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A single tree basal area growth model

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Highlights: What is the role of the structural and circular constraints on tree growth dynamics? Simple rules about growth and self-pruning result in a 2-dimensional dynamic growth model in a framework of structural and circular constraints. The results suggest that onset and rate of self-pruning are key factors in the partitioning of dry matter between foliage and wood.

Keywords: tree rings, heartwood, sapwood, self-pruning, partitioning

INTRODUCTION

Tree ring series are effective tools to study the impact of the environment on tree growth (Speer 2010). External factors influencing ring width often work on tree growth indirectly through their effect on the amount of foliage (Long et al. 2004). The amount of foliage is, according to the pipe model theory (Shinozaki et al. 1964), proportional to the sapwood cross section area. Because of the structural relationships between foliage, sapwood and heartwood, the pipe model sets constraints on tree growth and allocation (Mäkelä and Valentine 2006).

In this context it would be useful to know the role of the structural and circular constraints on the growth dynamics visible in tree ring series. Here I present a growth model based on the 2-dimensional cross section of the stem. Simple rules about growth and self-pruning result in a dynamic growth model. The aim is to get insight in the influence of structural and circular constraints on tree ring series and on tree growth in general.

THE MODEL

Self-pruning is the death of branches because of shading. Self-shading is biggest near the stem, creating a cavity inside the crown without foliage (Mäkelä and Valentine 2006). With an expanding crown, also this cavity becomes bigger. This suggests that the tree adjusts its amount of foliage according to the amount of light, and that there is a maximum thickness of the foliage layer (distance from surface to inner leaves).

The 2-dimensional model assumes that there are two forces causing structural changes: growth and self-pruning. Growth is a function of the sapwood area which results in a new growth ring, giving increase in basal area. At the same time the border between heartwood and sapwood shifts outward because of self-pruning, which will add a ring of transition wood to the heartwood. The growth rate of the sapwood area is calculated through the component of growth minus the component of transition from sapwood to heartwood. In the present model, the growth component is represented by the circumference of the basal area, and the transition component by the circumference of the heartwood area. If growth ring and transition ring have the same thickness, then the new growth ring becomes:

$$G_A(k+1) = x\ S_A(k)\ \frac{R_{CIRC}(k)}{R_{CIRC}(k) + H_{CIRC}(k)} \qquad (1)$$

where G_A is the growth ring area, k is current year, S_A is sapwood area, R_{CIRC} is circumference of the basal area, H_{CIRC} is circumference of the heartwood area, x is growth rate parameter, which depends on the nutrient status of the site; and the new transition ring becomes:

$$T_A(k+1) = x\ S_A(k)\ \frac{H_{CIRC}(k)}{R_{CIRC}(k) + H_{CIRC}(k)} \qquad (2)$$

where T_A is the area of transition from sapwood to heartwood. To account for a different width of the transition ring, a parameter of self-pruning q is added, which depends on the amount of shading. Equation (1) then remains the same, but equation (2) becomes:

$$T_A(k+1) = q \times S_A(k) \frac{H_{CIRC}(k)}{R_{CIRC}(k) + H_{CIRC}(k)} \quad (3)$$

The circumference of the basal area is proportional to the stem radius, and the circumference of the heartwood area is proportional to the heartwood area radius, so the equations can be simplified by:

$$G_A(k+1) = x\ S_A(k) \frac{R(k)}{R(k) + H(k)} \quad (4)$$

and

$$T_A(k+1) = q \times S_A(k) \frac{H(k)}{R(k) + H(k)} \quad (5)$$

When the tree ages, the non green parts become larger in relation to the leaf area, which reduces the growth efficiency and causes an age related growth decline (e.g. Hubbard et al.1999). Comparing simulations with real growth data is justified only when taking into account this growth decline. In the model the dependency of leaf area on tree dimension is expressed as S/R, where sapwood layer thickness (S) reflects the dimension of the leaf area, and stem radius (R) the dimension of the whole tree. This is also in agreement with recent studies indicating a strong dependency of metabolic processes on the amount of phloem, which causes a bottle neck for tree growth (Nikinmaa et al. 2013). The relationship is included in both equations by multiplying with S and dividing by R. Equation (4) can then be reduced to:

$$G_A(k+1) = \text{pi} \times S^2 \quad (6)$$

and equation (5) can be reduced to:

$$T_A(k+1) = \frac{\text{pi}\ q \times S^2 H}{R} \quad (7)$$

In a free standing tree the foliage expands outward also horizontally. This causes more shading inside the crown, so foliage is lost by self-pruning at the same rate. Thus in a free standing healthy tree the thickness of the foliage layer will tend to fluctuate around the same value. This will be reflected in the stem cross section as a tendency of constant width of the sapwood layer, while the area of sapwood increases. However, in a young vigorous tree the sapwood width may still increase because the crown also expands in upward direction, but when height growth slows down, sapwood width will fluctuate more and more around the same value.

The tendency of a constant sapwood layer makes that the transition ring between heartwood and sapwood is about as thick as the growth ring. In this case the parameter of self-pruning gets the value 1.

Growth of a tree in a stand depends on the level of competition. According to the level of competition we can divide trees in a closed stand roughly into two classes: dominant and suppressed. In dominant trees the self-pruning is less than growth, in suppressed trees the self-pruning is the same as or bigger than growth.

The parameter of self-pruning is easiest to calculate for suppressed trees where self-pruning is equal to growth, because the area of the transition ring is as big as the area of the growth ring. The equation for the transition ring is then the same as for the growth ring, equation (6), from which follows that the parameter of self-pruning has the value of R/H. In seriously suppressed trees, so where self-pruning is bigger than growth, this parameter is even bigger than R/H, and the crown will become smaller. In dominant trees the parameter has a value higher than in suppressed trees but lower than in free standing trees, so between R/H and 1. In trees released from suppression, the value will be less than 1.

RESULTS

Preliminary results show that

- growth simulations are conform general trends of growth and yield tables.
- simulations of suppression and release are in close accordance with tree ring data from Scots pine (see fig. 1a and b).

This suggests that the assumptions in the model are realistic. Model simulations further suggest that onset and rate of self-pruning are key factors in the partitioning of dry matter between foliage and wood.

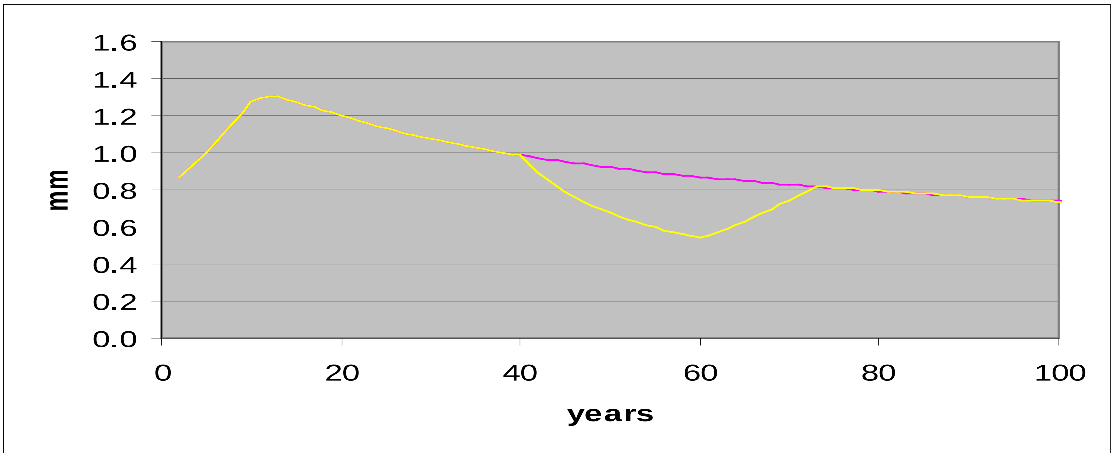

Fig.1a. Simulation: stand closure and suppression at age 40, release at age 60. The self-pruning parameter q is 1 until age 40, q =R/H between age 40 and 60, q = <1 after age 60 until sapwood thickness reaches the same value as before suppression.

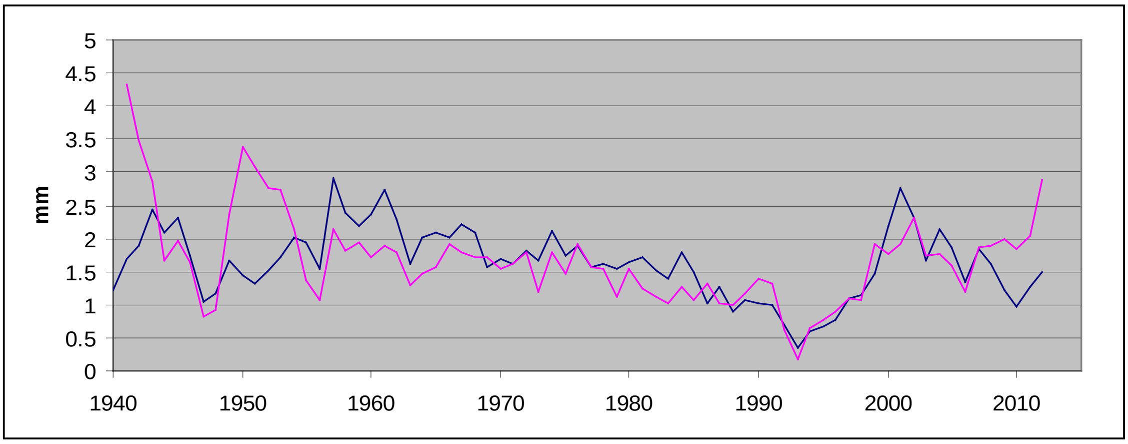

Fig. 1b. Ring width curves of two suppressed Scots pines in a stand, released by thinning in 1994.

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