Appendix I - analytical solution to the H:D in the stage/size structured model

Deduction

In order to deduce the analytical solution of the stage/size structured model to the H:D, an incomplete version of the conceptual model presented in Figure 1 was first created, where the sporophyte state variables and the clonal growth rates of the ramets are not considered. In addition, fecundity and survival of settled spores (which takes two projection times) were replaced by their product, fertility (which only takes one projection time). However, these will be solved later.

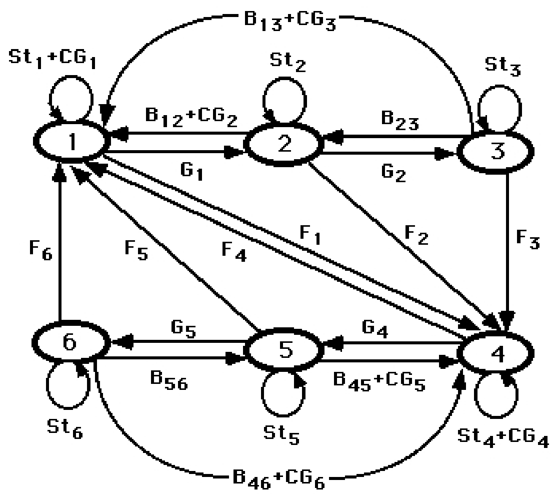


Figure 1- incomplete version of the stage/size structured model of a biphasic life-cycle: (1, 2 and 3) gametophyte fronds size classes and (4, 5 and 6) tetrasporophyte fronds size classes. (F) fertility, (G) growth, (St) stasis and (B) breakage.

From this life-cycle graph (or from its matrix) the dominant eigenvector was deduced, scaling to 1 one of its components:

$$\begin{cases} w_1 = 1 \\ w_2 = (G_1 + St_2.w_2 + B_{23}.w_3).\lambda^{-1} \\ w_3 = (G_2.w_2 + St_3.w_3).\lambda^{-1} \\ w_4 = (F_1 + F_2.w_2 + F_3.w_3 + St_4.w_4 + B_{45}.w_5 + B_{46}.w_6).\lambda^{-1} \\ w_5 = (G_4.w_4 + St_5.w_5 + B_{56}.w_6).\lambda^{-1} \\ w_6 = (G_5.w_5 + St_6.w_6).\lambda^{-1} \end{cases} \qquad \text{(eqn.1)}$$

then:

$$\begin{cases} w_1 = 1 \\ w_2 = \dfrac{(G_1 + B_{23}.w_3).\lambda^{-1}}{(1 - St_2.\lambda^{-1})} \\ w_3 = \dfrac{(G_2.w_2).\lambda^{-1}}{(1 - St_3.\lambda^{-1})} \\ w_4 = \dfrac{(F_1 + F_2.w_2 + F_3.w_3 + B_{45}.w_5 + B_{46}.w_6).\lambda^{-1}}{(1 - St_4.\lambda^{-1})} \\ w_5 = \dfrac{(G_4.w_4 + B_{56}.w_6).\lambda^{-1}}{(1 - St_5.\lambda^{-1})} \\ w_6 = \dfrac{(G_5.w_5).\lambda^{-1}}{(1 - St_6.\lambda^{-1})} \end{cases} \qquad \text{(eqn.2)}$$

Solving for w_2, replacing w_3:

$$w_2 = \frac{G_1.\lambda^{-1}.(1 - St_3.\lambda^{-1})}{(1 - St_3.\lambda^{-1}).(1 - St_2.\lambda^{-1}) - B_{23}.G_2.\lambda^{-2}} \qquad \text{(eqn.3)}$$

Solving for w_3:

$$w_3 = \frac{G_1.G_2.\lambda^{-2}}{(1 - St_3.\lambda^{-1}).(1 - St_2.\lambda^{-1}) - B_{23}.G_2.\lambda^{-2}} \qquad \text{(eqn.4)}$$

In order to solve for w_4, the equation was first solved for w_5 and w_6 as a function of w_4:

$$w_5 = \frac{G_4.w_4.\lambda^{-1}.(1 - St_6.\lambda^{-1})}{(1 - St_6.\lambda^{-1}).(1 - St_5.\lambda^{-1}) - B_{56}.G_5.\lambda^{-2}} \qquad \text{(eqn.5)}$$

$$w_6 = \frac{G_5.G_4.w_4.\lambda^{-2}}{(1 - St_6.\lambda^{-1}).(1 - St_5.\lambda^{-1}) - B_{56}.G_5.\lambda^{-2}} \qquad \text{(eqn.6)}$$

Now solving for w_4:

$$w_4 = \left(F_1 + \frac{G_1.\lambda^{-1}.\left[F_2.\left(1-St_3.\lambda^{-1}\right)+F_3.G_2.\lambda^{-1}\right]}{\left(1-St_3.\lambda^{-1}\right).\left(1-St_2.\lambda^{-1}\right)-B_{23}.G_2.\lambda^{-2}} \right).\lambda^{-1} \times \qquad \text{(eqn.7)}$$

$$\times \frac{\left[\left(1-St_6.\lambda^{-1}\right).\left(1-St_5.\lambda^{-1}\right)-B_{56}.G_5.\lambda^{-2}\right]}{\left[\left(1-St_6.\lambda^{-1}\right).\left(1-St_5.\lambda^{-1}\right)-B_{56}.G_5.\lambda^{-2}\right].\left(1-St_4.\lambda^{-1}\right)-\left[B_{45}G_4.\lambda^{-2}.\left(1-St_6.\lambda^{-1}\right)+B_{46.}G_5.G_4.\lambda^{-3}\right]}$$

Solving for w_5:

$$w_5 = \left(F_1 + \frac{G_1.\lambda^{-1}.\left[F_2.\left(1-St_3.\lambda^{-1}\right)+F_3.G_2.\lambda^{-1}\right]}{\left(1-St_3.\lambda^{-1}\right).\left(1-St_2.\lambda^{-1}\right)-B_{23}.G_2.\lambda^{-2}} \right) \times \qquad \text{(eqn.8)}$$

$$\times \frac{\mathrm{G}_4.\left(1-St_6.\lambda^{-1}\right).\lambda^{-2}}{\left[\left(1-St_6.\lambda^{-1}\right).\left(1-St_5.\lambda^{-1}\right)-B_{56}.G_5.\lambda^{-2}\right].\left(1-St_4.\lambda^{-1}\right)-\left[B_{45}G_4.\lambda^{-2}.\left(1-St_6.\lambda^{-1}\right)+B_{46.}G_5.G_4.\lambda^{-3}\right]}$$

And solving for w_6:

$$w_6 = \left(F_1 + \frac{G_1.\lambda^{-1}.\left[F_2.\left(1-St_3.\lambda^{-1}\right)+F_3.G_2.\lambda^{-1}\right]}{\left(1-St_3.\lambda^{-1}\right).\left(1-St_2.\lambda^{-1}\right)-B_{23}.G_2.\lambda^{-2}} \right) \times \qquad \text{(eqn.9)}$$

$$\times \frac{\mathrm{G}_4.G_5.\lambda^{-2}}{\left[\left(1-St_6.\lambda^{-1}\right).\left(1-St_5.\lambda^{-1}\right)-B_{56}.G_5.\lambda^{-2}\right].\left(1-St_4.\lambda^{-1}\right)-\left[B_{45}G_4.\lambda^{-2}.\left(1-St_6.\lambda^{-1}\right)+B_{46.}G_5.G_4.\lambda^{-3}\right]}$$

Solving for $(w_1+w_2+w_3)/(w_4+w_5+w_6)$, noting that w_4, w_5 and w_6 share part of their expressions, a provisory solution to the H:D is obtained:

$$\frac{w_1+w_2+w_3}{w_4+w_5+\mathrm{w}_6} =$$

$$= \frac{\left(1-St_3.\lambda^{-1}\right).\left(1-St_2.\lambda^{-1}\right)-B_{23}.G_2.\lambda^{-2}+G_1.\lambda^{-1}.\left(1-St_3.\lambda^{-1}+G_2.\lambda^{-1}\right)}{F_1.\left[\left(1-St_3.\lambda^{-1}\right).\left(1-St_2.\lambda^{-1}\right)-B_{23}.G_2.\lambda^{-2}+G_1.\lambda^{-1}.\left[F_2.\left(1-St_3.\lambda^{-1}\right)+F_3.G_2.\lambda^{-1}\right]\right].\lambda^{-1}} \times$$

$$\times \frac{\left[\left(1-St_6.\lambda^{-1}\right).\left(1-St_5.\lambda^{-1}\right)-B_{56}.G_5.\lambda^{-2}\right].\left(1-St_4.\lambda^{-1}\right)-\left[B_{45}G_4.\lambda^{-2}.\left(1-St_6.\lambda^{-1}\right)+B_{46.}G_5.G_4.\lambda^{-3}\right]}{\left(1-St_6.\lambda^{-1}\right).\left(1-St_5.\lambda^{-1}\right)-B_{56}.G_5.\lambda^{-2}+\mathrm{G}_4.\lambda^{-1}.\left(1-St_6.\lambda^{-1}+G_5.\lambda^{-1}\right)}$$

(eqn.10)

This is not the desired solution as some parameters are not accounted for because w_1 was scaled to 1. The H:D was determined by the following equation, were w_i is determined with w_1 scaled to 1 while w_i’ is determined with w_4 scaled to 1:

$$\mathrm{H:D} = \sqrt{\left(\frac{w_1 + w_2 + w_3}{w_4 + w_5 + w_6}\right) \times \left(\frac{w_1' + w_2' + w_3'}{w_4' + w_5' + w_6'}\right)} \qquad \text{(eqn.11)}$$

Solving for the second quotient of Equation 11 is similar to the procedures in equations 1 to 10. Once this done, Equation 11 can then be solved:

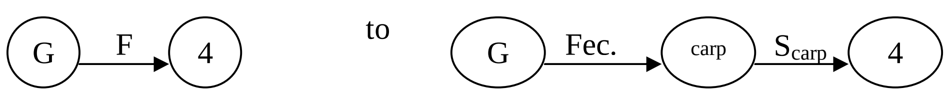
$$\mathrm{H:D} =$$

$$= \frac{\left(1 - St_3.\lambda^{-1}\right).\left(1 - St_2.\lambda^{-1}\right) - B_{23}.G_2.\lambda^{-2} + \mathrm{G}_1.\lambda^{-1}.\left(1 - St_3.\lambda^{-1} + G_2.\lambda^{-1}\right)}{\left(1 - St_6.\lambda^{-1}\right).\left(1 - St_5.\lambda^{-1}\right) - B_{56}.G_5.\lambda^{-2} + G_4.\lambda^{-1}.\left(1 - St_6.\lambda^{-1} + G_5.\lambda^{-1}\right)} \times$$

$$\left(\frac{F_4.\left[\left(1 - St_6.\lambda^{-1}\right).\left(1 - St_5.\lambda^{-1}\right) - B_{56}.G_5.\lambda^{-2} + G_4.\lambda^{-1}.\left[F_5.\left(1 - St_6.\lambda^{-1}\right) + F_6.G_5.\lambda^{-1}\right]\right]}{F_1.\left[\left(1 - St_3.\lambda^{-1}\right).\left(1 - St_2.\lambda^{-1}\right) - B_{23}.G_2.\lambda^{-2} + G_1.\lambda^{-1}.\left[F_2.\left(1 - St_3.\lambda^{-1}\right) + F_3.G_2.\lambda^{-1}\right]\right]} \right)^{1/2} \times \qquad \text{(eqn.12)}$$

$$\times \left(\frac{\left[\left(1 - St_6.\lambda^{-1}\right).\left(1 - St_5.\lambda^{-1}\right) - B_{56}.G_5.\lambda^{-2}\right].\left(1 - St_4.\lambda^{-1}\right) - \left[B_{45}G_4.\lambda^{-2}.\left(1 - St_6.\lambda^{-1}\right) + B_{46}.G_5.G_4.\lambda^{-3}\right]}{\left[\left(1 - St_3.\lambda^{-1}\right).\left(1 - St_2.\lambda^{-1}\right) - B_{23}.G_2.\lambda^{-2}\right].\left(1 - St_1.\lambda^{-1}\right) - \left[B_{12}G_1.\lambda^{-2}.\left(1 - St_3.\lambda^{-1}\right) + B_{13}.G_2.G_1.\lambda^{-3}\right]} \right)^{1/2}$$

Once again, this is not the final solution as two transformations need yet to be done: i) clonal growth has to be introduced. This is done by simply adding CG_i to the parameter in the same matrix entry a_{ij}, and ii) Fertilities have to be decomposed into fecundities and spore survival. In the life-cycle graph, this corresponds to change:



Where G represents any gametophyte size class. The symmetrical is done to the tetrasporophytes. Algebrically this change means that:

$$F_i.\lambda^{-1} = Fec_i \times S_{(spore)} \times \lambda^{-2} \qquad \text{(eqn.13)}$$

Introducing these changes in equation (12) yields the analytical solution to the H:D of the life-cycle in Figure 1 of the bulk article (equation 14).

$$\mathrm{H:D}=$$

$$=\frac{(1-St_3.\lambda^{-1}).(1-St_2.\lambda^{-1})-B_{23}.G_2.\lambda^{-2}+G_1.\lambda^{-1}.(1-St_3.\lambda^{-1}+G_2.\lambda^{-1})}{(1-St_6.\lambda^{-1}).(1-St_5.\lambda^{-1})-B_{56}.G_5.\lambda^{-2}+G_4.\lambda^{-1}.(1-St_6.\lambda^{-1}+G_5.\lambda^{-1})}\times$$

$$\times\sqrt{\frac{Fec_4.S_{tet}.\lambda^{-1}.\left[(1-St_6.\lambda^{-1}).(1-St_5.\lambda^{-1})-B_{56}.G_5.\lambda^{-2})\right]+G_4.\lambda^{-1}.\left[Fec_5.S_{tet}.\lambda^{-1}.(1-St_6.\lambda^{-1})+Fec_6.S_{tet}.G_5.\lambda^{-2}\right]}{Fec_1.S_{carp}.\lambda^{-1}.\left[(1-St_3.\lambda^{-1}).(1-St_2.\lambda^{-1})-B_{23}.G_2.\lambda^{-2})\right]+G_1.\lambda^{-1}.\left[Fec_2.S_{carp}.\lambda^{-1}.(1-St_3.\lambda^{-1})+Fec_3.S_{carp}.G_2.\lambda^{-2}\right]}}\times$$

$$\times\sqrt{\frac{\left[(1-St_6.\lambda^{-1}).(1-St_5.\lambda^{-1})-B_{56}.G_5.\lambda^{-2})\right].\left[1-(St_4+CG_4).\lambda^{-1}\right]-\left[(B_{45}+CG_5).G_4.\lambda^{-2}.(1-St_6.\lambda^{-1})+(B_{46}+CG_6).G_5.G_4.\lambda^{-3})\right]}{\left[(1-St_3.\lambda^{-1}).(1-St_2.\lambda^{-1})-B_{23}.G_2.\lambda^{-2})\right].\left[1-(St_1+CG_1).\lambda^{-1}\right]-\left[(B_{12}+CG_2).G_1.\lambda^{-2}.(1-St_3.\lambda^{-1})+(B_{13}+CG_3).G_2.G_1.\lambda^{-3})\right]}}$$

(eqn.14)

After introducing those changes in equation (14) it is still possible to simplify. Multiplying the first quotient by λ^2/λ^2 and the second and third quotients by λ^3/λ^3, gives the analytical solution to the H:D in the stable population structure (equation 15).

$$\mathrm{H:D}=\frac{(\lambda-St_3).(\lambda-St_2)-B_{23}.G_2+G_1.(\lambda-St_3+G_2)}{(\lambda-St_6).(\lambda-St_5)-B_{56}.G_5+G_4.(\lambda-St_6+G_5)}\times$$

$$\times\sqrt{\frac{Fec_4.S_{tet}.\left[(\lambda-St_6).(\lambda-St_5)-B_{56}.G_5)\right]+G_4.\left[Fec_5.S_{tet}.(\lambda-St_6)+Fec_6.S_{tet}.G_5\right]}{Fec_1.S_{carp}.\left[(\lambda-St_3).(\lambda-St_2)-B_{23}.G_2)\right]+G_1.\left[Fec_2.S_{carp}.(\lambda-St_3)+Fec_3S_{carp}.G_2\right]}}\times$$

$$\times\sqrt{\frac{\left[(\lambda-St_6).(\lambda-St_5)-B_{56}.G_5)\right].\left[\lambda-(St_4+CG_4)\right]-\left[(B_{45}+CG_5).G_4.(\lambda-St_6)+(B_{46}+CG_6).G_5.G_4)\right]}{\left[(\lambda-St_3).(\lambda-St_2)-B_{23}.G_2)\right].\left[\lambda-(St_1+CG_1)\right]-\left[(B_{12}+CG_2).G_1.(\lambda-St_3)+(B_{13}+CG_3).G_2.G_1)\right]}}$$

(eqn.15)

Interpretation

The expression $G_1.G_2.\lambda^{-1}$ represents the probability of a gametophytic ramet to reach the third size class (“3”) starting from the first (“1”) in the absence of ploidy self-looping. Multiplying it by w_1 it is obtained $w_1.G_1.G_2.\lambda^{-2}$ estimating the total number of individuals reaching “3”. In the deduction was established w_1=1,therefore:

$$G_1.G_2.\lambda^{-2} = w_1.G_1.G_2.\lambda^{-2} = w_3 \qquad \text{(eqn.16)}$$

wich represents the abundance of “3” relative to “1” when everything a ramet may due is either grow or die. From equation 2:

$$\left(1 - St_2\lambda^{-1}\right) = \left(G_1 + B_{23}.w_3\right)\lambda^{-1} / w_2 \qquad \text{(eqn.17)}$$

$$\left(1 - St_3\lambda^{-1}\right) = G_2.w_2.\lambda^{-1} / w_3 \qquad \text{(eqn.18)}$$

The expression $G_1.(1-St_3. \lambda^{-1}).\lambda^{-1}$ refers to the second size class of the gametophytic ramets as, from equations (16) and (18):

$$G_1\left(1 - St_3\lambda^{-1}\right)\lambda^{-1} = G_1.G_2.w_2.\lambda^{-2} / w_3 = w_2.w_3 / w_3 = w_2 \qquad \text{(eqn.19)}$$

wich represents the abundance of “2” relative to “1” when everything a ramet may due is either grow or die. The expression $(1-St_2. \lambda^{-1}).(1-St_3. \lambda^{-1})-B_{23}.G_2.\lambda^{-2}$ refers to the first size class of the gametophytic ramets as, from equations (17) and (18):

$$\left(1 - St_2\lambda^{-1}\right)\left(1 - St_3\lambda^{-1}\right) - B_{23}.G_2.\lambda^{-2} = \frac{\left(G_1 + B_{23}.w_3\right).\lambda^{-1}.G_2.w_2.\lambda^{-1}}{w_2.w_3} - B_{23}.G_2.\lambda^{-2} =$$

(eqn.20)

$$= \frac{G_1.G_2.w_2.\lambda^{-2} + B_{23}.G_2.w_2.w_3.\lambda^{-2}}{w_2.w_3} - B_{23}.G_2.\lambda^{-2} = \frac{G_1.G_2.\lambda^{-2}}{w_3} = \frac{w_3}{w_3} = 1 = w_1$$

wich represents the abundance of “1” relative to “1” when everything a ramet may due is either grow or die. An equivalent deduction can be made for state variables “4”, “5” and “6” refering to the tetrasporophytic ramets first, sencond and third size classes.

In Q_1 these haploid expressions appear isolated in the numerator whereas the diploid expressions appear in the denominator. Therefore, the Q_1 is estimating the haploid-to-diploid ratio of the “grow or die” paths. In Q_2 each of these expressions appears related to the respective fecundity and spore survival. Therefore, the Q_2 is estimating the haploid-to-diploid ratio of the “reproduce or die” paths that connect the first size classes of each ploidy. The ploidies trade places in the quotient because through these paths each ploidy phase is actually contributing to the dominance of the opposite ploidy phase. In Q_3 each of these expressions appears related to the respective looping vital rates. Therefore, the Q_3 is estimating the haploid-to-diploid ratio of the “loop or die” paths that keep individual in the same ploidy. Also in Q3 the ploidias trade places. However, the expressions are all subtracted to 1 and therefore work as if haploids were actually in the numerator and the diploids in the denominator.