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## A two-component dynamic stand model of natural thinning



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### ABSTRACT

Our investigation aims (1) to derive a dynamic model for mean volume and biomass growth projection over time, considering the competition-induced tree mortality (dynamic size-density model), (2) to design a compatible two-component modelling system composed of the dynamic size-density model and an appropriate density decrease function, and (3) to examine the applicability of this composite natural thinning model to describe the growth dynamics of even-aged coniferous and broadleaved stands.

The stand growth projection system was formulated to include three dynamic equations: a density decrease model expressing the reduction in tree number with dominant height growth, and two dynamic size-density models, for mean stem volume and tree biomass respectively. Two size-density formulations (M1 and M2) were derived, each including one local (site- or stand-specific) and three global (common to all stands of the species) parameters. Model M1 suggests a polymorphic set of size-density curves, while model M2 describes size-density curves with variable asymptotes. The goodness-of-fit statistics showed that for radiata pine (*Pinus radiata* D. Don) and Scots pine (*Pinus sylvestris* L.) datasets the three-model-system based on M1 performed better than the one based on M2. The growth trajectories of downy birch (*Betula pubescens* Ehrh.) and English oak (*Quercus robur* L.) stands were described only by model M2. The systems of projection equations explained more than 95% of the variation in most cases.

The two-component modelling system is implicitly defined by the stand density and mean tree size (biomass and/or volume) values for a given dominant stand height and set of global model parameters; it does not require any additional stand variables, constants of contested universality or standard-base variable values. It uses stand dominant height as a proxy for time, and inclusion of this growth stage indicator enables the bidirectional dependence between stand density and tree size to be reflected. The composite natural thinning model estimates sets of polymorphic curves with multiple asymptotes. Together with the stand-specific rate of density decrease, this also yields the stand-specific rate of size increase over time and the reduction in tree number, thus enabling prediction of contrasting individual growth patterns of stands of similar initial densities. It accounts for the isometric relationship between plant volume and biomass and can be considered for incorporation as a principal component of a dynamic Stand Density Management Diagram.

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### 1. Introduction

Conceptually, García (1988, 1994) defined two principal types of growth models: static models, which attempt direct prediction of the temporal course of the quantities of interest, and dynamic growth models, which predict the rates of change under various conditions, with the time trajectories obtained by adding or integrating these rates. Dynamic growth models comprise a state function, which characterizes the system at any point in time by using a

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fixed number of state variables, and transition functions, which describe the rate of change of the state variables and are typically given as a system of differential or difference (i.e. dynamic) equations (García, 1988, 1994). Stand Density Management Diagrams (SDMDs), a type of a stand-level growth model primarily used to derive density control schedules for specific management objectives, have also been subdivided into static and dynamic categories (Newton, 2003). According to Newton (2003), dynamic SDMDs explicitly include a mortality sub-model within their structure (unlike their static counterparts) and hence are able to describe stand developmental pathways throughout the entire size-density space. Mortality patterns including size-density trajectories as predicted from sub-models within the dynamic SDMD modelling framework are obtainable from algorithmic variants of

the SDMDs (Newton, 2009, 2012a, 2012b). The density decrease (mortality) sub-model usually included in dynamic SDMD requires supplementary information about stand age and/or site index (Castedo-Dorado et al., 2009; Newton, 2009, 2012a, 2012b; Pérez-Cruzado et al., 2011; Tewari and Álvarez-González, 2014). This information is not directly obtainable from the model, which is normally presented in graphical (diagrammatic) form and constructed using only spatial dimensions. Another approach for modelling the temporal dimension of growth, implemented in the classic-type SDMDs, is to express the temporal volume or biomass growth directly as a function of density decrease (Tadaki, 1964; Shibuya et al., 1997; Stankova and Shibuya, 2007; Stankova and Diéguez-Aranda, 2014a) in a set of natural thinning trajectories, thus bypassing the sub-model of density decrease over time. Such an approach for growth projection over time, however, is inherently static, because it does not include the time variable, expressed through age or some measure of tree size that is itself a function of time. Thus, if decrease of density in the stand does not occur, which is characteristic for the first (before the onset of the competition-induced mortality) and the last (the phase of growth-resources equilibrium) phases of stand growth, alteration in the tree size over time trajectory cannot be predicted. Consequently, this type of natural thinning model can be qualified as a size-density model rather than a transition function in a dynamic growth system.

Whereas SDMDs usually consider either a density decrease or a size-density model in stand growth projection, two-component systems composed of both density decrease and size-density models have also been developed in dynamic growth modelling. These composite systems involve a two-step application procedure which consists of projection of stand density to a future point in time through a dynamic mortality rate model and subsequent substitution of its estimate into a size-density relationship. The latter expresses the growth of some average stand size (e.g. mean stand diameter, biomass or stem volume) through the change in stand density and may (Cao et al., 2000) or may not (Smith and Hann, 1986; Puettmann et al., 1992) contain the time variable itself. The size-density models applied in the dynamic growth systems can be viewed as a product of an “asymptotic” and a “proportion” component. The “asymptotic” component is a function defining the maximum of an average stand size that can be reached at a given stand density, and is expressed either by the power function of Reineke (1933) for the mean stand diameter (Tang et al., 1994; Cao et al., 2000; Li et al., 2011) or by Yoda’s power law (Yoda et al., 1963) for the mean stand biomass or volume (Smith and Hann, 1984; Shibuya, 1995; Hagihara, 2000). The “proportion” component is presented by a density-dependent formulation, which yields values between 0 and 1 and which assures that the modelled average stand size is estimated as a proportion from the maximum attainable. The proportion component of the size-density model developed by Cao et al. (2000) can be viewed as derived from the Weibull cumulative distribution function, while the proportion component of the model by Smith and Hann (1984) resembles the double exponential function by Gompertz (*sensu* Zeide, 1993). The proportion components incorporated in the size-density models proposed by Shibuya (1995) and Hagihara (1998, 2000) consist of a direct subtraction from one of the ratio between current and initial stand density raised to a power.

The methodology for development of the first Stand Density Management Diagrams arose from a conjunction of two fundamental ecological postulates: the Competition-Density (C-D) theory proposed by Shinozaki and Kira (1956) and Yoda’s power law of self-thinning (Yoda et al., 1963). While the C-D theory studies the relationship between density and plant growth of even-aged populations at a particular growth stage (Shinozaki and Kira,

1956, 1961), Yoda’s power law formulates the dependence of plant growth on the decrease in population density over time (Yoda et al., 1963). Both theories were unified by Hagihara (1999, 2000) in a new reciprocal equation of the C-D effect, which is applicable to both self-thinning and non-self-thinning populations. It allows estimation of both the size-density relationship at a particular growth stage in space and the trajectory of stand growth over time, relative to the natural thinning process. Considering Hagihara’s fundamental research on the Competition-Density theory, the present investigation aims to achieve the following research objectives: (1) to derive a dynamic model for mean volume and biomass growth projection over time, given the process of competition-induced tree mortality (dynamic size-density model); (2) to design a compatible two-component modelling system composed of the dynamic size-density model and an appropriate density decrease function, which predicts stand survival with stand dominant height growth; and (3) to examine the applicability of the composite natural thinning model to describe the growth dynamics of even-aged coniferous and broadleaved stands and plantations.

## 2. Materials and methods

### 2.1. Data sets

Data from even-aged stands of four tree species – two coniferous and two broadleaved – were used to test the models derived in the present study. Measurements collected in permanent sample plots in natural stands of downy birch (*Betula pubescens* Ehrh.) and English oak (*Quercus robur* L.) and in radiata pine plantations (*Pinus radiata* D. Don) located throughout Galicia (NW Spain) composed three of the data sets, while the fourth data set was generated from measurements made in Scots pine (*Pinus sylvestris* L.) plantations in Bulgaria. The plot size varied depending on stand density, yielding a minimum of 30 trees per plot, and the plots were subjectively selected to cover the existing range of sites, densities and developmental stages of the stands. Only plots that were either not thinned or were only subjected to light thinning from below were considered. Since the investigated plant populations were either absolutely even-aged plantations or approximately even-aged natural stands with insignificant ingrowth, all trees in the plots were labelled with a number and diameter at breast height (1.3 m above ground level) of each tree was measured with callipers to the nearest 0.1 cm. Longitudinal data on stand density, expressed as number of trees per hectare (trees ha<sup>-1</sup>), dominant stand height, defined as the mean height of the 100 largest-dbh trees per hectare (m), mean stem volume (m<sup>3</sup>) and mean tree biomass (kg), were used for model parameterization. The data sets are graphically illustrated in Figs. 1–4, A1–A3 and are summarized by species in Table 1.

The birch stand data were obtained from permanent sample plots, of size 200–1000 m<sup>2</sup> in the altitudinal range 277–1370 m a.s.l., which were measured twice in the period 1997–2008. Plots of 225–1350 m<sup>2</sup> established in oak stands located at 338–845 m a.s.l. and measured two or three times in the period 1999–2009 were used to generate the data for this species. The plots, established in radiata pine plantations located below 900 m a.s.l., ranged from 625 to 1200 m<sup>2</sup> in size and were measured 2 or 3 times between 1995 and 2005. Total tree heights in a sample including the dominant trees (the proportion of the 100 largest-diameter trees per hectare, depending on plot size) were measured to determine the dominant stand height. The cumulative estimates of stand volume and biomass were based on stand-level allometric relationships of the stem volume and the weight of the aboveground tree compartments to stand basal area, dominant height, quadratic mean and dominant diameters, age and number

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