

TUNDRA Coexistence Model - for sp. i

$$A(L) = aL$$

↑
light intercepted

photosynthesis per unit leaf area, $A(L)$



$$V_i = C_i LAI_i$$

↑ C_i

total leaf area

N_i

ramet popⁿ density

$$C_i = \phi H_i^\theta$$

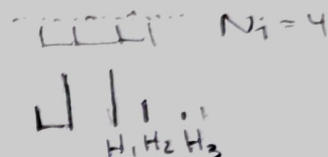
crown area of sp i

$$M_i = b H_i^p$$

carbon mass of ramet

H_i

ramet height - constant for sp. i



consider a system w/ Q species of heights H_i are ordered

$$H_Q < \dots H_i < H_j < \dots H_2 < H_1$$

↑ $j < i$ is the tallest species

$$\text{carbon gain} = A(L) v_i = a L^{\text{light}} C_i LAI_i$$

M_i = mass of carbon per ramet

$\frac{dM_i}{dt}$ = change in carbon per ramet per unit time

light situation:

$$L = e^{-k \sum_{j < i} N_j v_j}$$

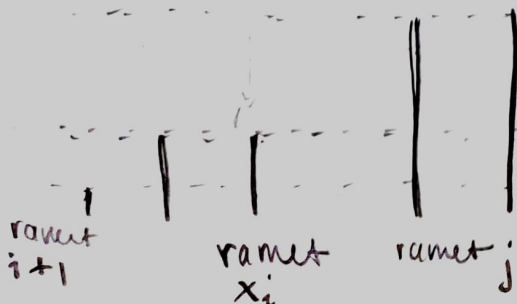
↑ everything above

$$\text{photosynthesis} = aL = a e^{-k \sum_{j < i} N_j v_j} - r v_i$$

respiration =

$$L_i = e^{-k \sum_{j \leq i} N_j v_j}$$

↑ extinction coefficient in



measure light here: $e^{-k \sum_{j < i} N_j v_j}$

measure light here: $e^{-k \sum_{j \leq i} N_j v_j}$

Light Environment

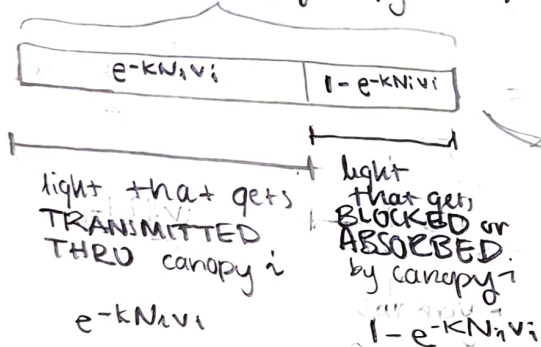
@ this level 100% illumination: $L_{Tot} = 100$

@ this level $L = L_{Tot} e^{-K \sum_{j=1}^i N_j V_j} =$ light that gets through $N_j V_j$ leaves and reaches top of i canopy

@ this level, $L = L_{Tot} e^{-K \sum_{j=1}^i N_j V_j} e^{-K N_i V_i} = L_{Tot} e^{-K \sum_{j=1}^i N_j V_j}$

$r_{j,1} \quad r_{i,1} \quad r_{i,2} \quad r_{i+1,1}$

total light hitting canopy $i = 1$



$$L_{r,i,x} = \frac{L_i}{N_i} \quad \text{light intercepted by an indiv. plant of sp. } i$$

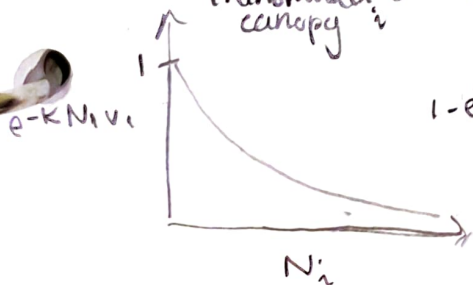
$$L_{r,i,1} + L_{r,i,2} = L_i$$

$$\text{Light intercepted by leaves of sp. } i = N_i V_i = e^{-K \sum_{j=1}^i N_j V_j} (1 - e^{-K N_i V_i})$$

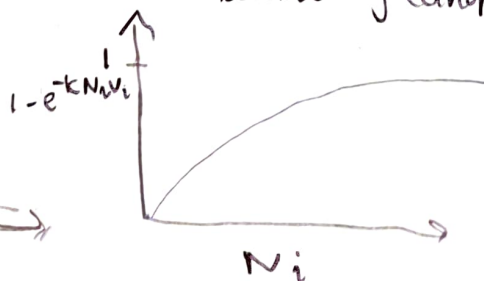
% of light that reaches canopy i

% of light absorbed by canopy $i = N_i V_i$

% light Transmitted THRU canopy i



% light BLOCKED by canopy i



CARBON accumulation per ramet

$$g_{r,i,x} = [A(L_{i,x}) - r_e - c_e] v_i$$

$$= \left[a \left(\frac{1}{N_i} \right) e^{-k \sum_{j=1}^n N_j v_j} (1 - e^{-k N_i v_i}) - r_e - c_e \right] v_i$$

we can write v_i in terms of height

$$\left[\frac{\text{carbon}}{\text{time}} \right] = \left[\frac{\text{carbon}}{\text{area} \cdot \text{time}} \right] \cdot \text{area}$$

per ramet

$$\frac{\text{carbon}}{\text{area} \cdot \text{day}} = \frac{\text{carbon}}{\text{area} \cdot \text{day}} \cdot \text{area}$$

Time required to make a baby ramet, T_i

$$g_{r,i,x} T_i = M_{i,x} = b H_i^\beta$$

↑

since babies are born full size, ramet must accumulate full biomass for its characteristic height H_i in order to reproduce

↓

$$b H_i^\beta = \left[a \left(\frac{1}{N_i} \right) e^{-k \sum_{j=1}^n N_j \phi H_j^\theta u} (1 - e^{-k N_i \phi H_i^\theta u}) - r_e - c_e \right] \phi H_i^\theta u T_i$$

assume that LAI_i per crown area is the same constant $u \forall i$ for now

$$v_i = C_i LAI_i = C_i u$$

$$= \phi H_i^\theta u$$

$$\frac{b}{\phi u} H_i^{\beta-\theta} = \left[a \left(\frac{1}{N_i} \right) e^{-k \phi u \sum_{j=1}^n N_j H_j^\theta} (1 - e^{-k \phi u N_i H_i^\theta}) - r_e - c_e \right] T_i$$

$$T_i = \frac{b H_i^{\beta-\theta}}{\phi u \left[a \left(\frac{1}{N_i} \right) \left(e^{-k \phi u \sum_{j=1}^n N_j H_j^\theta} - e^{-k \phi u N_i H_i^\theta} \right) - r_e - c_e \right]}$$

> 0 always

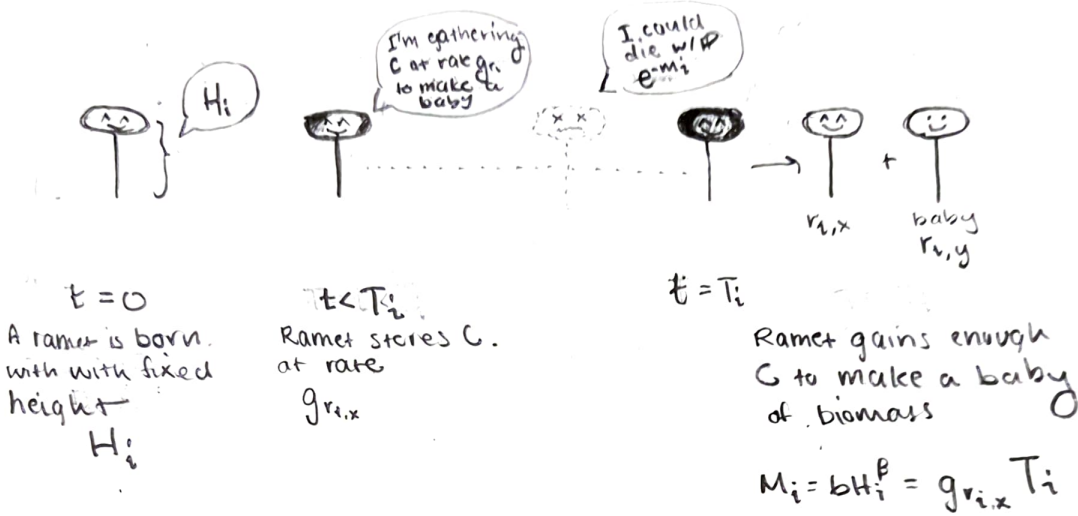
As $H_i \rightarrow \infty$, T_i increases as well

since $H_i^{\beta-\theta}$ increases

and from on the bottom $\rightarrow 0$

since essentially you move down the tail of e^{-x}

Formulation for lifetime reproductive success of Ramet $r_{i,x}$



Lifetime reproductive success = $\int_0^\infty (\text{survival to time } t) (\text{\# offspring born per time unit } dt) dt$

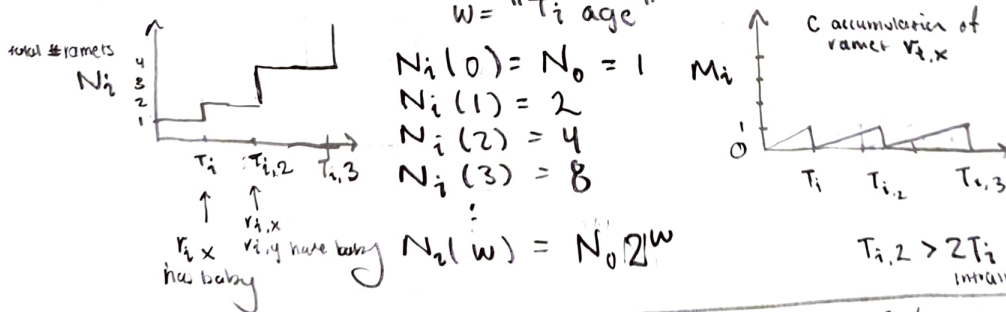
net reproductive rate (R_0) = $\sum_{w=0}^\infty (\text{survival to age } w) (\text{\# offspring produced at age } w)$

of offspring produced by Ramet in its lifetime

↑ "age" measured in time units T_i

↑ discrete individuals

We assume "pulsed" reproduction of discrete individuals ~ where once enough Carbon is accumulated, baby ramet "snaps" into being at full size. This means babies are only born at $t = T_i w$ ($w = 1, 2, \dots$) for each ramet



Note that $\int_0^\infty (e^{-m_i T_i}) (\text{\# offspring per unit time } T_i) dT_i = \frac{1}{T_i} \int_0^\infty e^{-m_i t} dt$

↑ survival to time T_i

↑ 1 per unit time T_i or $\frac{1}{T_i}$ per t

↑ but this is DISCRETE and can't be made int. small Δt i.e. $\lim_{T_i \rightarrow 0} dT_i = dt$ is FALSE biologically

if this were true $LRS = \left(\frac{1}{T_i}\right) \left(\frac{1}{m_i}\right) = 1$

$\Rightarrow T_i = \frac{1}{m_i}$

ALT. WORLD

as "bits of C" cannot also accumulate until full ramet size

In CLONAL RAMET WORLD, at equilibrium conditions $N_i(t) = \hat{N}_i$ $b(0) = 0$ $b(\infty) = 1$

$$LRS = \sum_{w=1}^{\infty} e^{-m_i T_i w} = \sum_{w=0}^{\infty} \left(\text{probability of survival to age } w \right) \left(\text{birth rate at age } w \right) \text{ of time increment } T_i$$

\uparrow
age measured in time units T_i

Recall the formulation for infinite sums of geometric series

$$\sum_{k=0}^{\infty} ar^k = \frac{a}{1-r} \quad \text{for } |r| < 1$$

$$= \sum_{w=1}^{\infty} (e^{-m_i T_i})^w \quad a=1, \quad r=e^{-m_i T_i}, \quad k=w$$

$$= - \left[e^{-m_i T_i} \right]_{w=0} + \sum_{w=0}^{\infty} e^{-m_i T_i w}$$

Subtract $w=0$ ↑
to change bounds

$$LRS = -1 + \left[\frac{1}{1 - e^{-m_i T_i}} \right]$$

rearranging

$$1 = -1 + \left[\frac{1}{1 - e^{-m_i T_i}} \right]$$



$$2 = \frac{1}{1 - e^{-m_i T_i}}$$

$$2(1 - e^{-m_i T_i}) = 1$$

$$2 - 2e^{-m_i T_i} = 1$$

$$e^{-m_i T_i} = \left(\frac{1-2}{-2} \right) = \frac{1}{2}$$

$$-m_i T_i = \ln\left(\frac{1}{2}\right) = -\ln(2) \quad \text{take the natural log}$$

$$T_i = \frac{\ln(2)}{m_i}$$

$$\text{Time to reproduce} = \frac{0.69}{\text{rate of death}}$$

*0.693147... transcendental number

Equilibrium values of \hat{N}_i

$$\frac{1}{T_i} = \frac{b}{\phi_u} H_i^{p-\theta} \left(a \left(\frac{1}{N_i} \right) \left[e^{-k\phi_u \sum_{j=1}^i \hat{N}_j H_j^\theta} - e^{-k\phi_u \sum_{j=1}^i N_j H_j^\theta} \right] - v_e - c_e \right) = \frac{\ln(z)}{m_i}$$

$$\frac{m_i b H_i^{p-\theta}}{\ln(z) \phi_u} = a \left(\frac{1}{N_i} \right) [e^{-\text{stuff}}] - v_e - c_e$$

$$N_i = a [e^{-i \text{stuff}} - e^{j \text{stuff}}] - N_i (v_e + c_e)$$

$$\frac{(1 + v_e + c_e) N_i}{a} = [e^{-\text{stuff}}] = e^{-k\phi_u \sum_{j=1}^i N_j H_j^\theta} (1 - e^{-k\phi_u N_i H_i^\theta})$$

$$\frac{(1 + v_e + c_e)}{a e^{-\sum_{j=1}^i N_j H_j^\theta}} N_i - 1 = -e^{-k\phi_u N_i H_i^\theta}$$

collect terms for ease

$$\frac{z}{j} N_i - 1 = -e^{-y N_i}$$

$$e^{-y N_i H_i^\theta} + \frac{z}{a e^{-y \sum_{j=1}^i N_j H_j^\theta}} N_i = 1$$

take ^{natural} log

$$\begin{aligned} y &= k\phi_u \\ z &= 1 + v_e + c_e \\ j &= \sum_{j=1}^i N_j H_j^\theta \\ h &= H_i^\theta \\ z' &= \frac{z}{a} \end{aligned}$$

$$-y N_i H_i^\theta + \log(z) + \log(N_i) - y \sum_{j=1}^i N_j H_j^\theta - \log(a) = 0$$

$$\log(N_i) - y H_i^\theta N_i - y \sum_{j=1}^i N_j H_j^\theta + \log\left(\frac{z}{a}\right) = 0$$

$$\log(x) - y h x - y j + \log\left(\frac{z}{a}\right) = 0 \quad \text{raise to exp}$$

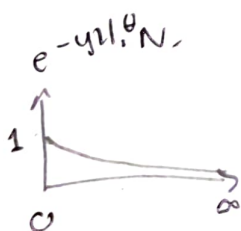
$$\left[\frac{1 - e^{-y H_i^\theta N_i}}{N_i} = \frac{\frac{m_i b H_i^{p-\theta}}{\ln(z) \phi_u + v_e + c_e}}{a e^{-y \sum_{j=1}^i N_j H_j^\theta}} \right]$$

$$x e^{-y h x} e^{-y j} \frac{z}{a} = 1$$

$$x e^{-y h x} = \frac{e^{y j}}{\frac{z}{a}}$$

$$x e^{-a x} = \frac{e^b}{\frac{c}{b}}$$

$$\log(x) - a x - b + \log(c)$$



ICK Lambert W???

At EQ we have

$$\frac{1 - e^{-\gamma N_i H_i^\theta}}{N_i} = \frac{Z}{a e^{-\gamma \sum_{j \neq i} N_j H_j^\theta}}$$

or you are the tallest sp. w/ height H_i

if all \hat{N}_j are small, then this becomes

"the sum of alot of small stuff" = "small" $\rightarrow 0$
 $e^{-[\text{small stuff} \approx 0]} = 1$

$$1 - e^{-\gamma N_i H_i^\theta} = \frac{Z}{a} N_i \Rightarrow N_i = \left(\frac{a}{Z}\right) (1 - e^{-\gamma N_i H_i^\theta})$$

but even this is still nasty?

Assume you are the best competitor.

$T_i =$... same expression

$$N_i = \left(\frac{a}{Z}\right) (1 - e^{-\gamma N_i H_i^\theta})$$

suppose your impact on your siblings was also minimal...

but this is weird bc you assume all competition terms are zero ?!!!??????

$$N_i \approx \frac{a}{Z}$$

rate of photosynthesis INCREASES w/ \hat{N}_i

$$\hat{N}_i \approx \frac{a}{Z} = \frac{a}{\frac{m_i b H_i^{1-\theta}}{\ln(2) \phi u} + r_e + C_d}$$

death rate m_i and height H_i both DECREASE \hat{N}_i

respiration of leaf area

construction cost of growth of leaf area