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AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(16 November - 10 December 1982)

PHENOTYPIC PLASTICITY: A STRATEGIC APPROACH TO PLANT ADAPTATION

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Phenotypic Plasticity: A Strategic Approach to Plant Adaptation

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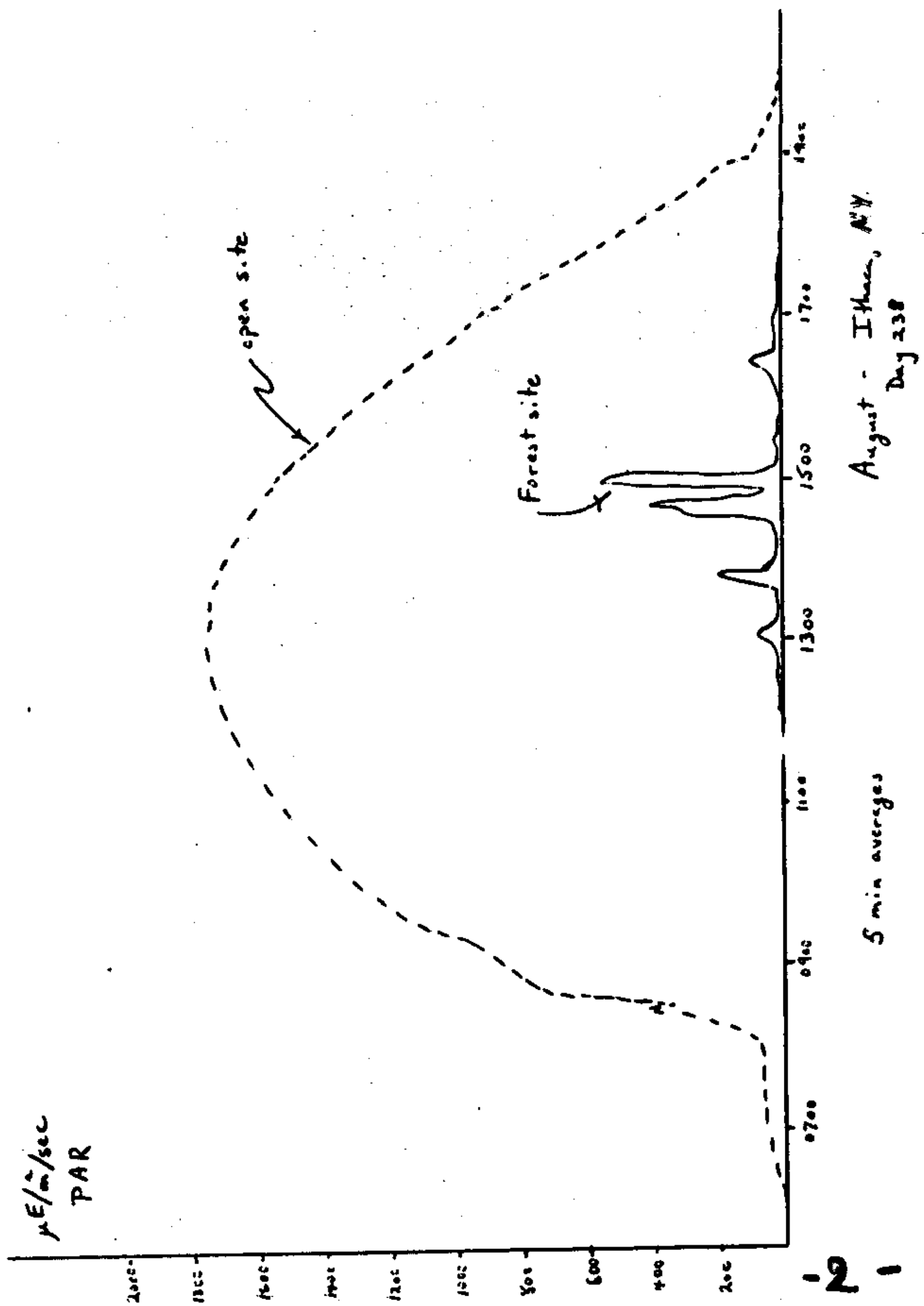
Environmental variability - spatial & temporal, plant dispersal mechanisms effectively allow averaging of spatial heterogeneity.

Phenotypic plasticity - a genotype has the capacity to express a range of phenotypes depending upon environmental conditions - e.g. a leaf's photosynthetic capacity, measured as light-saturated photosynthetic rate, is ened by light.

Review - (Bradshaw, 1965, Adv. Genetics 13: 115-155)

1. Plasticity is under genetic control.
2. Degree of control by detailed developmental pathways varies - rigourous canalization into 1 form - discrete switching between 2 or more forms - canalization only between wide limits.
3. Control is not uniform over whole genotype, but is specific for individual characters
4. Control is specific for individual environmental influences.



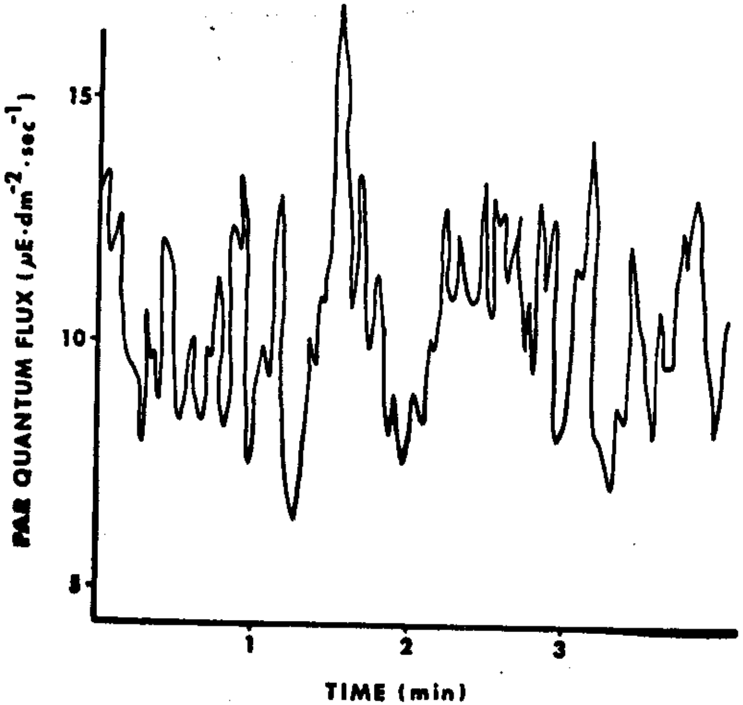


Figure II.2. Quantum flux in the photosynthetically active region of the spectrum beneath a mixed hardwood forest for a short time period on a day in early May.

Questions - How is plasticity range related to environmental variability? Can we predict plasticity ranges of characters from the frequency and amplitude of environmental variations which influence these characters? What are the "costs" of plasticity?

Approach - Strategic or a priori

1. Delineate a set of possible organism responses.
2. Describe state equations and constraints of the system
3. Define a fitness criterion, and assume evolution acts to maximize this, giving an optimal phenotype.

Examples of plasticity

Plastic	Non-plastic
Size of leaves, stem	Leaf shape
Number of shoots, leaves, flowers	Leaf margin serration
Hairiness	Flower shape

Case of Plasticity of Photosynthetic Capacity as influenced by light

1. Leaf maximum uptake capacities are determined during development, through light level.
2. This plasticity is under genetic control, e.g. different ecotypes have different plasticity ranges.

Steps 1-3 - Determine experimentally, Ps rates and responses to sudden light changes; determine the physiological causes for the observed response; mathematically model Ps response to evaluate energy gains in arbitrarily varying light environments.

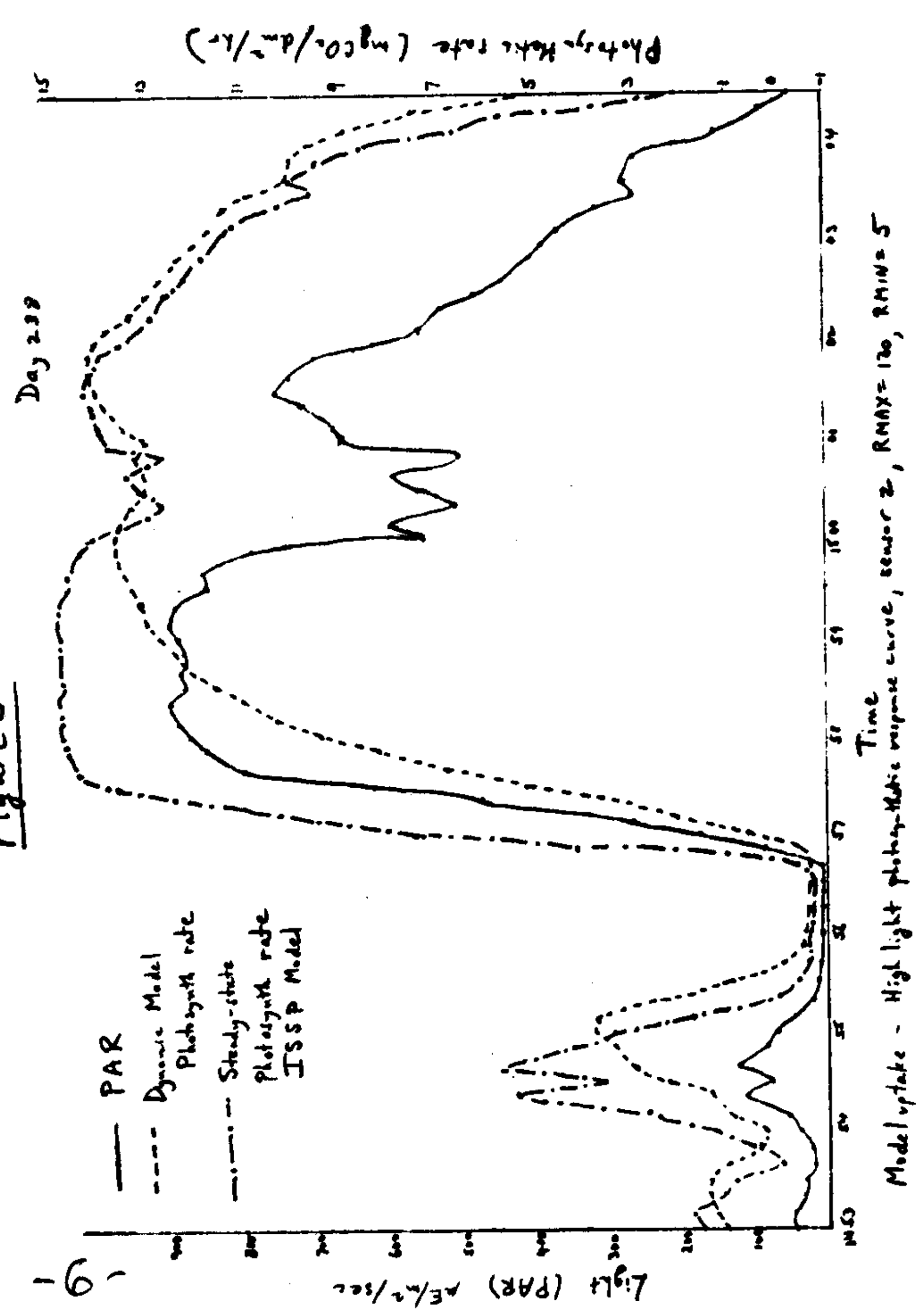
Results include: the energy gain of *Fragaria virginiana* is significantly affected by short-term light increases, lasting only minutes, and infrequently occurring through a day.

For the next step of determining optimal photosynthetic capacity, the "costs" of a given phenotype could be considered as:

1. Respiratory
2. Tissue construction
3. Maintenance of root and shoot tissue for adequate water supply
4. Effects of leaf lifespan

In what follows, the only cost considered is the higher respiration rates associated with higher photosynthetic capacity.

Figure 5



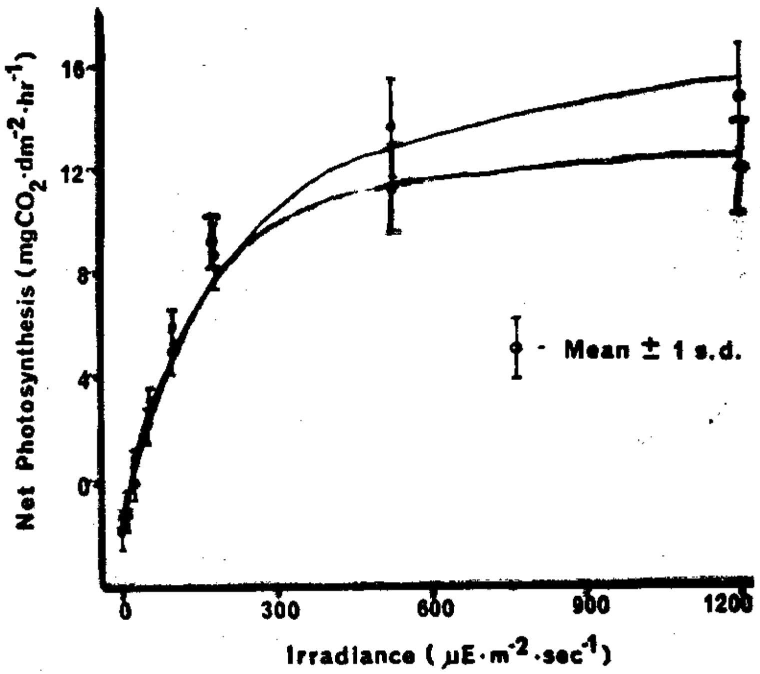


Figure IV.1. Fitted response curve for high light grown leaves. Least squares fit of equation (8) to the data means from Table I, Appendix I.

Low light grown leaves
F. virginiana

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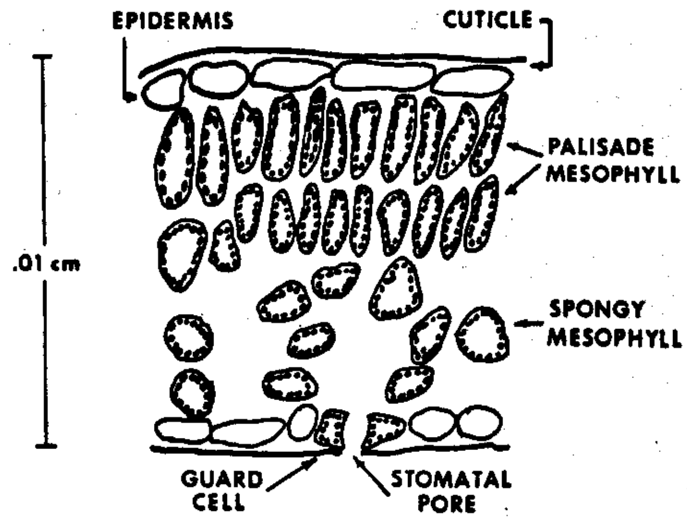

Figure III.1. Transverse section through a leaf (after Nobel, 1974)

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Step 4: Determine optimal Ps response in constant, deterministically varying, and randomly varying light conditions. Then, given a range of environmental conditions, determine optimal plasticity range.

Approach: View Ps plasticity as being under genetic control and proceed via strategic optimization.

Consider light-limited species, so other variations (temp., water) are ignored.

Optimization criterion - net carbon gain during a day.

Case I - Constant light level.

Total uptake is

$$\bar{P} = \int_{day} P(t)\,dt - \int_{night} R(t)\,dt$$

$P(t)$ = net Ps rate

$R(t)$ = night respiration rate

We take $\int_{night} R(t)\,dt = a \int_{day} P(t)\,dt + b\,t_N$

for constant a, b = basal metabolic rate, t_N = night length

Take $P(t) = \dfrac{K_1 K_2 L(t)}{K_1 L(t) + K_2} - f(K_2)$

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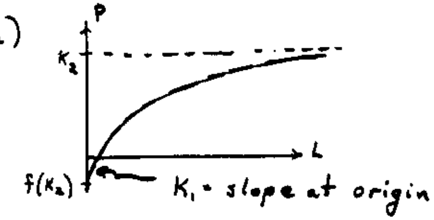


We assume

$$f(K_2) = c\,K_2^{\alpha} \qquad c, d, \alpha > 0$$
$$b(K_2) = d\,K_2^{\alpha}$$

so dark respiration rate during day, and basal metabolic rate are increasing functions of maximum photosynthetic capacity, K_2.

Then for a constant daily light level L, the problem is to choose K_2 to maximize total daily carbon gain:

$$\bar{P} = (1-a)\,t_D \left(\frac{K_1 K_2 L}{K_1 L + K_2} - c K_2^{\alpha} \right) - d K_2^{\alpha} t_N$$

For any fixed α, this is a simple calculus problem (transform to $\lambda = \frac{1}{K_2}$ variable).

Result:

Predict that respiration rate increases non-linearly with maximum photosynthetic capacity, possibly due to non-linear increase in mesophyll volume per unit leaf area with increasing K_2 caused by internal shading.

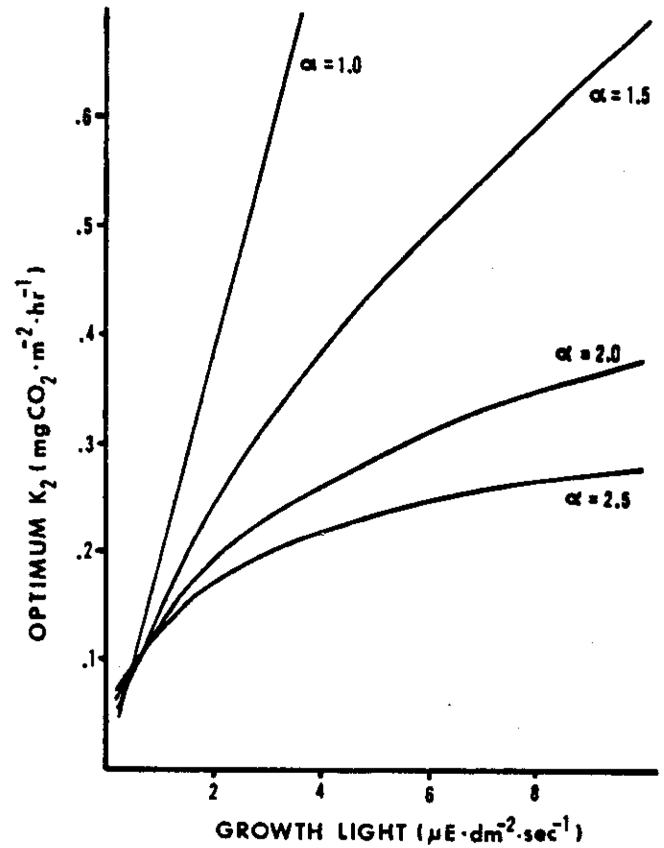
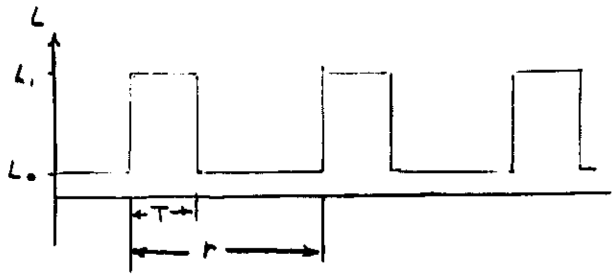


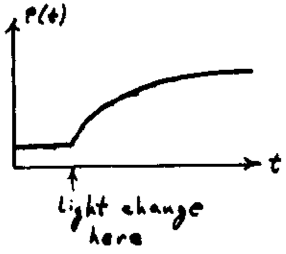
Figure V.1. Effect of varying α upon calculated values of K_2^{opt}, the optimal maximum photosynthetic capacity, using equations (8) and (9). Parameter values used are those of Table V.1 except a = .07, d = .8c; c is .02, .0047, .0011 for the cases α = 1.5, 2.0, 2.5 respectively.

Case II: Deterministically varying environment

Light switches between 2 levels:



Assume Ps response to light increase is exponential with time constant τ, and response to light decrease is instantaneous.



Then problem is to choose K_2 to maximize total daily gains:

$$\bar{P} = \frac{t_D(1-a)}{r}\Big\{ \underbrace{\frac{K_1K_2L_0}{K_1L_0+K_2}\left[r - T + \tau(1-e^{-T/\tau})\right]}_{\text{gains during low light}}$$

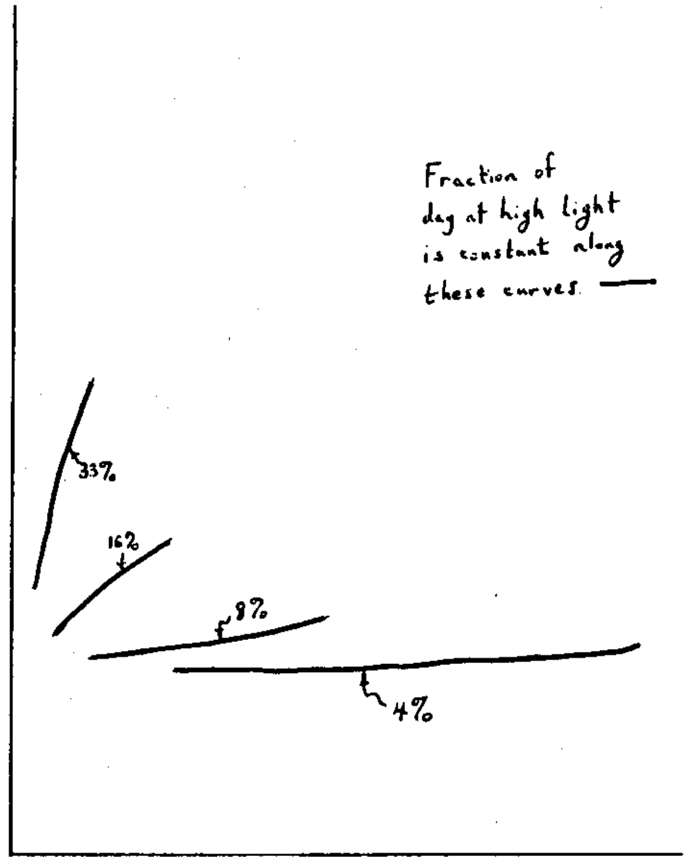
$$+ \underbrace{\frac{K_1K_2L_1}{K_1L_1+K_2}\left[T + \tau(e^{-T/\tau}-1)\right]}_{\text{gains during high light}}$$

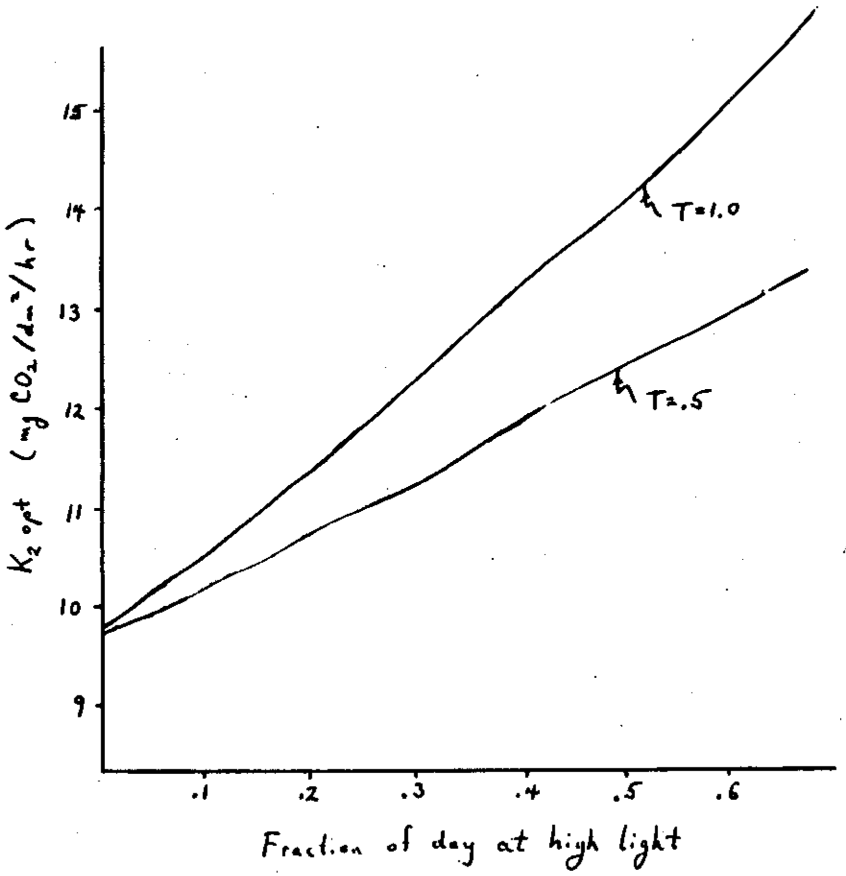
$$- \underbrace{\left[(1-a)c\,t_D + t_N d\right]K_2^{\alpha}}_{\text{respiratory losses}}$$

Utilizing $\alpha = 2.5$ estimated from response curves obtained in the lab, $\overline{P}$ becomes a non-linear equation in $\lambda = \frac{1}{K_2}$ which can be solved numerically for any fixed set of parameters to find K_2 opt = the optimum photosynthetic capacity.

Results :

1. Optimal photosynthetic capacity increases both as sunfleck length increases and as the frequency of sunflecks increase.
2. Optimal plasticity range increases non-linearly with both sunfleck length and fraction of day at high light.
3. There is more efficient utilization of a long sunfleck vs. several short ones with the same total quantum flux.
4. The manner in which light energy is packaged affects optimum Ps capacity.





Optimal light saturated photosynthetic rates as a function of fraction of day at high light, for high light periods of T = .5 & 1.0 min duration.

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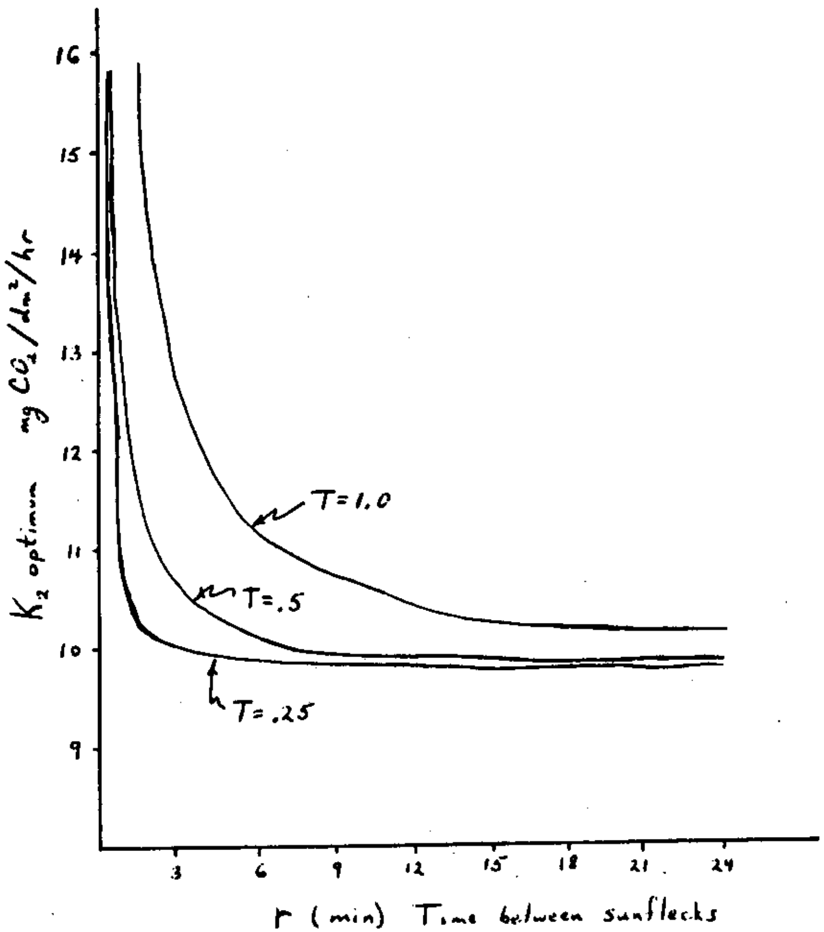

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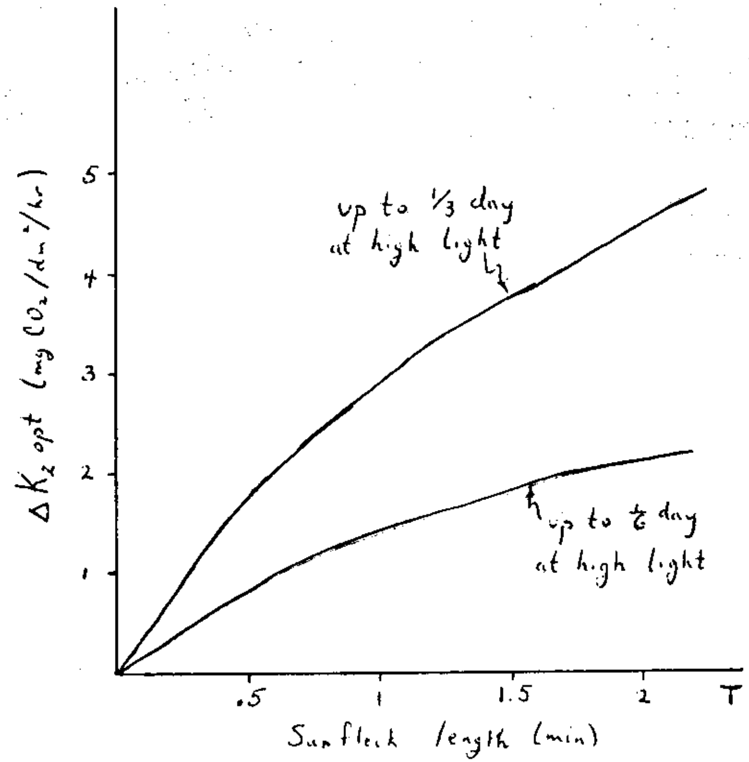
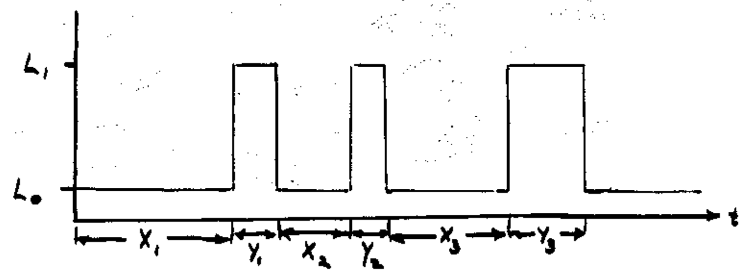


Optimal plasticity range for light saturated photosynthetic rate.

Case III : Randomly varying environment

Again, switch between 2 light levels, but have random lengths of time spent at each level.



X_i's are time between sunflecks

Y_i's are length of sunflecks

Suppose X_i i.i.d. mean δ, variance ρ^2, distribution $F(x)$

Y_i i.i.d. mean γ, variance ξ^2, distribution $G(y)$

$Z_i = X_i + Y_i$ i.i.d. mean $\delta+\gamma$, variance $\rho^2+\xi^2$, distribution $H = F * G$

Z_i's are sunfleck interarrival times and specify a renewal process $\{N(t), t \geq 0\}$ which counts the number of renewals (sunflecks) up to time t.

The uptake from the i^{th} sunfleck of length Y_i is

$$U_i = \frac{K_1 K_2 L_1}{K_1 L_1 + K_2}\left[Y_i + \tau\left(e^{-Y_i/\tau} - 1\right)\right] + \frac{K_1 K_2 L_0}{K_1 L_0 + K_2}\,\tau\left(1 - e^{-Y_i/\tau}\right) - Y_i\, c\, K_2^{\alpha}$$

The U_i's are i.i.d. and the total gain due to sunflecks up to time t is

$$V(t) = \sum_{i=1}^{N(t)} U_i$$

Letting $A(t) = E[V(t)]$ be expected gain from sunflecks occuring up to time t, then by a renewal argument (condition on time of 1st renewal Z_1) we obtain

$$A(t) = \underbrace{E[U_1]}_{\text{mean gain from 1st sunfleck}} + \int_0^t \underbrace{A(t-z)}_{\text{mean gain over remaining time given 1st sunfleck occurs at time } z} \, \underbrace{dH(z)}_{\text{probability 1st sunfleck occurs at time } z}$$

From renewal theory, the renewal function $M(t) = E[N(t)]$ satisfies

$$A(t) = E[U_1] + \int_0^t E[U_1]\, dM(t)$$

so $$A(t) = E[U_1]\,(1 + M(t))$$

The elementary renewal theorem gives

$$\lim_{t\to\infty} \frac{M(t)}{t} = \frac{1}{\delta+\gamma} \quad \text{with probability 1.}$$

So $\dfrac{A(t)}{t} \to \dfrac{E[U_1]}{\gamma+\delta}$ for t large. So we are justified in using

$$A(t_D) \approx \frac{t_D}{\gamma+\delta} E[U_1] \quad \text{for mean uptake}$$

due to sunflecks in a day of length t_D.

The mean fraction of day in sunflecks is

$$\frac{E[Y_1]}{E[Z_1]} = \frac{\gamma}{\gamma+\delta}.$$

We seek to find K_2 which maximizes expected total uptake during a day:

$$E[\bar{P}] \approx \underbrace{\left(\frac{K_1K_2L_0}{K_1L_0+K_2} - cK_2^{\alpha}\right) t_D(1-a)\left(1-\frac{\gamma}{\gamma+\delta}\right)}_{\text{uptake at low light}} +$$

$$\underbrace{t_D(1-a)\frac{E[U_1]}{\gamma+\delta}}_{\text{uptake at high light}} - \underbrace{t_N\, d\, K_2^{\alpha}}_{\text{respiratory losses}}$$

$$\approx \frac{t_D(1-a)}{\gamma+\delta}\left[\frac{K_1K_2L_1}{K_1L_1+K_2}\left(\frac{\gamma^2+\sigma^2}{2\tau}\right) - \right.$$

$$\left.\frac{K_1K_2L_0}{K_1L_0+K_2}\left(\frac{\gamma^2+\sigma^2}{2\tau}\gamma-\delta\right)\right] - \left[c(1-a)t_D + dT_N\right]K_2^{\alpha}$$

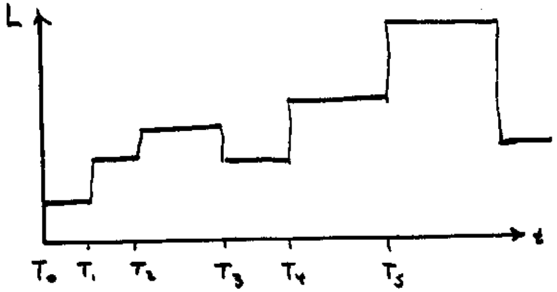
by using a second order approximation for $e^{-Y/\tau}$ term in U_i.

Result :

The random environment case can be reduced to the deterministically varying environment case by using mean times for sunfleck length and interarrival time, with some correction for the variance in these.

Case IV : Generalization to several environmental types

Here we view environment as shifting randomly between many different light levels.



Structure is a Markov-renewal process - the interarrival times $T_0 \le T_1 \le T_2 \le \cdots$ specify a renewal process. At each renewal the process shifts from one state (light level) to another according to a Markov Chain.

It is a Markov renewal process if

$$P[X_{n+1}=j,\ T_{n+1}-T_n \le t \mid X_0, \dots, X_n, T_0, \dots, T_n]$$
$$= P[X_{n+1}=j,\ T_{n+1}-T_n \le t \mid X_n]$$

$Q(i,j,t) = P[X_{n+1}=j,\ T_{n+1}-T_n \le t \mid X_n = i]$ is the semi-Markov kernel, and defines the process.

$P(i,j) = \lim_{t\to\infty} Q(i,j,t)$ are transition probabilities for the underlying Markov Chain.

If we assign a gain W_i to that obtained during the visit to the i^{th} state visited and suppose

$$W_n = f(X_{n-1}, X_n, T_{n+1}-T_n) \quad \text{and}$$

$S_0 = 0$, $S_{n+1} = S_n + W_{n+1}$ be total gains through the $n+1^{st}$ state visited and

$$N_t = \sum_n 1_{[0,t]}(T_n) = \#\text{ transitions in } (0,t)$$

then we have a strong law of large numbers for S_{N_t} = gains up to time t ;

Strong L.L.N. If $E_i[\,|W_1|\,] < \infty \;\; \forall i$ and $a(i) = E_i[W_1]$ then

$$\lim_{t\to\infty} \frac{S_{N_t}}{t} = \frac{\sum_i \pi(i)\,a(i)}{\sum_i \pi(i)\,m(i)} \quad \text{with probability 1}$$

where $\pi(j) = \sum_i \pi(i) P(i,j)$ is stationary dist. of M.C.

and $m(i) = E[\,T_{n+1} - T_n \mid X_n = i\,]$ is mean time in state i.

This is natural extension of case III above.

Extensions and Difficulties:

1. The above ignores differences in leaf ontogeny at different K_2 levels, e.g. differences in leaf lifespan.
2. The strategic approach includes all the problems inherent to optimization arguments in evolutionary theory, e.g. do we have "correct" optimization criteria, this bypasses evolutionary dynamics - "optimum" may not be obtainable due to genetic limitations.

Step 5: What limits the photosynthetic plasticity range? Why are there not infinitely plastic organisms?

Hypotheses: (Bradshaw, 1965)

1. Strong stabilising selection.
2. Plasticity incurs some cost - e.g. ability to attain one phenotype reduces the fitness of other phenotypes within the plasticity range.
3. Irreversibility of phenotypic modification may reduce future fitness (Waddington).
4. Plastic responses to sudden environmental changes may not occur rapidly enough
5. Genetic variability may not exist for the control of plasticity.

Development and Irreversibility

Consider a set of possible temporal environments $\xi \in \Omega$, phenotypes p chosen from some interval Q and a fitness function $f(p, \xi)$

For any particular environment ξ the optimal phenotype is
$$p^*(\xi) = \sup_{p\in Q} f(p, \xi).$$

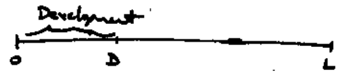
If ξ is a sample path of a stochastic process X_t, $t \in [0, L]$, where L is organism lifespan, we might take
$$p^*(\{X_t\}) = \sup_{p\in Q} E[\,f(p, \{X_t\})\,]$$

The optimal plasticity range is $I = [\rho_e^*, \rho_u^*]$ where

$$\rho_e^* = \inf_{\xi \in \Omega} \rho^*(\xi)$$

$$\rho_u^* = \sup_{\xi \in \Omega} \rho^*(\xi)$$

Now consider the simplest developmental case where development occurs during $[0, D]$



Then the chosen optimal phenotypes are in range $[\rho_{e,D}^*, \rho_{u,D}^*]$

$$\rho_{e,D}^* = \inf_{\xi \in \Omega_{[0,D]}} \rho^*(\xi)$$

$$\rho_{u,D}^* = \sup_{\xi \in \Omega_{[0,D]}} \rho^*(\xi)$$

If $\{X_t\}$ is non-stationary on $[0, L]$, then may well have $\rho_{e,D}^* < \rho_e^* < \rho_u^* < \rho_{u,D}^*$; implying that development restricts plasticity range which is optimal due to deleterious effects in later life ~~by~~ on phenotypes chosen in the extremes

$$(\rho_{e,D}^*, \rho_e^*) \;\&\; (\rho_u^*, \rho_{u,D}^*)$$