## Including the effect of biological processes in the allometric scaling relationships

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## Introduction

Allometric scaling relationships of the form  $Y = aX^b$  are widely utilized in many types of biological models. In the functional-structural plant models, for example, they can be used for estimating unmeasured plant traits based on some easily measurable traits such as the length or diameter of structures. Allometric scaling relationships are, however, usually viewed as static relationships where both the scaling exponent (*b*) and the normalization constant (*a*) are fixed according to their empirical values. This may have unpredictable effects in dynamic models where the structure of a plant, its physiological processes, and its growth environment are under a constant change. The value of the scaling exponent has been under intense theoretical and empirical investigation, but the allometric equations can incorporate also additional biologically relevant information.

## Normalization constant reflects the effect of dynamic processes

We show that by using a thoretically predicted fixed value for the exponent b, instead of an empirical value determined by regression, it is possible to make the normalization constant suitable for biological interpretation in terms of dynamically changing environment, along with improving the overall model fit.

Measurements on silver birch (*Betula pendula* Roth.) were used to establish allometric scaling equations relating the radius (r) of a branch to either the length (l) or the shoot number of the branch (n). It was assumed that the relationship between r and l can be modeled as  $l = ar^{2/3}$ , and the relationship between r and n as  $n = ar^2$ . The value of a was then predicted with a sample set of explanatory variables reflecting the dynamically changing structural traits of the study trees (tree age, breast diameter, crown length, tree height) and the characteristics of the stand surrounding the trees (two competition indices, neighbor species, relative availability of photosynthetic radiation). This procedure eliminated a significant proportion of variation from a, and improved the overall fit of the allometric models by up to 11%. The increased number of parameters did not explain the improvement.

Accordingly, there is potential for using the value of the normalization constant to depict biologically important information in a manner that improves the accuracy of model predictions.