Forest Ecology and Management 411 (2018) 90–100

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Intra- and inter-specific variation of the maximum size-density relationship along an aridity gradient in Iberian pinewoods

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ARTICLE INFO

Keywords:
Reineke
Self-thinning
Monospecific and mixed stands
Martonne
Competition equivalence coefficient

ABSTRACT

The diverse applications of the maximum size-density relationship (MSDR) in monospecific and mixed forests, such as in ecological and economic aspects, lead to continuous advances in our knowledge on this issue. One of the most recent advances was the inclusion of climatic variables in these studies, revealing the variation in MSDR depending on environmental conditions. However, the importance of climatic conditions on the intra- and inter-specific variation of MSDR is still poorly understood. The aim of this paper is to explore the dependence of MSDR on climatic conditions for the five principal pine species in the Iberian Peninsula (*P. halepensis* Mill., *P. nigra* Arn., *P. pinea* L., *P. pinaster* Ait., and *P. sylvestris* L.) and to analyse the importance of this dependence on the relative carrying capacities in mixed stands. Data from the Third Spanish National Forest Inventory (NFI) were used together with four simple climatic indices calculated from raster maps. Using a quantile regression, a MSDR basic model, relating the maximum number of trees and the quadratic mean diameter, was fitted to the data from the plots in monospecific stands. In a second step, the coefficients of basic model were parameterized as a function of climatic variables. The resulting climate-dependent model was also fitted to the plots. Competition equivalence coefficients (CEC) in mixed stands (i.e. ratio between maximum stand density indices of the two species) were calculated from the resulting models. The differences among species' MSDRs confirm the inter-specific variability of maximum densities and the need for species-specific models. According to the Akaike information criteria, the climate-dependent models, and particularly those dependent on Martonne aridity index, were always better than basic models. Although the higher the aridity the lower the maximum stand density, the influence of climate on the MSDR also varies according to the species considered, this influence being more evident for *P. pinaster* and *P. halepensis*, which also display high ecological plasticity. The CEC derived from the basic model for pine-pine mixtures range from 1.10 to 1.70. However, when aridity is considered, these coefficients almost always decrease. Our results highlight the importance of considering environmental variables to better describe and compare the potential density in monospecific and mixed stands and therefore, the utility of species-specific climate dependent models for management decision support.

1. Introduction

Resources needed for tree growth in forest stands are limited. Hence, as trees size increases the resources required increase and the self-thinning (i.e. tree mortality induced by competition) starts to be an active process in the forest dynamic. Self-thinning occurs when a stand approaches to the asymptote fixed by the maximum density, that is, the maximum number of trees of a given size that can grow per hectare in a stand (Smith and Hann, 1984, 1986; Puettmann et al., 1993; Tang et al., 1994). Knowing this maximum size-density relationship (MSDR) is an important issue in forest science because it is related to several ecological and economic aspects of forest management. Among other aspects, MSDR can be used as a tool to evaluate forest adaptation to climate change and carbon storage (Brunet-Navarro et al., 2016), as well as to assess risks due to abiotic and biotic factors (Ducey et al., 2017). The study of MSDR can also be an essential aspect of forest management, allowing managers to fix an optimal level of thinning as a percentage of this maximum stand density (Hynynen, 1993). In fact, MSDR or self-thinning lines are often used to develop stand density management diagrams (Newton, 1997; Long and Shaw, 2005; Valbuena et al.,

Abbreviations: M, Martonne aridity index; NFI, National Forestry Inventory; MSDR, maximum size-density relationship; CEC, competition equivalence coefficient

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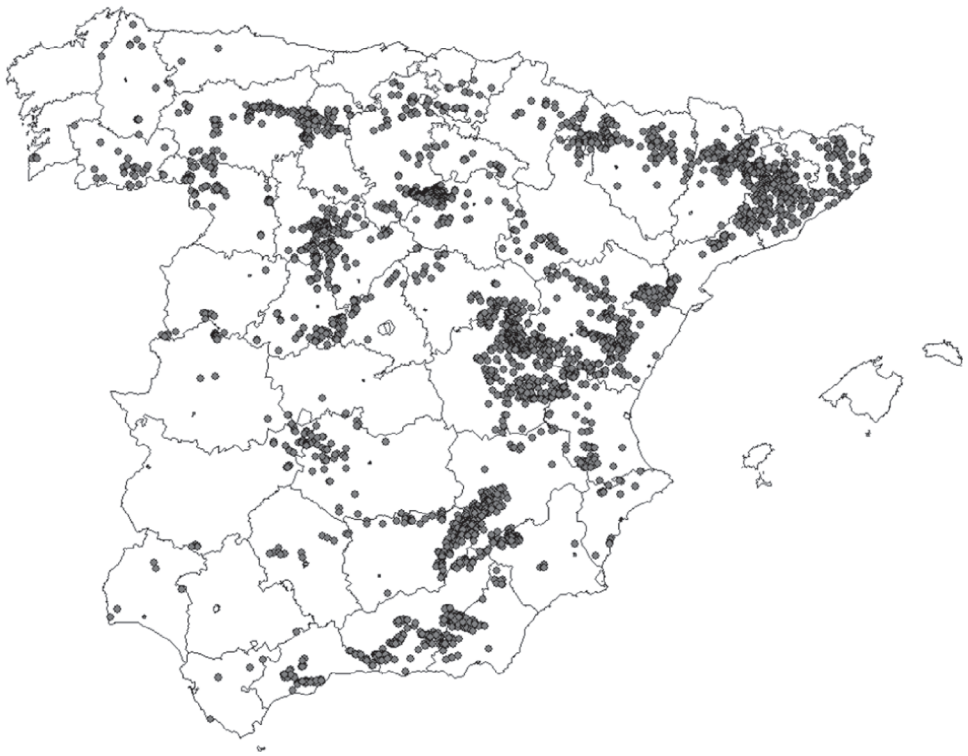
https://doi.org/10.1016/j.foreco.2018.01.017
Received 6 October 2017; Received in revised form 11 January 2018; Accepted 11 January 2018

(a) : Sample plots located in monospecific stands



(b) : Sample plot located in pine mixtures

Fig. 1. Location of the NFI sample plots used in this study.

2008), and growth models (e.g. Makela et al., 2000).(see Fig. 1.)

The most widespread approach to studying the MSDR is through a linear relationship, in double logarithmic scale, between mean plant size (as diameter, biomass or volume) and number of trees per hectare (Reineke, 1933; Yoda, 1963). In particular, Reineke (1933) studying monospecific stands at fully stocked stands, established a relationship between the maximum number of trees per hectare, N_{max}, and the quadratic mean diameter, dg, (Eq. (1a)) than can be written as a linear