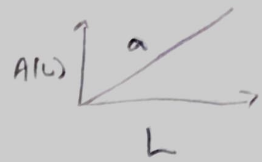
TUNDRA Coexistence Model - for sp. i

$A(L) = aL$ photosynthesis per unit leaf area.



$\uparrow$
light intercepted

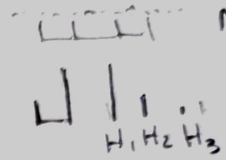
$V_i = C_i \, LAI_i$ ($\to C_i$) total leaf area

N_i ramet popⁿ density

$C_i = \phi H_i^{\theta}$ crown area of sp i

$M_i = bH_i^{\beta}$ carbon mass of ramet

H_i ramet height - constant for sp. i



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

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

$\underbrace{\qquad\qquad}_{j<i}$ $\uparrow$ is the tallest species

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 :

everything above

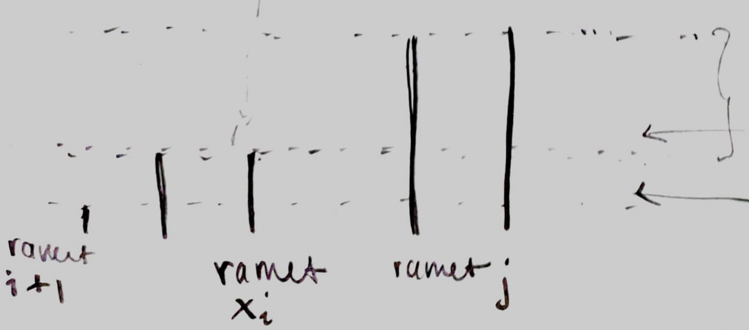
$$L = e^{-k \sum_{j<i}^{Q} N_j v_j}$$

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

respiration =

extinction coefficient in

$$L_i = e^{-k \sum_{j \le i}^{Q} N_i v_i}$$



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

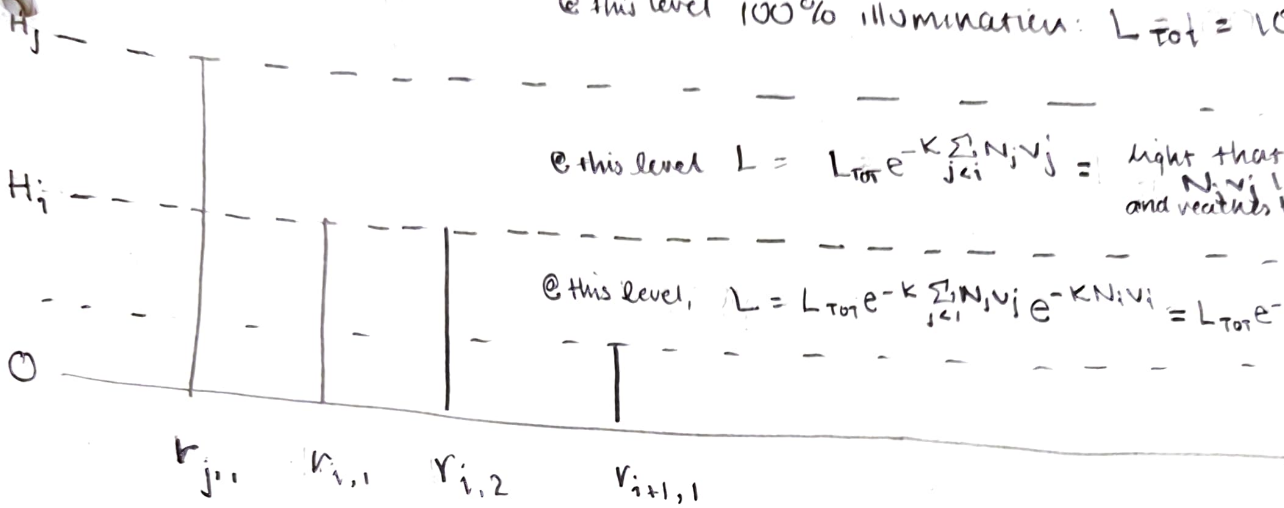
measure light here : $e^{-k \sum_{j=i}^{Q} N_j v_j}$

Light Environment

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

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

@ this level, $L = L_{TOT} e^{-K \sum_{j<i} N_j v_j} e^{-K N_i v_i} = L_{TOT} e^{-K \sum_{j=1}^{i} N_j v_j}$



total light hitting canopy i = 1

$\underbrace{\boxed{e^{-KN_iv_i}} \boxed{1-e^{-KN_iv_i}}}_{}$

light that gets TRANSMITTED THRU canopy i
$e^{-KN_iv_i}$

light that gets BLOCKED or ABSORBED by canopy i
$1-e^{-KN_iv_i}$

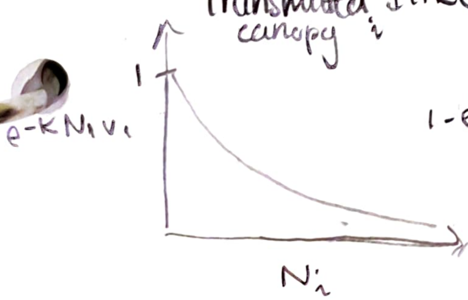
$L_{r_{i,x}} = \dfrac{L_i}{N_i}$ light intercepted by an indiv. ramet of sp. i

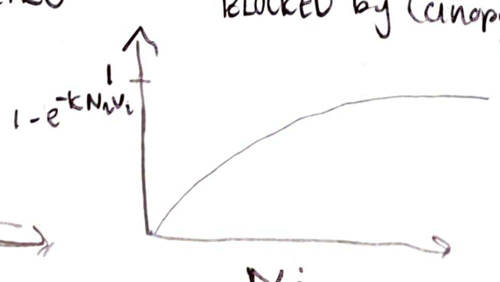
$L_{r_{i,1}} + L_{r_{i,2}} = L_i$

Light intercepted by leaves of sp i $N_i v_i$ $= e^{-K \sum_{j<i} N_j v_j} \left(1 - e^{-K N_i v_i}\right)$

% of light that reaches canopy i

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





CARBON accumulation per ramet

$$gr_{i,x} = \left[A(L_{i,x}) - r_e - c_e\right] v_i$$

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

we can write v_i in terms of height

$\left[\frac{\text{carbon}}{\text{time}}\right]$ per ramet $= \left[\frac{\text{carbon}}{\text{area}\cdot\text{time}}\right.$ $\frac{\text{carbon}}{\text{area}\cdot\text{day}}$ $\frac{\text{carbon}}{\text{area}\cdot\text{day}}$ area $=$

Time required to make a baby ramet: T_i

$$gr_{i,x} T_i = M_{i,x} = bH_i^\beta$$

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

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

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

$$v_i = C_i LAI_i = C_i u$$
$$= \phi H_i^\theta u$$

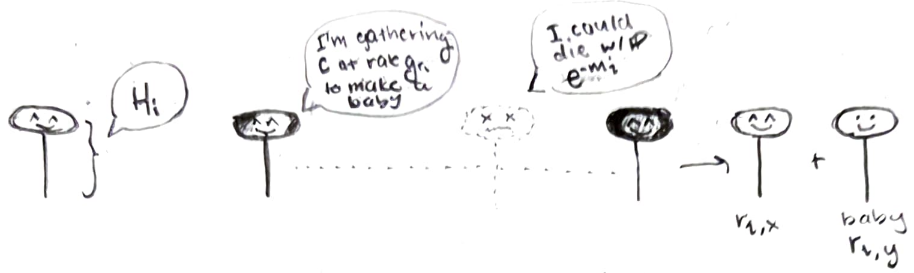
$$\frac{b}{\phi u} H_i^{\beta-\theta} = \left[a\left(\frac{1}{N_i}\right) e^{-k\phi u\sum_{j<i} N_j H_j^\theta}\left(1 - e^{-k\phi u N_i H_i^\theta}\right) - r_e - c_e\right] T_i$$

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

> 0 always

As $H_i \to \infty$, T_i increases as well
since $H_i^{\beta-\theta}$ increases
and term on the bottom $\to 0$
since essentially you move down the tail of e^{-x}

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



$t = 0$
A ramet is born with with fixed height H_i

$t < T_i$
Ramet stores C at rate $g_{r_{i,x}}$

$t = T_i$
Ramet gains enough C to make a baby of biomass

$$M_i = bH_i^{\beta} = g_{r_{i,x}} T_i$$

bc of "full ramet" reproduction this = 0 a lot of the time

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

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

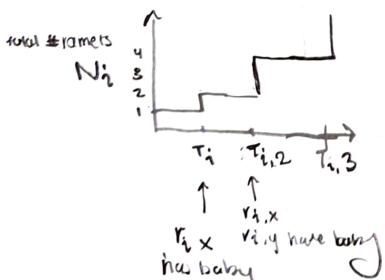
# of offspring produced by Ramet in it's lifetime

"age" measured in time units T_i

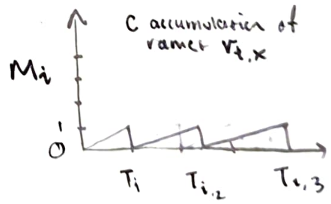
discrete individuals

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 $t = T_i w$ $(w = 1, 2, \ldots)$ for each ramet

$w =$ "T_i age"



$N_i(0) = N_0 = 1$
$N_i(1) = 2$
$N_i(2) = 4$
$N_i(3) = 8$
$\vdots$
$N_i(w) = N_0 2^w$



$T_{i,2} > 2T_i$ due to density intraspecific dependence

Note that $\int_0^\infty (e^{-m_i T_i})$ (# 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 inf. small i.e taking the limit

$\lim_{T_i \to 0} dT_i = dt$ is FALSE biologically as "bits of C" cannot also accumulate C until full ramet size

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

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

$b(>0) = 1$

age measured in time units T_i

$$LRS = \sum_{w=1}^{\infty} e^{-m_i T_i w} = \sum_{w=0}^{\infty} \underbrace{(\text{survival to age } w)}_{\text{probability of}} \underbrace{(\text{birth rate at age } w)}_{b(w)}$$

of time increment T_i

Recall the formulation for infinite sums of geometric series

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

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

$$= -\underbrace{\left[e^{-m_i T_i (0)}\right]}_{\substack{\text{subtract} \\ w=0}} + \underbrace{\sum_{w=0}^{\infty} e^{-m_i T_i w}}_{\text{to change bounds}}$$

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

rearranging

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

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

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

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

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

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

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

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

*0.693147... transcendental number

Equilibrium values of $\hat{N}_i$

$$\hat{T}_i = \frac{b}{\phi u} H_i^{\beta-\theta}\left(\frac{1}{a\left(\frac{1}{N_i}\right)\left[e^{-k\phi u\sum_{j<i}\hat{N}_j H_j^\theta} - e^{-k\phi u \sum_{j\le i} N_j H_j^\theta}\right] - r_e - c_e}\right) = \frac{\ln(2)}{m_i}$$

$$\underbrace{\frac{m_i b H_i^{\beta-\theta}}{\ln(2)\phi u}} = a\left(\frac{1}{N_i}\right)\left[e^{-\text{ stuff}}\right] - r_e - c_e$$

$$M N_i = a\left[e^{-j<i\text{ stuff}} - e^{j\le i\text{ stuff}}\right] - N_i(r_e + c_e)$$

$$\frac{(M + r_e + c_e)}{a} N_i = [e - \text{stuff}] = \underbrace{e^{-k\phi u\sum_{j<i}N_jH_j^\theta}}_{e^{-j\text{stuff}}}\left(1 - e^{-k\phi u N_i H_i^\theta}\right)$$

$$\frac{(M + r_e + c_e)}{a e^{-\text{sp}, j\text{ stuff}}} N_i - 1 = -e^{-k\phi u N_i H_i^\theta}$$

Collect terms for ease

$y = k\phi u$

$z = M + r_e + c_e$

$j = \sum_{j<i} N_j H_i^\theta$

$h = H_i^\theta$

$z' = \frac{z}{a}$

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

$$e^{-yN_iH_i^\theta} + \frac{z}{a e^{-y\sum_{j<i}N_jH_j^\theta}} N_i = 1$$

take natural log

$$-yN_iH_i^\theta + \log(z) + \log(N_i) - y\sum_{j<i}N_jH_j^\theta - \log(a) = 0$$

$$\log(N_i) - yH_i^\theta N_i - y\sum_{j<i}N_jH_j^\theta + \log\left(\frac{z}{a}\right) = 0$$

$$\log(x) - \underbrace{yh}_{a}\,x - \underbrace{yj}_{b} + \log\underbrace{\left(\frac{z}{a}\right)}_{c} = 0$$

raise to exp

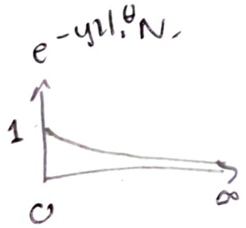
$$x e^{-yhx} e^{-yj}\frac{z}{a} = 1$$

$$x e^{-yhx} = \frac{e^{yj}}{c}$$

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

$$\left[\frac{1 - e^{-yH_i^\theta N_i}}{N_i} = \frac{\frac{m_i b H_i^{\beta-\theta}}{\ln(2)\phi u} + r_e + c_e}{a e^{-y\sum_{j<i}N_jH_j^\theta}}\right]$$

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



ICK lambert W??!?

At EQ we have

$$\frac{1 - e^{-yN_iH_i^0}}{N_i} = \frac{z}{a\, e^{-y\sum_{j\in 1} N_j H_i^0}}$$

if all $\hat{N}_j$ are small, then this becomes
"the sum of alot of small stuff" = "small" → 0
$e^{-[\text{small stuff} \approx 0]} = 1$

$$1 - e^{-yN_iH_i^0} = \frac{z}{a} N_i$$

but even this is still nasty?