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A review of the growth behaviour of stands and trees in even-aged, monospecific forest

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Abstract

Key message Metabolic, physiological and inter-tree competitive processes interact to determine long-term growth behaviour of stands and individual trees of even-aged, monospecific forests.

Context Even-aged, monospecific forests go through an initial phase from seedling establishment to full canopy development, then follows a progressive decline in growth rate, leading eventually to tree senescence and death. Individual trees show a relationship between their maximum possible growth rates and their sizes (hence ages), maxima that show a progressive decline as the trees grow larger. Growth rates are further restricted by competition with their neighbours for access from the site to the light, water and mineral nutrients essential to their growth. To ensure they remain standing upright and can access the resources they need, trees must maintain a balance between the sizes of both their above- and below-ground parts.

Aims This review aimed to summarise what is known about the various biological factors that control these growth processes, both at the stand and individual tree levels.

Conclusions The principal factors determining growth behaviour are species characteristics, environmental circumstances of the site on which the forest is growing, availability from the site of the resources essential to growth, sizes (hence ages) of individual trees, competition between neighbours for growth resources and partitioning of growth between the parts of individuals to maintain an appropriate balance between their sizes.

Keywords Growth phases, Growth decline, Mortality, Self-thinning, Competition, Partitioning

1 Introduction

Model systems exist that describe the development of forests, based broadly on an understanding of their ecology (e.g. Oliver and Larson 1996; Franklin et al. 2002). These consider a wide range of processes that can encompass site disturbance leading to development of a new cohort of trees of various species together with an understory, growth of the stems, crowns and root systems of

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the individual trees, effects on growth of the environmental circumstances of the site on which they are growing (temperature, humidity, sunlight, water and mineral nutrient availability) and effects of competition between trees for the growth resources each requires.

Following Oliver and Larson (1996, p. 147), an even-aged cohort of trees may develop over a period as '…narrow as 1 year or as wide as several decades, depending on how long trees continue invading after a disturbance'. Such disturbances leave open ground, usually following disastrous fire or weather events or clear-felling to obtain timber. Of course, in plantation forestry, planting is usually done over a short period, usually no more than a few weeks. Once a cohort has been established, there are then periodic losses of trees due to competition between them as well as chance events of

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wind, fire, flood, insect damage or disease. As well, succession processes may occur as shade tolerant species develop beneath the original canopy. Eventually, trees mature and some may survive for hundreds of years.

The present review is restricted to only a part of this whole ecology of forest development. It is concerned with growth development of trees, both of forest stands (a term used in forest science for a more or less homogeneous group of trees in a forest) and of the individual trees within the stand. Further it is restricted to trees of even-aged, monospecific forests. Such forests, of many different species, occur around the world and many are managed to produce commercial timber products.

The Section 'Some principles of forest growth behaviour' establishes the basic principles of the physiological and environmental factors that determine tree growth from seedlings through to maturity. The Section 'Phases of growth with age' discusses growth of whole forest stands as they pass through four phases, (1) seedling to full canopy, then (2) growth dominance by larger trees over smaller and mortality occurring amongst smaller, then (3) increased spacing allowing smaller trees to contribute proportionately more to total stand growth and finally (4) an old growth phase as larger, overstorey trees senesce and die. Once a stand enters its second growth phase, the Section 'Changes in stand growth rates with age' describes the year-by-year decline in whole stand growth rate that then occurs and discusses the physiological processes believed to cause that decline. The Section 'The balance between stand growth, stocking density and mortality' describes the balance that is then maintained between average tree size and the number of trees remaining in the stand, a balance defined by what is known as the 'self-thinning rule'.

The Section 'Individual tree growth and development' then turns to the growth behaviour of the individual trees in the stand. The Section 'Maximum possible growth rates' considers the maximum growth rates, at any particular stand age, that individual trees display when they do not compete with each other for the growth resources each needs (light, water and mineral nutrients) and how those maxima change with tree size. The Section 'Inter-tree competition' describes the effects on individual tree growth rates when they do compete with each other for growth resources. Sections 'Partitioning net primary production' and 'Stem taper' then describe the factors that control the maintenance of the balance between sizes of the different parts of individual trees, their canopies, branches stems and root systems, balances that are essential both to ensure their growth continues and that they remain standing upright. Learning from the earlier discussions, the Section 'Conclusions' then draws

conclusions about how tree and stand growth behaviour are controlled.

2 Some principles of forest growth behaviour

To develop systems to manage even-aged, monospecific forests for timber production or other purposes requires an understanding of their growth behaviour as a whole and of the individual trees within them. Various texts consider forest management practices (e.g. Davis et al. 2001; Savill et al. 1997; West 2014). Growth of a forest stand involves accumulation of the growth behaviour of the individual trees within it. There are three principal factors that control the growth of each individual. The first is its genetic makeup, which determines its anatomy and physiological behaviour (e.g. Li et al. 2012; Park et al. 2012; Swain et al. 2013; Wang et al. 2014; Arnold et al 2015; Yañez et al. 2015; Belaber et al. 2018; Pavan et al. 2021). The second is its size at any time (Pretzsch et al. 2012a; Cordonnier et al. 2019; Ogawa 2019; Pretzsch 2021); this reflects the amount of living tissue (foliage and fine roots particularly) it contains to undertake growth processes (Weiskittel et al. 2011, chap. 12). The third is the amount of the resources necessary for growth it can acquire (light, water, and mineral nutrients); this depends on the circumstances of the site itself and the extent of the competition for those resources that each tree suffers from neighbouring trees (Burkhart and Tomé 2012, Chap. 9; West and Ratkowsky 2022a). Ultimately tree growth is a consequence of the physiological and metabolic processes its environmental circumstances then allow it to undertake. In the present work, it is assumed the reader has a general understanding of those processes; substantial texts are available to describe them (e.g. Atwell et al. 1999; Lambers et al. 2008; Landsberg and Sands 2011).

Much of the present work is concerned with growth behaviour as it develops and changes with age, hence, tree and stand circumstances. Year-by-year forest growth behaviour is considered to involve three elements. Firstly, the trees replace some fruiting bodies, leaves, outer bark and fine roots that have been shed as above- or below-ground litter in the previous year. Secondly, they grow bigger in height and overall biomass by adding to their (largely) dead tissue, wood, that makes up branches, stem and the large roots that anchor them in the ground. Thirdly, some die from time to time. In this work, growth periods of a year or so will be considered; in any such period, seasonal and dormancy effects will determine just when growth occurs.

Leaves use carbon dioxide, light and water to undertake photosynthesis and provide a tree with its 'food' and, hence, the energy to undertake growth; this is often termed 'gross primary production' (GPP), the units of

which are commonly given as the equivalent amount of tree biomass it represents. As essential as leaves are the living, fine roots that are located at the extremities of the root system; they take up from the soil the water and mineral nutrients essential to the metabolic processes of the tree, usually aided by mycorrhizal fungi and other soil microbes (e.g. Razgulin 2022; Balestrini et al. 2024; Ku et al. 2024; Maitra et al. 2024). At any time, the total growth of the trees on a site will be limited by whichever of these resources is most limited in supply; this is a principle known as Liebig's 'law of the minimum' (Liebig 1840; van der Ploeg et al. 1999), although it has been suggested that multiple stresses acting on plants can jointly limit their growth behaviour (Niinemets 2010a).

Over any growth period, respiratory costs to maintain existing live tissues and to construct new tissues are subtracted from GPP, leaving 'net primary production' (NPP). NPP is then the amount of new biomass that may be added to a tree as growth: note that for a stand, its NPP is the amount of new biomass to be added to those trees that remain alive during the growth period being considered. As will be discussed later, the 'efficiency' with which a tree (or stand) uses its photosynthetic production is then an important determinant of its growth behaviour. Two statistics used commonly to quantify this are 'carbon use efficiency' (CUE) and 'resource use efficiency' (RUE). CUE (discussed by Manzoni et al. 2018) is defined as NPP/GPP whilst RUE is defined as NPP/R, where R is a measure of the amount of the resource required for growth (light, water or nutrients) that was used to produce the GPP. It follows from their definitions that CUE and RUE are related as $CUE = R(RUE/GPP)$. NPP and GPP may be measured directly (West 2015, Chap.8, 2020; Liao et al. 2023) or estimated from models that, in effect, involve R (Weiskittel et al. 2011; Pei et al. 2022).

Many different measures are used to describe the sizes and/or growth of individual trees and stands. Commonly used are tree stem diameter (usually measured at 'breast height', most commonly defined as 1.3–1.4 m above ground level), basal area (stem cross-sectional area at breast height), tree height, volume of wood contained in stems and oven-dry biomass (weight of plant material after drying for several days in an oven at 60–80 °C until it reaches a constant weight). Biomass may be determined as the total of the above-ground parts and/or roots of a tree or of its separate parts, leaves, branches, bark, stem wood, woody roots or fine roots. The difficulty of measurement of these various characteristics is progressively more difficult and time consuming in the order they are listed here; the methods to do so are discussed in works on forest measurement (e.g. Avery and Burkhart 2002; van Laar and Akça 2007; West 2015; Westfall et al. 2024). Ground measurement techniques for many

of these variables are being replaced by remote sensing instruments (e.g. West 2015, Chap. 13; Jucker et al. 2017; Kangas et al. 2018; Park et al. 2019; Ahmad et al. 2022; Mo et al. 2023). Such instruments can measure individual trees or whole stands at scales that vary from ground level, to being airborne or to satellite imagery. Even root systems may be measured at ground level, using ground penetrating radar and other electronic devices (Butnor et al. 2003; Zhu et al. 2014; West 2015, Sect. 13.1.3; Li et al. 2022; Gates et al. 2023; Loiseau et al. 2023; Sharma et al. 2024). Recent technological development in these fields has been extremely rapid. It is conceivable that, over the next few decades, much of the labour intensive measurement of individual trees on the ground will be superseded by the use of electronic equipment that measures them remotely. As will be discussed later, many of these characteristics are correlated with each other and any or all are used when discussing forest growth behaviour.

Much of what has been learnt about tree and stand growth behaviour has come through the development of model systems that describe them. A great variety of such models has been developed over the years for many different forest types around the world. Major texts offer substantial reviews of this work (e.g. Vanclay 1994; Weiskittel et al. 2011; Burkhart and Tomé 2012). Many of these models are based on observed growth in relation to observed tree or stand characteristics and environmental circumstances. These are termed 'empirical' models. Others have been developed that attempt to predict growth through the physiological processes and environmental factors that control it. These are termed 'process-based' models and have often been reviewed for agricultural crop systems (Loomis et al. 1979; DeJong 2022) and for forest systems (Dixon et al. 1990; Mäkelä et al. 2000; Le Roux et al. 2001; Landsberg and Sands 2011; Weiskittel et al. 2011; Merganičová et al. 2019). Reference will be made later to some conclusions about forest growth behaviour that have been drawn from model systems.

3 Growth and development of forest stands
3.1 Phases of growth with age
Studies of various forest types have led to a model system that describes development of a forest stand (Binkley 2004; Binkley et al. 2006). This system has four phases and reflects how different tree sizes develop as the forest ages. In turn, this determines which tree sizes tend to dominate stand growth at different times. The system has come to be used widely (e.g. Pothier 2017; West et al. 2021; Liu et al. 2022; Pommerening et al. 2022; Li et al. 2024; Pretzsch et al. 2024). It can be related to the well-known, four phase system of development of forest structure and size of Oliver and Larson (1996, Chap. 5). The

growth processes that are likely to be occurring in each phase of the Binkley et al. system are described below.

Phase 1: This phase starts from the time of germination of seeds or planting of seedlings to develop an even-aged forest. It may continue for 20 years or more, depending on the seedling stocking density, the species involved and the environmental properties of the site on which the forest is growing. This phase is probably closest to the 'stand initiation' stage, as defined by Oliver and Larson (1996). As they point out, during the early stages of this phase, plants other than the trees may develop including grasses, herbs and shrubs. If dense enough, these may smother the tree seedlings until some grow tall enough to overtake them. Of course, in plantation forests, it is normal practice to control the development of 'weeds' such as these, so they will not interfere with the development of the forest. The present work will concentrate on circumstances where such influences have passed and will consider the development of the trees alone.

From the start of this phase, each seedling grows at a rate determined by its individual genetic capabilities and the site circumstances (e.g. Yang et al. 2006; Wang et al. 2012; Keenan 2015; Thomas et al. 2017; Xia et al. 2019; Anderson-Texeira et al. 2022). Initially, the space around each seedling from which it obtains the resources essential to its growth (sunlight and water and mineral nutrients from the soil) does not overlap that of any of its neighbours, so the seedlings do not compete with each other to obtain those resources. Each seedling will then be able to acquire amounts of the growth resources that are proportional to the size of its leaf and fine root systems; its growth can then be expected to be proportional to its size. Note that carbon dioxide, whilst being essential for photosynthesis, hence, plant growth, is not generally considered as being in limited supply because it blows in continuously with the wind. However, plant growth may increase as carbon dioxide concentration in the air increases, a factor presently of interest when considering the role of forests in response to climate change (Maschler et al. 2022).

The root systems and canopies of the trees eventually expand and become large enough to meet each other. This fills the space on the site from which they might acquire the essential growth resources and so they start to compete with each other for those resources. By this time, the stand leaf and fine root biomasses will have reached a maximum and will change little thereafter as they will be using all the available resources that the site can supply (Asner et al. 2003; Hilty et al. 2021). From this time on, it will be only the amounts of their woody tissue that will continue to increase with time as the trees grow further and distribute their net primary production between their parts. This marks the end of Phase 1 of stand development.

Up to this stage of growth, it is believed that the competition between neighbours is principally below ground for water and nutrient uptake by roots. Each tree will be able to take up amounts of these that are proportional to the size of their root systems, hence to the volume of space their root systems are occupying (Putz and Canham 1992; Weiner et al. 1997; Schwinning and Weiner 1998; Casper et al. 2003; Bartelheimer et al. 2008; Coates et al. 2009; Pommerening and Meador 2018); this is termed 'symmetric' competition. Growth of each tree might then be expected to continue to be proportional to its size (Fernández-Tschieder and Binkley 2018; West 2023a). However, the larger trees, which have larger leaf and fine root biomasses, will be able to grow more than the smaller trees and hence dominate the total growth of the stand; methods are available to assess the extent of this dominance from individual tree growth rates (West 2018).

As an example, Fig. 1 shows the change with age in stand biomass of woody tissues (branches, stems and coarse roots) and the living tissues (leaves and fine roots) over the first 20 years of life of a eucalypt plantation in Australia. Also shown is the development of stand leaf area index (the one-sided area of all its green leaves per unit ground area). Many studies have shown such development with age of leaf area index (Long and Smith 1992; Vose et al. 1994; O'Hara and York 2014; Behling et al. 2016; Huong et al. 2016; Cattanio 2017; Parker 2020); because leaf area index correlates closely with stand leaf biomass at any age, its trend is illustrating also the rise to a maximum of stand leaf biomass, which then correlates in turn with stand fine root biomass (see discussion of leaf and fine root allometry in the Sect. 'Partitioning net primary production'). This plantation ended Phase 1 at only 2–3 years of age, when its leaf and fine root biomasses and leaf area index had reached their maxima. Its Phase 1 was very short because it was fast growing on an intensively managed, highly productive, well fertilised site with a very favourable, sub-tropical climate.

Phase 2: The next phase of this system is perhaps closest to the 'stem exclusion' stage of Oliver and Larson (1996). It is notable in Fig. 1 that leaf area index rose to a maximum at the end of Phase 1 and then declined to subsequently maintain a more or less steady state. By contrast, after reaching their maxima, leaf and fine root biomasses continued subsequently at much the same levels, with small changes year-by-year as weather conditions varied slightly. This apparent contrasting behaviour of leaf area index is believed to be a result of leaves becoming thicker, hence denser, after its maximum, a phenomenon that has been found to occur
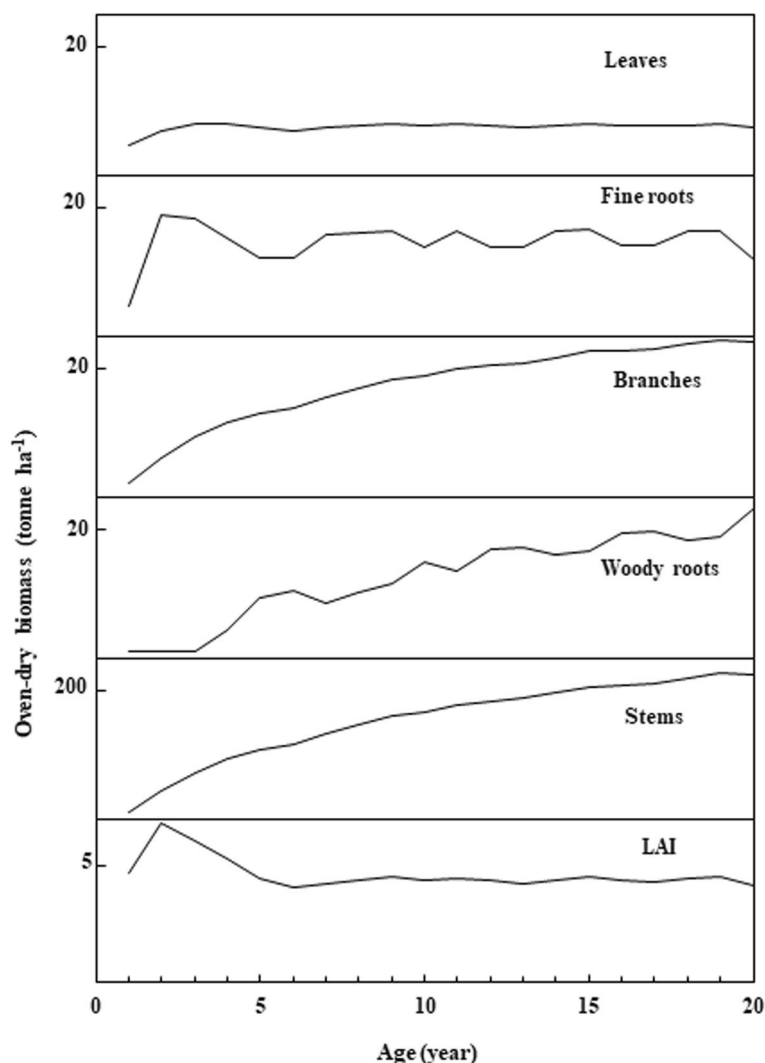
Fig. 1 Change with age in stand biomass of leaves, fine roots, branches, woody roots, stems and leaf area index (LAI) of an experimental plantation of flooded gum (*Eucalyptus grandis* Hill ex Maiden) planted in 1987 in southeast Queensland, Australia. Note that units of leaf area index are m^2 m^{-2}. Trees were sampled for biomass measurement at various ages. Methods and results are described in Cromer et al. (1993a, b). This figure is reproduced in part from Fig. 2.1 of West (2014) who used and extrapolated the results of Cromer et al. using a forest growth modelling system

with leaves of many species at different stage of stand development (Linder 1985; Steele et al. 1990; Niinemets and Kull 1995; Whitehead and Beadle 2004; West 2014, Sect. 2.3.1). Once the living tissues had reached their maxima, branch, stem and woody root biomasses continued to increased progressively as the trees grew. This forest will have still been in Phase 2 when it passed beyond the oldest age shown in Fig. 1.

As Phase 1 progressed, differences in growth of individual trees will have led to differences in tree heights; the taller trees will have been either genetically superior for height growth or will have chanced to have particularly favourable, local availability of growth resources from the site. As Phase 2 then progresses, these height differences allow taller trees to both shade smaller trees and to sway rather more violently in the wind. This leads to smaller trees having reduced photosynthetic capacity due to both the shading and a relatively greater loss of leaves through mechanical abrasion within their crowns (Putz et al. 1984; Umeki 1997; Niinemets et al. 1998; Koike 1989; Rudnicki et al. 2004; Reiter et al. 2005; Meng et al. 2006a; Dong et al. 2015; Hajek et al. 2015). Growth rates of the taller trees will then be disproportionately large with respect to their sizes, whilst the reverse will be true of the smaller trees. This is then a consequence of what is termed 'asymmetric' competition, where one group of trees is able to access an amount of a growth resource, light in this case, that is disproportionately large with

respect to its size (Fernández-Tschieder and Binkley 2018). It leads to the formation of a well-defined group of suppressed trees in the stand, amongst which deaths are then likely to start occurring. Larger trees will continue to dominate stand total growth as started in Phase 1.

Until a stand reaches Phase 2, the total amount of growth it will have achieved at any time will vary directly with its 'stocking density' (the number of trees per unit area present in the stand). This occurs because the total leaf mass, hence photosynthetic capability, of the stand will vary directly with the number of trees present (Forrester et al. 2013; Zhao et al. 2012; West 2014, Sect. 7.2; Gabira et al. 2023; Hakamada et al. 2023). However, once suppressed trees start dying in Phase 2, this direct proportionality will be lost as their biomasses become part of the litter of the stand; unlike 'fine' litter, which is made up largely of shed leaves, twigs, bark and fine roots from living trees, the much larger stems, branches and woody roots of trees that have died are often termed 'deadwood' litter. As Oliver and Larson (1996, p. 215 et seq.) discuss, live tree stand biomass will reach a maximum at some time during Phase 2, subsequent reductions reflecting net losses due to tree deaths.

Figure 2 illustrates how stands of different stocking densities might develop as their ages change through Phases 1 and 2. It shows data from an experimental plantation in Turkey of Turkish red pine (*Pinus brutia* Ten.),

a species native to eastern Mediterranean regions (Erkan and Aydin 2016). The experiment used one of the novel designs of Nelder (1962). These allow plants to be grown at a very wide range of stocking densities on a conveniently sized area of land; the layout of the plants in the present case, a circular design that occupied a total of 0.94 ha, is shown in Fig. 2a. The results reported here came from the third to seventeenth tree circles, where the tree stocking densities at planting declined progressively from 5618 stems ha^{-1} to 539 stems ha^{-1}, as circle radius increased. Figure 2b shows how the stand stem wood volume of trees related to the stocking density of the trees surviving in the various circles at 7, 9 and 12 years of age. At 7 years of age, the seedlings at all stockings were still in Phase 1 and their stand stem wood volumes were directly proportional to stocking density. By 9 years of age and later, parts of the experiment with higher stocking densities had entered Phase 2 and mortality was starting, so the direct proportionality was lost.

Phase 3: After there have been appreciable deaths amongst suppressed trees in Phase 2, Phase 3 involves a transition to the next phase. The increase in intertree spacing resulting from the deaths will reduce the level of asymmetric competitive advantage of taller trees over smaller. West (2018) has given an example of growth development as a stand moves through Phase 3. The reduced competitive advantage of taller trees in
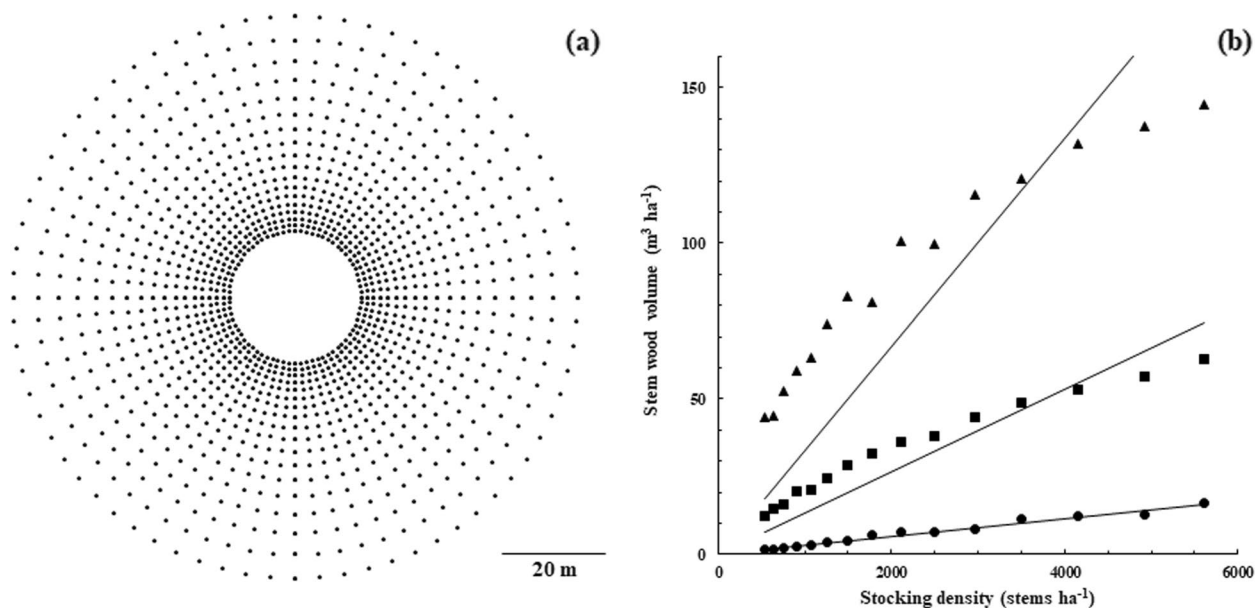
Fig. 2 **a** Using design 1a of Nelder (1962), an aerial view of the layout of tree planting positions in the experimental plantation of *Pinus brutia* Ten. established at Duaci, Turkey in 2005 (Erkan and Aydin 2016). **b** Stand stem wood volume in relation to surviving stocking densities in the circles of the experiment at (●) 7, (■) 9 and (▲) 12 years of age as shown in Erkan and Aydin's Fig. 7. The solid lines are the ordinary least-squares straight-line fits through the origin of the data in each case; if there was direct proportionality between volume and stocking density, the data points would fall directly on the line, as they appear to do so for the age 7-year data, but not for the later ages

this phase allows the smaller trees to contribute rather more to the overall growth of the population, reducing the growth dominance of larger trees, with a consequent decrease with increasing age in the degree of inequality (variability) of plant sizes in the population. Others have described similar changes with age in stand structure at these stages of development for various species (Lundqvist 1994; Tschieder et al. 2012; McGown et al. 2016; Pothier 2017). This phase is perhaps closest to the 'understory reinitiation' stage of Oliver and Larson (1996), where the canopy opening may allow understory species to develop.

Phase 4: This phase involves a reversal of growth dominance, where smaller trees contribute proportionally more to total stand growth than larger trees and grow at rates disproportionately large relative to their sizes. There have been a number of reports of this occurring, but it is not always the case (Binkley et al. 2003, 2006; Doi et al. 2010; Binkley and Kashian 2015). Binkley and Kashian (2015) suggested it occurs because larger trees may have lower resource use efficiency than smaller trees (see Sects. 'Changes in stand growth rates with age', 'Inter-tree competition').

As this phase continues, the trees pass maturity, reach old age and eventually die. As Roach (1993) discusses, individuals of some species can survive for over 1000 years. Whilst the processes of ageing and death have been studied extensively for animals, much less is known about them for plants. In plants such as trees, there is often a long period of 'senescence', which Roach defined as '... a decline in age-specific survival and reproduction with advancing age'.

Phase 4 is equivalent to the 'old growth' stage of Oliver and Larson (1996) in which overstory trees start to die and, if understory trees have developed, they may begin to grow into the overstory.

3.2 Changes in stand growth rates with age

During growth Phase 1, trees grow progressively larger from the seedling stage, with correspondingly larger total amounts of leaf material on the site. This allows for progressively increased amounts of photosynthesis and so the overall stand growth rate increases progressively with time. It reaches a maximum to coincide with the maximum leaf biomass of the stand as it enters Phase 2. As growth continues through Phase 2 and beyond, stand growth rate declines even though leaf biomass does not. The decline continues progressively and may do so for the rest of the lifetime of the forest. This phenomenon has long been recognised in forest science; various reviews and texts describe it (Gower et al. 1996; Ryan et al. 1997;
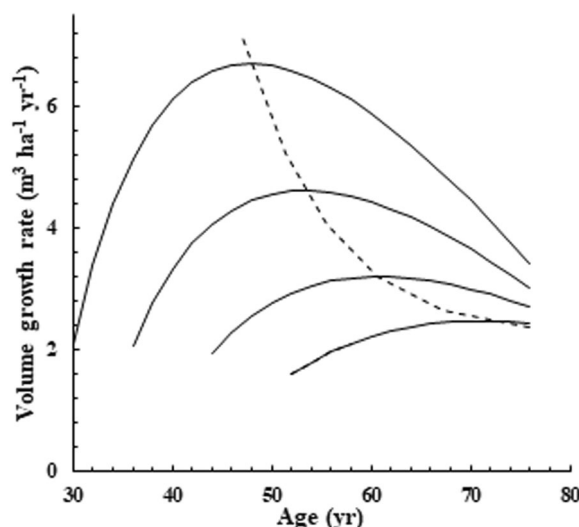
Fig. 3 Growth rate against age (——) in stand stem wood volume of Alaskan paper birch (*Betula papyifera* Marsh.) forest, predicted using Eq. (1), for stands with a site index of 11 m (lowest line) and site indices of 14, 17 or 20 m for successively higher lines. The line (----) shows how the maximum growth rate observed at any site index changes with age

Davis et al. 2001, Chap. 4; Skovsgaard and Vanclay 2013; West 2015, Sect. 8.10; Binkley 2023; Pretzsch et al. 2023).

Figure 3 gives an example to illustrate this phenomenon. It was derived using predictions from a model to predict stand stem wood volume of well stocked, even-aged stands of paper birch (*Betula papyifera* Marsh.) growing in interior regions of Alaska, USA (Gregory and Haack 1965). This species occurs extensively across Alaska and Canada; it can grow for up to 100 years and is considered to be fast growing, albeit for a species in a cold climate. The model was given in Gregory and Haack's Table 12 and, after taking its derivative and transforming its units, was.

$$dV/dA = 4.30 + 0.0493S^2 - 0.000603S^2A - 13218/A^2 \quad (1)$$

where V was stand stem wood volume (to a small end diameter under bark of 10 cm of trees in the stand with diameters at breast height ≥ 11 cm) (m^3 ha^{-1}), A was age (year) and S was a measure of site productivity, site index (m). Site index was defined as the height at 50 years of age of the tree of mean stem basal area, amongst dominants and codominants. Site index based on tree heights is used commonly in forest science as a measure of site productive capacity; there are various other measures of productive capacity, measures based on various other stand characteristics (e.g. Avery and Burkhart 2002; Skovsgaard and Vanclay 2013; West 2015, Sect. 8.7.3). The progressive rise in growth rate at younger ages to a maximum is

evident in Fig. 3 and is followed by a progressive decline at later ages. As discussed by Ryan et al. (1997) and as is evident from the dashed line in Fig. 3, the decline starts at younger ages in stands growing on sites of higher productivity and declines more rapidly in those stands; this occurs because stands on more productive sites reach growth Phase 2 earlier than those on less productive sites. In his review of this growth decline phenomenon, Binkley (2023) discussed three mechanisms that have been advanced as possible causes of it. The first was that there might be declines with age in the amount of foliage held in tree canopies due to physical losses of leaves as trees become taller, sway more in the wind and their crowns collide, and/or the amount of nutrients available from the soil or an increases in water stress in the leaves as taller trees need to transport water from their roots to successively greater heights. The second possibility was that the resource use efficiency of trees might decline as they grow larger. The third was that larger trees have larger amounts of tissue that they need to support metabolically through respiration, so reducing their net primary production. Binkley concluded that evidence favoured the second of these suggestions, tree resource use efficiency. A theory that that has received much support in times past and is consistent with this suggestion of a decline in resource use efficiency, is the 'hydraulic limitation theory'. This proposed that, as water coming from the roots has to be raised against gravity to increasing heights as trees grow taller, this leads to increased water stress in the leaves which will reduce their photosynthetic capability (Ryan et al. 1997, 2006; Koch et al. 2004; Mencuccini et al. 2005). More recently, detailed study of a wide range of forest types throughout the world has suggested that photosynthetic capabilities of taller tree crowns may not decline (West 2020). Rather, it is their resource use efficiency that declines through increased respiratory losses as trees grow taller and larger, hence older. One cause of this may be respiratory costs involved with the construction and maintenance of more complex morphologically and/or anatomically structured leaf tissues in response to reduced light availability and/or increased water stress, changes that maintain the photosynthetic capability of leaves and may also render them more efficient with respect to water use (Nock et al. 2011; Peñuelas et al. 2011). Other possible causes of increased respiratory losses are the need to maintain an increasing live tissue biomass within the wood, to increase the turnover rates of fine roots in older forests, to transport carbohydrates and hormones through an increasing length of phloem and to maintain alive smaller, competitively unsuccessful trees or taller trees that are indeed subject to hydraulic limitation. Much research remains to be done to ascertain the relative importance of each of these factors.

## 3.3 The balance between stand growth, stocking density and mortality

Once the forest has entered growth Phase 2, it carries the maximum amount of the tree live tissues (principally leaves and fine roots) that the site can support (Fig. 1). As individual trees then grow bigger, the amount of live tissue each carries will increase with its size. Thus, as the stand ages and moves into Phase 3, smaller, suppressed trees will die to ensure the total live tissue carried by the remaining trees does not exceed this maximum. In the absence of some environmental catastrophe, this is usually the driving force behind regular, progressive mortality in a forest.

Yoda et al. (1963) examined the balance between the sizes of plants in a population and their stocking density. They proposed that after mortality had become steady and ongoing in a plant population, the following relationship would hold at any time thereafter,

$$\bar{B} = \alpha N^{-\beta} \tag{2}$$

where $\bar{B}$ is average plant biomass, N is stand stocking density, and α and β are parameters. In effect, this relationship defines a limit beyond which the plants in a population cannot grow because the site cannot support any greater total biomass. Initially, Yoda et al. suggested that β took a value of 3/2. Gorham (1979) provided a remarkable test of this theory. From the scientific literature, he collated data of average, aboveground oven-dry biomasses and stocking densities of plant stands undergoing steady mortality that ranged from large trees, through tree saplings to much smaller plants (different types of sedges, rushes and ferns) and right through to very small plants, mosses. The stocking densities varied enormously in this data set, from tree stands with just over 700 stems ha^{-1} to mosses with over 164 million stems ha^{-1}. Likewise, the average aboveground biomasses of the plants varied enormously, from just over 1 tonne plant^{-1} in the trees to about 20 mg plant^{-1} in the mosses. Gorham's data are reproduced in Fig. 4. Using the logarithmic transformation of Eq. (2), he determined a value for β of 1.49, very close to Yoda et al.'s assumption of 3/2; the model he fitted is shown as the solid line drawn on Fig. 4. This theory appears to hold widely across plant populations (White 1981) and is commonly termed the 'self-thinning rule'; the straight line based on the logarithmic conversion of the rule is known as the 'self-thinning line'. There have been numerous suggestions as to what circumstances lead to particular values of the parameters of Eq. (2). During growth Phase 1, before competition-induced tree mortality starts and when total stand growth at any time varies directly with its stocking density (the Sect. 'Phases of growth with age'), $\beta = 1$. When that applies, Eq. (2) is termed the 'law of
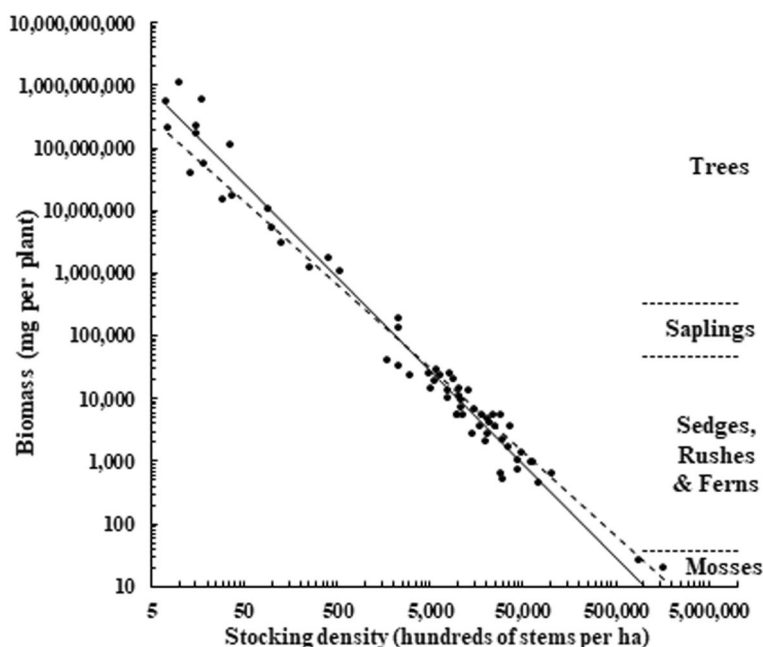
Fig. 4 Adapted from Gorham ([1979](#)), a scatter plot (●) is shown of average aboveground plant biomass against stand stocking density, for stands undergoing steady mortality, of a wide range of plant types from trees to mosses as indicated. The data are plotted in (base 10) logarithmic form or they would not fit reasonably on the page. The solid self-thinning line (——) is a trend line for the data, based on the logarithmic form of Eq. (2), for which Gorham determined $\beta = 1.49$. The dashed line (- - - - -) is the fit to the data when $\beta = 4/3$, the smallest value Mrad et al. ([2020](#)) suggested it might take

constant final yield' (Weiner and Freckleton [2010](#)). This reflects the situation shown at 7 years of age in Fig. 2b. Such cases are often found to be of practical interest for agricultural crops that may be grown for only a year or with wide spacing between individuals. Once continuing mortality has started in growth Phase 2, it has been suggested that the value of β may take values other than the 3/2 suggested originally by Yoda et al. and apparently confirmed by Gorham. Mrad et al. ([2020](#)) described various 'mechanisms' that might determine its value. These include one or other of metabolic, biomechanical, inter-tree competition or mortality rate effects, each of which might apply during different growth phases and under different environmental circumstances. Each suggested mechanism involves an interaction between tree sizes and the number of trees in a stand as they develop with time. Mrad et al.'s arguments suggested that β should take a value within the range 4/3–3/2, depending on which of the mechanisms was operating in a stand.

It might be felt that Mrad et al.'s suggested range for β is not large. However, it is sufficient to lead to substantial differences in predictions made using the self-thinning rule. To illustrate this, the dashed line shown on Fig. 4 is the self-thinning line determined as the fit to Gorham's data when $\beta = 4/3$, the lowest value suggested by Mrad et al.. This contrasts with the solid line where $\beta = 1.49$, as

determined by Gorham and very close to the maximum value of 3/2 suggested by Mrad et al. At the lowest stocking density shown in the data, the line with $\beta = 4/3$ predicts stand average biomass to be 62% smaller than that predicted from Gorham's line and, at the highest stocking density, to be 159% larger. The fit to the data of both lines looks reasonable to the eye and not greatly different, but the use of logarithmically transformed axes in the figure disguises the magnitude of the differences of biomass predictions that can arise in each case. Mrad et al. were unable to suggest which of the various mechanisms they proposed is most common or, indeed, when and if different mechanisms operate at different phases of stand development or are more important for different species. Considerable research work is necessary to investigate these matters further.

Yoda et al.'s theory was a variation of the theory advanced much earlier, in a forestry context, by Reineke ([1933](#)). Reineke used a reversed form of Eq. (2) and a different measure of average plant size. His version was

$$N = \alpha' D_q^{-\beta'} \qquad (3)$$

where D_q is stand quadratic mean diameter (the diameter equivalent of the average basal area of live trees in a stand) and α' and β' are parameters. It is referred to often

in forest measurement texts and its usage has continued in recent years (e.g. Avery and Burkhart 2002, Sect. 15–5; Schütz and Zingg 2010; Kweon and Comeau 2017; Zhang et al. 2018; de Prado et al. 2020; Pavel et al. 2023; Chivhenge et al. 2024). Reineke proposed that a value of $\beta' = 1.605$ held generally across forest types, just as Yoda et al. subsequently proposed $\beta = 3/2$ generally. However, the proposals of Mrad et al. (2020) and the results of many empirical studies suggest these particular values often do not apply. For example, Aguirre et al. (2018) and Pretzsch (2019) collated results from over 30 studies in monospecific forests of eight softwood and two hard-wood species spread widely across Europe. Using units of stem ha^{-1} for N and cm for D_q, they found β' varying over the range 1.33–2.14, with a mean of 1.79, and α' varying over the range 0.64–8.01×10^5, with a mean of 3.06×10^5. These α' and β' values correlated positively with each other, with Pearson's correlation coefficient of 0.83. Other work with many species, in both single- and mixed-species populations, has found all of α, α', β and β' varying sometimes, and sometimes not, on sites with different environmental circumstances, at different phases of the life of stands and even when the stand has been subject to different management practices early in its life, such as different initial stocking densities or thinning (Tang et al. 1995; Pretzsch 2010; Schütz and Zingg 2010; Zeide 2010; Zhang et al. 2018; Kweon and Comeau 2017; Wade 2018; de Prado et al. 2020; West 2021; Marqués et al. 2023; Pavel et al. 2023; Caicoya et al. 2024). An example will illustrate the use of Reineke's version of the self-thinning rule. It comes from Trouvé et al. (2017), using data from river red gum (*Eucalyptus camaldulensis* Dehnh.) forests growing in Victoria, Australia. This species is widespread across Australia and occurs along watercourses. Trouvé e al. had data available from repeated measurements made over 9–117 years of age in a set of plots in these forests. These data are shown as the light grey lines on Fig. 5 for individual plots. It is evident that, early in the life of a plot (during growth Phase 1), the quadratic mean diameter of the trees tended to increase steadily with little change in stand stocking density. Then, as Phase 2 started, mortality of smaller trees commenced and stocking density declined progressively, whilst the average size of the remaining trees continued to increase. The solid black line on Fig. 5 shows the Reineke self-thinning line that Trouvé e al. determined for their data set. It was positioned as the upper limit of the data above which stands were unlikely to be found anywhere in river red gum populations. There are various methods available by which lines positioned near the boundary of data sets such as this may be fitted; West (2023b) lists a number of these. Trouvé et al. also used their plot data to develop a model that related stand stocking density to stand
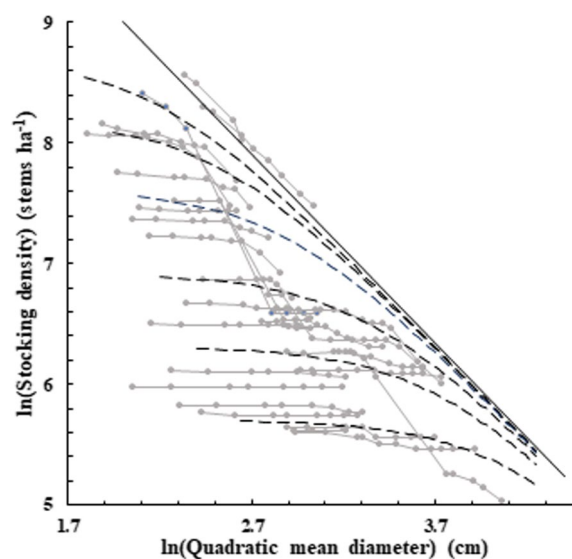
Fig. 5 Data (●——●) showing the progressive trend of the natural logarithm [ln()] of stand stocking density and quadratic mean diameter in each of a set of plots of *E. camaldulensis* in Victoria, Australia, as provided in the Supplementary information of Trouvé et al. (2017). The line (——) is Reineke's self-thinning line (Eq. 3) that they determined using a nonlinear least-squares procedure. For a set of stands chosen with arbitrary starting points, the lines (- - - -) show predictions of the change in stocking density with quadratic mean diameter from their model (6)

quadratic mean diameter. The dashed lines on Fig. 5 show predictions made with that model for a set of stands with arbitrarily chosen start points. Note that the predictions for each of the examples shown there tend ultimately towards the self-thinning line itself and not above it, consistent with the concept of the line. Note that other versions of diagrams such as Fig. 5, versions based on other measures of tree average size, such as stem wood volume, are known as 'density management diagrams' and have practical application in forest management practice (e.g. Drew and Flewelling 1977; Davis et al. 2001, pp.170–174; West 2014, Sects. 7.1.3, 8.4).
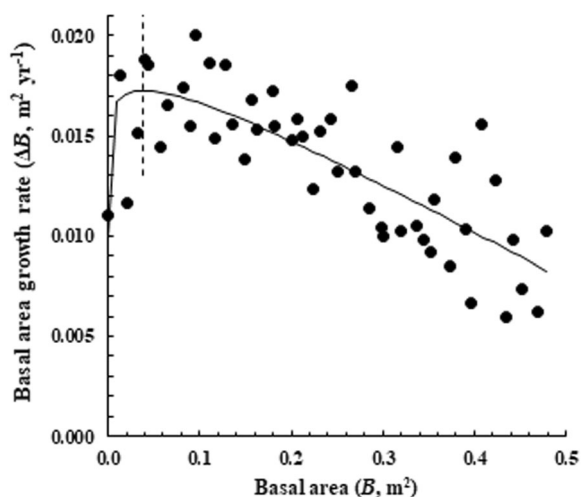
4 Individual tree growth and development
4.1 Maximum possible growth rates
A technique used commonly in modelling growth behaviour of individual trees in forest stands is to develop an initial model that predicts the 'maximum' (sometimes termed 'potential' or 'optimum') growth rate possible, or at least the maximum ever observed in nature, that a tree might have in relation to its size at the time growth is occurring. Subsequently, terms are added to the model to predict the reductions from this maximum that are a consequence of both the particular environmental circumstances of the site on which the tree is growing and the competition it faces from its neighbours for

the resources it requires for growth (Smith et al. 1992; Pretzsch and Biber 2010; Weiskittel et al. 2011; Pommerening et al. 2022; West 2023b).

An example to illustrate the derivation of a model to determine this maximum growth rate comes from West (2023b). He had data from 96 inventory plots in blackbutt (*Eucalyptus pilularis* Smith) forest growing over a region of sub-tropical eastern Australia. The plots had been measured numerous times and ranged in age over 2–63 years at the start of measurements. They provided stem basal area growth rates for 35,876 individual trees over their 0.4–5-year-long growth periods. The tree basal areas at the start of growth periods were divided into 50 equal sized classes and the observation in each class that had the maximum growth rate was selected (Bi and Turvey 1997). It was then assumed that the range of stand circumstances over the 96 plots would have allowed that some trees had an opportunity, at some time during their lifetime, to grow at rates close to the maximum possible for blackbutt. Figure 6 shows a scatter plot of the selected data. Maximum growth rates tended to increase to a maximum of their own with increasing tree size. They then declined progressively as tree size increased further. The fit to the data of the well-known Chapman-Richards function (Pienaar and Turnbull 1973) is shown.

These results are consistent with the earlier discussion that surrounded Figs. 1 and 3, where stand growth rates reach a maximum as a stand is moving from growth Phase 1 to 2. For the present case and following

West (2023b) '… during early stand development, individual tree growth rates increase with size, hence age. Stand growth is the sum of individual tree growths, so as trees become larger, stand growth rate will become correspondingly bigger. However, after some years, some trees will reach a size at which their growth rates decline, consistent with the trends in maximum possible growth rates shown in [the present Fig. 6]. Over time, more and more trees will reach this size and stand growth rates will continue to decline, the decline increasing steadily with increasing tree size, that is, with increasing stand age.' Thus, and as also discussed in the Sect. 'Changes in stand growth rates with age', it may be assumed that as individual trees become larger, hence taller, their growth rates decline in consequence of increased respiratory costs.

Numerous authors have studied tree maximum possible growth rates in relation to tree size for various tree species around the world. Table 1 lists 17 such cases that used data sets and methods of analysis to produce results equivalent to those described here in Fig. 6. For each of the cases shown in Table 1, Fig. 7 shows the relationship that their authors established between maximum possible basal area growth rates and tree basal areas. Note that the line numbered 14 is a reproduction of the solid line of Fig. 6. It is evident from Fig. 7 that there are substantial differences between species in both their maximum possible growth rates and the tree basal areas at which those maxima occur. This reflects the genetic capabilities of different species and the environmental circumstances in which their populations occur. Notably, several of the hardwoods (numbers 12–15) and two of the softwoods (2, 7) appear to be particularly capable of rapid growth for given tree sizes. Perhaps that helps to explain why those species have often been favoured for use in commercial plantation forestry.

Some of the studies listed in Table 1 have found that maximum possible growth rates can be related to the productive capacity of the site on which the trees are growing (Hahn and Leary 1979; Teck and Hilt 1991; Coomes and Allen 2007; Pretzsch and Biber 2010). This is to be expected of course, since growth rates are limited ultimately by the amount of the resources required for growth available on the site. West (2023b) has given an example of this for the same population of blackbutt in sub-tropical Australia as discussed above in relation to Fig. 6. To do that, the entire data set available was subdivided into a number of site index classes, defined in this case as the average height of the 50 largest diameter trees per hectare at 20 years of age and thence into tree basal area classes as done in the example above. The Chapman-Richards function was then fitted to the data for each site index class and the trends then apparent with different site indices were examined.

Fig. 6 Scatter plot (●) of maximum tree basal area growth rates of individual trees against their corresponding basal areas, as selected from a population of blackbutt (*E. pilularis*) trees growing in sub-tropical eastern Australia. The solid line is the ordinary least-squares fit to the data of the function $\Delta B = 0.022B^{0.0567} - 0.0268B$. The dashed line indicates that maximum growth rate was itself predicted to reach a maximum at a basal area of 0.039 m.² (a diameter at breast height over bark of 22.3 cm)

Table 1 Details of forest species for which models have been published predicting maximum possible growth rates in individual tree stem diameter or basal area. The population sizes shown are the total number of trees for which data were available to construct the model concerned; note that in the case of *Pinus taeda*, the trees were open-grown

Number	Species	Location	Population size	Reference
Softwoods				
1	*Abies balsamea*	Northeastern USA	4456	Teck and Hilt (1991)
2	*Picea abies*	Bavaria, Germany	15,281	Pretzsch and Biber (2010)
3	*Picea rubens*	Northeastern USA	4968	Teck and Hilt (1991)
4	*Pinus banksiana*	Lake States, USA	4625	Hahn and Leary (1979)
5	*Pinus resinosa*	Lake States, USA	11,663	Hahn and Leary (1979)
6	*Pinus sylvestris*	Bavaria, Germany	15,281	Pretzsch and Biber (2010)
7	*Pinus taeda*	Southeastern USA	115	Smith et al. (1992)
8	*Tsuga canadensis*	Northeastern USA	3431	Teck and Hilt (1991)
Hardwoods				
9	*Acer rubrum*	Northeastern USA	6591	Teck and Hilt (1991)
10	*Acer saccharum*	Northeastern USA	4237	Teck and Hilt (1991)
11	*Eucalyptus delegatensis*	Temperate Australia	4608	West (2023c)
12	*Eucalyptus grandis*	Sub-tropical Australia	10,123	West (2023c)
13	*Eucalyptus obliqua*	Temperate Australia	24,060	West (2023c)
14	*Eucalyptus pilularis*	Sub-tropical Australia	35,876	West (2023c)
15	*Eucalyptus regnans*	Temperate Australia	12,422	West (2023c)
16	*Fagus sylvatica*	Switzerland	5591	Pommerening et al. (2022)
17	*Nothofagus solandri* var. *cliffortioides*	New Zealand	3334	Coomes and Allen (2007)
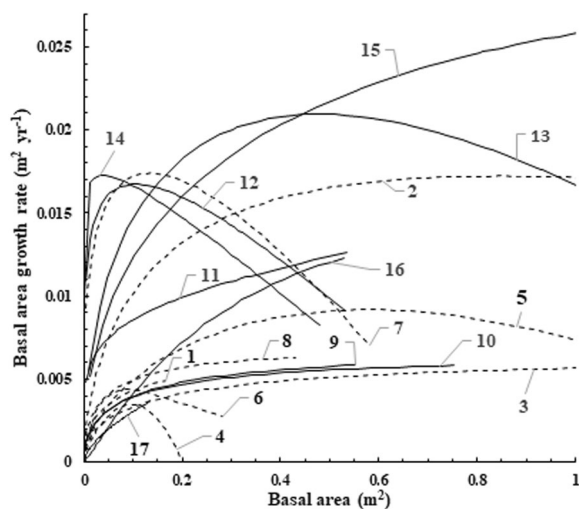
Fig. 7 Fitted maximum possible growth rate models reported for various softwood (- - - -) and hardwood (——) species around the world. The numbers identify the species details as shown in Table 1. Some of the models (species numbers 1–3, 6, 8–10) included stand site index as a predictor variable; the results shown here for those species were determined using the maximum site index reported for their populations
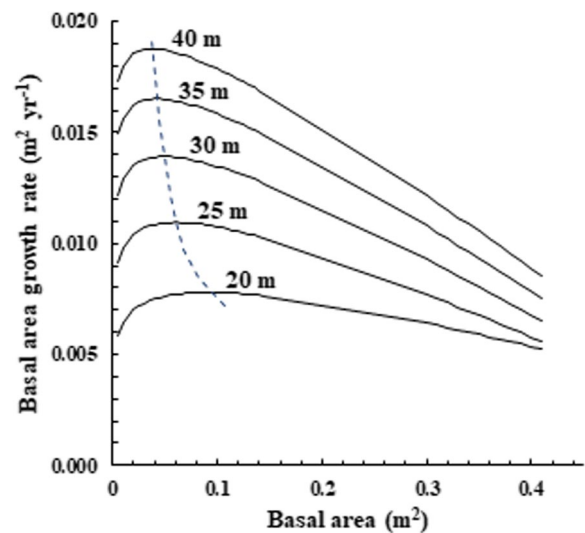
Fig. 8 For forests of blackbutt (*E. pilularis*) in subtropical eastern Australia, predictions (.——) for five stands of varying site productive capacities (as assessed by site indices, as indicated) of the maximum possible stem basal area growth rates of individual trees against their basal areas. The line (- - - - -) shows how, in any stand, the basal area of the tree that shows the greatest growth rate of all trees in that stand tends to decline with increasing site productivity. This figure is a reproduction of Fig. 4 of West (2023a)

Figure 8 is reproduced from West (2023b) and shows how the model he developed predicted the change of maximum growth rate with tree size for each of a set of site index classes. The dashed line there shows that the less productive the site, the larger was the tree basal area at which maximum basal area growth rate was itself a maximum. This result is consistent also with the studies described above that have shown tree and stand growth rates declining with age, hence, tree size. For a tree of given stem basal area, many studies have shown that the height of such a tree is smaller in stands of lower site productive capacity. That is, on sites of lower productive capacity, it will be larger diameter trees that have reached a height at which increased water stress in the upper crown threatens to limit photosynthetic capability of the tree and requires it to incur higher respiratory costs to prevent that happening.

4.2 Inter-tree competition

The previous section has been concerned with growth rates of trees that are, presumably, free of competition from their neighbours for the growth resources they require from the site. In normal forest circumstances many trees are present, so this is not usually the case and inter-tree competition for resources may occur.

As discussed in the Sect. 'Phases of growth with age', two forms of inter-tree competition have been recognised 'size-symmetric' and 'size-asymmetric' (Fernandez-Tschieder and Binkley 2018). The development of inter-tree competition for resources starting in growth Phase 1 was considered earlier (the Sect. 'Phases of growth with age'). Initially, competition is believed to be symmetric, below ground for water and nutrients. When

height differences appear in Phase 2, above-ground asymmetric competition may apply in addition to the ongoing symmetric competition. Some circumstances have been identified where asymmetric competition for below ground resources has been found favouring larger trees. These have included spatial heterogeneity of resources in the soil or of litter layers (Casper and Jackson. 1997; Rajaniemi 2003; Hodge 2006; Forrester 2019; Garlick et al. 2021), conditions of low water availability (Forrester 2019; Forrester et al. 2022) or development of ectomycorrhizal systems on roots (Franklin et al. 2014). Both symmetric and asymmetric competitive processes can be expected to continue as a stand moves into Phases 3 and 4. However, progressive opening of the stand due to tree mortality will reduce the intensity of the competition experienced by any individual as there will be reduced overlap with its neighbours of the spaces from which each obtains the resources it needs for growth.

Figure 9 was compiled from the data set used by West (2023a) when examining the processes of inter-tree competition in the same blackbutt forests in eastern Australia as were discussed through Figs. 6 and 8. Individual tree stem basal area growth rates are shown plotted against stem basal area for three growth periods at various stages of development of three plots in those forests. In the case of Fig. 9a, the forest was still in growth Phase 1 and growth was directly proportional to size. In Fig. 9b, the forest was just entering Phase 2 so growth was just starting to deviate from direct proportionality to size, but no obvious group of suppressed trees had yet developed. In Fig. 9c, the forest was well into Phase 2 and a group of small, suppressed trees, showing little or no growth, had clearly developed; the model fitted in that case was the
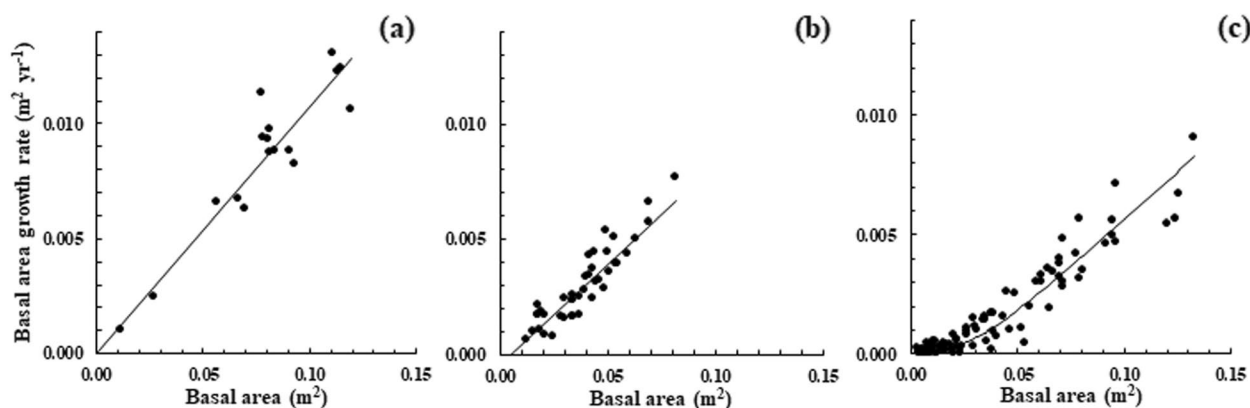

Fig. 9 Scatter plots (●) of individual tree stem basal area growth rates (ΔB, m^2 year^{-1}) against stem basal area (B, m^2) at the start of the growth period concerned for three plots of blackbutt (*E. pilularis*) in subtropical eastern Australia. Plots were **a** 15–18 years of age with site index 36 m, **b** 19–21 years, 29 m and **c** 24–26 years, 29 m. The solid lines show the ordinary least-squares fit to the data of the models **a** $\Delta B = 0.107B$, **b** $\Delta B = -0.000399 + 0.0868B$ and **c** $\Delta B = 0.0402\{B - 0.0349 + [(0.0349 + B)^2 - 0.1252B]^{1/2}\}$. These figures are redrawn from parts of Figs. 2c, b, a, respectively, of West (2023c)

'bent stick' model, found useful to describe such growth behaviour by West and Ratkowsky (2022b). Similar growth behaviour has been reported for plantations of radiata pine (*Pinus radiata* D. Don) in South Australia (West and Borough 1983) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in England (Ford 1975) as well as for native forests of some other eucalypt species in Tasmania, Australia (West 1980, 1981) and some hardwood species in Canada (from Ellis 1979, as reported by West 1980).

West (2023a) then attempted to quantify the levels of both symmetric and asymmetric competition in these blackbutt forests. The methods to do so are illustrated through Fig. 10, which is based on the information for the plot shown in Fig. 9c. Three solid lines are drawn there. The first shows the maximum growth rate that trees in that plot might have in the absence of competition; that was based on the model used to compile Fig. 8, for a blackbutt stand with a site index of 29 m. The second line shows the fit to the data of the actual growth behaviour of trees in that plot; that repeats the solid line shown on Fig. 9c. The third line shows the growth behaviour the trees in the plot *would* have if symmetric competition only was occurring between the trees; the method and justification for drawing that line are discussed in West (2023a).

The two dashed lines, marked A and B on Fig. 10, were drawn to help illustrate the inferences on the levels of competitive processes that may be drawn for a larger tree in the plot (A) and a smaller tree (B). Following Welden
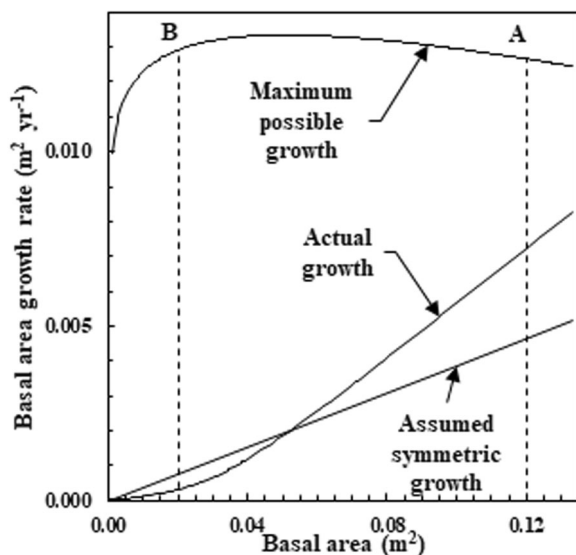
Fig. 10 As discussed in the text, the solid lines are model predictions of growth behaviour of individual trees in the blackbutt (*E. pilularis*) plot shown in Fig. 9c. The dashed lines denote individual trees, the behaviour of which is discussed in the text

and Slauson (1986), the level of competition 'intensity' suffered by a plant may be defined as the decrease it causes in its growth rate from what it would have under optimal circumstances and its 'importance' as the relative decrease. Based on those definitions and as discussed in detail by West (2023a), for the larger tree (A) symmetric competition is much more important than asymmetric (75% versus 25%, respectively). The asymmetric competition in that case has a negative intensity because larger trees achieve a disproportionate gain in photosynthetic capability, hence growth rate, over smaller trees (Sect. 'Phases of growth with age'). For the smaller tree (B), symmetric competition is still much more important than asymmetric (96% versus 4%). However, in that case the asymmetric competition has a positive intensity because smaller trees have disproportionately reduced growth rates due to the asymmetric competition from taller trees.

West (2023a) explored these issues for a large number of growth periods in a large number of plots in the blackbutt forests for which he had data. Across the entire data set, it was found that symmetric competition was consistently much more important than asymmetric. This result was rather surprising, since various studies have led to an impression that asymmetric competitive processes are the more influential in determining individual tree growth rates (Biging and Dobbertin 1992; van Breugel et al. 2012; West and Ratkowsky 2022a; Melis et al. 2023). West concluded that this view may have arisen because, with time, asymmetric competition very obviously alters the shape of the frequency distribution of tree sizes in the stand, whereas symmetric competition leads to no such change. But, none of these works quantified competitive processes formally as West (2023a) did; much work remains to explore this issue in other forest types. West concluded that '… it is essentially the size of a tree at any time that is the prime determinant of its subsequent growth behaviour. This defines the extent of the spread of its root system below ground and the size of its canopy. In turn, these determine, firstly, the maximum possible amount of growth resources the tree can access from whatever resources are available on the site on which it is growing. Secondly, they determine the intensity of competition between it and its neighbours, competition that limits the proportion of the total resources on the site that are actually available to each tree.'

4.3 Partitioning net primary production

The previous two sections have considered growth behaviour of individual trees in forests through their stem basal area growth rates in relation to their stem basal areas. Stem basal area usually correlates well with tree biomass (West 2015, Sects. 7.3–7.4) so that discussion of basal

area growth can usually be taken to be a good descriptor of overall tree growth. The present section expands this tree growth concept to consider more fully the first two elements of growth described in the Sect. 'Some principles of forest growth behaviour', that is, where biomass shed as litter in a previous growth period is replaced or biomass is added to the stems and woody roots to make the tree larger. In particular, it considers the 'partitioning' (often also termed 'allocation') of net primary production to these parts of trees or stands. Litton et al. (2007) have collated stand data from a wide range of forest types at different ages showing their annual net primary production of leaves, above-ground wood and roots (fine with woody); these data are useful to give some idea of the biomass quantities involved and their allocations to different tree parts.

Friedlingstein et al. (1999) pointed out that, in modelling tree growth behaviour, one of three assumptions has generally been used to predict this partitioning of net primary production. The first of these is that there is a constant proportion for each part, as determined by empirical observation for any particular vegetation type. Models based on this assumption may have limited flexibility as they are often constrained by the environmental circumstances of the forests from which the empirical observations were obtained. These circumstances may limit the total biomass of leaf and fine root tissue that may be supported on a site and the balance between them. However, this assumption does not then allow for changes in the proportions of the various tree parts as trees pass through the various growth phases.

A second assumption used is that leaf growth is optimised to ensure photosynthetic production, hence growth rate, is maximised. To support this proposal, it may be argued that trees have evolved to grow to great sizes and heights (King 1990). In doing so, they are aided by an ability to adopt an arrangement of the leaves within their crowns to maximise photosynthetic production (Hirose 2005). These attributes give them the best chance of survival and allow them to compete successfully with other forms of vegetation that have a shorter habit and that might be attempting to occupy the site. Thus, it seems reasonable to assume that trees will, when possible, favour leaf production or canopy condition to maximise their photosynthetic production and so, ultimately, their growth and ability to maintain a dominant position in the stand. A number of studies and process-based model systems have adopted strategies that favour this proposition, which leads to maximisation of the overall growth rate of a stand as a whole or of the individual trees within it (Iwasa et al. 1984; West 1993; Lüdeke et al. 1994; Sterck and Schieving 2007; Duchateau et al. 2015; Schippers et al. 2015; Seidel and Ammer 2023).

The third assumption used is that different parts of the tree must maintain a balance between their sizes to ensure they retain their physiological capabilities or their structural integrity, a balance termed 'allometry', which may be defined generally as the relationship between the sizes of the various parts of an organism. Many such relationships have been identified for many species around the world (e.g. Cheng and Niklas 2007; Pretzsch 2010; Pretzsch et al. 2012a; Anitha et al. 2015; Yuen et al. 2016; Gonçalves 2022). Thus, whilst the second assumption above suggests that individual tree development over any growth period may favour maximisation of leaf production where possible, this third assumption imposes constraints that require concomitant development of other parts of the tree, hence partitioning of net primary production to those parts. This has led to an approach to model tree growth that has been termed 'allometric partitioning theory' (McCarthy and Enquist 2007).

For stands and individual trees, there are various allometric relationships that may be important to allometric partitioning theory. These require that:

- Foliage and fine root biomasses be closely related, relationships often see through those with other tree parts such as stem diameter, to ensure the root system is large enough to take up from the soil the water and nutrient needs of the leaves (Sievänen et al. 2000; Pretzsch 2010; Pretzsch et al. 2012b; Anitha et al. 2015; Yuen et al. 2016),
- Branch biomass is related to the leaf biomass, so it is sufficient to support the weight of the foliage the branches must carry (West 1993; Horn 2000; Duchateau et al. 2015; Anitha et al. 2015; Yuen et al. 2016),
- Stem diameter, height and overall size must be related to ensure that the stem has the structural ability, as a vertical pole, to remain standing upright to support the weight of its above ground parts and resist the wind forces or snow weights to which it is subject (King and Loucks 1978; King 1981; West et al. 1991; Horn 2000; Ilomäki et al. 2003; Read and Stokes 2006; Iida et al. 2012; Anitha et al. 2015; Yuen et al. 2016; Gao et al. 2023; Zubkov et al. 2024),
- Height of a tree must reflect the length and width of its crown (Iwasa et al. 1984; King 2005; Iida et al. 2012; Qiu et al. 2023),
- Cross-sectional area of the sapwood within the tree stem, coarse roots and branches must relate directly to the foliage biomass in the crown (termed the 'pipe model theory') to ensure there is sufficient sapwood to maintain the necessary flow rate of water from the roots so that the leaves may undertake photosynthesis satisfactorily (Shinozaki et al. 1964a, b; West

and Wells 1990; Medhurst et al. 1999; Horn 2000; Sievänen et al. 2000; Anitha et al. 2015; Yuen et al. 2016; Aye et al. 2022),

- Biomass of the entire root system must reflect the overall tree size to ensure it is large enough to hold the tree firmly in the soil and to avoid uprooting by wind forces (Cheng and Niklas 2007; Anitha et al. 2015; Yuen et al. 2016; Zeng and Makoto 2023),
- Biomass of fruiting bodies be sufficient to ensure the reproductive requirements of the species are met (Sterck and Schieving 2007).

Model systems have been developed that involve some or other of such allometric relationships (Lüdeke et al. 1994; King 2005; Sterck and Schieving 2007; Potkay et al. 2022). One, a process-based model devised by the present author (West 1993), will be described briefly here. That model predicts, year by year, above-ground biomass growth of each tree in a stand. Initial values, at some age, must be provided for each tree in the stand of the oven-dry biomasses of its leaves, branches and stem, its height, stem diameter, sapwood cross sectional area at breast height and the dimensions and position above ground of the tree crown, which is assumed to be ellipsoidal in shape. As well various allometric relationships must be available for the forest concerned, relationships that will have been established in prior studies of the forest. These include some of the relationships that were alluded to above, and relate tree stem diameters and heights to tree biomasses, leaf biomasses to branch biomasses and leaf biomass to sapwood cross sectional area at breast height. As well, values of numerous parameters that apply to the physiological and structural characteristics of the species concerned, such as the average density of its stem wood, the life-span of the leaves, the stand conditions that will lead to death of the tree and various others. Information allowing predictions of sunlight availability to the trees throughout the year are required also. Thus, much information about the stand and species concerned are necessary to apply models of this nature; these require considerable study of forests of the species concerned before such models may be used.

Given these requirements, the model then predicts the annual oven-dry biomass growth rate (kg year^{-1}) of the various above-ground parts of each tree in the stand as

$$\Delta G/\Delta t = n_G P - l_G \qquad (4)$$

where G denotes biomass of each of the leaves (L), branches (B) or stem (S) (kg), t denotes time (year), P is net primary production (kg year^{-1}) as a consequence of photosynthesis of above-ground tree parts, n_G is the proportion of net primary production that is partitioned to each biomass part ($n_L + n_B + n_S = 1$) and l_G is the loss in

biomass as litter of each biomass part. Above-ground net primary production is predicted using a sub-model that estimates it from the amount of sunlight intercepted by the crown of each tree over the year concerned. The model then assumes that leaf biomass growth ($\Delta L/\Delta t$) in any year is maximised, but is subject to the constraints imposed by the allometric relationships that are assumed to apply between the tree parts. West applied this model to predict growth from 8 to 35 years of age of an 0.6 ha plantation forest of mountain ash (*Eucalyptus regnans* F. Muell) in Victoria, Australia. This is a fast-growing species, native to south-eastern temperate Australia; it produces the tallest trees of any hardwood species in the world, with heights that can exceed 100 m. Sizes of the individual trees in the stand were summed and Fig. 11 shows how the model predicted the change with age in the stand stem biomass growth rate. Note that it reaches a maximum at about 21 years of age, suggesting that this plantation was moving into growth Phase 2 at that age. Contrast this result with those of Fig. 3, for the Alaskan paper birch forest, which was growing far more slowly in a much colder climate, where the maximum growth rate did not occur any earlier than about 45 years of age. Of particular note is that the empirical model describing stand growth of Alaskan paper birch (Model 1) has a chosen, quadratic form that allows the maximum growth rate to be predicted. Nothing in the West model makes any such assumption. The maximum in that case is a consequence of the constraints on individual tree growth rates imposed by the allometric relationships between the tree parts as they grow taller and larger. This, perhaps,
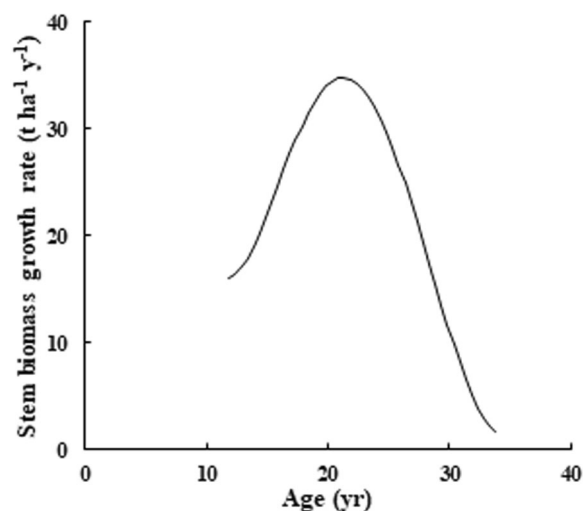
Fig. 11 Change with age in stand stem biomass growth rate of a plantation forest of mountain ash (*E.regnans*) in Victoria, Australia, as predicted using the model of West (1993). This diagram was derived from Fig. 1a of the original publication
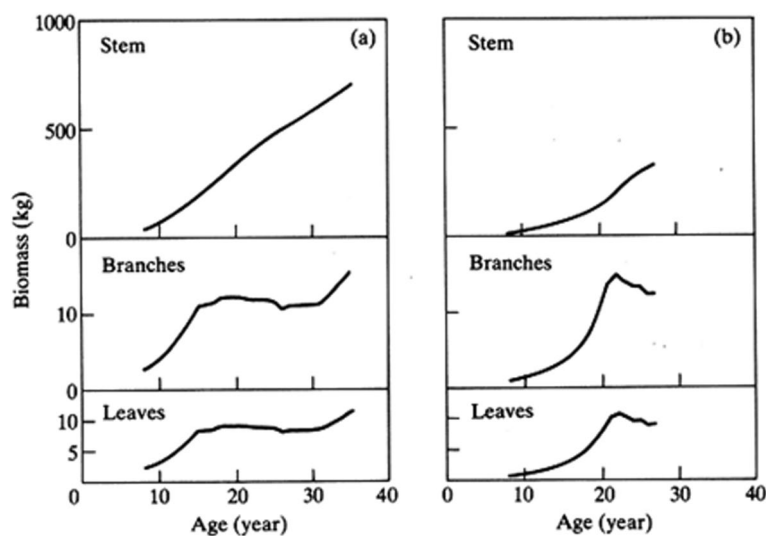
Fig. 12 Change with age in biomass of stem, branches and leaves of individual trees in the plantation forest shown in Fig. 11. Results are for **a** a well-lit, dominant tree and **b** a suppressed tree that died at 27 years of age. This is a reproduction of Fig. 3 of West (1993) and is reproduced here with the kind permission of Elsevier, publisher of the Journal of theoretical Biology

emphasises that a process-based model, one that is based around the physiological processes that determine growth, may yield a better understanding of how that growth occurs than an empirically derived model that adopts a form simply chosen to fit a data set of observed growth rates.

Figure 12 shows the biomass development with age predicted for two individual trees from the mountain ash stand, one (a) being a dominant tree and the other (b) a suppressed tree that died at 27 years of age, before the end of the simulation period. It can be seen that after about 30 years of age, the canopy of the dominant tree enlarged, as it over-topped other trees and was able to intercept progressively more sunlight. By contrast, after about 21 years of age the leaf biomass of the suppressed tree declined as it became progressively more over-topped by taller trees, until it could survive no longer. Not shown here, but available in Figs. 4 and 5 of West (1993), partitioning of above-ground net primary production for both trees was around 80–90% to stem growth, 10–15% to leaf development and the remainder to branches. The proportion to leaves and branches tended to increase slightly with time, no doubt reflecting the condition of the model that leaf growth was favoured and that stand stem growth rate declined after about 21 years of age as trees grew larger (Fig. 11). So, whilst this example appeared to predict satisfactorily both stand and individual tree growth behaviour, it relied on allometric relationships between various tree parts

to allocate net primary production between them as the tree grows. Those relationships were developed empirically for the species concerned and there is a risk that they may change with age or the environmental circumstances on which the forest is growing.

Since the work of Friedlingstein et al. (1999), mentioned above, much further consideration has been given to understanding what determines growth partitioning of net primary production as trees grow. Over the years, there have been many studies done, suggestions made and reviews of its operation (Lacointe 2000; Sievänen et al. 2000; Le Roux et al. 2001; Enquist and Niklas 2002; Litton et al. 2007; Ryan et al. 2010; Franklin et al. 2012; Poorter et al. 2012; Vicca et al. 2012; de Kauwe et al. 2014; Schippers et al. 2015; Li et al. 2016; Collalti and Prentice 2019; Gonçalves 2022; Potkay et al. 2022). However, as Merganičová et al. (2019) point out, the processes determining growth partitioning vary with species, environmental circumstances, phenology, ontogeny, stand circumstances and various other things that are still not well understood. It is clear that the many complexities involved with these processes need to be the subject of separate reviews and their ramifications are too complex to discuss further here.

4.4 Stem taper
A further aspect of the growth of the different parts of individual trees is the way in which new biomass is distributed down the tree stem and, hence, how the stem

tapers. This is important from a forest management point of view since it determines the taper of individual logs that can be cut from the stem. This determines the sizes and quality of the boards that can be sawn from them.

The most enduring theory to explain stem taper is the 'mechanistic' theory (Larson 1963). It is based on the concept that a tree stem is a vertical pole that has to stand upright to support the weight of the above ground parts of the tree and resist the forces to which it is subjected both by gravity and the wind. A number of studies have invoked engineering theory to suggest that stems are shaped so that the bending stresses to which they are exposed are constant along most of their length; this is termed the 'constant (or uniform) stress' theory (Dean and Long 1986; Morgan and Cannell 1987; West et al. 1989a, b; Dean 1991; Mattheck 1994; Meng et al. 2007; Dean et al. 2002, 2013). It has been found that this theory does not apply always and there may be a need for 'safety factors' in stem diameter against damaging winds (Niklas and Spatz 2000; Minamino and Tateno 2014). Certainly, experimental work has shown that altering the distribution of bending stresses along tree stems stimulates diameter growth where stress is greater (Jacobs 1954; Telewski and Jaffe 1986; Valinger 1992; Valinger et al. 1994, 1995; Lundqvist and Valinger 1996; Osler at el. 1996; Meng et al. 2006b; Dranski et al. 2018; Nicoll et al. 2019). Where the wind tends to blow rather more in one direction than another, the stem, crown and root systems may develop non-circular, cross-sectional shapes, the asymmetry being to windward (Wang et al 2023); such a growth response, to an external 'touching' stimulus, is known as thigmomorphogenesis. Tree stems can adopt quite peculiar shapes under unusual environmental circumstances, such as when they lean against other trees or some other solid object, grow on steep slopes or have odd branching habits (Mattheck 1991, 1994). Particularly in tropical rainforests, large trees may develop extensive flutes or buttresses that can extend to several metres above ground. These are believed to give additional structural support to the tree and may have other effects on the forest ecosystem (Pandey et al. 2011; Bhatta et al. 2021; Kuwabe et al. 2021; Tyukavina and Popova 2022; Alencar et al. 2023; Wang et al. 2023).

The progressive increase in height and distribution of growth along the stem leads to the stem tapering from tip to ground. Many models have been developed for many species around the world that predict how stem diameter changes with height and whether this varies with genetic or environmental circumstances (Gomat et al. 2011; Schneider 2019; Aye et al. 2022; Boczniewicz et al. 2022; Valverde et al. 2022; Kangas et al. 2023).

5 Conclusions

This work has examined the principal issues determining the growth behaviour in even-aged, monospecific forests of both whole stands and the individual trees within them. Growth was considered as it occurs progressively over periods of no more than a few years. It was defined as involving the replacement of tissue biomass lost as litter in a previous growth period and the addition of new biomass to the various parts of the tree as it grows taller and larger. The issues that were concluded as being important determinants of growth were:

- The genetic properties of the species concerned. These determine the different physiological and metabolic characteristics of each tree species which, in turn, determine their responses to different environmental circumstances and the speed with which they are able to grow. These matters were not considered in detail here,

- The environmental circumstances of the site on which trees are growing, particularly its temperature and humidity regimes, which affect the rate of metabolic processes, and the availability of the essential resources trees require for growth, carbon dioxide, sunlight, water and mineral nutrients. These factors determine the amount of leaf (and corresponding fine root) biomass that may be supported on the site. In turn, this determines the amount of photosynthesis the leaves may undertake, hence the amount of growth that may occur,

- The four phases of growth through which the forest stands go, from seedling establishment, through development of the full leaf biomass the site can support, the start of competition between neighbours for access to the essential growth resources each needs, the start of deaths amongst the less competitively successful individuals, until ageing leads to maturity, senescence and eventual death,

- The progressive decline in growth rate of whole stands that follows development of the full leaf biomass on a site. This is believed to be due to increased respiratory demands on trees as they grow taller; that is consequent on increased water stress in leaves as water is raised to greater heights,

- Development of a well-defined relationship between average tree size and the number of live trees remaining in a stand at any time, as smaller trees die due to competitive suppression by larger trees,

- That the maximum growth rate of individual trees, when free from competition with neighbours, depends on their size, not their age. This maximum declines progressively beyond a certain size, presumably because larger, taller trees experience increased

water stress in their leaves leading to increasing respiratory costs,

- Competition between individuals for growth resources is initially for water and nutrients below ground until some have grown tall enough to shade their neighbours and sway more vigorously so abrading their crowns, hence competing successfully with them for use of light. However, competition below ground appears to remain the principal determinant of the growth rates that individuals may achieve, and,
- The adoption by trees of an evolutionary strategy to grow tall and dominate other vegetation on a site. This imposes constraints on the sizes of the various tree parts (leaves, branches, stems, roots, etc.) to ensure that their respective roles can be performed and the tree remains standing upright. The processes that control partitioning of growth to different parts are poorly understood, but this is constrained by the need for those parts to maintain their relative sizes to each other (termed allometric relationships).

Much experimental work has been undertaken over the last century or so to observe the growth behaviour of trees in forests. However, much remains to be done to understand properly the physiological and metabolic processes that control that behaviour and their relationship with the environmental circumstances of the site on which a forest is growing. Issues that were discussed here and obviously need further work include an understanding of how environmental circumstances of a site limit the potential for growth of vegetation on it (as determined by principles such as Liebig's law of the minimum), the factors determining the timing, degree and cause of tree senescence and death and the decline in growth rates with tree age or size, the mechanisms determining the timing and effects of environmental circumstances on self-thinning in forest stands, the intensity and importance of inter-tree competitive processes and the factors that determine the partitioning of growth between the different parts of trees and forest ecosystems. The limited understanding of one or other of these matters has no doubt led to the plethora of stand and individual tree growth models that have been developed for many different forest types around the world. The research work necessary to investigate these matters properly to allow development of better model systems to predict tree and stand growth is likely to be complex and require considerable time. Improved models will aid matters such as response to climate change, maintenance of biodiversity and management of wood yields.

Finally, it must be appreciated that this review has considered even-aged, monospecific forests particularly. Many of the processes discussed for them will operate in a similar fashion in the more complex, multi-aged, mixed-species forests. However, different species can vary greatly in their growth behaviour through differences in physiological processes, such as their tolerance to shading by taller trees, reaction to availability of growth resources or ability to exploit growth resources advantageously from different niches within the forest ecosystem. Numerous works address the issues surrounding tree growth behaviour in these more complex forests (e.g. Niinemets 2010b; Pretzsch et al. 2015; Forrester and Bauhaus 2016; Lévesque et al. 2016; Ali 2019; Trogisch et al. 2021; Feng et al. 2022; Gonçalves 2022; Ding et al. 2023; Looney et al. 2024) and the development of management systems for them (e.g. Diaci et al. 2011; Ciccarino and Fernandes 2023; Himes et al. 2023; Chivenge et al. 2024; Looney et al. 2024; Pommerening et al. 2024).

Declarations

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