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A comprehensive framework of forest stand property-density relationships: perspectives for plant population ecology and forest management

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Abstract:	Context: There are many stand property-density relationships in ecology which represent emergent properties of plant populations. Examples include self-thinning, competition-density effect, constant final yield, and age-related decline in stand growth. We suggest that these relationships are different aspects of a general framework of stand property-density relationships. Aims: To illustrate the generalities and ecological implications of stand property-density relationships, and organize them in a comprehensive framework. Methods: We illustrate relationships between stand property and density (1) at one point in time, (2) over time, and (3) independent of time. We review the consequences of considering different variables to characterize stand property (mean tree size, mean tree growth, stand growth, stand yield, stand leaf area). Results: We provide a framework which integrates the broad categories of stand property-density relationships, and individual expressions of these relationships. For example, we conclude that constant final yield is a special case of the growth-growing stock relationship for life forms were yield is a reasonable approximation of growth (non-woody plants). Conclusion: There is support in the literature for leaf area being broadly integrative with respect to various expressions of stand property-density relationships. We show how this is and suggest implications for plant population ecology and forest management.

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Annals of Forest Science
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Object: cover letter for article submission

Dear Editor,
following you positive feedback to our inquiry of last June 2012, please receive our draft of a review of the rich literature dealing with stand property-density relationships in tree populations.

The novelty of the review is in identifying a common theoretical background for different processes related to stand density which are treated independently by plant population ecologists.

We are qualified to conduct this review. The influence of population density has been the focus of much of our research, resulting in over 60 papers and book chapters in which plant population density is the focus or an important component.

The submission consists of this cover letter, a MS Word file with text, references, tables, and figure captions, and 7 figures in separate EPS files.

The paper has not been presented elsewhere. We believe that the topic will be of great interest to AFS readers, both from a theoretical (forest ecology) and applied (forest management) point of view.

We look forward to publish our review in Annals of Forest Science.
Thank you very much,

Sincerely,
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Response to reviewers

A comprehensive framework of forest stand property-density relationships: perspectives for plant population ecology and forest management

-the way the article is organised should be reconsidered as it appears difficult for the reader to disentangle syntheses from opinions and discussions in each relationships category. I suggest thus the author(s) to first present briefly the stand property-density relationships as well as the logic of the general framework (the synthesis itself) and then to structure the article around their discussions based on connections between categories, leaf area index and perspectives for plant population ecology and forest management.	**We restructured the paper and moved most of our interpretations to a novel chapter before the summary. This chapter is inclusive of explicit perspectives for forest ecology and management, along with an outlook on research on mixed and uneven-aged forests and related references).** **We also added sub-headings to the longest chapters for better clarity.**
-the author(s) should give more elements on the validity or the modifications of the relationships in multi-cohorts and mixed forests. It is very frustrating in the end to notice that this topic is hardly addressed, especially for the time independent category. See for instance Rivoire, M., Le Moguedec, G. (2012). A generalized self-thinning relationship for multi-species and mixed-size forests. AFS 69(2): 207-219.	**See above.** **After closer inspection of the literature (including that suggested by the reviewer) we concluded that most research on mixed and/or uneven-aged stands is still at a preliminary stage, i.e., detailing only certain types of mixtures (limited to two species, anyway), and is far from developing a more general framework. We inserted these considerations in the text.**
-the implication for plant population ecology and for forest management are explicitly announced in the abstract but actually are not well developed in the current version (diluted in all the sections). The authors should dedicate specific sections for these two topics.	**See above.**
A recent study has been published on the plant size-density relationships that could help the author(s) to deepen their discussion: Deng, J. et al. 2012. Insights into plant size-density relationships from models and agricultural crops. PNAS 109 (22): 8600-8605.	**Reference added**
The title should be more explicit: for instance « A comprehensive framework of forest stand property-density relationships: perspectives for plant population ecology and forest management».	**The title was changed as suggested**
Correct the units through the whole text: m3 and m2 instead of m-3 and m-2.	**Corrected**
L31: remove the brackets.	**Removed**
L64: relative density is based itself on a density-stand property relationship which can be confusing.	**A sentence was inserted that acknowledges the fact and points to further explanations in the following chapters.**

L73-78: such experiments can be also used for stand-property density relationships over time. I suggest the authors either to remove this part or to develop it in the previous section.	**Removed**
L73: density does not vary in simple replacement series experiments (it is used to study species mixtures). Use other appropriate references or be more explicit.	**Changed to "thinning trials"**
L77-78: in an experiment with true replicates and with random allocations of treatments, the variability of edaphic factors is expected to be the same among treatments. In my opinion, the sentence can be removed as it is not informative and not essential for the article.	**Removed**
L80-81: check the sentence.	**Sentence edited: "The way stand property is characterized…"**
L80-84: This is redundant with L61-65. It can be removed.	**Removed**
L148: remove « is ».	**Removed**
L198-220: distinguish better growth from yield. Growth is addressed in the next paragraph.	**Yield and growth relationships were divided into separate paragraphs**
L298: see also Charru et al. 2012. Significant curvilinear in the self-thinning relationships of 11 temperate tree species assessed from forest inventory data. AFS 69: 195-205.	**Reference added**
Table 1 caption: replace "3" by "three". In the table, provide entire words instead of acronyms. It would be relevant to show in the table that CFY and growth-growing stock are linked.	**The table and caption were edited as requested.**
Figure 1b : top height is not indicated in the figure (replace t ?).	**Top height was added to the figure and caption**
Figure 4a: for the sake of homogeneity, add letters for the different initial densities.	**Letters were added to the figure**

*Title Page

A comprehensive framework of forest stand property-density relationships: perspectives for plant population ecology and forest management

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Total number of characters: 44227
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Number of figures: 7

Contribution of the co-authors: JL coordinated the review and wrote much of the early draft. GV wrote Part 2.3. Both authors contributed to draft revisions.

A comprehensive framework of forest stand property-density relationships: perspectives for plant population ecology and forest management

Abstract

Context: There are many stand property-density relationships in ecology which represent emergent properties of plant populations. Examples include self-thinning, competition-density effect, constant final yield, and age-related decline in stand growth. We suggest that these relationships are different aspects of a general framework of stand property-density relationships.

Aims: To illustrate the generalities and ecological implications of stand property-density relationships, and organize them in a comprehensive framework.

Methods: We illustrate relationships between stand property and density (1) at one point in time, (2) over time, and (3) independent of time. We review the consequences of considering different variables to characterize stand property (mean tree size, mean tree growth, stand growth, stand yield, stand leaf area).

Results: We provide a framework which integrates the broad categories of stand property-density relationships, and individual expressions of these relationships. For example, we conclude that constant final yield is a special case of the growth-growing stock relationship for life forms were yield is a reasonable approximation of growth (non-woody plants).

Conclusion: There is support in the literature for leaf area being broadly integrative with respect to various expressions of stand property-density relationships. We show how this is and suggest implications for plant population ecology and forest management.

Keywords: *Competition, Leaf area, Population ecology, Self-thinning, Stand density, Stand dynamics*

1. Introduction

Most plant populations, ranging from annuals to long-lived trees, experience competition, in the form of increasing density of individuals under a limited amount of needed resources. The remarkable range of responses of plants to competition is the driver of important emergent properties of plant populations (*sensu* Goldstein 1999) and has been the subject of a rich literature in both basic and applied (i.e., agronomy and forestry) plant ecology. Examples include self-thinning (Reineke 1933; Yoda et al. 1963), competition-density (C-D) effect (Kira et al. 1953), constant final yield (Weiner and Freckleton 2010) and age-related decline in stand growth (Smith and Long 2001). All of these relationships have in common that some attribute of the population (e.g., a "stand" property such as mean size, total yield, or growth) is related to population density. Examples of differences between these relationships include: does the attribute being related to density represent a population mean or a population total; does the relationship include time, either implicitly or explicitly; does the relationship include potential productivity, i.e., is it dependent on site quality?

When one of these relationships is invoked in a particular situation or context, it is typical to treat it as independent from other stand property-density relationships. In this review, however, we illustrate how these seemingly disparate relationships are, in fact, each examples of different aspects, and in some cases, simply different formatting, of a general framework of stand property-density relationships. Our focus in this review will be trees; we will, however, ground our synthesis in the context of terrestrial vascular plant communities.

2. Rationale: stand property-density relationships

This synthesis concerns the diverse class of stand property-density relationships. In this context, stand property is "performance" *sensu* Weiner and Freckleton (2010), and the attribute of the population being related to density. Stand property can be represented by an expression of yield per unit area (standing biomass, stem volume or basal area with units such as g m^{-2}; m^3 ha^{-1} or m^2 ha^{-1}), mean size (a transformation of yield), or an expression of growth (with units such as g m^2 yr^{-1}; m^3 ha^{-1} yr^{-1}). The way stand property is characterized can make the basic relationship appear fundamentally different, but there is insight to be gained from comparing and contrasting different forms. Density can be expressed in absolute (e.g., seedlings m^{-2} or trees ha^{-1}) or relative terms. Relative density (RD) is a quantification of

the current density of a forest stand in comparison to some maximum level (Woodall et al. 2006). The existence of a maximum level is another consequence of stand property-density relationships, and will be discussed below.

There are three basic ways to characterize relationships between stand properties and density (Weiner and Freckleton 2010) (Table 1). A stand property-density relationship can represent a point in time. Alternatively, a relationship may be over time, such as in a stand development trajectory. In both cases, a key assumption is that except for density, important variables influencing potential productivity, such as stand age and edaphic factors, are constant (Weiner and Thomas 1986). Finally, a stand-property relationship may be analyzed independently of time, as in the case of naturally occurring populations (as opposed to controlled experiments) spanning a wide range of site quality and stand ages.

2.1 Stand property-density relationships at a point in time

This version of stand property-density relationships is typically represented with data from a controlled experiment, like a spacing trial or thinning experiment (e.g., Harms et al. 2000; Laroque 2002), with a single species and relatively uniform distributions of stems and site condition. The densities represented can be either initial or surviving following self-thinning. The most important examples of this version of stand property-density are the competition-density (C-D) effect (Kira et al. 1953), the yield-density (Y-D) effect (Shinozaki and Kira 1956; Drew and Flewelling 1977), growth-growing stock (G-GS) relations (Long et al. 2004) and constant final yield (CFY) (Weiner and Freckleton 2010).

The C-D and Y-D effects are the relationships between stand property and density, at a given point in time, where stand property is characterized as either mean size or yield, respectively. The C-D effect is represented in Figure 1a by four hypothetical populations with relatively low (ρ_1) to high (ρ_4) initial density. Each curve represents the influence of density at a given point in time. Early (t_1) in the development of these populations, mean size is independent of density, but eventually a negative relationship emerges as competition affects mean size first at the highest densities and progressing to the lower densities (t_3). For trees, the C-D effect is convincingly represented on density management diagrams (Jack and Long 1996) by a given top height line, with a family of top height lines showing the time progression of the C-D effect (Figure 1b) (Newton et al. 1997). With site quality held constant, any combination of stand property and density along a given top height line corresponds to a given point in time (Drew and Flewelling 1977).

The growth-growing stock effect (G-GS) is the stand property-density relation at a given point in time where stand property is characterized as growth. In the forestry literature, the stand property is typically tree stem volume increment (Husch et al. 1982) and is represented for both the population (m^3 ha^{-1} yr^{-1}) (Figure 2a) or for the population mean (mean tree growth with units of m^3 yr^{-1}) (Figure 2b). The shape of the G-GS relationship for stand growth is illustrated as asymptotic in Figure 2a (after Langsaeter 1941); this is consistent with some (e.g., Curtis et al. 1997), but by no means all, experimental results (e.g., Zeide 2001). The alternative is a unimodal form to the stand G-GS relationship, with maximum growth occurring at somewhat less than maximum density. The asymptotic form implies that even a very light thinning must result in at least a modest reduction in stand growth. In contrast, the unimodal form implies that stands, particularly young ones (Pretzsch 2010 pg 409), are able to compensate and even overcompensate for thinning removals.

In considering the G-GS effect, it is important to be mindful of the diversity of ways 'growth' is represented. In the forestry literature, for example, the choice of net versus gross growth affects the nature of the G-GS effect at high densities (Figure 2a). It is also important to clearly understand which component of growth is being represented by stand property, e.g., which trees or tree parts are included in the definition. In agronomy the concept of 'harvest index' (reviewed in Hay 1995) is analogous to only considering the growth of those trees greater than merchantable size.

The law of constant final yield (CFY) is another important example of a stand property-density relationship at one point in time (although the words 'constant' and 'final' incorrectly suggest development over time). The fundamental difference between CFY and G-GS is that stand property is represented by yield rather than growth (Weiner and Freckleton 2010 Figure 1); this relationship was originally held valid for herbaceous species only.

2.2 Stand property-density relationships over time

As before, stand property can be characterized as yield, mean size, or growth, but here the focus is on changes in the stand property over time, typically analyzed in even-aged stands. These changes can be represented as a trajectory (i.e., ordered values of stand property as a function of density), or a time series (i.e., time on the x-axis).

2.2.1 Self-thinning trajectory

In the trajectory approach (Figure 3), time is represented implicitly, as the population moves along the trajectory, and displays simultaneous changes of both stand property and density. A population occupying a site with high potential productivity will move along the trajectory faster than if it were occupying a poorer site, but will nevertheless move on the same trajectory if the starting values are the same (Long et al. 2004).

Along the trajectory of a given population, e.g. with larger mean size over time, relative density tends to increase asymptotically. The asymptote, or 100% RD, represents the maximum size-density boundary, i.e., the upper limit to all combinations of mean size and density observed in fully stocked pure or nearly pure populations. This limit has an analog in the concept of carrying capacity, but the reasons for its existence have been a source of intense debate in the ecological literature (discussed in paragraph 2.3).

The stand property-density trajectory of a population of trees spans several more or less distinct stages of stand development (Long and Smith 1984; Oliver and Larson 1996). When the trees are small relative to their number, individual tree growth is great relative to the potential growth (which is a function of species, site quality and age). In contrast, the degree of site occupancy is low and, therefore, stand growth is modest relative to its potential. At this stage of development, the stand would occupy a point on the left side of the G-GS relationships (Figure 2a-b). With time, mean tree size and RD increase and competition results in a reduction of individual tree growth relative to its potential. With further increases in mean size and RD, the population approaches full site occupancy and stand growth approaches a maximum for the given species, site and age (Long and Smith 1984). Further increases in RD are accompanied by self-thinning (i.e., competition-induced mortality), and, indeed, the entire trajectory is commonly referred to as the self-thinning trajectory (Smith and Hann 1986).

2.2.2 Time series of yield

With the time series approach, the influence of density on a stand property is often represented by comparing populations of different initial densities. In forest populations, time series of stand properties display two fundamentally different patterns of yield over time – one for stem volume or woody biomass, and another for foliage.

When yield is represented as either stand volume or basal area ($m^3\ ha^{-1}\ yr^{-1}$ or $m^2\ ha^{-1}\ yr^{-1}$) these can be gross, net, or merchantable, but regardless of how these stand

property-density relationships over time are characterized, the basic patterns are similar. For a given initial density, yield increases over time even with the on-set of self-thinning (Figure 4). However, even as the amount of foliage on individual trees also continues to increase more or less indefinitely, the amount of foliage for the population (i.e., total leaf area or leaf biomass) reaches an upper limit at some threshold tree density (Figure 5a-b) (Kira and Shidei 1967). This is a dynamic equilibrium, resulting from a constant loss of foliage during self-thinning, and the simultaneous increase in crown size of survivors (Holdaway et al. 2008). For a population with a high initial density, arriving at the foliar upper limit happens at a relatively young age; with low initial density, arriving at the plateau occurs later (Turner and Long 1975) (Figure 5a). At this point, the stand is said to "fully occupy" the site, i.e., exploiting all the resources (light, nutrients, and possibly water) that the site has to provide.

During stand development, the woody component of yield must increase as long as full site occupancy, as represented by maximum foliage, is maintained. This is an architectural imperative for trees resulting from the way foliage is supported. At some point in stand development, however, this pattern changes. Very large trees simply are not collectively capable of completely occupying the site, or reoccupying the site following mortality within the cohort. Mortality, of course, can occur almost from the beginning of stand development – the key difference is that now, the residual trees are not capable of fully reoccupying the site because there are not enough of them and their growth is too slow. This behavior has been confirmed by many experimental observations (White and Harper 1970; Zeide 1987; Cao et al. 2000), although alternative explanations have been provided, ranging from mechanical limits to individual crown size (Long and Smith 1990), to physiological limits of the respiration/assimilation balance (Yoder et al. 1994). On the mean size-density plane, this results in a curvilinear, downward-concave maximum self-thinning line (e.g., Zeide 1987, Shaw and Long 2007, Charru et al. 2012, Vacchiano et al. 2013). This so-called "mature stand boundary" emerges only when sufficient data from stands with sparse, large-sized trees are analyzed, but is sufficient to alter mortality predictions based on a linear self-thinning limit, with important silvicultural implications (DeRose et al. 2008). The failure to account for this process, and the associated change in the pattern of yield accumulation over time, has resulted in confusion in the literature.

The development of stand-level foliage over time is further influenced by what Weiner and Freckleton (2010) refer to as 'aggressive interaction'. While trees are, of course, sessile, their crowns are not. The crowns of tall trees are subjected to considerable sway in the wind and the resulting collisions can lead to substantial twig and foliage abrasion (Long and Smith

1992; Rudnicki et al. 2003) and what has been referred to as crown "shyness" (Putz et al. 1984, Fish et al. 2006) or "disengagement" (Assmann 1970). Competitive interaction can lead to greater uniformity in the spatial distribution of crowns than is reflected in the spatial arrangement of the trees at ground level (Vacchiano et al. 2011). The observation that for some stands the amount of foliage actually culminates and begins to decline with crown closure (Smith and Long 2001) is almost certainly related to the physical interaction of swaying trees (Meng et al. 2006).

2.2.3 Time series of growth

Finally, stand property-density relationships can be characterized as an expression of growth, i.e., the difference in yield over time (as before, $m^3\ ha^{-1}\ yr^{-1}$ or $m^2\ ha^{-1}\ yr^{-1}$). The 'time course of yield' and the 'time course of growth' are simply different formatting of the same fundamental stand property-density relationship. At any time in stand development, current annual increment (CAI) is computed as the derivative of the yield curve, while mean annual increment (MAI) is the accumulated stand yield divided by stand age. CAI starts off slowly, gradually accelerates, continues to increase but at a decreasing rate, reaches a peak (i.e., culmination) and begins to decelerate (Figure 6a) (Assmann 1970). The culmination of CAI is, of course, coincident with the inflection in the yield curve; the culmination of CAI of the population always anticipates culmination of CAI of individual trees (Assmann 1970).

Density influences the CAI relationship, in that CAI will culminate sooner and at a higher level for a stand with a higher density (Figure 6a). Immediately after culmination, even though growth is declining, it is still *nearly* as high as it was at culmination, thus mean annual increment (MAI) continues to increase even as CAI has begun to decline (Figure 6b). On one hand, while MAI is merely a mathematical manipulation of the basic ecological phenomena (time course of CAI), it provides important insight. For example, in forestry, the age of culmination of MAI corresponds to the rotation length for maximum yield over many rotations (Assmann 1970).

Various mechanisms have been proposed as potential drivers of the age-related decline in CAI (Figure 6a). In a recent analysis, Xu et al. (2012) concluded that the decline in growth in a *Quercus*- dominated forest was primarily due to mortality of large, dominant trees and not to changes in productivity associated with tree physiology (e.g., Ryan et al. 1997, Magnani et al. 2000) or in stand structure (Binkley et al. 2002). Smith and Long (2001) argued that as a consequence of how foliage is supported by stems and branches, stem

volume growth must decline once stand-level foliage reaches its maximum (Figure 5a). It is possible that multiple mechanisms are involved in this important stand property-density relationship, or that different ones emerge in different taxa, sites, or stand developmental stages (e.g., Berger et al. 2004, Martinez-Vilalta et al. 2006, Thomas 2010).

2.3 Stand property-density relationships independent of time

2.3.1 Self-thinning plane

A third type of relationship is correlative, relating stand property and density for different sites and species (e.g., White et al. 2007). The most common expression of this class of stand property-density relationships is a log-log plot of mean size and density in which each datum represents a snapshot of a different site or population. The populations displayed represent different combinations of mean size and density and usually have one or more things in common. Often, for example, all are dominated by the same species (Figure 7). In a typical dataset they can represent a wide range of site quality and stand age (Long 1985). In such cases, there is a fundamental relaxation of the 'all else being equal' assumptions typical of the 'point in time' and 'over time' classes of stand property-density relationships.

An extremely important product of this class of stand property-density relationships is the derivation of a line, or plane, connecting all the maximum achievable combinations of size and density for the populations under scrutiny. Great attention has been focused on how best to estimate this maximum size-density boundary (e.g., Bi 2000, Zhang et al. 2005) and the best metric to measure mean size, i.e., diameter, volume, or top height (e.g., Vanclay 2009, Burkhart 2013). The slope of the maximum size-density boundary has been characterized as -1.6 (Reineke 1933) or -1.5 (Yoda et al. 1963) depending on whether the dependent variable is mean diameter or mean tree volume, respectively. Pretzsch (2010 pg. 404) showed that Yoda's exponent, originally calibrated with herbaceous plants, could apply to tree populations if only living bole biomass is considered (i.e., excluding heartwood). Recently, proponents of the metabolic scaling theory of ecology (WBE) have postulated the generality of quarter-power scaling, based on fractal networks of transportation systems in individual plants, predicting a self-thinning slope of -4/3 (West et al. 1997, Enquist et al. 1998, Simini et al. 2012). The -4/3 value is of critical importance for the applicability of the energetic equivalence rule in plants (Deng et al. 2008, 2012). However, we agree with

Pretzsch (2010) and suggest caution in transferring seamlessly between individual and stand tree allometry. In fact, individual-plant allometric exponents cannot be generalized in the stand, but depend on tree size, competition, crown ratio (e.g., Makela and Valentine 2006; Pretzsch and Mette 2008), and possibly ontogenic stage (Charru et al. 2012). This may be a very important reason why tests of observed self-thinning slopes versus Yoda's or WBE's predictions have yielded contrasting results (e.g., Pretzsch and Biber 2005; Pretzsch and Dieler 2012; Reyes-Hernandez et al. 2013).

Two basic postulates serve as a starting point for considering maximum size-density relationships: the slope is universal, regardless of species (while the intercept is species-specific); and for a given species the slope and intercept are independent of site quality (Reineke 1933). There is considerable ambiguity in the literature, and it is certainly true that neither postulate is universally accepted (e.g., Pretzsch and Biber 2005). Part of the ambiguity stems for the difficulty in accurately determining the location of a species' or metapopulation's maximum size-density line, because stands experiencing "maximum" crowding are by definition rare (Long and Shaw 2012), and statistical techniques used to characterize boundary lines have not been consistently applied (Zhang et al. 2005).

The postulate that the slope of maximum size-density lines is universal is almost certainly true only in the most general sense. Even small differences in slopes among species may convey important ecological insight relating, for example, to species' relative tolerance and what Zeide (1985) referred to as self-tolerance. It has been observed, however, that relatively small differences in slope and, therefore the coefficient used in an index of RD (e.g., Reineke's SDI), may have limited practical silvicultural importance (Long and Shaw 2005).

The second basic postulate is that for a given species, the maximum size-density relation is independent of site effects. Several sources, however, suggested that maximum potential density is to be understood as a site property (Assmann 1970; Sterba 1987). Different site qualities, therefore, have been characterized by different self-thinning lines within the same species (Sterba 1981; Hynynen 1993; Morris 2002; Monserud et al. 2004; Schutz and Zingg 2010). Recent studies have found that intra-specific variation of the self-thinning slope could also be due to (a) the mode of competition, i.e., symmetric (competition for belowground resources) versus asymmetric for light (Lin et al. 2011), or (b) accounting for the self-thinning of separate tree parts, i.e., root systems, boles, or crowns (Xue and Hagihara 2008; Deshar et al. 2012).

2.3.2 Intraspecific scaling

Interspecific scaling is touted as an important advantage of the last class of stand property-density relationships (Weiner & Freckleton 2010). An example of scaling starts with Eichhorn's (1904) rule and its evolution to a framework which spans all three classes of the stand property-density relationships. Eichhorn postulated that stand volume is a function of stand height, independent of age and site quality, but, implicitly, dependent on RD (Skovsgaard and Vanclay 2008). His abstraction was, in effect, an early characterization of a stand property-density relationship. The original relationship can be effectively expanded with an index of relative density, i.e., VOL = *f* (HT, RD). Further expansion of the expression to include an index of site quality (SQ) allows stand property to be represented by growth, e.g., CAI = *f* (HT, RD, SQ). Long and Shaw (2010) used this formulation to explore the influence of compositional and structural diversity on stand growth.

3. Implications for forest ecology and management

It is clear that the broad array of stand property-density relationships are part of an overarching framework. Competitive effects at the level of individuals and populations are reflected in emergent behaviors (Clark 1990).

There is a great deal of support in the literature for leaf area being broadly integrative with respect to various expressions of stand property-density relationships. This is an extremely important emergent property of even-aged populations of trees, which is something like a species-specific carrying capacity. Additional support to this model is provided by the CFY theory: for trees, CFY does not apply for total yield represented by stem volume (i.e., $m^3\ ha^{-1}$). However, we propose that CFY can be considered a special case of G-GS for non-woody species, for which yield is actually a reasonable approximation of growth. Consequently, CFY might apply to stand foliage mass or leaf area.

A stand's approach to full site occupancy and subsequent self-thinning are associated with, and almost certainly directly linked, to the existence of a stand's foliage upper limit (Long and Dean 1986). For example, two stands with the same total amount of foliage, but with different absolute densities, have their foliage distributed differently (Smith and Long 1989). In the stand with the lower absolute density, the trees are on average carrying greater amounts of foliage and proportionately even greater amounts of branch and stem wood biomass. These differences in canopy architecture are almost certainly associated with

growth efficiencies, which, in turn, affect both ecosystem functions, e.g., NPP and rate of carbon accumulation (Toda et al. 2009) and management strategies, e.g., maximizing timber production in a given time according to the G-GS relationship (Long et al. 2004; Pretzsch 2010 pg 414). The G-GS effect has a central place in silviculture, particularly as it relates to the development of thinning prescriptions. A comparison of the two versions of the G-GS effect (Figure 2a-b) illustrates the impossibility of simultaneously maximizing stand and individual tree growth. This is at the heart of the observation that an effectively designed thinning regime is in fact an appropriate (in the context of specific stand management objectives) trade-off between stand and individual tree growth (Smith et al. 1997).

The relationship between total leaf area and size-density might also account for observed intraspecific differences in the intercept of the maximum size-density boundary. Maximum total leaf area has been shown to vary with factors such as temperature, light, nitrogen, and water balance (Grier and Waring 1974, Lonsdale and Watkinson 1982). Any site factor or treatment that affects the total leaf area which a population can support may also affect that population's self-thinning trajectory (Long and Dean, 1986).

Finally, stand property-density relationships are at the hearth of forest dynamics models at any scale, from stand to landscape and continental level (e.g., Jack and Long 1996, Bonan et al. 2003, Reynolds and Ford 2005). Knowledge of plant population responses to competition, e.g., of the shape of the size-density relationship and its determinants, is strictly connected to accurate predictions of competition intensity and tree mortality, and may provide a blueprint for validation of model behavior (Leary 1997, DeRose et al. 2008).

For these reasons, additional research is needed to characterize stand property-density relationships (e.g., self-thinning dynamics) in mixed-species and multi-cohort tree populations. Recent work has used a traditional approach, i.e., characterizing mean size and density of a series of forest stands with varying structural heterogeneity or species composition, albeit limited to individual two-species mixtures (Shaw 2000; Long and Shaw 2012; Rivoire and Le Moguedec 2012; Ex and Smith 2013). However, this approach ignores the mechanisms underlying species coexistence, and cannot address the variations in the competition-facilitation balance that may occur between any two or more species under different site conditions. Physiological approaches to self-thinning yield promising results (Simini et al. 2010) towards a more general model, but contradictions between the geometric and metabolic scaling models will need to be resolved in order to develop a general framework for competition response at the population level in any forest stand.

4. Summary and outlook

There are many density-based relationships in plant population ecology. High profile examples include self-thinning, the C-D effect, CFY and age-related decline in stand growth. All of these have in common that some attribute of the population, a stand property (e.g., mean size, total yield, growth) is related to population density (e.g., absolute, relative, initial, or subsequent to self-thinning). While it is typical to treat the various expressions of stand property-density relationships as independent from the others, these seemingly disparate relationships are, in fact, each examples of different aspects (in some cases simply differently formatted) of a general framework of stand property-density relationships.

Stand property-density relationships can be broadly categorized in the context of time: 1) a point in time; 2) a trend over time; and 3) independent of time. Our synthesis provides a framework that integrates the broad categories of stand property-density relationships, and individual expressions of these relationships. We made explicit important linkages between basic and applied population ecology, and suggested unifying ecological processes behind the various stand property-density relationships.

There is a great deal of support in the literature for leaf area being broadly integrative with respect to various expressions of stand property-density relationships. The upper limit to population-level leaf area and the mechanical constraints on how this total leaf area is allocated to individuals in the population is a promising candidate for the mechanism of self-thinning, especially in populations of trees. Similarly, the dynamics of stand and individual leaf area have a clear influence on growth-related phenomenon, including age-related decline.

Even with a history of research spanning more than a century, stand property-density relationships still represent fertile ground for basic and applied research. The fundamental physiological or biomechanical processes driving stand property-density relationships remain elusive, as do fundamental questions about the mechanisms responsible for tree mortality, the extent and role of physiological and evolutionary plasticity, the tradeoffs between competition and facilitation under stress conditions, and the functioning and allometry of belowground competition. Answers to these questions are critical to better understanding the ecology of stand property-density relationships and to more effectively applying in forest management.

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Tables

Table 1 – Stand property-density relationships treated in this review, and organized by three major variations in context of time

Stand property-density…	Relationship	Source
…At a point in time	Competition-Density effect	Kira et al. (1953)
	Yield-Density effect	Shinozaki and Kira (1956)
	Growth-growing stock (growth-based)	Long and Smith (1984)
	Constant Final Yield (yield-based)	reviewed by Weiner and Freckleton (2010)
…Over time	Self-thinning trajectory	Yoda et al. (1963)
	Foliage over time	reviewed by Holdaway et al. (2008)
	Yield over time	Assmann 1970
	Growth over time (Current or Mean Annual Increment)	Assmann 1970
…Independent of time	Log mean size – log density	Reineke (1933)
	Eichhorn's rule	Eichhorn (1904)

Captions of figures

Fig. 1 (a) C-D effect in a hypothetical spacing trial of 4 population grown at different densities ($\rho_1 \ldots \rho_4$) and monitored at three points in time ($t_1 \ldots t_3$); (b) stand development trajectories and top height (TH) isolines in a density management diagram for pure, even-aged tree populations. Self-thinning limit in bold. If coupled with local site index curves, top height is indicative of stand age

Fig. 2 Growth-growing stock relationship where growth is portrayed as (a) total or (b) mean over the population

Fig. 3 Self-thinning trajectory of two stands with differing initial density (ρ_1, ρ_2) and relative density isolines

Fig. 4 Time series of yield in stands with differing initial densities ($\rho_1 \ldots \rho_3$)

Fig. 5 Time series of (a) population total and (b) individual mean foliage mass. Dashed lines represent stands with differing initial densities ($\rho_1 \ldots \rho_3$)

Fig. 6 (a) Time series of current annual increment (CAI) in stands with differing initial densities ($\rho_1 \ldots \rho_3$); (b) CAI and MAI (mean annual increment) time series in a given stand

Fig. 7 Log-log plot of mean size-density relationship in different tree populations with maximum size-density and mature stand boundary lines (*sensu* Shaw and Long 2007).

Figure 1
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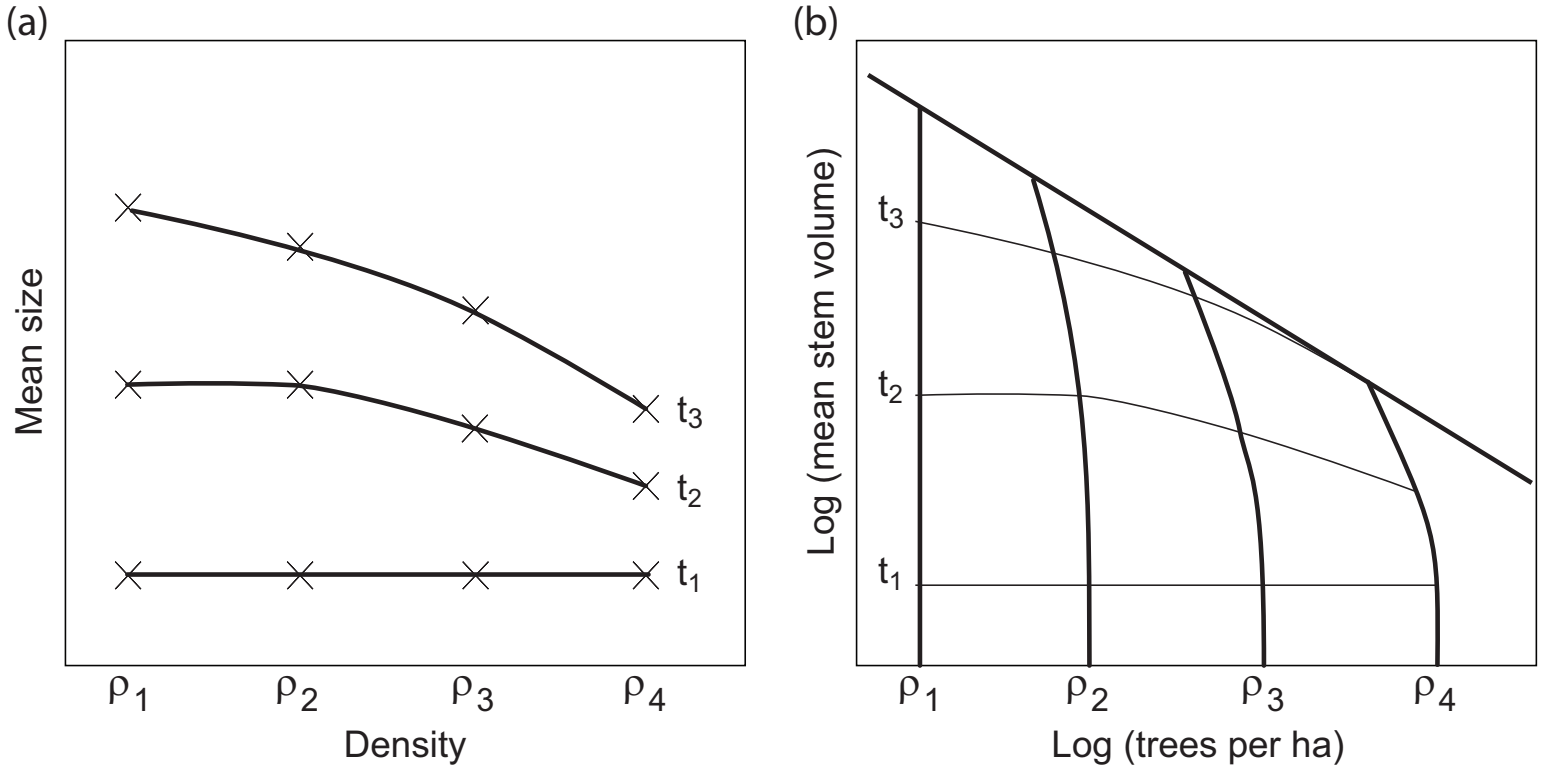

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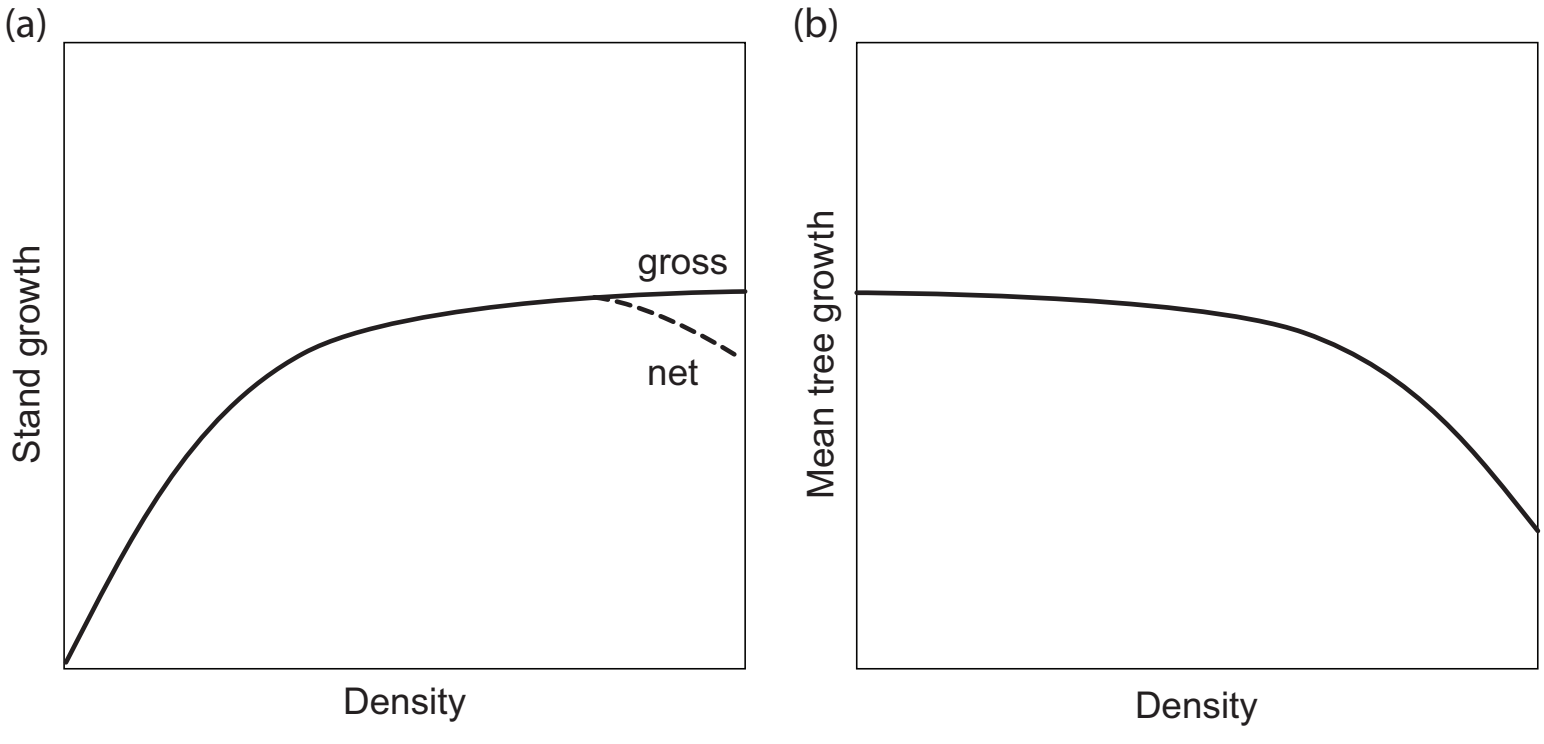

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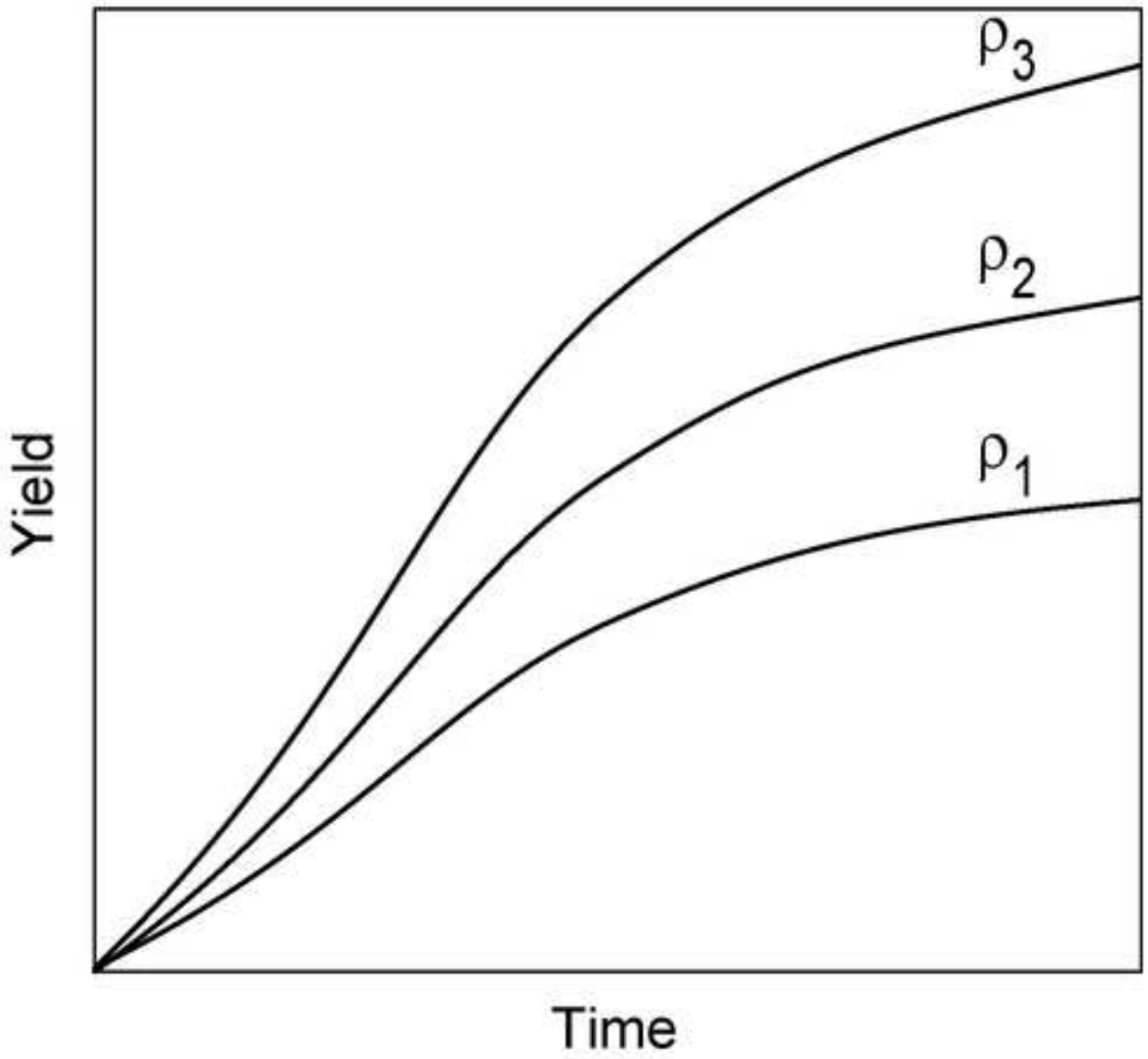

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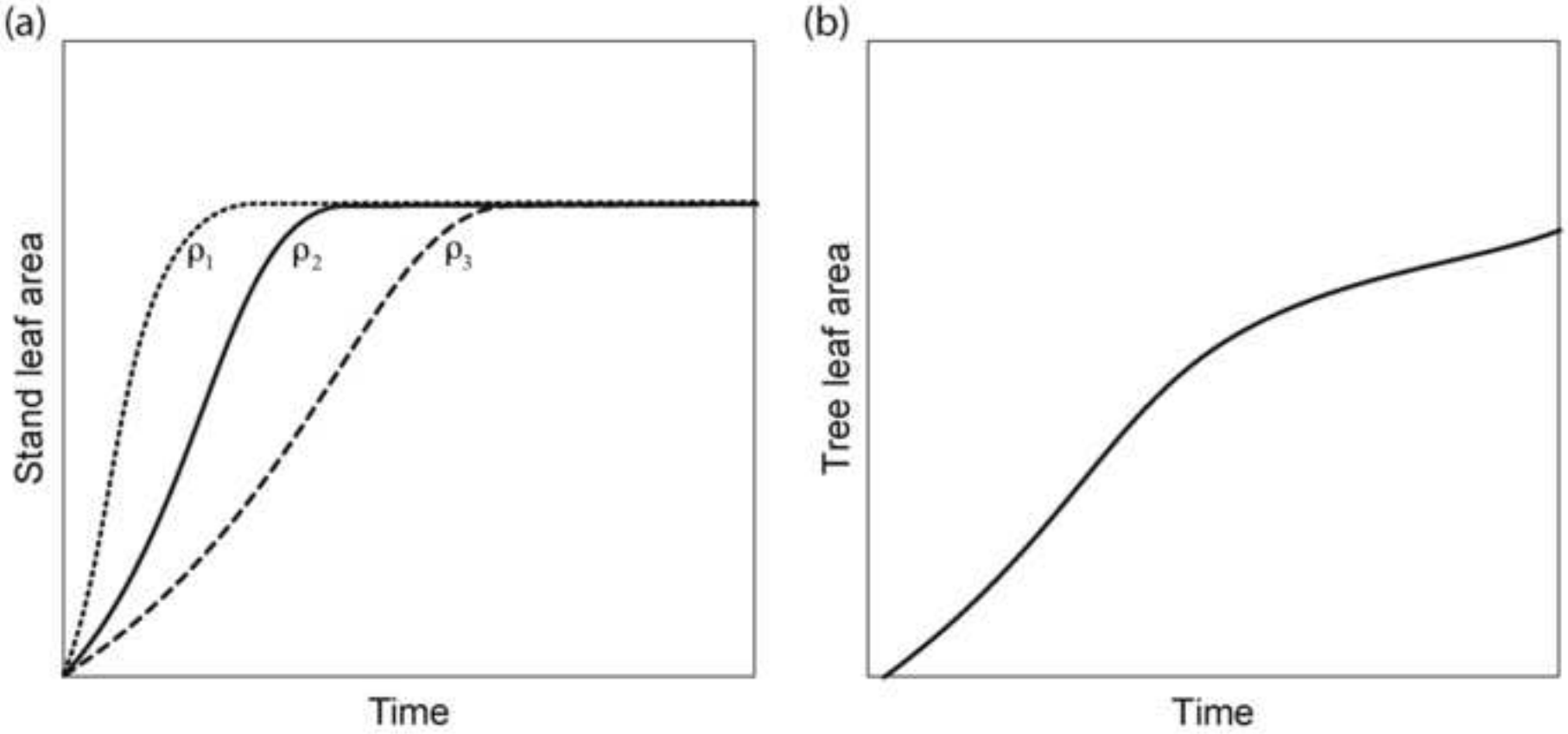

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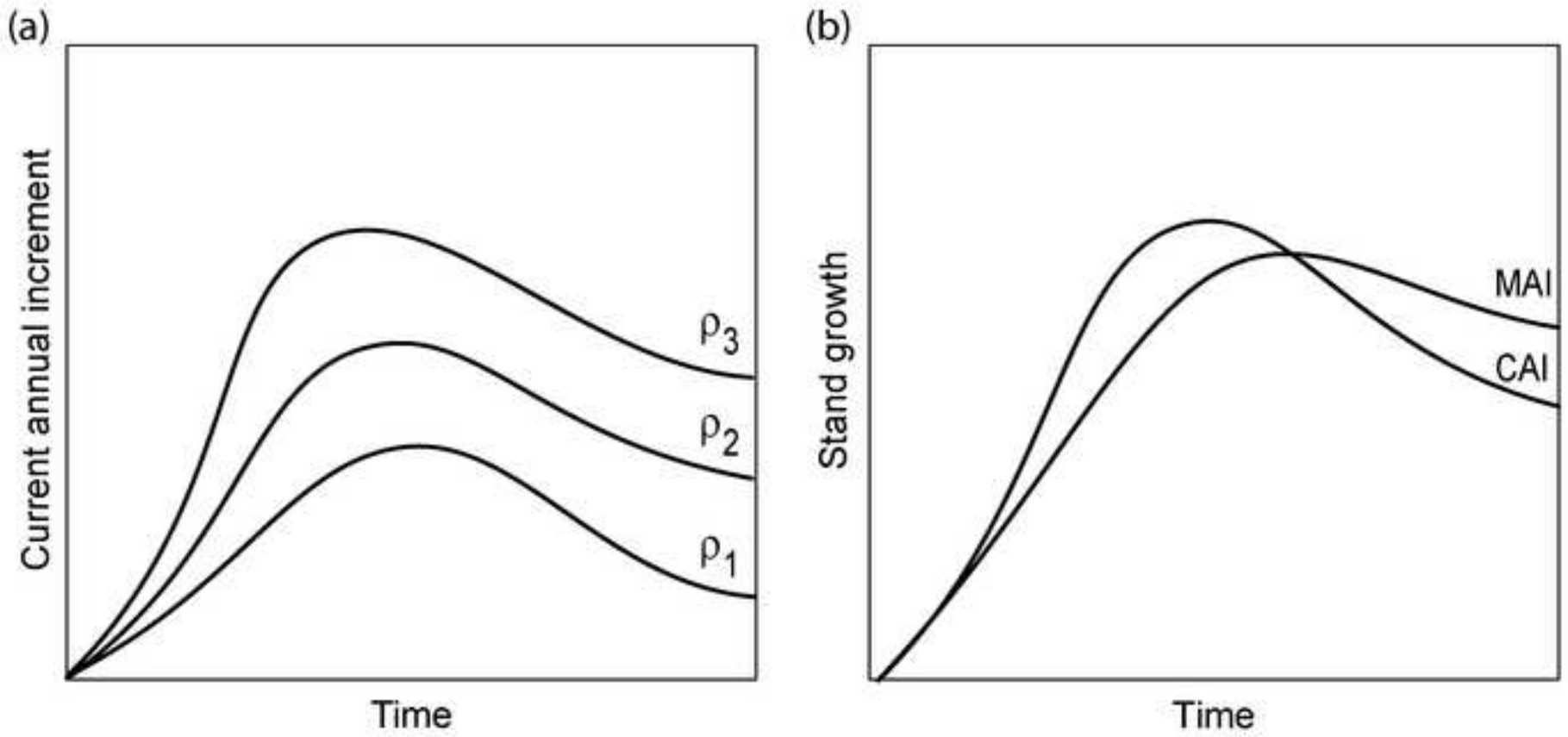
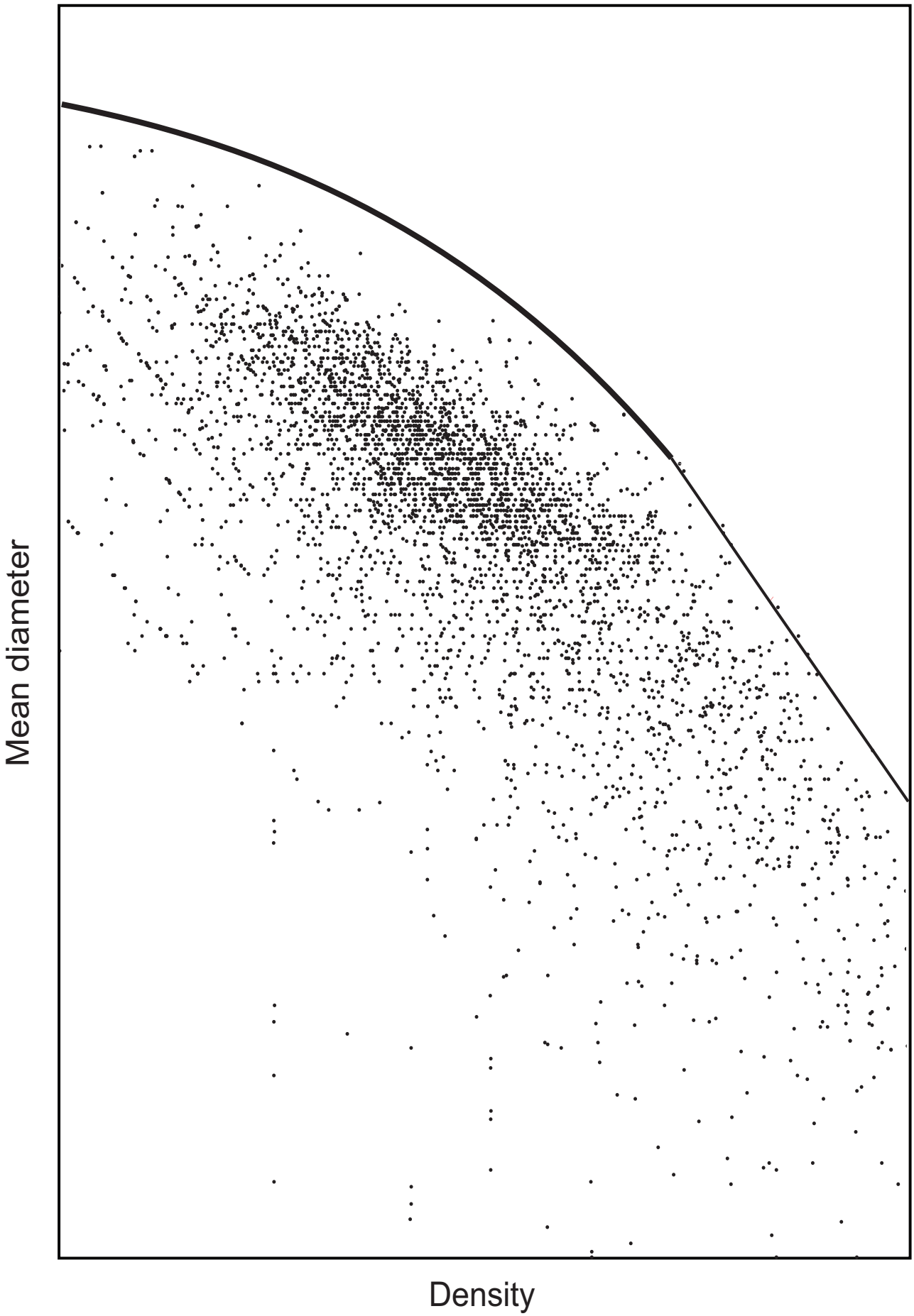
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