Forest Ecology and Management 414 (2018) 99–107

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Linking competition with Growth Dominance and production ecology

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ARTICLE INFO

Keywords:
Gini coefficient
Size hierarchy
Resource use
Resource use efficiency
Size-growth relationships

ABSTRACT

The development of forests over time is influenced by competition for resources among trees, leading to patterns of size hierarchy. These two aspects – competition and size hierarchy – can be examined in conjunction with a production ecology perspective. Competition for resources between individuals has often been represented as a continuum between absolute symmetry and absolute asymmetry. Symmetric competition implies that trees capture resources proportional to size, whereas asymmetric competition implies that large trees capture a disproportional share of contested resources over small trees. Furthermore, the competitive ability of a tree is also determined by the efficiency with which the resources are used to grow. Competition is often inferred indirectly from size inequality or size hierarchy of the size structure using the Gini coefficient. This approach assumes that the predominant mode of competition is asymmetric, and that size hierarchy reflects a degree of competition. This presumption is not always valid, and in this case size hierarchy does not reliably represent competition. A more insightful examination of competition might be interpreted from the Growth Dominance approach. Growth dominance summarizes the growth distribution in relation to size structure, and characterizes how effectively large trees dominate growth in a population. When competition is not asymmetric, size hierarchy does not imply a hierarchy on growth relative to size. For example, two stands experiencing opposite modes of competition could have the same Gini coefficient, but will show different Growth Dominance coefficients. We propose that the connection between competition and Growth Dominance relates to specific resource use and resource use efficiency patterns among trees in a stand. Growth dominance can be positive (if larger trees dominate growth), null (if no particular group of trees dominate growth) or reverse (if smaller trees dominate growth). Positive Growth Dominance should relate to asymmetric competition for resources and (or) to increasing resource use efficiency with tree size in a stand. Null Growth Dominance should result from symmetric competition for resources and similar resource use efficiency among trees in a stand. Reverse Growth Dominance should arise from symmetric competition for resources and (or) from a decreasing resource use efficiency with tree size in a stand. We look forward to the development of many case studies that will challenge our idea, either refining or refuting it.

1. Introduction

Competition occurs between neighboring individuals and involves the effect on the partitioning of environmental resources (light, water and nutrients) between individuals, and the efficiency with which these resources are used to support growth. Competition may be defined as the difference in growth between an individual growing in a crowded stand and a same-size individual growing under isolated conditions (Hara, 1993). Competition is difficult to study as a process, and it has been often assessed as a pattern. Most work on competition has concentrated on studying the size structure of populations. Some degree of size hierarchy is common in forests, and even homogeneous clonal plantations often have coefficients of variation in tree size of more than 15% (Binkley et al., 2010).

In this paper, we analyze how competition can be examined with two stand metrics: the Gini coefficient and Growth Dominance coefficient. We also explore how these indices relate to the production ecology equation (Monteith, 1977). Patterns of Gini and Growth Dominance coefficients derive from the combined influence of resource use (resource uptake) and resource use efficiency distribution among

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https://doi.org/10.1016/j.foreco.2018.01.052
Received 3 November 2017; Received in revised form 29 January 2018; Accepted 30 January 2018
Available online 22 February 2018

Table 1
A glossary of terms used in forest competition and forest production ecology.

Term	Definition	Source
Complete size asymmetry	One individual, the largest, captures all the contested resources (also called absolute size asymmetric competition)	Schwinning and Weiner (1998)
Complete symmetric competition	All individuals capture the same amount of resources irrespective of their sizes (also called absolute size symmetric competition)	Schwinning and Weiner (1998)
Growth Dominance	Growth dominance describes the growth distribution of trees in relation to tree size distribution	Binkley (2004)
Partial size symmetric competition	Capture of contested resources increases with size but less than proportionally	Schwinning and Weiner (1998)
Partial size asymmetric competition	Capture of contested resources increases with size and larger individuals obtain a disproportionate share of resources	Schwinning and Weiner (1998)
Perfect size symmetric competition	Capture of contested resources is proportional to size (also called relative size symmetric competition)	Schwinning and Weiner (1998)
Resource	An element or form of energy used by plants in direct or indirect processes of production; light (energy form), water (lost in transpiration), and nutrients (catalysts for biochemical reactions, and components of cells) are the resources of interest	Binkley et al. (2004)
Resource use	The quantity of resources used by a plant at a defined scale of space and time (=resource capture, resource uptake, resource acquisition)	Binkley et al. (2004)
Resource use efficiency	Production per unit of resource used. It needs to be defined clearly for any particular plant component (e.g., stem production)	Binkley et al. (2004)
Size hierarchy	Size hierarchy describes the degree to which biomass is concentrated among a few individuals	Weiner and Solbrig (1984)
Size-growth relationship	Functions relating growth to size of individuals plants in a population at a point in time (also called distribution modifying functions)	Westoby (1982)

trees within a population. We use case studies and simulated stands to illustrate some points. This focus on size and growth of individuals is not identical to reproductive success, but if competitive dominance and genotype are correlated, size and growth will relate to evolutionary fitness (Weiner, 1990). This paper concerns processes that lead to differences in growth rate of tress, without analyzing the effect of competition on fitness of individuals trees (see Table 1 for definition of terms used in this paper).

2. Competition and stand structure

Competition is usually considered as a continuum between absolute symmetric competition and absolute asymmetric competition. Asymmetric competition develops when larger individuals have a disproportional competitive advantage over small individuals, resulting from greater proportional preemption of resources (Schwinning and Weiner, 1998; Weiner, 1990). A crown of a large tree intercepts light, preempting the supply to a smaller tree with little or no influence of a smaller tree's light capture on the larger tree. Symmetric competition implies that the competitive effects of larger and smaller individuals are similar, with either equal resource use (absolute symmetry), or resource use that scales less than proportional with tree size (partial size symmetry) or proportionally with tree size (perfect or relative size symmetry) (Schwinning and Weiner, 1998; Weiner, 1990). For example, equal use of soil water by all plants would be symmetric competition, and water use in constant proportion to tree size would be relative-size symmetric.

Size hierarchy describes the degree to which biomass is concentrated among a few individuals, and refers to a concept of size inequality or concentration in the size distribution of a population (Weiner and Solbrig, 1984). Scientists have assumed size hierarchy as the outcome of competition, and various characteristics of size distribution have been used to evaluate size hierarchy. These include: skewness, bimodality, size inequality or size variation, and growth distribution (Bendel et al., 1989; Damgaard and Weiner, 2000; Ford, 1975; Weiner and Solbrig, 1984; Westoby, 1982). The Gini coefficient has been recommended as a statistic to measure size hierarchy in plant populations (Weiner and Solbrig, 1984).

The effect of competition on size hierarchy varies according to the mode of competition. While asymmetric competition increases size hierarchy over time (in a stand without intense mortality), symmetric competition sustains the current size hierarchy over time (Weiner, 1990; Westoby, 1982).

The size distribution of a forest results in part from the distribution of growth among trees, with feedback effects on subsequent growth among trees. The "distribution modifying functions" (Westoby, 1982) (also called size-growth relationships) are functions relating growth to size of individuals plants in a population at a point in time. The shape of these functions influences the development of size distributions, and relates to the mode of competition (Weiner, 1990). Using the relationship between growth and size, competition is considered size-symmetric if individuals grow proportional to their size (all individuals experience similar relative growth rate), and competition is considered size-asymmetric if large individuals grow more than proportionally to size (larger individuals experience higher relative growth rate). Finally, competition is considered inverse size-asymmetric (also called partial size-symmetric) when small individuals grow disproportionately more relative to their size (Metsaranta and Lieffers, 2010; Pretzsch and Biber, 2010; Weiner, 1990; Weiner and Damgaard, 2006). Asymmetric competition is the most likely explanation for those cases with size-asymmetric growth, however, size-asymmetric growth is not a good measure of the strength of asymmetric competition (Weiner and Damgaard, 2006).

Another representation of the relationship between growth and stand structure is Growth Dominance (Binkley, 2004; Binkley et al., 2006). Growth dominance describes the growth distribution of trees in relation to tree size, and has been used as a quantitative method to evaluate stand structure. Growth Dominance varies across species and forest stands. For example, stands of *Eucalyptus* species often show high positive Growth Dominance at young ages (Binkley et al., 2003), declining but remaining positive with age (Doi et al., 2010). In contrast, stands of *Pinus* species show a relatively small positive Growth Dominance or null Growth Dominance (Bradford et al., 2010; Fernández and Gyenge, 2009; Fernández Tschieder et al., 2012). Fernandez et al. (2011) proposed that differences in Growth Dominance patterns could be related to species traits as leaf physiological plasticity. Explicitly or implicitly, Growth Dominance has been related to symmetric or asymmetric competition (Bradford et al., 2010; Doi et al., 2010; Fernández and Gyenge, 2009; Fernández Tschieder et al., 2012; Keyser, 2012; Pothier, 2017). Positive Growth Dominance has been related to asymmetric competition, null Growth Dominance to perfect symmetric competition, and reverse Growth Dominance to absolute or partial symmetric competition (Doi et al., 2010; Fernández Tschieder et al., 2012; Pothier, 2017).