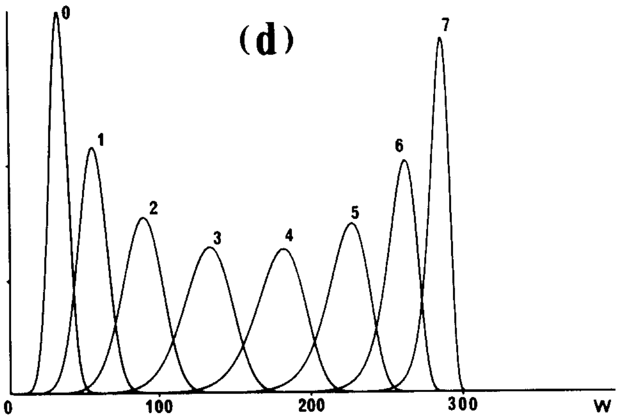


Fig. 2. Time development of size frequency distribution, $f(W, t)$. In all cases $r = 0.2$, $K_0 = 320.0$; (a) $ASD = 0.2$; (b) $ASD = 0.6$; (c) $ASD = 1.0$; (d) $ASD = 0.0$. Starting from a normal distribution, $f(W, t)$ moves to the right with time and finally it converges to the steady state distribution, equation (9), indicated by the dotted line. The number attached to each distribution curve represents the time step.

1975; Nagano, 1978) the mortality is very low except for the early growth stage. For $M \neq 0$, however, equation (7) cannot be solved analytically, thus computer calculations are used. Figure 3 shows the numerical result for the time development of the frequency distribution under the condition that the

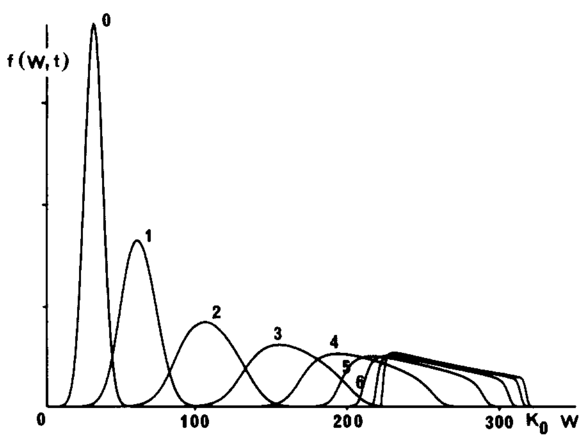


Fig. 3. Time development of $f(W, t)$ for the case that $ASD = 0.6$, $K_0 = 320.0$, and M given by equation (10). Between $W = 0.0$ and 100.0 the individuals die and the plant density decreases (compare with Fig. 2b). The individuals which survive this mortality barrier finally establish the L-shaped pattern.

mortality term in equation (7) is given by:

$$M(W) = 0.1 \qquad 0.0 < W < 100.0$$
$$= 0 \qquad 100.0 \leq W < 320.0 \tag{10}$$

and $ASD = 0.6$. As might be expected, the individuals which survive by overcoming the mortality barrier finally establish the same distribution pattern as that for the case of $M = 0$.

DISCUSSION

The growth rate of a plant is affected by many factors, which can be classified into three major categories: genetic factors; inorganic environmental factors; and intraspecific competition. In experimental populations, it can be assumed that each plant is affected equally by the inorganic environment; soil nutrients, water and CO_2 concentration; etc. However, each plant is affected differently by the genetic and competitive factors. Focussing attention on the genetic factor, Koyama and Kira (1956) presented a model to explain the appearance of the L-shaped distribution. In their model they assumed that both the initial size and the growth rate have a normal distribution. By a computer calculation under these assumptioins, they showed that the size distribution becomes skewed with time. Under the same assumptions Hara (1984) represented a Kolmogorov equation describing the dynamics of size distribution and showed that a log-normal distribution was realized. However, since they derived these results without considering the competition for light, they could not explain why the skewedness of the size distribution depended on the plant density.

For simplicity we consider only the competition for light in the present model, disregarding genetic variation. Since competition for light has a one-sided nature, it leads to the asymmetric variation in the growth rate of plants. As the plant density increases, i.e. the number of neighbouring plants increases, the asymmetric variation increases and the advantage of taller individuals is amplified. Therefore, the L-shaped distribution becomes more skewed with increased plant density. The combined effect of the genetic and the competitive factors should contribute to the appearance of the L-shaped distribution.

Although we have used the 'size rank' N as a simple index of the intraspecific competition in this paper, the 'weighted size rank' can be used as an alternative index:

$$N_1 = S\int_W^\infty W'\, n(W', t)\, \mathrm{d}W'$$

which assumes that a larger individual has a greater shade-effect on other plants. If we replace N in equation (7-3) by N_1, the steady state distribution is obtained by a procedure analogous to the derivation of equation (9):

$$f(W, \infty) = \frac{K_0}{ASDW^3} \qquad \frac{K_0}{\sqrt{1 + 2ASDK_0}} < W < K_0 \tag{11}$$

A time-dependent solution has not yet been obtained in this case. Equation 11 gives a steady state distribution with an L-shaped pattern similar to that calculated with the size rank N (equation 9), but this pattern is even more skewed: the weighted size rank N_1 means that the shade-effect of large-sized individuals is greater than that with the simple size rank N.

Although we chose equation (5) for the functional form of v, a different function may be used without significantly changing the qualitative feature of the L-shaped size distribution, so long as it satisfies equation (4). However, in order to analyze the observed data quantitatively, we have to specify the growth equation (5) in a suitable form for each specific population.

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APPENDIX

By integrating equation (7-1) with respect to W from W to K_0 and using the relationship $N(K_0, t) = 0$ and $V(K_0, N(K_0, t)) = 0$, given by equations (7-2) and (7-3), we can derive the partial differential equation about N:

$$\frac{\partial N}{\partial t} = -rW\left(1 - \frac{1+AN}{K_0}W\right)\frac{\partial N}{\partial W} \tag{A-1}$$

The initial condition of size rank N is given by:

$$N(W, 0) = S\int_W^{K_0} q(W')\,\mathrm{d}W' \equiv g(W) \tag{A-2}$$

Since the right-hand-side of equation (A-1) for $W = 0$ becomes zero, we have $\mathrm{d}N(0, t)/\mathrm{d}t = 0$. This means that the total number of plants in area S is kept constant. Thus we put $N(0, t) = SD$.

According to a standard method of solving the first order partial differential equation (Ames, 1965; Williams, 1980), the characteristic curves of equation (A-1) are given by two first-order ordinary differential equations:

$$\frac{\mathrm{d}W}{\mathrm{d}t} = rW\left(1 - \frac{1+AN}{K_0}W\right) \tag{A-3}$$

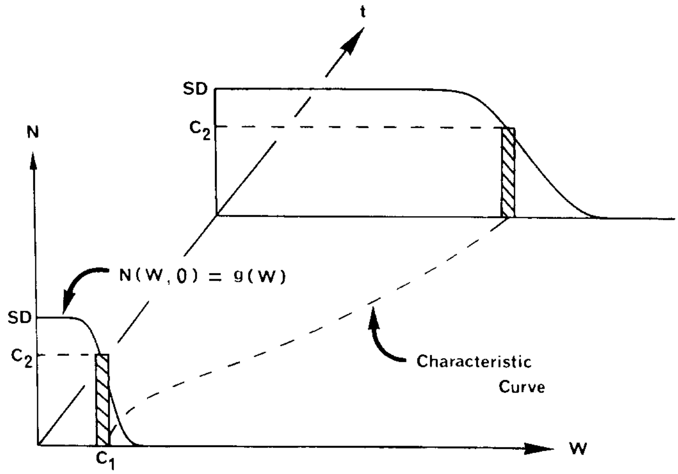

Fig. 4. Time development of size rank, $N(W, t)$. The initial distribution localized on the left side, $g(W)$, moves to the right with time. The dotted line on the $W-t$ plane represents the characteristic curves, which is the growth trajectory of the individuals with the size rank $N = C_2$.

$$\frac{\mathrm{d}N}{\mathrm{d}t} = 0 \tag{A-4}$$

From equation (A-4), N is a constant and can be denoted by $N = C_2$; equation (A-3) then becomes:

$$\frac{\mathrm{d}W}{\mathrm{d}t} = rW\left(1 - \frac{1 + AC_2}{K_0}W\right) \tag{A-5}$$

This can be easily solved, and gives the following solutions:

$$W = \frac{C_1 K'}{C_1 + (K' - C_1)\exp(-rt)} \tag{A-6-1}$$

$$N = C_2 \tag{A-6-2}$$

$$K' = \frac{K_0}{1 + AC_2} \tag{A-6-3}$$

The differential equation (A-5) represents the growth rate of individuals with size rank $N = C_2$. Thus equation (A-6-1) describes how the size of a plant with a fixed size rank $N = C_2$ changes with time. The growth trajectory given by equation (A-6-1) is shown by the characteristic curves on the $W - t$ plane in Fig. 4. Substituting equation (A-6-1) for $t = 0$ (i.e. $W = C_1$) and $N = C_2$ into the initial condition (A-2), we have:

$$C_2 = g(C_1) \tag{A-7}$$

If we eliminate C_1 and C_2 from the set of equations (A-6) and (A-7) we have the following equation:

$$N = g(x)$$

where

$$x = \frac{KW\exp(-rt)}{K - W(1-\exp(-rt))}, \quad K = \frac{K_0}{1+AN} \tag{A-8}$$

Inverse transformation of equation (A-8) leads to the solution of equation (A-1):

$$N(W,\, t) = g(0) = SD \quad \text{for } 0 < W \leq W_1^* \tag{A-9-1}$$

$$N(W,\, t) = \frac{K_0(g^{-1}(N) - W\exp(-rt))}{AW\, g^{-1}(N)(1-\exp(-rt))} - \frac{1}{A} \tag{A-9-2}$$

$$\text{for } W_1^* < W < W_2^*$$

$$N(W,\, t) = 0 \quad \text{for } W \geq W_2^* \tag{A-9-3}$$

where

$$W_1^* = \frac{W_1 K_1}{W_1 + (K_1 - W_1)\exp(-rt)}$$

$$W_2^* = \frac{W_2 K_0}{W_2 + (K_0 - W_2)\exp(-rt)}$$

$$K_1 = \frac{K_0}{1+ASD}$$

Here, W_1 is the maximum value of W which satisfies $g(W) = SD$ and W_2 is the minimum value of W which satisfies $g(W) = 0$ (see Fig. 4). As $t \to \infty$, $N(W,\, t)$ tends to:

$$\begin{aligned} N(W,\, \infty) &= \frac{K_0}{AW} - \frac{1}{A} && \text{for } K_1 < W < K_0 \\ N(W,\, \infty) &= g(0) && \text{for } 0 < W \leq K_1 \end{aligned} \tag{A-10}$$

Differentiating equation (A-10) with respect to W, gives the following steady state solution:

$$f(W,\, \infty) = -\frac{1}{SD}\frac{\partial N}{\partial W} = \frac{K_0}{ASDW^2} \quad \text{for } \frac{K_0}{1+ASD} < W < K_0$$

$$f(W,\, \infty) = 0 \quad \text{for } 0 < W \leq \frac{K_0}{1+ASD} = W_{\min}$$

This is exactly the same as equation (9) which has been heuristically obtained as shown in the text. (Q.E.D.)