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Commentary

The diameter growth–height growth relationship as related to the
diameter–height relationship

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The relationship between stem diameter at breast height (D) and tree height (H) among trees (D – H relationship) has provided some of the most basic information for forest studies. Uses of this relationship include the allometric relationship for estimating stem volumes and stand biomass, an index of forest productivity (site index) (Vanclay 1994), and studies of various constraints on height growth including mechanical support (King 2011) and life-history strategies (Iida et al. 2011). However, some attributes of the D – H relationship may not always be correctly understood among researchers (Henry and Aarssen 1999). For example, the D – H relationship among the plants of a stand at a given point in time (static D – H relationship) is known to change with time in both herbaceous (Weiner and Thomas 1992, Nagashima and Terashima 1995) and tree populations (Kohyama et al. 1990, Sumida et al. 1997, 2013). Hence, a single static D – H relationship obtained at a point in time may not be sufficient to analyse long-term physiological and ecological processes, and time-trajectories of D and H of individual trees should be investigated (King 2011). However, the huge size and long-lived nature of trees are obstacles to the long-term monitoring of D and H , and it is generally impossible to regulate the growth conditions of the trees in a stand.

In this issue of Tree Physiology, Trouvé et al. (2015) reports a unique method for the analyses of the relationship between height growth rates (Δh) and diameter growth rates at breast height (Δd ; here we use this term for convenience, instead of their original term 'circumference growth' with its abbreviation Δc). They performed a pooled analysis of the Δd – Δh relationship using a large number of data sets selected from a network of long-term experiment for the growth of sessile oak (*Quercus petraea* (Liebl.)) stands in France. Each of the stands in the selected data sets was an even-aged monoculture and was managed at a specific level of crowding called the Relative Density Index (RDI), whereas the ages and the RDI levels differed among stands. There were measurements

of meteorological conditions common to those stands, but their values also varied among the stands. Trouvé et al. applied nonlinear mixed models to their analysis, in which the relationship between Δd and Δh was assumed to be a curvilinear relationship (the Mitscherlich equation). By pooling the data from all stands, the factors that could affect the shape of the curvilinear line, such as stand ages, RDI levels and some meteorological factors, were examined. An example of a prediction deduced from their results is shown in Figure 1a, which is based on Figure 5b in Trouvé et al. (2015).

In Figure 1a, the two curvilinear lines represent the among-tree relationship between Δd and Δh resulting from different RDI treatments. They found that the maximum height growth rate was greater in the sparsely managed stand (stands with a low level of RDI) than in the densely managed stand. Although D (circumference) and H were not incorporated as explanatory variables in their mixed models equations, Trouvé et al. empirically assumed that Δd represented the 'social status' in a stand, i.e., dominant trees had greater Δd values. Hence Figure 1a illustrates that the height growth rates of the dominant trees tended to reach the ceiling, especially in the densely managed stand, and that the ratio of Δh to Δd was greater in suppressed trees than in the dominant trees. King (2011) demonstrated that height growth rates of some coniferous species peaks at about 20-30 years of stand age. This phenomenon was reproduced in the analysis of Trouvé et al. in such a way that the asymptote of the height growth in the Δd – Δh curve changed with stand age (Figures 3 and 5a in Trouvé et al. 2015).

Unfortunately, as stated by Trouvé et al., some explanatory variables and other unused attributes, e.g. stand age and the stand dominant height at that age, were strongly correlated. Hence, although the explanatory variables of their final model included the stand age by discarding the dominant height, the model could not separate the effect of dominant height from that age, and care must be taken with the interpretation of their

results.

In the analysis by Trouvé et al., the effect of the Soil Water Deficit in summer (summer SWD; an index of water stress) on the Δd – Δh relationship was not significant (Table 3 in Trouvé et al. 2015), though in the sparsely managed stand the Δd – Δh curve is seen to shift toward the lower side under the conditions of high summer SWD (Figure 1b; Figure 4 in Trouvé et al. 2015). However, the failure to detect significant results may be because the 'resolution' of the data was not high enough to detect its effect, for the measurements of the tree sizes in a stand were conducted at four year intervals, and the value of summer SWD used in the model was the average of those four years. In addition, the shift in the Δd – Δh curve may have been accompanied by a shift in the frequency distribution of Δd values towards the lower side of Δd (Figure 1b) although this was not considered. While reduction of both height growth and diameter growth by water stress is not always the case for all species (Larchevêque et al. 2011), a tree under a chronic water stress often exhibits not only a shorter tree height but also a thinner stem diameter than trees without any water stress (Ryan and Yoder 1997).

The method introduced by Trouvé et al. implies the possibility of analysing changes with time in the static D – H relationship by using pooled data sets. Figure 2a is a schema of the Δd – Δh curve assumed in Trouvé et al. The shape of this ceiling curve is similar to that of the static D – H relationship (illustrated as the data cloud in Figure 2b), but the relationship between the two curves in Figures 2a and b is a little tricky. Figure 2c illustrates how a data point (D, H) in the static D – H relationship (Figure 2b) moves in the next time step, or the time-trajectory of an individual in the static D – H relationship in Figure 2b. The movement of the whole D – H cloud in the next time step would be obtained by giving ($\Delta d, \Delta h$) values to all data points of (D, H) in Figure 2b. Note here that the curvilinear line assumed in Figure 2a indicates that a tree with a small Δd has a

greater $\Delta h/\Delta d$, which means that a tree with a small Δd implicitly has a steeper trajectory. Let us further assume that a tree with a small D in a static $D-H$ relationship also has a proportionately small Δd . Then it follows that a tree with a small D in the static $D-H$ relationship (Figure 2b) should have a steeper trajectory than does a large tree. Resultant time-trajectories of (D, H) of individuals would be like the solid arrows in Figure 2d. That is, the $\Delta d-\Delta h$ curve which is asymptotic against Δh (Figure 2a) will yield a time trajectory of the (D, H) of an individual which is asymptotic against D , if D of a tree is relatively small (Figure 2d, dashed arrows). This accords with the time-trajectory patterns of individuals in some herb species (Weiner and Thomas 1992, Nagashima and Terashima 1995) and in a conifer species (Sumida et al. 2013). Hence the $\Delta d-\Delta h$ curve assumed in Trouvé et al. suggests a method of connection between the static $D-H$ relationship and time-trajectory of individuals.

Although the study of Trouvé et al. was not aimed to link between the $D-H$ and $\Delta d-\Delta h$ relationships, from the viewpoint of the study of carbon allocation in trees, it would be important to propose a way of explicitly connecting them in future studies; if two trees have the same diameter growth rates (Δd) but different tree sizes (D), the increment of the cross-sectional area would be greater in the tree with a larger D , and so would the volume increment of the stem at breast height. In other words, the importance of a value of Δd to a given tree may vary according to the value of D (or some other index of tree size) of the tree. In fact, as tree size reflects the sizes of internal water and carbohydrate stores (Sala et al. 2012, McDowell et al. 2013), the importance of tree size has been emphasized. Hence it would be meaningful to consider the effects of individual tree size into the $\Delta d-\Delta h$ modelling. Unfortunately, however, it is impossible to directly connect the $\Delta d-\Delta h$ relationship and the $D-H$ relationship from the result of Trouvé et al., as neither D nor H was included as an explanatory variable of their

models. Thus, the $(\Delta d, \Delta h)$ values of a tree are known but its (D, H) values are unknown in Figure 2c, thus in Figure 2d the location of the initial point of the vectors of $(\Delta d, \Delta h)$ cannot be determined.

There is another basic issue to keep in mind when the growth of D (at breast height) is used as a surrogate for stem thickening, which is that the diameter growth rate at breast height does not always represent the diameter growth rates of the other parts of a stem. Sumida et al. (2013) reported that some suppressed trees in an evergreen conifer stand had low rates of diameter growth in the stem below the crown base, but the height growth rates and the diameter growth rates in the stem within the crown was often high. This indicates that, in trees with suppressed conditions, the stem within the crown has priority of thickening over the stem below the crown base, possibly due to physiological reasons related to the necessity of leaf turnover (Sumida et al. 2013). The reason why the priority could be low for the stem below the crown in suppressed individuals was also discussed (Sumida et al. 2013). This nature of stem diameter growth rate at breast height must be paid attention in studies of carbon allocation using the $D-H$ and $\Delta d-\Delta h$ relationships.

It is poorly known how factors other than light, such as drought, extreme temperatures and strong wind, may affect the size inequality among the trees within a stand. The method by Trouvé et al. is suitable for such an analysis. The difference in $\Delta h/\Delta d$ ratio among trees in a stand is likely to be related to the difference in light quality above their crowns. Presence of taller neighbours will decrease the red/far-red light (R/FR) ratio above the crowns of shorter trees, which would trigger their shoot elongation of the main trunk and inhibition of branching (Schmitt and Wulff 1993). This is thought to be a morphological adaptation for trees to anticipate and avoid increasing competitive intensity for light with stand development (Schmitt and Wulff 1993).

However, in a stand where height inequality has occurred among individuals, height growth rates of shorter or suppressed individuals are never large enough to overtake the heights of the taller or dominant ones, resulting in a bimodal frequency distribution of plant height, and death of some shorter or suppressed individuals result (Ford 1975, Mohler et al. 1978, Nagashima and Terashima 1995, Watanabe et al. 2004). This is the case in Trové et al. in the sense that $\Delta h/\Delta d$ values were greater, but Δh values were smaller, in suppressed individuals than in dominant ones, meaning that an increase in the $\Delta h/\Delta d$ ratio would not improve competitive disadvantages of the suppressed individuals. If so, why do they continue to maintain Δh at the expense of Δd ? Answers to this question may be related to the role of non-structural carbohydrates (NSC) within a tree body (e.g., Sala et al. 2012); it has been pointed out that NSC is important for suppressed trees as they need to survive under occasional environmental stresses, such as drought, with little supply of light energy (Myers and Kitajima 2007; O'Brien et al. 2014). Thus, the significance of the increased $\Delta h/\Delta d$ in suppressed individuals may be for survival rather than for competition; possibly the increased $\Delta h/\Delta d$ should be interpreted such that the suppressed trees restrict allocation of photosynthate for uses of less priority, which is probably the thickening of the stem below the crown, in order to secure a certain level of NSC necessary for the survival under stressful conditions (Saffell et al. 2014). This hypothesis seems to be an interesting issue for a study concerning the Δd – Δh analysis, as it may extend the study of morphological strategy of species to studies of internal NSC levels. Such a study would also contribute to better understanding of the static D – H relationship among individuals.

Analysis of the Δd – Δh relationships using a large number of data sets may be useful for phenology studies of diameter and height growth, considering that Δh can be regarded as the current-year shoot extension on the crown surface of sessile oak.

Current-year shoots flush a few times a year on the crown surface in sessile oak (Buck-Sorlin and Bell 2000), and the timing of bud break for shoot growth is later than that of radial growth (Michelot et al. 2012). In an evergreen oak *Quercus ilex* L., radial growth is limited by the length of growing season which is affected by winter temperatures and summer drought (Lempereur et al. 2015). These facts may suggest that the phenology of shoot growth and that of radial growth are governed by different environmental conditions, thus Δh and Δd of a year may be determined by different environmental factors. Given a large number of data sets that allow us to determine meteorological factors in detail, factors affecting the balance between Δd and Δh may be clarified by the method of Trouvé et al. The nonlinear mixed models analyses using the pooled data sets is no easy, but further development of the method developed by Trouvé et al. could provide an important new tool in the analysis of stem growth.

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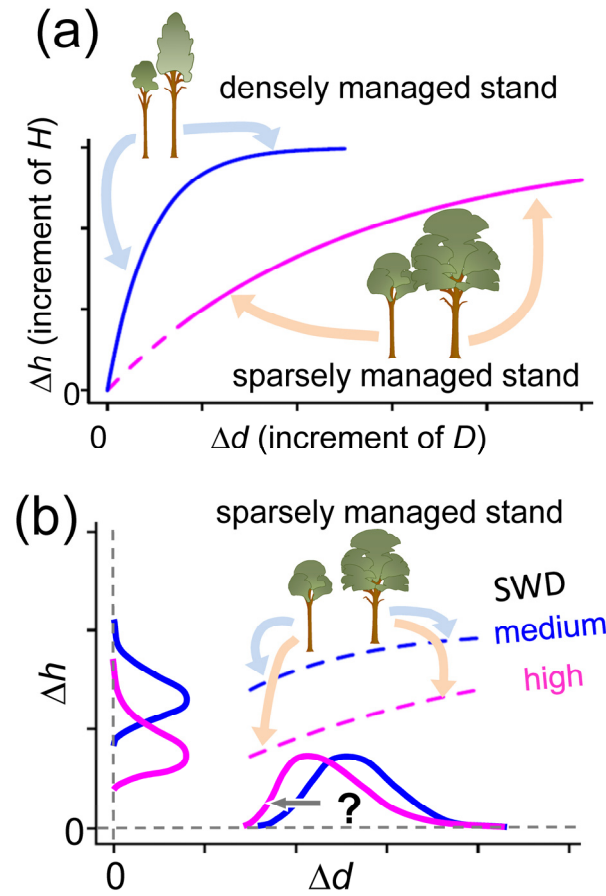


Figure1. Schematic illustrations explaining the Δd – Δh relationships in Trouvé et al. (2015). (a) A comparison of the Δd – Δh relationships between a densely managed stand (blue line) and a sparsely managed stand (pink line), schematically modified from Figure 5b in Trouvé et al. (2015). Each curvilinear line represents the among-tree relationship of a stand, where dominant trees were assumed to have greater Δd values. (b) The effects of SWD on the Δd – Δh relationship (dashed lines) in two sparsely managed stands with different levels of SWD, schematically modified from Figure 4 in Trouvé et al. (2015). The bell-shaped curves assume possible changes in frequency distributions of Δd and Δh values, from the medium (blue) to high (pink) levels of SWD.

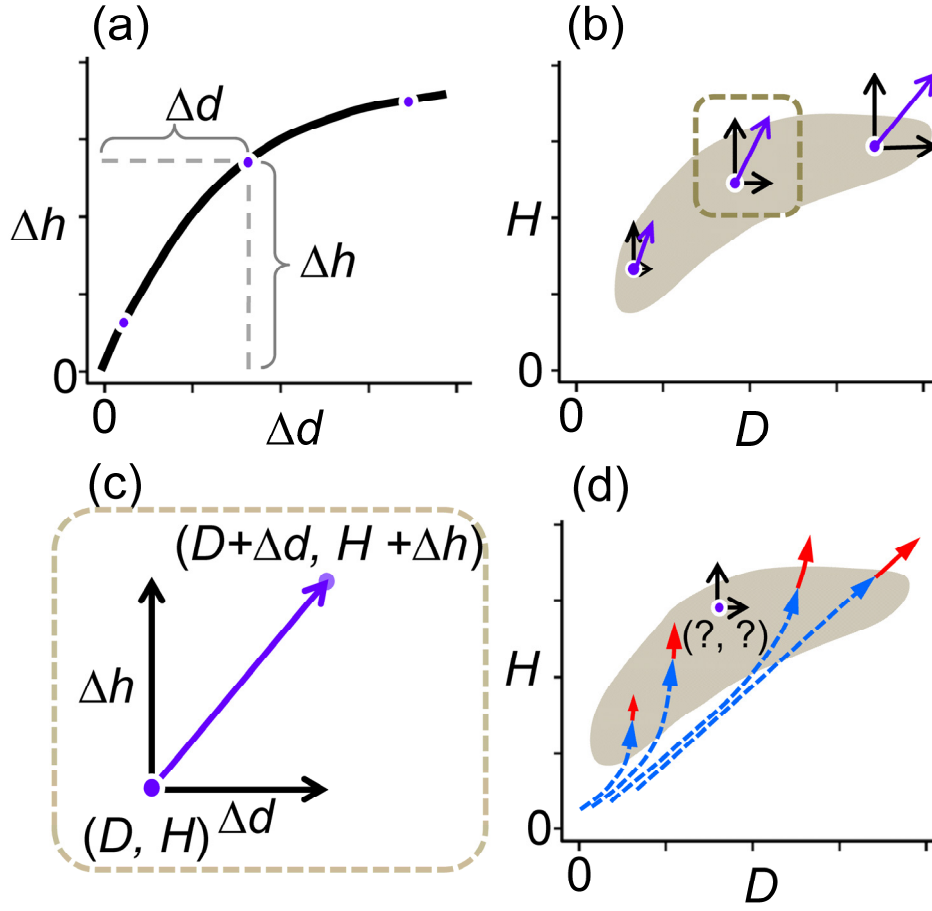


Figure 2. Explanations for the linkage between the Δd – Δh relationship and the static D – H relationship. (a) The Δd – Δh relationship assumed by Trouvé et al. (2015). (b) The relationship between D and H among trees at a given point in time (static D – H relationship), illustrated as the cloud assuming many (D, H) data points. Vectors indicate the movement of (D, H) data points in the next time step. (c) A magnified illustration of a (D, H) data point and the vectors shown in (b). The vector sum indicates the time-trajectory of the (D, H) point. (d) Time-trajectories of D and H of four individual trees in the past (dashed arrows) and the in the next time step (solid arrows), assuming the Δd – Δh relationship in (a).