

2 Timber Growth Theory

Thinnings offer the opportunity to gain access to the control of density in a forest stand through the harvest of trees. Typically, timber growth is assumed to be density-dependent, i.e., the change in the timber volume is dependent on the current stock size (cf. Conrad and Clark 1987, p. 62). The term “density”, though, is not used consistently in forestry science (Zeide 2005). Depending on the problem, density might refer to the stem number, the basal area, the timber volume, the biomass or various density indices. However, in order to derive relevant propositions concerning the influence of thinnings on the profitability of timber production, it is necessary to evaluate the impact of the removal of some trees on the remaining trees. In order to meet the abstraction level of the following investment models (cf. Chapter 3), a simple growth model is required which offers guidance within the complex structures of forest stands and allows to deduce concrete hypotheses about the basic relationships of timber production. Due to the lack of such a qualitative model, this chapter tries to outline density-dependent timber growth in even-aged and pure forest stands with the help of some basic theories of natural science.

In view of the problem to define density, the proposed model follows a different approach. It analyzes the relationship between the stand age and the initial density, which is the number of plants at the beginning of a rotation cycle. In this way, density – however defined (Zeide 2005) – is the consequence of the magnitudes of both these characteristics. In effect, density is introduced into timber growth by the initial density. The initial density is convenient for several reasons. First, it is a tangible, easily assessable and logical variable as it represents a concrete action of forest management. Second, all commonly applied density measurements arrange the initial densities at the moment of the establishment in the same order as long as the regenerated trees are all equal, i.e., those stands with the highest number of trees at the beginning of the rotation are inevitably the densest stands at that moment, which makes it meaningful to speak of dense stands. Third, the ini-

tial density is directly related to thinnings as both focus on the relevant actions: to purposefully increase or to decrease the number of trees in the stand.

Timber growth, or the change in the timber volume over the age, denotes a growth function as it describes the temporal behavior of the timber volume in the system of a forest stand. Density-dependent timber growth might then comprise both positive and negative relationships between simultaneously growing trees. The proposed model, however, focusses solely on the negative relationship which might be termed competition as this term is frequently defined by its harmful effects on the involved individuals (cf. Begon et al. 1990, p. 197). The restriction of the diverse mutual interdependencies between trees solely to the negative influences on the timber volume, though, might only be acceptable in pure stands as trees of the same species might not occupy different ecological niches thus competing for the same niche. In mixed stand, mutually reinforcing timber growth might evolve when different tree species are intermingled in specific ways.

A basic assumption might be necessary in order to justify timber growth at all. If it is assumed that trees maximize their individual fitness by producing many, healthy and widespread seeds within their species-specific reproductive strategy which are capable of establishing maximal reproductive offspring in turn, timber growth might be derived thereof. In order to produce and disseminate these seeds, trees must develop large and high crowns with a large photosynthetic mass in comparison to their neighboring trees which guarantees to utilize enough resources for a large number of healthy seeds that can be easily spread by wind or animals from their raised position on the tree. The productive mass, again, can only be supplied and supported by timber. It should be noted that this assumption might not hold for mixed forest stands (Pretzsch 2009, p. 340 f.).

2.1 The Homogenous Stand

Homogeneous timber growth or a homogeneous forest stand is defined as equal timber volumes of all trees in the stand at equal ages. As a consequence, all trees necessarily share equal timber increments and equal impacts upon each other as, otherwise, the timber volumes will diverge at some age. Trees might be growing homogeneously when they are all of the same age, of equal genetic constitution, are growing on equally fertile land and in an equal climate, are evenly distributed and treated.

Timber production focusses on the timber volume of a stand Q as the means to generate an income stream. Since a forest stand is composed of different trees, the timber volume of a stand is the sum of the volumes of each tree q^i belonging to the stand, i.e.,

$$Q = \sum_{i=1}^n q^i, \quad [2-1]$$

where n is the number of trees (stem number) in the stand, and i is the index for each tree. In a homogeneous stand, every tree has exactly the same timber volume. The calculation of the timber volume thus simplifies to

$$Q = nq^i. \quad [2-2]$$

Accordingly, the timber volume of stand depends on the stem number and the volume of one tree.

2.1.1 Stem Number

The stem number is the number of trees in a stand. It is the direct consequence of the initial density. The latter is the number of trees when a stand is established. While the alternatives to establish a stand are numerous – e.g. planting, sowing, natural regeneration, or even coppicing – it is irrelevant for the purpose in this paragraph how the trees have been established. In the homogeneous stand, only the number of plants matters since all trees are

distributed evenly and are of the same age, which might not apply necessarily to all regeneration techniques.

Just after a stand has been established, the stem number is equal to the initial density. Thereafter, though, both might diverge. Due to natural regeneration from seeds of adjacent stands or even from trees of the same stand, the stem number might increase. Since these phenomena are highly dependent on the vicinity of a stand, they have to be excluded from this analysis in order to focus on the basic relationships occurring in all stands. On the other hand, the stem number might also decrease after initial stand establishment. The reasons for the death of trees are even more various; e.g., fungal or insect infestation, browsing damage, forest management operations, vandalism, air pollution, etc. Since all these sources are again highly dependent on the vicinity of a stand, they have to be excluded. The only relevant source for the displacement of trees that is solely influenced by the processes within a stand is density-dependent mortality. This phenomenon, which is also referred to as natural mortality or self-thinning (Zeide 1985), might reduce the stem number during the development of the stand (cf. Weiskittel et al. 2011, p. 139 ff.). For convenience, density-dependent mortality will be simply termed mortality hereafter.

As long as mortality has not occurred, the stem number equals the initial density. After mortality has taken place, the stem number is less than the initial density. The relation between stem number and density-dependent mortality in forests has been examined first by Reineke (1933). In his empirical study, he found indications of an exponentially decreasing relationship between the number of trees per unit area and their average diameter in fully-stocked and untreated stands. As a result, he derived an age-independent density index thereof. Although his investigations gave rise to controversial discussions, the index is widely accepted in forest mensuration science (Zeide 2005). Various studies have since then observed similar relationships for different tree species, locations and site qualities (e.g. Zeide 1995; Pretzsch 2000; Inoue et al. 2004).

Analogous observations were made by Yoda et al. (1963). They found decreasing weights of herbaceous plants with an increasing number of plants. Consequently, they derived the “ $-3/2$ th power law of self-thinning” which describes the relation between the average living plant mass and the plants per unit area. The analyses of both Reineke (1933) and Yoda et al. (1963) can be transformed into each other by substituting plant mass for diameter (White 1981); in this way, the former is special case of the latter.

Eventually, the reciprocal changes in tree size and tree number have been derived allometrically (cf. Mohler et al. 1978; Tang et al. 1994; Zeide 2004; Pretzsch and Biber 2005). As the size of the trees in a fully-stocked stand increases, the number of plants has to decrease in order to supply enough space for each individual. By the same token, it is possible to show a very similar relationship between equal volumes of balls and their numbers when lying close to each other on a fixed area, on the one hand, and the number and size of trees, on the other (Pretzsch 2009, p. 406 ff.). The size of a tree may be either measured in volume or living plant mass as these units are isometrically related (White 1981).

If it is necessary, then, for trees to grow in size over the age, the number of trees has to decrease once the stand is fully stocked, i.e., once a maximum of photosynthetically active mass is reached. The positive change in the size of a tree with respect to the age is assumed to be given for all relevant situations. Necessarily, trees increase their diameters as long as they are alive when old sapwood cells are no longer functional. Their capabilities to achieve this, though, are limited. Single trees and untreated stands exhibit a typical growth pattern (Assmann 1970): beginning to grow on a low level with an increasing acceleration, culminating at some age, and growing with a decreasing acceleration afterwards. At some point, they might even reduce their size due to decay. However, this stage of the development of a stand can be ignored in an analysis of profitable timber production.

In a perfectly homogenous stand, however, there is no reason why single trees should be eliminated due to density-dependent mortality. Since the timber growth of all trees is equal in every aspect, no tree has any advantage

over any other tree which could then be expanded (proportional or disproportional) to depress their neighbor until his death. Therefore, all trees would be dying off simultaneously when the small photosynthetic mass is unable to maintain the growing metabolism of the tree. For instance, this stagnation phase in timber growth can be observed in comparatively dense and almost homogeneously growing stands (e.g. pine plantations) where the timber increments tend to cease. In consequence, density-dependent mortality has to be assumed as exogenously given and to take place on a regularly distributed random basis at any age in which some crucial density factor (defined as a combination of tree size and number of trees) is reached. Mortality thus occurs when a stand enters a zone of imminent competition-mortality (Drew and Flewelling 1977). According to the self-thinning line (White 1981), mortality takes place in the initially densest stands first while it never occurs in comparatively sparse stands (Valentine 1988).

In summary, the stem number in this approach is determined by the age s of the stand and its initial density m , i.e.,

$$n = n(s, m). \quad [2-3]$$

2.1.2 Diameter

The second determinant of the timber volume of a homogeneous stand is the timber volume of a single tree q^i . Since the growth of a tree is a phenomenon in a highly complex ecosystem, myriads of factors influence the formation of timber (cf. Oliver and Larson 1996, p. 21 ff.). In order to focus the analysis on the relevant aspects, the factors which are working independently of the vicinity of a stand have to be isolated.

In forest mensuration science the timber volume of a tree is typically calculated as (cf. West 2009, p. 36)

$$q^i = \hat{h}^i * (d^i)^2 * \pi/4 * b^i, \quad [2-4]$$

where $\hat{h}^i$ is the height of the tree, d^i its stem diameter and b^i a taper reduction factor which reduces the volume of a cylinder generated by $\hat{h}^i$ and d^i to the volume equivalent of the shape of the tree. According to this calculation, the diameter, the height, and the taper reduction factor are three basic determinants of the tree volume. This separation is convenient as the last two determinants are only negligibly affected by the initial density.

As various empirical observations (e.g. Altherr 1966; Petersen and Spellmann 1993; Mäkinen and Hein 2006) as well as analytical considerations (e.g. Oliver and Larson 1996, p. 335; Pretzsch 2009) reveal, tree height is hardly affected by the initial density. Although there is a tendency of higher trees in more densely planted stands, the differences are insubstantial and negligible for the purposes of this work. Nevertheless, in actual forest stands, this proposition does only apply to the dominant height, which is the average height of the tallest trees in a stand. In homogeneous stands, though, all trees are of the same height. The shape of a tree, on the other hand, is definitely influenced by the initial density (Assmann 1970, p. 57ff). If comparing the shape of solitary grown trees with those cultivated in densely planted stands, the differences are obvious, especially for deciduous trees. However, the reduction factors might be assumed to be of equal magnitude as the timber increments are only differently distributed on the stem such that solitarily growing trees grow thicker stem bases but thinner upper sections. In this way, the independence of the taper reduction factor from the initial density must follow from the limited supply of resources.

In consequence, since tree height and reduction factors are constant over varying initial densities, they will not affect the qualitative differences between stands of the same age. Only the diameter is influenced by both age s and initial density m of a stand, i.e.,

$$d^i = d^i(s, m). \quad [2-5]$$

Since this analysis only focuses on growing trees, the diameter increases with an increasing age of a stand. Furthermore, it is irrelevant where the diameter is evaluated as long as it is the same for all trees and the taper reduction factor is adjusted.

The relationship between stand density and tree diameter might be explored with the help of the pipe model theory. Although elaborated analytically by Shinozaki et al. (1964a; 1964b), empirical observations of the relationship between diameter increment and assimilation organs are already made by Pressler (1865) or Huber (1928). Pressler (1865) pointed out that the area of timber increment in any part of the stem is proportional to the leaf area above this part. Shinozaki et al. (1964a) found a linear relation between the weight of assimilation organs and the weight of non-photosynthetic tissue. They concluded that every unit of assimilation mass is supported by a unit of non-photosynthetic tissue. Therefore, the form of a plant is a consequence of the assemblage of unit pipes.

In the case of trees, Shinozaki et al. (1964a) made another important observation. For any part of a tree which lies below all photosynthetic organs, the constant ratio between photosynthetic and non-photosynthetic mass does not hold. They understood this phenomenon as the consequence of the accumulation of disused pipes. Pipes can become inoperable for various reasons; e.g., senescence, embolisms, seasonal activity. Since a tree is unable to dispose disused pipes, they are preserved in the interior of the stem as heartwood, and, therefore, do not share a functional relationship with the active photosynthetic organs. Consequently, the relationship is only valid for the active non-photosynthetic tissue of the tree, the sapwood. Numerous empirical observations (e.g. Kaufmann and Troendle 1981; Withehead et al. 1984; Kimmins 1987; Vertessy et al. 1995; Scott et al. 1998; Eckmüller and Sterba 2000) underlie this conclusion for various tree species and sites. It also served as a basement for several, more sophisticated growth models (e.g. Waring et al. 1982; Valentine 1985; Deleuze and Houllier 1995; Mäkelä 2002).

As a tree grows in size, newly formed sapwood cells have to support newly formed photosynthetic organs as well as they have to replace disused pipes. This "secondary growth" (Nultsch 2001, p. 296) forms the timber volume as a byproduct of the need to grow. It might be interrupted periodically or irregularly due to climatic changes. The important implication for this study, however, is that the stem diameter, as a fundamental determinant of the timber volume, is a function of the photosynthetic mass of the tree. Since this mass is concentrated on the crown surface, the potential of a tree to produce timber volume is dependent on the potential to expand its crown.

The space which the crown of a tree can possibly occupy is called the potential growing area (Assmann 1970, p. 101), or area potentially available (Brown 1965). Naturally, this concept might be extended to include the rhizosphere. However, as both areas are correlated, it is not necessary for the purposes of this work. Since the trees in a homogeneous stand are of equal height, this might also be reduced to the potential ground coverage of a tree. In the clear setting of a homogeneous stand, each tree has the same potential ground coverage which determines its diameter growth because the trees are distributed evenly over the area. Therefore, higher initial densities offer limited opportunities for crowns to expand freely. As the trees grow in size, each tree occupies more and more of its potential growing area until it is filled out and the canopy is thus closed.

The potential growing area, though, is not a homogenous source of resources. This is particularly evident when comparing a nearly solitary growing tree and one out of a closed stand. A further extension of the potential growing area will hardly promote the timber increment of the former, but will substantially raise the increment of the latter. Furthermore, the effect varies with the tree height. The detailed reaction of trees due to enlargements of the potential ground coverage cannot be evaluated here; it is not even necessary. The only relevant aspect is that the function relating enlarged growing areas to increment reactions is strictly monotonically increasing within the competitive domain; i.e., a comparatively larger growing area gives rise to both higher crown surfaces and timber volumes if solitary growth is ruled out. Without any competition between the trees of the stand

(solitary growth), the increment reaction function has to be constant because genetics and site constraints make it impossible to convert more resources into photosynthetic mass. The threshold of competition was empirically analyzed, for instance, for Loblolly pine (*Pinus taeda* L.) by Clason (1994) or Zhang et al. (1996), and for Norway spruce (*Picea abies* L.) by Lässig (1991).

Eventually, lower initial densities give rise to thicker tree, and *vice versa*, if trees compete for resources. By inference, solitary growth maximizes the timber volume of a single tree as it is provided with the maximal possible supply of resources that a site can offer and the tree can utilize. The same analysis remains valid for other diameters, such as branch diameter. Therefore, all branch diameters respond equally to the stem diameter to changes in the growing area as they represent, along with their associated photosynthetic mass, small trees within the tree.

2.1.3 Stand Volume

As equation [2-2] reveals, the timber volume of a stand depends on the stem number n and the timber volume of a tree of the stand q^i . In turn, both determinants vary with the age and the initial density. Therefore, it holds that

$$Q = Q(s, m). \quad [2-6]$$

According to the argumentation in the preceding sections, higher stem numbers and larger diameters increase, lower stem numbers and smaller diameters reduce stand volume, *ceteris paribus*. However, higher initial densities give rise to higher stem numbers but smaller diameters since they reduce the potential growing area, and *vice versa*. Therefore, both effects on the stand volume are related oppositely with respect to the initial density (cf. von Thünen 1875, p. 90; 2009, p. 92). In order to evaluate which effect prevails when, the conclusions of the preceding paragraphs have to be put together.

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