MaxW optimisation hypothesis - as in McM & Dewar (2013, New Phytol accepted)

Following referee reports from New Phytol, N concns were converted to N:C ratios, units were converted from DM to C & g N to kg N (10/4/2013, Bk38, p102).

Eqns for leaf photosynthesis in Dewar et al (2012 Tree Physiol) Book 35, p 210

Roddy's comments in red

Parameters are from Dewar et al (2012) (kN<kL paper, Tree Physiol)

Photosynthesis & C balance parameters (from Dewar et al 2012, Tree Physiol)

$\omega := 0.49$ C content of biomass

$Mastar := 0.181$ Leaf mass per unit area at base of canopy (kg DM/m2)

$Nf := \frac{14}{\omega} \cdot 0.001$ $Nf = 0.029$ Leaf N:C ratio (g N / g C) (used as initial guess for root fn, taken from simulated value in Dewar et al 2012, Table 3))

$Nabase := Nf \cdot Mastar \cdot \omega$ Fix Narea at base of canopy (kg N/m2) $Nabase = 2.534 \times 10^{-3}$

$KL := 0.43$ Light extinction coefft

$Ntot := 21.6 \cdot 10^{-3}$ Total canopy N content (kgN/m2) (Simulated value from Table 3 of Dewar et al 2012)

$An := 2.09 \cdot 10^{-3}$ Slope of Amax vs Narea relationship (mol/kgN/s)

$No := 4 \cdot 10^{-4}$ Minimum N area for photosynthesis (kgN/m2)

$\alpha := 0.06$ Quantum efficiency

$Rleaf := 0.09 \cdot 2 \cdot 10^{-3}$ Leaf maintenance respiration rate (mol/kgN/s) Multiplied by 2 to account for CUE = 0.5

$Rleaf := 0.0$ Set Rleaf = 0 and redefine CUE to be whole-plant CUE.

$Io := 611 \cdot 10^{-6}$ Incident photosynthetically active radiation (mol/m2/s), Dewar et al 2012

$CUE := 0.5$ Check value in Dewar et al (2012) Tree Physiol): value in Dewar et al (2012) is probably too low since it referred to non-foliar CUE.

$CUE := 0.45$ With Rleaf = 0, CUE = whole-plant CUE (10% reduction because our CUE is net of leaf respiration, whereas Dewar (2012) included leaf daytime respiration in eqn for leaf net photosynthesis)

$Tauf := 8$ Leaf lifespan (yrs)

$Taur := 1$ Root lifespan (yrs)

Conversion of GPP from mol/m2/s to kg C/m2/y (Dewar et al 2012)

$Daysperyear := 209$ Growing season length (days)

$Hoursperday := 14.15$ Daylight length (hrs) $Daysperyear \cdot Hoursperday \cdot 60 \cdot 60 = 1.0646 \times 10^{7}$

$Convfactor := Daysperyear \cdot Hoursperday \cdot \frac{60 \cdot 60 \cdot 12}{10^{3}}$ Conversion factor: Seconds per year (cf Dewar et al 2012 Tree Physiol 1.0646*10^7) $Convfactor = 1.278 \times 10^{5}$

Root & N uptake paramters (McM et al 2012, Ecol & Evoln):

Use parameter values for sweetgum in McM et al (2012) (Bk34, p185-190) . Code is from file OptRootDepth201204261.mcd:

$ro := 0.017$ root radius (cm)

$\rho r := 0.38$ root tissue density (g/cm3)

$Lro := 0.76678$ root length density at half max U /cm2 (Bk35, p145)

$Ro := \pi \cdot ro^{2} \cdot \rho r \cdot Lro$ $Ro = 0.000265$ root mass density at half max U g DM/cm3

$Ro := Ro \cdot 1000 \cdot \omega$ $Ro = 0.129628$ Convert to kg C /m3

$Umax1 := 0.012$ $Umax2 := 0.008$ Annual supply of available soil N. aka Potential annual N uptake (gN/m2 ground/year)

$Do := 0.6$ Length scale for exponential decline (m) $Ro \cdot Do = 0.07778$

$Nr := \frac{7}{\omega} \cdot 10^{-3}$ Root N:C ratio $Nr = 0.01429$

$Nw := \frac{1.5}{\omega} \cdot 10^{-3}$ Wood N:C ratio $Nw = 0.003061$

$Nr := 0.015$ $Nw := 0.003$ Rounded values of N:C ratios used in McM & Dewar (2013) New Phytol

$Retrans := 0.5$ Fraction of leaf N retranslocated at senescence

Photosynthesis Eqns (rectangular hyperbolic light response, Dewar et al 2012, Tree Physiol)

$Asat(na) := An \cdot (na - No)$ Light saturated photosynthesis (umol/m2/s)

$I(lai) := KL \cdot Io \cdot \exp(-KL \cdot lai)$ Light incident on leaves at canopy top(umol/m2/s)

$$Aa(lai, na) := \left[\frac{1}{\left(\frac{1}{Asat(na)} + \frac{1}{\alpha \cdot I(lai)} \right)} - Rleaf \cdot na \right] \cdot Convfactor$$

Net leaf photosynthesis (kgC/m2/y). Respiration - see Bk 36, p149; Bk 37, p14-23; p 38- $Aa(0, 0.003) = 0.516$

$$dAdN(lai, na) := \left[\frac{An}{\left(1 + \frac{Asat(na)}{\alpha \cdot I(lai)}\right)^{2}} - Rleaf \right] \cdot Convfactor$$

Slope (kgC/kgN/y) of Aarea versus Narea relationship

Solution derived by Lagrange multiplier method (Bk 35, p210)

Dimensionless variable

$\varsigma(nabase) := \frac{An \cdot nabase}{\alpha \cdot KL \cdot Io}$ $\varsigma(Nabase) = 0.336$

$$ExpKLcrit(ltot, nabase) := \frac{\sqrt{\frac{1}{\left(1 - \frac{No}{nabase}\right)} + \zeta(nabase)\,\exp(KL \cdot ltot) - 1}}{\zeta(nabase) \cdot \left(1 - \frac{No}{nabase}\right)}$$

$$Lcrit(ltot, nabase) := \frac{1}{KL} \cdot \ln(ExpKLcrit(ltot, nabase)) \qquad Lcrit(5, Nabase) = 2.977 \qquad Lcrit(0.5, Nabase) = -0.139$$

For given Ntot, value of Lcrit < 0 when ltot is low. Then Na = Nabase throughout canopy. Ltot=Ntot/Nabase and Lcrit = 0 (Bk 36, p104)

$$Lcrit(ltot, nabase) := if(Lcrit(ltot, nabase) > 0, Lcrit(ltot, nabase), 0) \qquad Lcrit(5, Nabase) = 2.977 \qquad Lcrit(0.5, Nabase) = 0$$

$$ExpKLcrit(ltot, nabase) := if(Lcrit(ltot, nabase) > 0, ExpKLcrit(ltot, nabase), 1) \quad ExpKLcrit(5, Nabase) = 3.597 \quad ExpKLcrit(0.5, Nabase) = 1$$

Total canopy N (kg N/m2 ground) as function of total LAI & Lcrit (Bk 37, Eqn14.5):

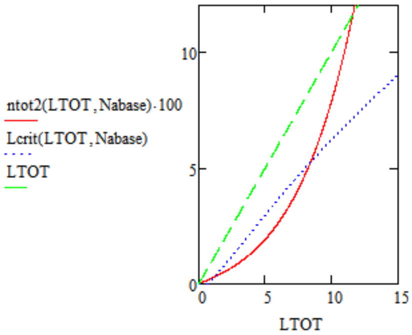
$$ntot2(ltot, nabase) := \left[\frac{\alpha \cdot Io}{An} \cdot \left(\sqrt{\frac{1}{1 - \frac{No}{nabase}} + \zeta(nabase) \cdot \exp(KL \cdot ltot) - 1}\right) \cdot \left(1 - \frac{1}{ExpKLcrit(ltot, nabase)}\right)\right] + nabase \cdot ltot - (nabase - No) \cdot Lcrit(ltot, nabase) \qquad ntot2(5, Nabase) = 0.019207$$

NB If Lcrit<=0, Ntot=Ltot*Nabase (Bk35, p105)

$$ntot2(ltot, nabase) := if(Lcrit(ltot, nabase) > 0, ntot2(ltot, nabase), ltot \cdot nabase) \qquad ntot2(5, Nabase) = 0.019207 \qquad ntot2(0.5, Nabase) = 0.001267$$

$$LTOT := 0, 0.01 .. 15$$

Check for continuity of ntot2 at L = Lcrit



Contributions to canopy photosynthesis (mol/m2/s) from upper canopy (0<lai<Lcrit) (**atotup**) & lower canopy (Ltot<lai<Lcrit) (**atotlow**):

Simplifed expression for Atot (Bk 36, p10-12) (Next 2 eqns apply only when No=0):

$$atotup(ltot, nabase) := \alpha \cdot Io \cdot \left(1 - \frac{1 + \zeta(nabase)}{\sqrt{1 + \zeta(nabase) \cdot \exp(KL \cdot ltot)}}\right) \qquad atotup(5, Nabase) = 1.181 \times 10^{-5} \qquad atotup(0.5, Nabase)$$

$$atotlow(ltot, nabase) := An \cdot nabase \cdot \left(ltot - \frac{1}{KL} \cdot \ln\left(\frac{1 + \zeta(nabase) \cdot \exp(KL \cdot ltot) - \sqrt{1 + \zeta(nabase) \cdot \exp(KL \cdot ltot)}}{\zeta(nabase)}\right)\right) \qquad atotlow(5, Nabase) = 5.054 \times 10^{-6} \qquad atotlow(0.5, Nabase$$

Expressions for Atot (mol/m2/s) as function of Ltot & Lcrit (Bk 37, p16-17; Bk 36, p10-12):

$$atotup(ltot, nabase) := \alpha \cdot Io \cdot \left(1 - \frac{1}{ExpKLcrit(ltot, nabase)}\right) \cdot \left(1 - \frac{1}{\sqrt{\frac{1}{1 - \frac{No}{nabase}} + \zeta(nabase) \cdot \exp(KL \cdot ltot)}}\right) \qquad atotup(5, Nabase) = 1.335 \times 10^{-5} \qquad atotup(0.5, Nabase$$

$$atotlow(ltot, nabase) := An \cdot (nabase - No) \cdot \left[ltot - Lcrit(ltot, nabase) - \frac{1}{KL} \cdot \ln\left[\frac{1 + \zeta(nabase) \cdot \left(1 - \frac{No}{nabase}\right) \cdot \exp(KL \cdot ltot)}{1 + \zeta(nabase) \cdot \left(1 - \frac{No}{nabase}\right) \cdot ExpKLcrit(ltot, nabase)}\right]\right]$$

$$Lcrit(5, Nabase) = 2.977 \qquad Lcrit(0.5, Nabas$$

$$atotlow(5, Nabase) = 3.522 \times 10^{-6} \qquad atotlow(0.5, Na$$

$$atot2(ltot, nabase) := atotup(ltot, nabase) + atotlow(ltot, nabase) \qquad atot2(5, Nabase) = 1.687 \times 10^{-5} \qquad atot2(0.5, Nab$$

NB If Lcrit<=0, Na(L)=Nabase throughout canopy. Incorporate in Eqn for Atot (Bk35, p105),(Bk37,eqn 16.3 with Lcrit=0)

$$atot2(ltot, nabase) := if\left[Lcrit(ltot, nabase) > 0, atot2(ltot, nabase), An \cdot (nabase - No) \cdot \left[ltot - \frac{1}{KL} \cdot \ln\left[\frac{1 + \zeta(nabase) \cdot \left(1 - \frac{No}{nabase}\right) \cdot \exp(KL \cdot ltot)}{1 + \zeta(nabase) \cdot \left(1 - \frac{No}{nabase}\right)}\right]\right]\right] \qquad atot2(0.5, Na$$

Incorporate leaf maintenance respiration (mol/m2/s) = Rleaf (mol/kgN/s) *Ntot (kgN/m2) (Bk 37, p16-23;p38-)

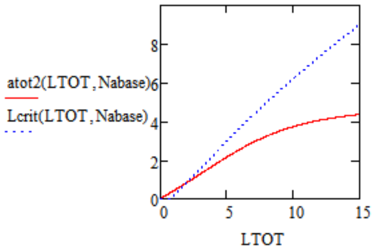
$$atot2(ltot, nabase) := atot2(ltot, nabase) - Rleaf \cdot ntot2(ltot, nabase)$$

Convert Atot from mol/m2/s to kg C / m2 /year

$$atot2(ltot, nabase) := atot2(ltot, nabase) \cdot Convfactor$$

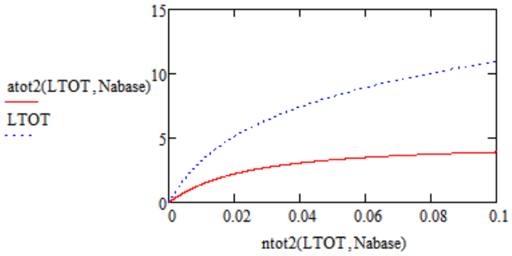
Convfactor

Check for continuity of Atot at L=Lcrit



GRAPH Atot (kgC/m2/s) & Ltot versus Ntot (kg N/m2):

Atot (kgC/m2/s) & Ltot versus Ntot (kg N/m2):



Determine optimal Ltot for given total canopy N (Ntot):

$\mathrm{Ltotsoln} := 3$ $\qquad$ $\mathrm{TOL} := 10^{-9}$ $\qquad$ NB: Roddy reduced TOL from 10-3 (default) to 10-6

$\mathrm{Ltotopt2(nabase, ntot)} := \mathrm{root(ntot2(Ltotsoln, nabase) - ntot, Ltotsoln)}$ $\qquad$ $\mathrm{Ltotopt2(Nabase, Ntot)} = 5.357$ $\qquad$ $\mathrm{ntot2(Ltotopt2(Nabase, Ntot), Nabase)} = 0.022$

Determine Atot as function of Ntot (after Ltot is eliminated numerically):

$\mathrm{AtotVsNtot(nabase, ntot)} := \mathrm{atot2(Ltotopt2(nabase, ntot), nabase)}$ $\qquad$ $\mathrm{AtotVsNtot(Nabase, Ntot)} = 2.304$

Does Atot Vs Ntot relationship pass through origin? (Bk 36, p104):

$\mathrm{AtotVsNtot(Nabase, 0)} = 0$

is this discrepancy related to the discrepancy between lambda1 and dAtot/dNtot (below)?
YES it is. Reducing TOL to 10-6 resolves both discrepancies.

Optimal profiles of Leaf N (kg N m-2) & Aa (kgC m-2 y-1):

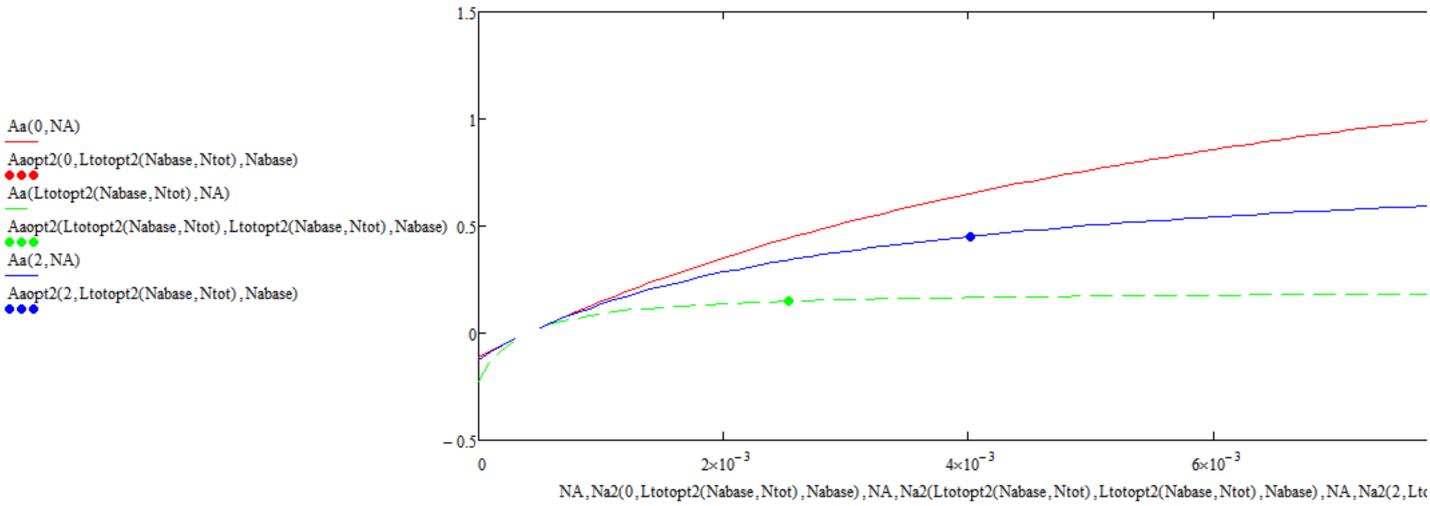
$$\mathrm{Na2(lai, ltot, nabase)} := \mathrm{if}\left[\mathrm{lai} < \mathrm{Lcrit(ltot, nabase)}, \mathrm{No} + \frac{\alpha\cdot \mathrm{KL}\cdot \mathrm{Io}\cdot \exp(-\mathrm{KL}\cdot \mathrm{lai})}{\mathrm{An}}\cdot\left[\sqrt{\frac{1}{\left(1-\frac{\mathrm{No}}{\mathrm{nabase}}\right)} + \zeta(\mathrm{nabase})\cdot\exp(\mathrm{KL}\cdot\mathrm{ltot})} - 1\right], \mathrm{nabase}\right]$$

$\mathrm{Na2}(0, 5, 0.003) = 8.979 \times 10^{-3}$

$\mathrm{Aaopt2(lai, ltot, nabase)} := \mathrm{Aa(lai, Na2(lai, ltot, nabase))}$ $\qquad$ kg C/m2/y $\qquad$ $\mathrm{Aaopt2(0, Ltotopt2(Nabase, Ntot), Nabase)} = 1.07$

$\frac{\mathrm{Aaopt2(0, Ltotopt2(Nabase, Ntot), Nabase)}}{\mathrm{Convfactor}}\cdot 10^{6} = 8.374$ umol /m2/s

$\mathrm{NA} := 0, 0.0001 .. 0.01$



Slope at L=0 $\quad \mathrm{dAdN(0, Na2(0, Ltotopt2(Nabase, Ntot), Nabase))} = 58.686$

Slope at L=2 $\quad \mathrm{dAdN(2, Na2(2, Ltotopt2(Nabase, Ntot), Nabase))} = 58.686$

Slope at L=Ltot $\quad \mathrm{dAdN(Ltotopt1, Na2(Ltotopt2(Nabase, Ntot), Ltotopt2(Nabase, Ntot), Nabase))} =$

N balance: MaxNup hypothesis (Root optimisation paper - McM et al 2012 Ecol & Evoln):

$$utot1(dmax, umax) := umax\cdot\left(1 - \exp\left(\frac{-dmax}{2\cdot Do}\right)\right)^2$$

Utot (kgN/m2/y) as fn of Dmax (m) (McM et al 2012, Ecol & Evoln, Eqn 10)

$$rtot1(umax, utot) := 2\cdot Ro\cdot Do\cdot\left(\frac{\sqrt{\frac{utot}{umax}}}{1-\sqrt{\frac{utot}{umax}}} + \ln\left(1-\sqrt{\frac{utot}{umax}}\right)\right)$$

Rtot (kg C/m2) as fn of Utot (McM et al 2012, Ecol & Evoln Eqn 12)

$$rtot2(dmax) := Ro\cdot\left[2\cdot Do\cdot\left(\exp\left(\frac{dmax}{2\cdot Do}\right)-1\right) - dmax\right]$$

Max rooting depth (m) (McM et al 2012, Ecol & Evoln, Eqn 8)

$rtot2(1.1) = 0.091$

$dmaxsoln := 1$

$dmax1(rtot) := root(rtot2(dmaxsoln) - rtot, dmaxsoln)$

$dmax1(0.543) = 2.216$

Determine Utot (kg N/m2/y) from Rtot (kg C/m2/y):

$Utotsoln := Umax1\cdot 0.5$

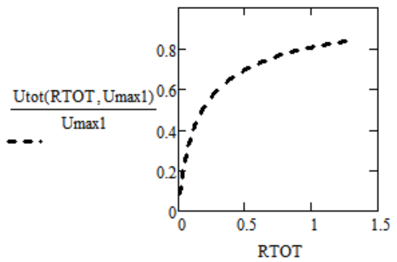
Initial guess of Utot (kg N /m2/y) must be < Umax. (If problem converging, I could make Utotsoln non-rectang hyp fn of Rtot (Umax/(1+Ro*Do/Rtot)

$Utot(rtot, umax) := root(rtot1(umax, Utotsoln) - rtot, Utotsoln)$

$Utot(0.2, Umax1) = 6.197\times 10^{-3}$

$RTOT := 0.01, 0.02 .. 2$

N uptake as fraction of Umax (f) versus Rtot:



NB This function may not converge. If wish to plot, might be better to graph both Utot & Rtot as functions of max rooting depth Dmax (variable Z in OptRootDepth201204261.mcd)

Does Utot Vs Rtot relationship pass through origin? YES!

$rtot1(Umax1, 0) = 0$

N balance (Phi = Utot/Umax, see McM et al (2012, Ecol & Evoln)

$$Phi(cw, nr, ntot, rtot, umax) := \left[\frac{ntot\cdot(1-Retrans)}{Tauf} + \frac{rtot\cdot nr}{Taur} + cw\cdot Nw\right]\cdot\frac{1}{umax}$$

USE FORMULA BASED ON BOTTOMS OF CANOPY & ROOT SYSTEM TO EXPRESS Dmax AS FUNCTION OF Ltot (Bk 36, p122):

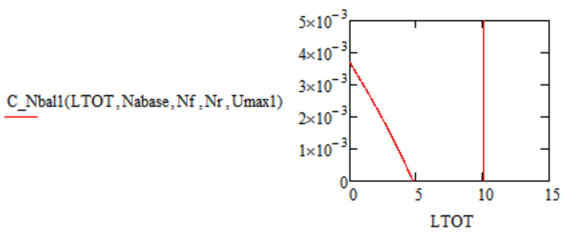
$$DmaxVsLtot(ltot, nabase, nf, nr, umax) := Do\cdot\left[\ln\left(\frac{umax\cdot Taur}{Ro\cdot Do}\right) - \ln\left[\frac{(1-Retrans)}{CUE\cdot Convfactor\cdot Tauf\cdot\left(\frac{An}{\frac{1}{1-\frac{No}{nabase}} + \zeta(nabase)\cdot\exp(KL\cdot ltot)} - Rleaf\right) - \frac{1}{nf}} + nr\right]\right]$$

$DmaxVsLtot(5, Nabase, Nf, Nr, Umax1) = 1.306$

Relnsp betw Dmax & Ltot derived from C-N conservation eqn (Bk 36, p123):

$$C\_Nbal(dmax, ltot, nabase, nf, nr, umax) := utot1(dmax, umax) - Nw\cdot CUE\cdot atot2(ltot, nabase) - \frac{ntot2(ltot, nabase)}{Tauf}\cdot\left(1 - Retrans - \frac{Nw}{nf}\right) - \frac{rtot2(dmax)}{Taur}\cdot(nr - Nw)$$

$C\_Nbal1(ltot, nabase, nf, nr, umax) := C\_Nbal(DmaxVsLtot(ltot, nabase, nf, nr, umax), ltot, nabase, nf, nr, umax)$



$$cwmax(dmax, ltot, nabase, nf) := CUE\cdot atot2(ltot, nabase) - \frac{ntot2(ltot, nabase)}{nf\cdot Tauf} - \frac{rtot2(dmax)}{Taur}$$

Determine optimal Ltot, Dmax, Atot, Ntot, Cw

$Ltotsol := 5$

Ltotopt(nabase, nf, nr, umax) := root(C_Nbal1(Ltotsol, nabase, nf, nr, umax), Ltotsol)

Ltotopt(nf, nr, umax) := Ltotopt(nf·Mastar·ω, nf, nr, umax)　　Ltotopt(Nf, Nr, Umax1) = 4.757

Dmaxopt(nf, nr, umax) := DmaxVsLtot(Ltotopt(nf, nr, umax), nf·Mastar·ω, nf, nr, umax)　　Dmaxopt(Nf, Nr, Umax1) = 1.313

Atotopt(nf, nr, umax) := atot2(Ltotopt(nf, nr, umax), nf·Mastar·ω)　　Atotopt(Nf, Nr, Umax1) = 2.052

Ntotopt(nf, nr, umax) := ntot2(Ltotopt(nf, nr, umax), nf·Mastar·ω)　　Ntotopt(Nf, Nr, Umax1) = 0.0177

Rtotopt(nf, nr, umax) := rtot2(Dmaxopt(nf, nr, umax))　　Rtotopt(Nf, Nr, Umax1) = 0.139

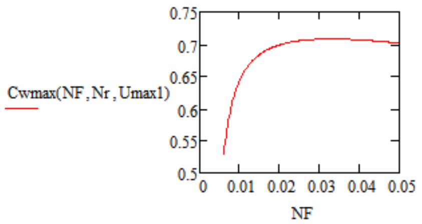
Cwmax(nf, nr, umax) := cwmax(Dmaxopt(nf, nr, umax), Ltotopt(nf, nr, umax), nf·Mastar·ω, nf)　　Cwmax(Nf, Nr, Umax1) = 0.707

Utotopt(nf, nr, umax) := Phi(Cwmax(nf, nr, umax), nr, Ntotopt(nf, nr, umax), Rtotopt(nf, nr, umax), umax)·umax　　Utotopt(Nf, Nr, Umax1) = 0.005312

Is there also an optimum for Nf? Graph max Cwmax versus Nf

What are optimal GPP, Ftot, LAI, SLA?

NF := 0.006, 0.0062 .. 0.05



Are optimal values of other variables sensitive to value of Nf?

$$\mathrm{Cfopt}(nf, nr, umax) := \frac{\mathrm{Ntotopt}(nf, nr, umax)}{nf \cdot \mathrm{Tauf}}$$

$$\mathrm{SLAopt}(nf, nr, umax) := \frac{\mathrm{Ltotopt}(nf, nr, umax) \cdot \omega}{\mathrm{Cfopt}(nf, nr, umax) \cdot \mathrm{Tauf}}$$

$$\mathrm{Cropt}(nf, nr, umax) := \frac{\mathrm{Rtotopt}(nf, nr, umax)}{\mathrm{Taur}}$$

$$\mathrm{Ftotopt}(nf, nr, umax) := \frac{\mathrm{Ntotopt}(nf}{n}$$

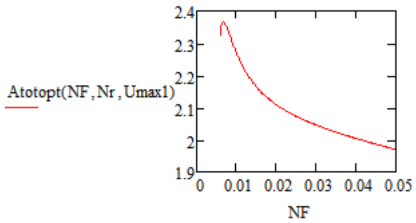
$$\mathrm{LMAav}(nf, nr, umax) := \frac{\mathrm{Ftotopt}(nf, nr, umax)}{\mathrm{Ltotopt}(nf, nr, umax) \cdot \omega}$$

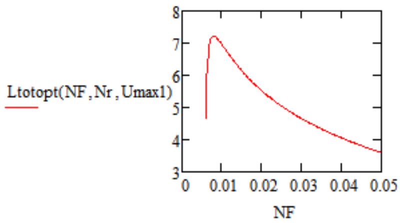
$$\mathrm{Rav}(nf, nr, umax) := \frac{\mathrm{Rtotopt}(nf, nr, umax)}{\mathrm{Dmaxopt}(nf, nr, umax)}$$

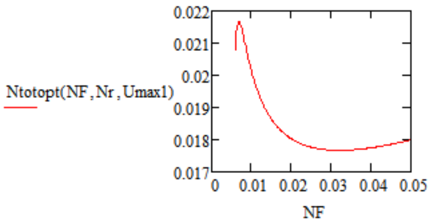
$$\mathrm{RLDav}(nf, nr, umax) := \frac{\mathrm{Rav}(nf, nr, umax)}{\pi \cdot ro^2 \cdot \rho r \cdot 1000 \cdot \omega}$$

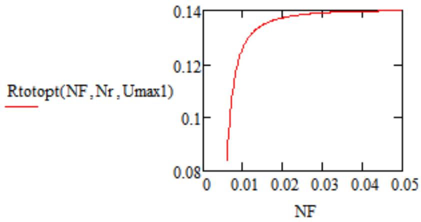
Average root length density (cm/cm3 soi volume)

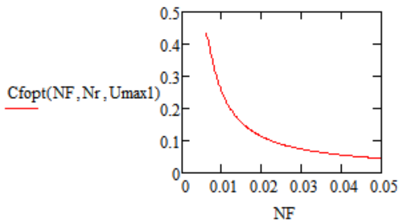
NPPopt(nf, nr, umax) := Cfopt(nf, nr, umax) + Cropt(nf, nr, umax) + Cwmax(nf, nr, umax)

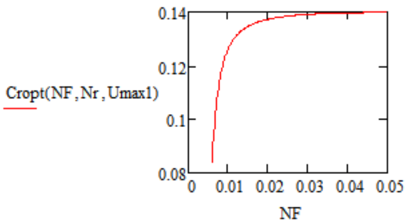


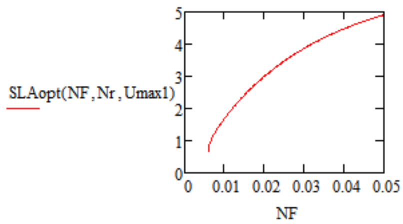






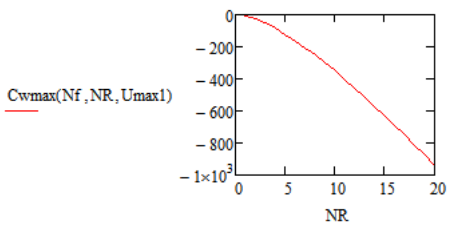






Is there also an optimum for Nr? Graph max Cw versus Nr

NR := 1, 2 .. 20



Determine optimal soln for leaf N:C ratio Nfopt (kg N / kg C) **& other variables for Umax1 & Umax2** (If problem converging, try changing initial guess for nf): $CUE = 0.45$ Rl

Initial guess: $nf := 0.04$

$Umax1 = 0.012$

$Cwmax1(nf) := Cwmax(nf, Nr, Umax1)$

$Nf1 := Maximize(Cwmax1, nf)$ $Nf1 = 0.033$ $Cw1 := Cwmax1(Nf1)$ $Cw1 = 0.708$ $Ntotopt(Nf1, Nr, Umax1) = 0.0177$ $Rtotopt(Nf1, Nr, Umax1) = 0.139$ $Dmaxopt(Nf1, Nr, Um$

$Atotopt(Nf1, Nr, Umax1) = 2.032$ $Cfopt(Nf1, Nr, Umax1) = 0.067$ $Cropt(Nf1, Nr, Umax1) = 0.139$ $SLAopt(Nf1, Nr, Umax1) = 4.065$ $Ftotopt(Nf1, Nr, Umax1) = 0.538$ $LMAav(Nf1, N$

$Rav(Nf1, Nr, Umax1) = 0.106$ $RLDav(Nf1, Nr, Umax1) = 0.627$ $CUE \cdot Atotopt(Nf1, Nr, Umax1) = 0.915$ $NPPopt(Nf1, Nr, Umax1) = 0.915$ $Atotopt(Nf1, Nr, Umax1) \cdot C$

N uptake fraction: $\frac{Utotopt(Nf1, Nr, Umax1)}{Umax1} = 0.44317$ $Ltot1 := Ltotopt(Nf1, Nr, Umax1)$ $Ltot1 = 4.465$

Leaf N at top of canopy (gN/m2): $Natop1 := Na2(0, Ltot1, Nf1 \cdot Mastar)$ $Natop1 = 0.012$ Avge leaf N content: $\frac{Ntotopt(Nf1, Nr, Umax1)}{Ltot1} = 3.957 \times 10^{-3}$

$af(Nf1, Nr, Umax1) := \frac{Cfopt(Nf1, Nr, Umax1)}{NPPopt(Nf1, Nr, Umax1)}$ $af(Nf1, Nr, Umax1) = 0.074$ $aw(Nf1, Nr, Umax1) := \frac{Cw1}{NPPopt(Nf1, Nr, Umax1)}$ $aw(Nf1, Nr, Umax1) = 0.774$ $ar(Nf1, Nr, Umax$

$af(Nf1, Nr, Umax1) + aw(Nf1, Nr, Umax1) + ar(Nf1, Nr, Umax1) = 1$

$Umax2 = 0.008$

$Cwmax2(nf) := Cwmax(nf, Nr, Umax2)$

$Nf2 := Maximize(Cwmax2, nf)$ $Nf2 = 0.0283$ $Cw2 := Cwmax2(Nf2)$ $Cw2 = 0.357$ $Ntotopt(Nf2, Nr, Umax2) = 0.00718$ $Rtotopt(Nf2, Nr, Umax2) = 0.092$ $Dmaxopt(Nf2, Nr, U$

$Atotopt(Nf2, Nr, Umax2) = 1.07$ $Cfopt(Nf2, Nr, Umax2) = 0.032$ $Cropt(Nf2, Nr, Umax2) = 0.092$ $SLAopt(Nf2, Nr, Umax2) = 4.882$ $Ftotopt(Nf2, Nr, Umax2) = 0.254$ $LMAav(Nf2,$

$Rav(Nf2, Nr, Umax2) = 0.083$ $RLDav(Nf2, Nr, Umax2) = 0.4935$ $CUE \cdot Atotopt(Nf2, Nr, Umax2) = 0.481$ $NPPopt(Nf2, Nr, Umax2) = 0.481$ $Atotopt(Nf2, Nr, Umax2) \cdot CU$

N uptake fraction: $\frac{Utotopt(Nf2, Nr, Umax2)}{Umax2} = 0.36332$ $Ltot2 := Ltotopt(Nf2, Nr, Umax2)$ $Ltot2 = 2.532$

Leaf N content at top of canopy (gN/m2): $Natop2 := Na2(0, Ltot2, Nf2 \cdot Mastar)$ $Natop2 = 6.136 \times 10^{-3}$ Avge leaf N content: $\frac{Ntotopt(Nf2, Nr, Umax2)}{Ltot2} = 2.836 \times 10^{-3}$

$af(Nf2, Nr, Umax2) = 0.066$ $aw(Nf2, Nr, Umax2) := \frac{Cw2}{NPPopt(Nf2, Nr, Umax2)}$ $aw(Nf2, Nr, Umax2) = 0.742$ $ar(Nf2, Nr, U$

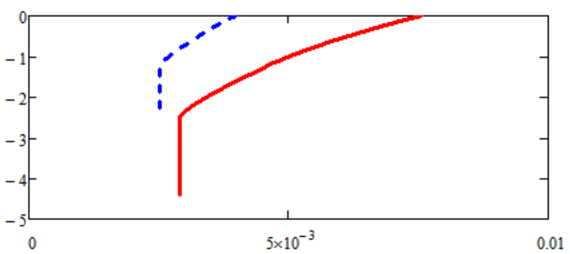
$af(Nf2, Nr, Umax2) + aw(Nf2, Nr, Umax2) + ar(Nf2, Nr, Umax2) = 1$

Vertical profiles of leaf N content (Na(L), kg N/m2), photosynthesis (Aa(L), kg C/m2/s), leaf C payback (Xc, kg C/m2), leaf C export per unit N investment (ef, kg C / kg N):

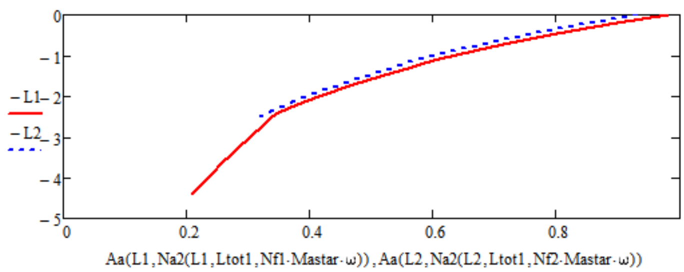
$L1 := 0, 0.1 .. Ltot1$ $Umax1 = 0.012$ $Ltot1 = 4.465$

$L2 := 0, 0.1 .. Ltot2$ $Umax2 = 8 \times 10^{-3}$ $Ltot2 = 2.532$

Fig 1(a) Optimal vertical profile of leaf N content (kg N / m2) versus canopy depth (L)



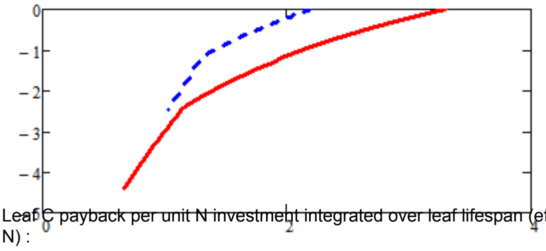
Leaf photosynthesis (kg C/m2/y) versus L:



$Aa(0, Na2(0, Ltot1, Nf1 \cdot Mastar \cdot \omega)) = 0.98$

Fig 1(b) Optimal vertical profile of leaf C payback (kg C / m2) versus canopy depth (L)

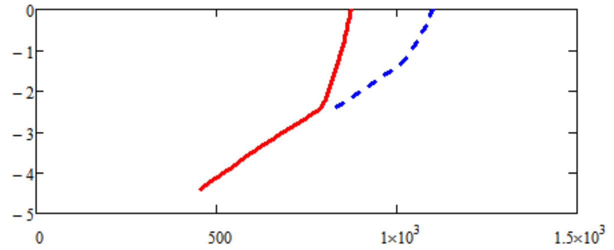
$XC(lai, nf, nr, umax) := CUE \cdot Tauf \; Aa(lai, Na2(lai, Ltotopt(nf, nr, umax), nf \cdot Mastar \cdot \omega)) - \frac{Na2(lai, Ltotopt(nf, nr, umax), nf \cdot Mastar \cdot \omega)}{nf}$



Leaf C payback per unit N investment integrated over leaf lifespan (ef, LCEPUN, kg C / kg N) :

$$\mathrm{LCEPUN}(lai,nf,nr,umax) := \left(\mathrm{CUE}\cdot\mathrm{Tauf}\,\frac{\mathrm{Aa}(lai,\mathrm{Na2}(lai,\mathrm{Ltotopt}(nf,nr,umax),nf\cdot\mathrm{Mastar}\cdot\omega))}{\mathrm{Na2}(lai,\mathrm{Ltotopt}(nf,nr,umax),nf\cdot\mathrm{Mastar}\cdot\omega)}-\frac{1}{nf}\right)\cdot\frac{1}{1-\mathrm{Retrans}}$$

Fig 1(c) Optimal vertical profile of leaf C payback per unit leaf N investment (kg C / kg N) versus canopy depth (L)



$$\mathrm{LCEPUN}(\mathrm{Ltotopt}(\mathrm{Nf1},\mathrm{Nr},\mathrm{Umax1}),\mathrm{Nf1},\mathrm{Nr},\mathrm{Umax1}) = 446.051$$

$$\mathrm{LCEPUN}(\mathrm{Ltotopt}(\mathrm{Nf2},\mathrm{Nr},\mathrm{Umax2}),\mathrm{Nf2},\mathrm{Nr},\mathrm{Umax2}) = 812.281$$

Eqns for vertical profiles of root-mass density (R(z), kg C/m3), N uptake (Ur(z), kg N/m3/year):

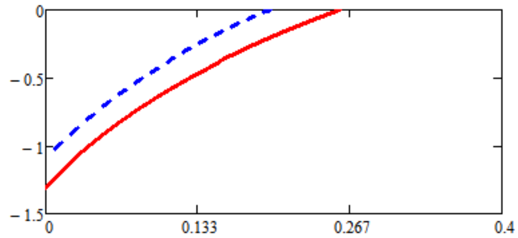
$$R(dmax,z) := \mathrm{Ro}\cdot\left(\exp\left(\frac{dmax-z}{2\cdot\mathrm{Do}}\right)-1\right)$$

$$\mathrm{Ur}(dmax,umax,z) := \frac{umax\cdot\exp\left(\frac{-z}{\mathrm{Do}}\right)}{\mathrm{Do}}\cdot\left(1-\exp\left(-\frac{dmax-z}{2\cdot\mathrm{Do}}\right)\right)$$

$\mathrm{Zmax1} := \mathrm{Dmaxopt}(\mathrm{Nf1},\mathrm{Nr},\mathrm{Umax1})$ $\qquad$ $\mathrm{Zmax2} := \mathrm{Dmaxopt}(\mathrm{Nf2},\mathrm{Nr},\mathrm{Umax2})$

$Z1 := 0, 0.01 .. \mathrm{Zmax1}$ $\qquad$ $\mathrm{Zmax1} = 1.315$ $\qquad$ $Z2 := 0, 0.01 .. \mathrm{Zmax2}$ $\qquad$ $\mathrm{Zmax2} = 1.108$

Fig 2(a) Optimal vertical profile of root mass density (kg C / m3) versus soil depth (z, m)



$$R(\mathrm{Zmax1},0) = 0.258$$

N uptake (kg N/m2/y) versus z:

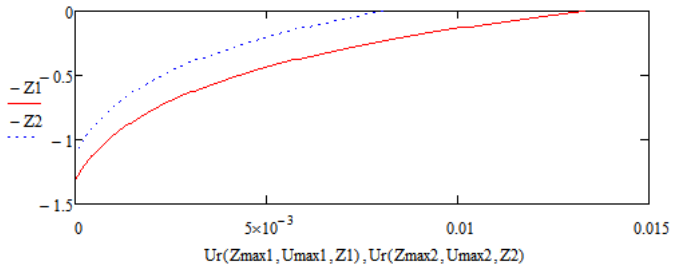


Fig 1(b) Optimal vertical profile of root N payback integrated over root lifespan (kg N / m3) versus soil depth (z)

$$\mathrm{XN}(dmax,nr,umax,z) := (\mathrm{Ur}(dmax,umax,z)\cdot\mathrm{Taur}-nr\cdot R(dmax,z))$$

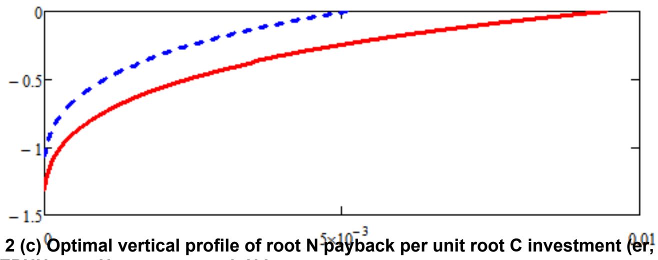
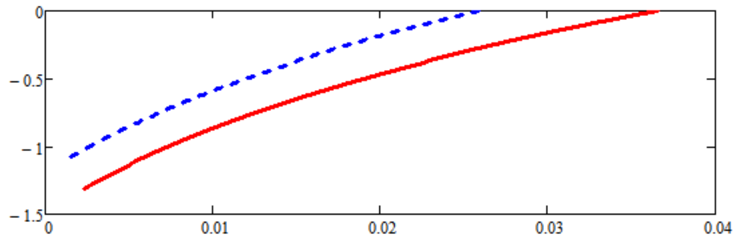


Fig 2 (c) Optimal vertical profile of root N payback per unit root C investment (er; kg N / kg C)
RNEPUN=root N export per unit N investment

$$RNEPUC(dmax, nr, umax, z) := \left(\frac{Ur(dmax, umax, z)}{R(dmax, z)}\cdot Taur - nr\right)$$



Evaluate ef (LCEPUN, kg C/kg N) at base of canopy & er (RNEPUC kg N/kg C) at base of root system & their product at Umax1 & Umax2:

$Dmaxopt(Nf1, Nr, Umax1) = 1.315$

$Ltotopt(Nf1, Nr, Umax1) = 4.465$

$LCEPUN(Ltotopt(Nf1, Nr, Umax1), Nf1, Nr, Umax1) = 446.051$

CHECK LCEPUN: compare with value (CUE*Lamda1*Tauf-1/Nf)/(1-Retrans) calculated from Lamda1 below:

$$\frac{70.413\cdot 8\cdot CUE - \frac{1}{Nf1}}{1 - Retrans} = 446.052$$

$RNEPUC(Dmaxopt(Nf1, Nr, Umax1), Nr, Umax1, Dmaxopt(Nf1, Nr, Umax1) - 0.00001) = 0.00224$

CHECK RNEPUC: compare with value (Lambda2*Taur-Nr) calculated from Lamda2 below:

$0.017242\cdot 1 - Nr = 0.00224$

$RNEPUC(Dmaxopt(Nf1, Nr, Umax1), Nr, Umax1, Dmaxopt(Nf1, Nr, Umax1) - 0.00001)\cdot LCEPUN(Ltotopt(Nf1, Nr, Umax1), Nf1, Nr, Umax1) = 1$

$Dmaxopt(Nf2, Nr, Umax2) = 1.108$

$Ltotopt(Nf2, Nr, Umax2) = 2.532$

$LCEPUN(Ltotopt(Nf2, Nr, Umax2), Nf2, Nr, Umax2) = 812.281$

$RNEPUC(Dmaxopt(Nf2, Nr, Umax2), Nr, Umax2, Dmaxopt(Nf2, Nr, Umax2) - 0.00001) = 0.00123$

$RNEPUC(Dmaxopt(Nf2, Nr, Umax2), Nr, Umax2, Dmaxopt(Nf2, Nr, Umax2) - 0.00001)\cdot LCEPUN(Ltotopt(Nf2, Nr, Umax2), Nf2, Nr, Umax2) = 1$

Optimal annual C allocation (kg C/m2/year) at Umax1=0.012 & at Umax2 = 0.008 kg N/m2/year:

$$cfopt(nfol, umax) := \frac{Ntotopt(nfol, Nr, umax)}{nfol\cdot Tauf} \qquad cropt(cw, nfol, umax) := \frac{Rtotopt(nfol, Nr, umax)}{Taur}$$

$Umax1 = 0.012$

$cfopt(Nf1, Umax1) = 0.067$

$cropt(Cw1, Nf1, Umax1) = 0.139$

$Cw1 = 0.708$

$NPP1 := cfopt(Nf1, Umax1) + cropt(Cw1, Nf1, Umax1) + Cw1$

$NPP1 = 0.9145$

$Umax2 = 0.008$

$cfopt(Nf2, Umax2) = 0.032$

$cropt(Cw2, Nf2, Umax2) = 0.092$

$Cw2 = 0.357$

$NPP2 := cfopt(Nf2, Umax2) + cropt(Cw2, Nf2, Umax2) + Cw2$

$NPP2 = 0.481$

Optimal partitioning fractions:

$$\frac{cfopt(Nf1, Umax1)}{NPP1} = 0.074$$

$$\frac{cropt(Cw1, Nf1, Umax1)}{NPP1} =$$

$$\frac{cfopt(Nf2, Umax2)}{NPP2} = 0.066$$

$$\frac{cropt(Cw2, Nf2, Umax2)}{NPP2} = 0.192$$

$$\frac{Cw1}{NPP1} = 0.774 \qquad \frac{cfopt(Nf1, Umax1)}{(Cw1 + cropt(Cw1, Nf1, Umax1))} = 0.079$$

$$\frac{Cw2}{NPP2} = 0.742 \qquad \frac{cfopt(Nf2, Umax2)}{(Cw2 + cropt(Cw2, Nf2, Umax2))} = 0.071$$

$$\frac{NPP2}{NPP1} = 0.526$$

Is Cwmax sensitive to Nf? Plot relationship between annual wood production (Cw, kg C/m2) and leaf N:C ratio (kg N/kg C) for high & low Umax. (To check optimum of Cw wrt Nf)

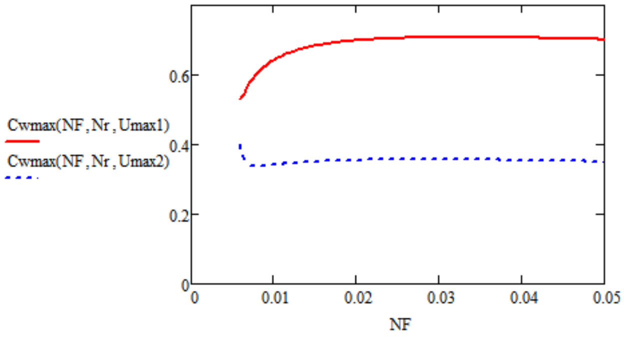
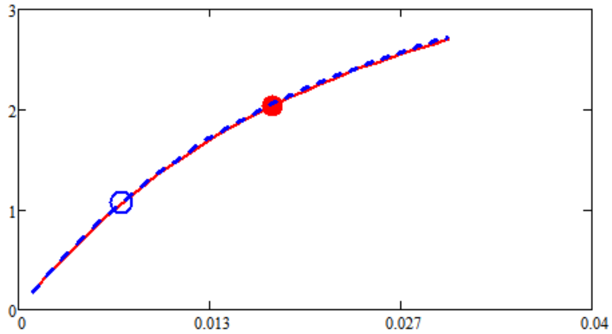


Fig 3a: Show Atot (kgC/m2/y) - Ntot (kgN/m2) relationship & optima at Umax1 & Umax2:

$NTOT := 0.001, 0.002 .. 0.03$



$atot2(Ltotopt2(Nf1 \cdot Mastar \cdot \omega, 0.02), Nf1 \cdot Mastar \cdot \omega) = 2.188$

$atot2(Ltotopt2(Nf2 \cdot Mastar, 0.02), Nf2 \cdot Mastar) = 2.061$

Slope of Atot - Ntot relnsp (kg C / kg N / y):

$$SlopeAtotNtot(nf, ntot) := \frac{atot2(Ltotopt2(nf \cdot Mastar \cdot \omega, ntot + 0.000001), nf \cdot Mastar \cdot \omega) - atot2(Ltotopt2(nf \cdot Mastar \cdot \omega, ntot - 0.000001), nf \cdot Mastar \cdot \omega)}{0.000002}$$

$$SlopeAtotNtot(nf, ntot) := \frac{atot2(Ltotopt2(nf \cdot Mastar \cdot \omega, ntot + 0.0000001), nf \cdot Mastar \cdot \omega) - atot2(Ltotopt2(nf \cdot Mastar \cdot \omega, ntot - 0.0000001), nf \cdot Mastar \cdot \omega)}{0.0000002}$$

Slope at intersections (kgC / kgN / y):

$SlopeAtotNtot(Nf1, Ntotopt(Nf1, Nr, Umax1)) = 70.412954 \qquad SlopeAtotNtot(Nf2, Ntotopt(Nf2, Nr, Umax2)) = 122.645997$

Compare slope of Atot-Ntot relnsp versus Lagrange multiplier (lambda1=Aa(Ltot)/Na(Ltot)) from MaxNup optimisation hypothesis (kg C / kg N / year):

$$lambda1(ltot, nf) := \frac{Aa(ltot, Na2(ltot, ltot, nf \cdot Mastar \cdot \omega))}{Na2(ltot, ltot, nf \cdot Mastar \cdot \omega)}$$

$lambda1(Ltot1, Nf1) = 70.412954 \qquad lambda1(Ltot2, Nf2) = 122.645997$

Check value of Lagrange multiplier versus slope of Aa vs Na relnsp. They should be the same when L < Lcrit:

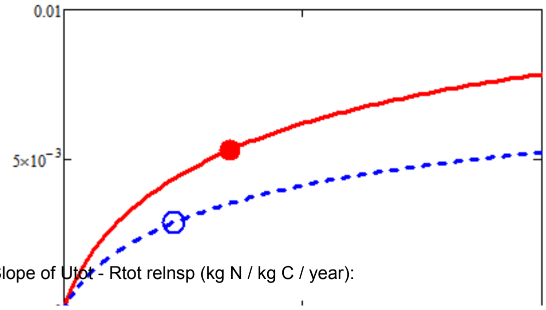
$dAdN(0, Na2(0, Ltotopt2(Nf1 \cdot Mastar \cdot \omega, Ntotopt(Nf1, Nr, Umax1)), Nf1 \cdot Mastar \cdot \omega)) = 70.412954$

$dAdN(1, Na2(1, Ltotopt2(Nf1 \cdot Mastar \cdot \omega, Ntotopt(Nf1, Nr, Umax1)), Nf1 \cdot Mastar \cdot \omega)) = 70.412954$

Fig 3b: Show Utot (kg N/m2/y) - Rtot (kg C/m2) relationship & optima at Umax1 & Umax2:

$Dmax1 := Dmaxopt(Nf1, Nr, Umax1) \qquad Dmax2 := Dmaxopt(Nf2, Nr, Umax2)$

$DMAX := 0, 0.01 .. 2$



Slope of Utot - Rtot relnsp (kg N / kg C / year):

$$\text{SlopeUtotRtot}(\text{dmax}, \text{umax}) := \frac{\text{utot1}(\text{dmax} + 0.000001, \text{umax}) - \text{utot1}(\text{dmax} - 0.000001, \text{umax})}{\text{rtot2}(\text{dmax} + 0.000001) - \text{rtot2}(\text{dmax} - 0.000001)}$$

Slope at intersections (kg N / kg C / y)

$\text{SlopeUtotRtot}(\text{Dmax1}, \text{Umax1}) = 0.017242$ $\quad$ $\text{SlopeUtotRtot}(\text{Dmax2}, \text{Umax2}) = 0.016231$

Compare slope of Utot-Rtot relnsp versus Lagrange multiplier
(lambda2=Ur(Dmax)/R(Dmax)=Umax*exp(-Dmax/Do)/(Ro*Do)) from MaxNup optimisation hypothesis (kg N / kg C / y):

$$\text{lambda2}(\text{dmax}, \text{umax}) := \frac{\text{umax}}{\text{Do} \cdot \text{Ro}} \cdot \exp\left(\frac{-\text{dmax}}{\text{Do}}\right)$$

$\text{lambda2}(\text{Dmax1}, \text{Umax1}) = 0.017242$ $\quad$ $\text{lambda2}(\text{Dmax2}, \text{Umax2}) = 0.016231$