Chapter 2
From Primary Production to Growth and Harvestable Yield and Vice Versa: Specific Definitions and the Link Between Two Branches of Forest Science

2.1 Link Between Forest Growth and Yield Science and Production Ecology

Forest science and management, which is focussed on wood production, is interested primarily in timber, i.e. the harvestable part of the standing crop. In other words, all growth and management processes are geared to attaining net growth and yield of the commercially viable wood. Net growth is that part of gross primary production that is not respired for maintenance metabolism, is not consumed by animals, is not lost due to physical damage or self-thinning, or remains unused in the forest after the harvest.

Growth and yield are quantified conventionally in terms of stem-wood volume, or merchantable wood volume (>7 cm at the smaller end), in units of m^3 (yield) and $m^3\,yr^{-1}$ (growth) per tree or per hectare. Sometimes these volume units are converted into calorific units (GJ or kWh) for the inventory of fuelwood production, or into tons of biomass or carbon for climate change research. However, the process-oriented research carried out in ecological science is concerned with the magnitude of and the relationships between gross and net primary production; the costs of respiration; the allocation patterns among leaves, seeds, wood, and root production; and the turnover. The principle growth and yield units in ecology are kilograms or tonnes of biomass and biomass production per year, or the energy equivalents Giga Joule (GJ) and GJ yr^{-1}. Such information not only characterises the biomass and energy balance of a system, it is also the key to a more accurate estimation of production potential and to optimising management strategies.

The difference between the approaches in forestry and ecology is also evident in the experimental designs. Forest research looks at the total life span of a tree or stand. Hence, it is usually sufficient to record growth and yield of the wood volume in discrete time intervals, typically 5 or 10 years. Observation series, sometimes of more than 150 years, provide data on growth, yield mortality at the tree and stand level, and thus facilitate the study of long-term growth responses to

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disturbances. Yet, the 5- to 10-year intervals only partly permit the identification of cause-and-effect relationships, for example the effects of a short drought, cold periods, or fertilisation on growth.

On the other hand, ecophysiological experiments aim to provide an understanding of the relationship between growth and the factors influencing growth, such as resource availability and environmental conditions. The measurements are typically very intensive and may need to be investigated at time resolutions of seconds or minutes. Due to the complex experimental design, often only a part of the system can be studied, e.g. a leaf, a plant organ, or plant, and the experiment can only be run for a limited time period, e.g. a growing season or a few years, but rarely a decade or more. The time series resulting allow a much more differentiated analysis of cause-and-effect chains. However, the results from studies on plant organ level may not necessarily be transferable to the plant or stand level. Therefore, long-term records from forest growth and yield science are needed to support the validation of ecophysiological findings, to scale-up these findings from a plant organ to the plant or stand level, and then to develop applicable generalisations.

We see that both disciplines, forest growth and yield science and production ecology, have their own aims, approaches, and units. Both make complementary contributions to quantifying and understanding tree and stand development. The goal of this chapter is to establish a link between the volume-oriented forestry measures and the biomass measures used in production ecology. Tools and rules of thumb are provided for translating forestry growth and yield values into primary productivity and production efficiencies, and vice versa. The biomass allocation of a tree to needles, leaves, twigs, branches, stem and roots, or the root to shoot ratio, aboveground and belowground turnover, wood density, and carbon content, for example, are dependent on species, provenance, age, site conditions, and the silvicultural treatment. Yet, because exact knowledge about these dependencies is still incomplete and often missing, the factors introduced in this chapter represent estimations based on measurements and literature available to the author. Despite all the uncertainties remaining, the chapter links the measures used in forestry and ecology to bridge the gap between these two disciplines.

2.2 General Definitions and Quantities: Primary Production, Growth and Yield

The following paragraph presents definitions and the relative proportions of primary production, growth, and yield. The term primary *production* is used to address the production process in general, while primary *productivity* means the amount of photoproduction over a given time period for a given area.

Gross primary productivity (GPP, t $ha^{-1}\,yr^{-1}$) refers to the total biomass produced in photosynthesis over a given time period for a given area.

Net primary productivity (NPP, t $ha^{-1}\,yr^{-1}$) is defined as the biomass remaining after subtracting the continuous losses through respiration. The term net primary productivity equates with gross growth (GG). The choice of either term depends on the focus of the topic. Net growth (NG_{total}, t ha^{-1} yr^{-1} is obtained by subtracting the continual loss of biomass, i.e. the turnover, as well, which includes the loss of leaves, branches, and roots as a plant grows (short-term or ephemeral turnover of plant organs) and the loss of entire individuals, which die or are removed during stand growth (long-term turnover of whole individual plants). The intermediate state, net growth + turnover of individuals is an important variable in forestry and, therefore, is discussed in this chapter (cf. Sect. 2.3.2).

Net growth of stem wood harvested ($NG_{harvested}$, t ha^{-1} yr^{-1}) reduces the amount of biomass further still as it excludes the volume of roots, tree stumps, the treetops, and brushwood. Merchantable wood volume only refers to the trunk (and branches) above a certain diameter (>7 cm at the smaller end). Here, the net growth (merch) + turnover (merch) of individuals is of special importance.

In forestry, where the general aim is to produce stem wood, the approximate proportion of NPP, net biomass productivity, and net stem growth harvested in relation to 100% GPP is 50%, 25%, and 10%, respectively (Fig. 2.1). This means that 50% of the assimilated carbon is respired, 25% is lost through turnover and recycled, and 15% is unmerchantable or lost through harvesting techniques. Hence, ultimately only 10% of GPP (or 20% of NPP) is commercially viable and measured during the inventory. While this is an important component, it certainly does not represent

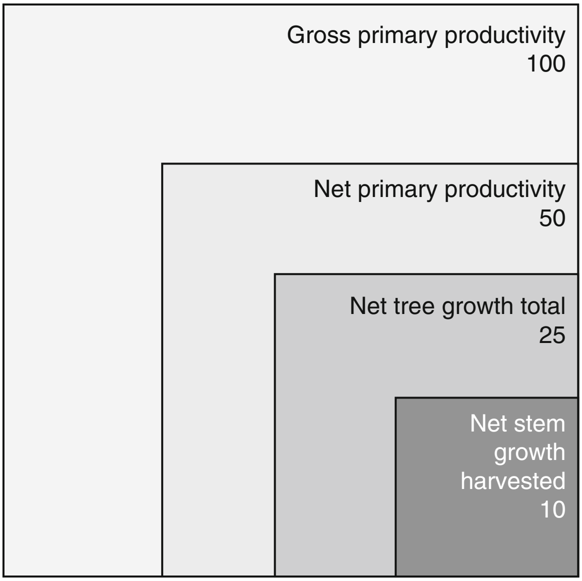

Fig. 2.1 Relative proportions of GPP of biomass, NPP, net tree biomass growth (NG_{total}), and net stem growth harvested ($NG_{harvested}$). Rough guess of the portion for a European beech stand over a 100-year growing period. The relations GPP:NPP:NG_{total}:$NG_{harvested}$ amount to 100:50:25:10. Loss due to respiration, turnover (organs and whole plants), unused root and shoot biomass, and loss due to logging techniques result in a relationship of 10:1 between GPP and $NG_{harvested}$

adequately the elements or energy cycle of the ecosystem. In the following section we refine these proportions.

Figure 2.1 illustrates the relative proportions of the production measures above in a 100-year-old European beech stand under mediocre site conditions. The proportional relationship of 100% GPP to NPP, net biomass growth, and harvested net stem growth is 50%, 25%, and 10%, respectively. This relationship is derived from the long-term means of the production parameters in an evenaged stand. A harvestable net stem growth of 3 t $ha^{-1} yr^{-1}$ corresponds to a net biomass production of 7.5 t $ha^{-1} yr^{-1}$, a NPP of 15 t $ha^{-1} yr^{-1}$, and a GPP of 30 t $ha^{-1} yr^{-1}$.

2.2.1 Gross and Net Primary Production

Gross primary productivity includes the production of organic substance (i.e. NPP, or gross growth) plus the respiration losses (R). Gross primary productivity can be determined directly only in chamber experiments. Field experiments estimate NPP directly from energy balances, litter fall, and net yield or indirectly from evapotranspiration measurements (Brünig 1971). The respiration $\sum R$ of stems, roots, and leaves is then added to NPP, or NPP is multiplied as a factor f_r, giving

$$GPP = NPP + \sum R = NPP \times f_r. \tag{2.1}$$

Herbaceous plants respire 20–50% of their net C-uptake (Larcher 1994, p. 133). Woody plants, especially in forests with a high fraction of photosynthetically inactive biomass (cf. Chap. 2, Sect. 2.5 and Chap. 10, Sect. 10.4), respire 40–60% of the net C-uptake in temperate forests and up to 75% in tropical rainforests (Assmann 1961; Larcher 1994, p. 134; Mar-Möller 1945). In a pure stand, the respiration loss increases from 15% to 30% of GPP in the juvenile stage to 50% in early mature stands to more than 90–100% in old growth stands (Kira and Shidei 1967; Sprugel et al. 1995). In a selection forest with a relatively stable relationship between standing biomass and foliage biomass, the percentage respiration loss relative to GPP should be steady between 30% and 70%. Grier and Logan (1977) describe old grown temperate rainforests along the North American west coast where up to 93% of the C-uptake is used in respiration.

For our purposes, we estimate that a respiration loss of about 50% applies. This corresponds to the respiration factor $f_r = 2$. This reference value holds for temperate regions. Due to the higher temperatures in tropical forests, the percentage respiration loss is higher, and the level of NPP is only slightly higher than in temperate forests. Here GPP, which is higher in tropical forests, is consumed largely in respiration so that NPP is comparable (Kimmins 1996, pp. 46–47). There are still large gaps in knowledge about the absolute magnitude of respiration, the ratio between crown and root respiration, and the dependency of respiration on the factors influencing growth such as site conditions, treatment, and stress.

Net primary productivity quantifies the entire production of organic substances as well as the turnover in a given time period. It is synonymous with gross growth, and we can divide NPP into net growth and turnover.

$$\text{NPP} = \text{net biomass growth} + \text{plant organs and whole plant losses}. \quad (2.2)$$

The net growth of biomass (NG) is still comparably easy to measure although, in forests, some uncertainty still exits about the measurement of wood density and the leaf, brushwood, and root biomass. Moreover, the long-term turnover, affected by the loss of whole trees, can be recorded in repeated surveys at the forest level at least. However, determinations of the turnover of individual plants in herbaceous ecosystems would require an intensive experimental design. The ephemeral turnover in forest and herbaceous vegetation is equally difficult to measure.

According to Brünig (1971, p. 240), the NPP reaches 2–3 $\text{t ha}^{-1}\,\text{yr}^{-1}$ in boreal conifer forests, 7–17 $\text{t ha}^{-1}\,\text{yr}^{-1}$ in temperate deciduous broadleaved and evergreen conifer temperate forests, and 18–22 $\text{t ha}^{-1}\,\text{yr}^{-1}$ in tropical rainforest. Thus, it ranges from 2 to 22 $\text{t ha}^{-1}\,\text{yr}^{-1}$, or 0.2 to 2.2 $\text{kg m}^{-2}\,\text{yr}^{-1}$. These values correspond to those from Körner (2002, p. 945) and Larcher (1994, p. 129, Table 2.18). Larcher reports values of 0.1–0.2 $\text{t ha}^{-1}\,\text{yr}^{-1}$ for tundra, desert and savannah vegetation, 10–15 $\text{t ha}^{-1}\,\text{yr}^{-1}$ for temperate forests, and 18–30 $\text{t ha}^{-1}\,\text{yr}^{-1}$ for tropical rainforests. The considerable differences among the vegetation zones are mainly attributable to the length of the growing season. When divided by the length of the growing season, NPP lies between 1.7 and 2.5 $\text{t ha}^{-1}\,\text{month}^{-1}$ for most vegetation types. The strong dependence of NPP on favourable temperature and precipitation conditions supports the assumption that the increased growth rates in central Europe are at least partly due to the extended growing season (Pretzsch 1999; Spiecker et al. 1996).

The above mentioned NPP values have been averaged over long survey periods and should not be confused with peak values found for a day or a month. Such maxima easily can exceed the average rates by a factor of 10–50, and show the physiological capacity of a plant at a given site. The NPP of plants on sites with superior short-term peak values can be surpassed, in the long run, by plants, which have lower peak values but which maintain constant moderate rates as a consequence of the longer growing season, continuous precipitation, and nutrient availability.

In comparison with the older value of NPP for the world's forests of 67.2 Gt yr^{-1} from Whittaker and Likens (1973), the Intergovernmental Panel of Climate Change IPCC (2001) calculates the current annual NPP at 46.6 Gt yr^{-1} ($\text{Gt} = 10^9\,\text{t}$). This corresponds to 22–46% of the entire biospheric NPP, including marine ecosystems. For forest cover, the annual NPP is 11.2 and 15.7 $\text{t ha}^{-1}\,\text{yr}^{-1}$ (1.12–1.57 $\text{kg m}^{-2}\,\text{yr}^{-1}$) according to IPCC (2001) and Whittaker and Likens (1973), respectively. The global annual NPP of forests of 23.3 and 33.6 Gt C yr^{-1} from IPCC (2001) and Whittaker and Likens (1973), respectively, makes up 3–5% of the total atmospheric C-pool of 750 Gt C yr^{-1}. The annual C-emissions from the combustion of fossil fuels were in the order of 6.3 Gt C yr^{-1} during the 1990s; the C-emissions resulting from land-use change and deforestation, 1.6 Gt C yr^{-1} (IPCC 2001). Given a terrestrial and marine carbon sink of 5 Gt C yr^{-1}, C-emissions are higher than the ecosystem uptake leading to an annual atmospheric increase in carbon of 3.5 Gt C yr^{-1}, i.e. approximately 0.5%.

Körner (2002, p. 945) points out many sources of uncertainty in the upscaling from biomass increase to NPP. For example, methodological hurdles essentially make it difficult to quantify branch and root turnover. In addition, the estimation of the mycorrhizal assimilate uptake or root exudation is somewhat uncertain. Yet, the current state of research allows us to propose a range in NPP of 10–20 t $ha^{-1}\,yr^{-1}$ or 1–2 kg $m^{-2}\,yr^{-1}$ for central European forests.

As indicated above, this range of NPP values needs to be multiplied by $f_r = 2$ to obtain the total amount of synthesised biomass, and subsequently derive GPP. This produces a GPP of about 20–40 t $ha^{-1}\,yr^{-1}$, or 2–4 kg $m^{-2}\,yr^{-1}$. Given the uncertainties associated with the estimation of respiration losses mentioned above, this range is purely theoretical.

2.2.2 Gross and Net Growth

Growth is defined as the entire biomass produced by a plant or a stand within a defined period (e.g. a day, a year, 5 years). Depending on whether the biomass lost and turned over within this period (i.e. leaves, fine roots, branches, or entire plant individuals) is included or not, we refer to gross or net growth. Whereas GPP and NPP refer to growth including and excluding respiration loss, respectively, gross growth and net growth includes and excludes the turnover of plant organs and individual plants, respectively. The distinction between gross and net growth is of special importance in forests where high levels of mortality and whole trees turnover occur because of their long life spans (Landsberg 1986, p. 172). Thus gross growth, which includes turnover, equals NPP.

$$\text{Gross growth} = \text{net growth} + \text{losses} + \text{mortality} = \text{NPP}. \qquad (2.3)$$

The quantity net growth typically is determined from the difference between periodical measurements. For plant biomass w_1 and w_2 at times t_1 and t_2, net growth is

$$\text{NG} = (w_2 - w_1)/(t_2 - t_1). \qquad (2.4)$$

For an individual plant, net growth (NG) can be expressed as an absolute value in kg yr^{-1}, as a relative growth rate (RGR)

$$\text{RGR} = (\ln w_2 - \ln w_1)/(t_2 - t_1) \qquad (2.5)$$

in kg $kg^{-1}\,yr^{-1}$ (Harper 1977, pp. 27–28), or as

$$\text{ULR} = (w_2 - w_1)/\text{LA}/(t_2 - t_1). \qquad (2.6)$$

The unit leaf rate (ULR) expresses the biomass growth per leaf area and time in $kg\,m^{-2}\,yr^{-1}$ (Larcher 1994, p. 117). For a stand, the absolute values are given relative to an area unit, e.g. $t\ ha^{-1}\,yr^{-1}$ (Assmann 1961), or as crop growth rate (CGR) in biomass per leaf area and time in $kg\,m^{-2}\,yr^{-1}$ (Larcher 1994, p. 127).

Therefore, NPP is derived from net growth by adding the measured or estimated losses within the measurement period (2.3). The determination of losses and mortality in herbaceous communities such as grasslands is difficult by comparison as one needs to monitor frequently the individual plant losses and the turnover of roots and other plant material. Due to the spatial and temporal scales that apply in forests, the loss of individual trees can be recorded more easily through frequent surveys. In Sect. 2.2 of this chapter, special factors are introduced in the calculation that reduces the gross growth by 40–50% to account for the losses. If NPP = 1–2 $kg\,m^{-2}\,yr^{-1}$ in central European forests, then net growth is about 0.5–1.0 $kg\ m^{-2}\,yr^{-1}$, or 5–10 $t\ ha^{-1}\,yr^{-1}$ when we assume a 50% loss due to turnover and mortality.

2.2.3 Gross and Net Yield

Yield is defined as the entire biomass produced and accumulated from stand establishment onwards. The difference between gross and net yield is analogous to that between gross and net growth. Gross yield includes the entire aboveground and belowground ephemeral biomass such as leaf litter, fine root turnover, and tree mortality. Gross yield can be calculated as the sum or integral of gross growth from stand establishment t_0 up to a specific time t_n:

$$\text{Gross yield} = \int_{t=t_0}^{t_n} \text{gross growth}\,dt \tag{2.7}$$

or, on the basis of the net growth and turnover:

$$\text{Gross yield} = \int_{t=t_0}^{t_n} \text{net growth}\,dt + \int_{t=t_0}^{t_n} \text{turnover}\,dt. \tag{2.8}$$

Net yield only refers to the current, remaining component of biomass production.

$$\text{Net yield} = \text{gross yield} - \int_{t=t_0}^{t_n} \text{turnover}\,dt. \tag{2.9}$$

Yield can be determined at the individual plant level as an absolute value (e.g. kg per plant), or for whole stands for a unit area (e.g. $kg\,m^{-2}$ or $t\ ha^{-1}$). Net yield is also termed standing crop or standing biomass. It gives the dry weight of a whole plant or a whole stand in both the aboveground and belowground compartments at a given time (Helms 1998, p. 175). Herbaceous plants can be harvested and weighted simply as entire plants. For woody plants, especially in old forest stands, diameter and height dimensions, or other measurements of individual tree size are used to extrapolate the unknown biomass compartments in upscaling functions (cf. Chap. 9).

Net yield or standing crop increases continuously until a threshold biomass stocking, an equilibrium between growth and decline, is reached. On a global perspective, 85% of the vegetation biomass is stored in forests, of which 80% is located aboveground. The range in net yield, or standing crop, is broad: 0.1–1.2 kg m^{-2} in half deserts; 2–6 kg m^{-2} in grasslands, shrublands and agricultural crops; 6–14 kg m^{-2} in seasonal subtropical and tropical forests; 10–22 kg m^{-2} in boreal forests; 10–34 kg m^{-2} in temperate forests; and 14–40 kg m^{-2} in evergreen subtropical and tropical forests.

As 1 kg m^{-2} = 10 t ha^{-1}, the net yield for temperate forests given above translates into 100–340 t ha^{-1}. According to Burschel et al. (1993, p. 42), the net yield in Germany's forests is 260 t ha^{-1} in managed forests, and 310–620 t ha^{-1}, i.e. 31–62 kg m^{-2} in relict primary forests. Clearly, these are average values, which incorporate a broad range of site conditions, age classes and management practices. For old growth coastal rainforest stands in British Columbia, biomass stocks of 1,000 t ha^{-1} (100 kg m^{-2}) or more are found (Grier and Logan 1977). The standing biomass of managed forests in central Europe is estimated roughly at 30 kg m^{-2}, or 300 t ha^{-1}.

About 70% of the earth's surface (510×10^6 km^2) is covered with water. Of the remaining 30% (150×10^6 km^2), forest accounts for only 26% (FAO, 2001, 2005), or 32% (Constanza et al. 1997), i.e. $40–50 \times 10^6$ km^2. Yet, about 77–93% of the entire living biomass of $0.93–1.65 \times 10^{12}$ t (IPCC 2000, 2001; Whittaker et al. 1973) is concentrated in these forests. The global mean value of 6.16–10.94 kg m^{-2} or 61.6–109.4 t ha^{-1} is therefore much lower than the average value for managed forests in central Europe (30 kg m^{-2} or 300 t ha^{-1}) quoted above, which is explained largely by the relative large percentage of open, mainly subtropical forests.

2.3 Specific Terminology and Quantities in Forest Growth and Yield Science

The definition of growth and yield adopted in forest yield science, introduced in Sect. 2.2, essentially relates to stem wood or the merchantable wood, which are quantified in relation to tree height (m), stem diameter at 1.3 m (cm), or volume (m^3 per tree, m^3 ha^{-1}). By growth, we mean the increase in size or weight of a plant or a stand in a given period of time. Depending on whether the plant organs or trees that die in the given time period are included or not, we refer to gross growth or net growth. The same applies for the definitions of gross and net yield.

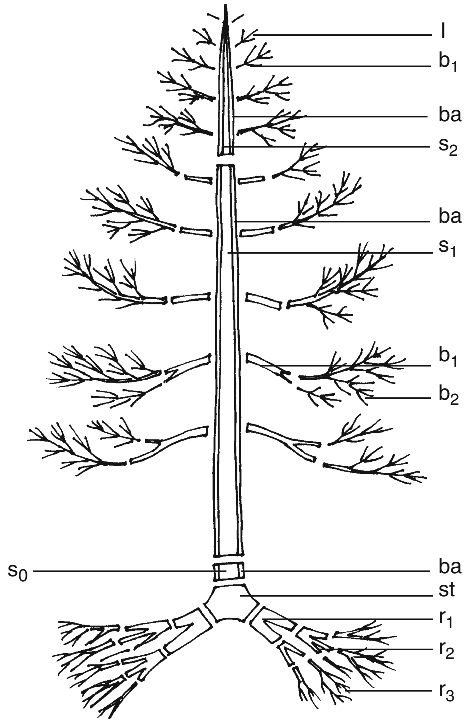

Fig. 2.2 Compartmentalisation of a tree with differentiation of stem volume and merchantable volume <7 cm, standing volume, and harvested volume: l leaves, b_1 branches $\geq$7 cm at the smaller end, b_2 branches <7 cm, ba bark, s_0, s_1, s_2 stem wood, s_0 trunk base left in the stand due to harvesting techniques, s_1 stem wood $\geq$7 cm in diameter at the smaller end, s_2 top stem wood <7 cm; st stump wood; r_1, r_2, r_3 root wood of decreasing diameter classes, e.g. >5 mm, 2–5 mm, <2 mm

Figure 2.2 illustrates the partitioning of the woody tree parts into the following compartments: s_t tree stump; s_0 trunk base, which normally is not harvested; s_1 tree trunk of >7 cm diameter between trunk base and tree top; s_2 tree top with <7 cm diameter; b_1 branches with >7 cm diameter; b_2 branches with <7 cm diameter (branch wood); and ba bark. Belowground, we distinguish between coarse, medium, and fine roots (r_1, r_2, r_3).

The standing merchantable wood and stem-wood volume over bark, v(merch) and v(stem), are defined as

$$v(\text{merch}) = s_0 + s_1 + b_1 + \text{ba}, \tag{2.10}$$

$$v(\text{stem}) = s_0 + s_1 + s_2 + \text{ba}. \tag{2.11}$$

The merchantable wood and stem-wood volume harvested under bark, v(merch harv) and v(stem harv), are

$$v(\text{merch harv}) = s_1 + b_1, \tag{2.12}$$

$$v(\text{stem harv}) = s_1 + s_2. \tag{2.13}$$

Unless explicitly stated, the following discussion always refers to the volume of standing merchantable wood or stem wood over bark because these are the basic forestry units for growth and yield, and also the basic parameters for upscaling to the standing biomass, NPP and GPP. In Sect. 2.4.3, we introduce estimates for the percentage of stump base (s_0) and the percentage of bark (b_a) used to estimate the harvesting losses.

2.3.1 Growth and Yield of Individual Trees

2.3.1.1 Definitions and Examples for Standing Volume, Growth, and Yield

To introduce the most important growth and yield variables, we adopt the 131-year-old Scots pine tree No. 5 from the experimental plot NUE 141/4 near Nürnberg, Southern Germany, by way of example (Figs. 2.3 and 2.4). Figure 2.3 shows the current annual increment in height (CAI_h in $m\,yr^{-1}$), diameter ($CAI_d\,cm\,yr^{-1}$), and stem volume (CAI_v in $l\,yr^{-1} \hat{=} 10^{-3}\,m^3\,yr^{-1}$) after high-precision stem analysis. Despite the oscillations caused by the factors influencing growth for a brief period, these growth curves conform to unimodal optimum curves with culmination in the early to early-mature stages. Traditionally, the change in volume, as well as the change in diameter and height, at the tree and stand level is referred to as *increment*. Whereas the term *growth* is used to quantify the increase in weight, biomass, and dry weight, the term *increment* is used when referring to structural increases such as height, diameter, basal area, or volume. Essentially growth and increment describe the same thing, i.e. the rate at which the plant or stand increases in weight or size in a given time period. If, instead of annual measurements, periodic surveys at n-year intervals are carried out, then the recorded increment in height, diameter, and volume must be divided by n and is called the periodic annual increment PAI (e.g. PAI_h, PAI_d, PAI_v). Figure 2.3d shows the periodic annual increment of volume in litres per year. Because the stem continually increases in size, and losses in stem or merchantable wood rarely occur, e.g. through crown break or bark loss, the turnover of stem and merchantable wood is minimal to negligible. Thus, at the individual tree level, gross stem growth approximately equals net stem growth. This approximation holds for trees up to 50–150 years at least, the typical harvesting age in central Europe. For old trees with diameters exceeding 50–100 cm, a certain amount of turnover of large branches (b_1) occurs, which affects the merchantable wood volume (but not the stem volume).

By adding the current annual increment CAI over the life span, t_0 to t_n, one obtains the yield,

$$\text{yield} = \int_{t=t_0}^{t_n} \text{growth}\,dt. \tag{2.14}$$

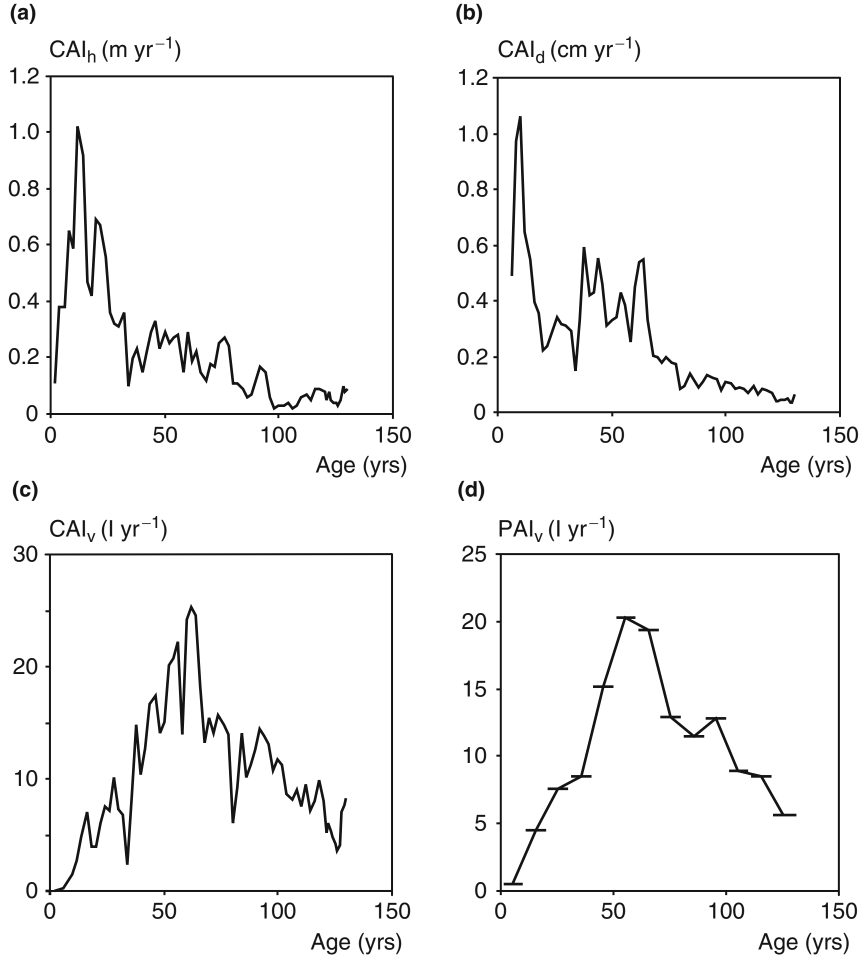

Fig. 2.3 Current annual increment (CAI) and periodic annual increment (PAI) for an individual tree, synonymous with current annual growth and mean periodical annual growth: (**a**) current annual increment of tree height (m yr^{-1}), (**b**) stem diameter at height 1.30 m (cm yr^{-1}), (**c**) stem volume (l yr^{-1}), and (**d**) periodic annual volume increment (l yr^{-1}) over 10-year periods. Results from a stem analysis of the 131-year-old Scots pine No. 5 from long-term plot Nürnberg 141/4

Figure 2.4a–c shows the S-shaped yield curves for height, diameter and volume (Y_h, Y_d, Y_v). The height, diameter, or the volume of the tree stems at a particular point in time represents net yield; and when turnover of stem wood or merchantable wood during ontogenesis is negligible, then

$$\text{Gross yield} \cong \text{net yield} = \int_{t=t_0}^{t_n} \text{net growth}\,dt. \tag{2.15}$$

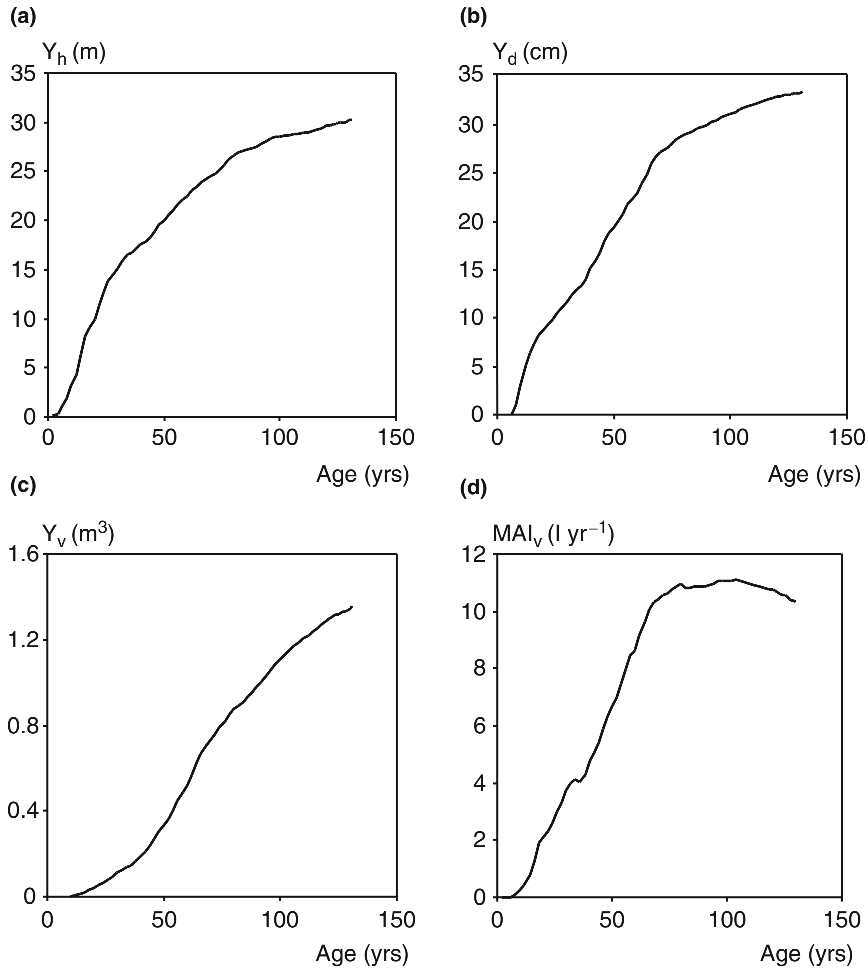

Fig. 2.4 Yield curve for (**a**) tree height (m), (**b**) stem diameter (cm), and (**c**) stem volume (m^3) of Scots pine No. 5 from long-term plot Nürnberg 141/4 (cf. Fig. 2.3). (**d**) Mean annual volume increment (MAI_v) is a synonym for mean annual volume growth

CAI or PAI in selected years or periods are age-dependent, and indicate little about the long-term productivity of a plant or the quality of the site. The long-term productivity is expressed better by the mean annual increment (MAI) (synonymous with mean annual increment); since the time required for woody and herbaceous species to mature differs, it is difficult to make comparisons on the basis of yield data. To overcome this difficulty, the yield at a given time is divided by the age, giving the MAI

$$\text{Mean annual increment (MAI)} = \text{yield}_n/\text{t}_n. \tag{2.16}$$

Mean annual increment characterises site quality and delimits the suitable harvesting age. The MAI value resulting reflects the mean long-term productivity level and is an appropriate value for comparisons. Figure 2.4d shows the development of MAI $(1\,yr^{-1})$ for selected Scots pine trees in plot NUE 141/4.

In the literature and in practice, a clear differentiation rarely is made between growth (Fig. 2.3) and yield (Fig. 2.4a–c). In contrast to the strict definitions employed here, all too often yield curves are termed growth curves, e.g. Harper (1977, pp. 5–9). This inconsistency in terminology has led to the misunderstanding and confusion already remarked upon by Bruce and Schumacher (1950, p. 376): "While these curves are commonly called growth curves, it will be noted, that this term is not strictly applicable. [...] The true growth curve is the one showing the relation between the increase in diameter (or height as the case may be) and age. This yearly increase is called the current annual growth." I strongly recommend a more consistent differentiation between the growth curve and its integral, the yield curve.

2.3.1.2 Reference Values for Growth and Yield for Individual Trees

Table 2.1 presents some growth and yield characteristics of a number of 118- to 166-year-old trees after stem analysis (cf. the Chap. 3). The volumes of conifers are given as stem volume and of broadleaves as merchantable wood volume. The final volumes of the selected trees vary between $v = 0.96–8.27\,m^3$, the maximum annual increment for diameter $CAI_{d\ max} = 0.37–1.37\,cm\,yr^{-1}$, height $CAI_{h\ max} = 0.32–0.94\,m\,yr^{-1}$, and volume $CAI_{v\ max} = 13–165\,l\,yr^{-1}$ $(1\,l = 10^{-3}\,m^3)$. Usually, diameter growth culminates first (age 8–53), followed by height growth (age 8–68) and, finally, volume growth (age 33–161). Light-demanding species such as Silver birch, Sweet cherry, European ash, and Scots pine reach higher CAI maxima and culminate earlier than shade tolerant species such as European beech, Norway spruce, and Silver fir. The MAI_d, MAI_h, MAI_v at the respective ages 118–166 reach only a half or a third of the maximum CAI_{max} values: $MAI_d = 0.24–0.49\,cm\,yr^{-1}$, $MAI_h = 0.16–0.32\,m\,yr^{-1}$, and $MAI_v = 7–52\,l\,yr^{-1}$. If the turnover of stem wood or merchantable wood is ignored, the standing volume = net yield $\cong$ gross yield. Then, the net yield and gross yield values of the 118- to 166-year-old trees presented range between 0.96 and $8.27\,m^3$.

Tree size at a given age may vary strongly in the same stand depending on the resource availability of the individual tree. Table 2.2 lists some selected growth and yield values obtained from stem analysis for very slender and very large trees on various experimental plots.

Under favourable site conditions, and with silvicultural promotion, the size difference among the large trees in a stand may be 2–5 times larger in diameter, 1–2 times larger in height, and 5–74 greater in volume than that of the small trees of the same age (cf. lines max : min). The maximum annual increment in diameter, height, and volume in the dominant trees may be as much as 10, 8, and 103 times the suppressed neighbours of the same age, respectively (cf. max:min on the right side of Table 2.2). This demonstrates clearly the potential of thinning to enhance the

Table 2.1 Size (d, h, and v), maximum current annual increment ($CAI_{d\,max}$, $CAI_{h\,max}$, and $CAI_{v\,max}$), and mean annual increment (MAI) of various tree species. The details result from stem analysis and shoot length measurements of individual trees on experimental plots with medium stand density

Tree species	Experiment	Age years	d cm	h m	v m^3	$CAI_{d\,max}$ cm yr^{-1}	Age years	$CAI_{h\,max}$ m yr^{-1}	Age years	$CAI_{v\,max}$ l yr^{-1}	Age years	MAI_d cm yr^{-1}	MAI_h m yr^{-1}	MAI_v l yr^{-1}
Norway spruce	DEN 05	160	77.8	44.6	8.27	0.77	12	0.67	12	125	153	0.49	0.28	52
Scots pine	BAY 51	145	40.9	34.3	2.18	1.37	8	0.94	8	23	33	0.28	0.24	15
Silver fir	RUH110	166	65.6	38.1	5.59	0.58	36	0.65	36	88	161	0.40	0.23	34
European larch	MUE 140	150	69.4	35.5	5.03	0.91	19	0.60	19	75	135	0.46	0.24	34
Sessile oak	KEH 804	118	42.1	31.8	2.30	0.43	15	0.66	10	67	115	0.36	0.27	19
European beech	ROT 634	121	49.1	38.3	3.25	0.59	15	0.60	35	165	125	0.41	0.32	27
White hornbeam	MUE 140	159	40.7	26.2	1.35	0.37	53	0.32	68	30	157	0.26	0.16	8
Silver birch	MUE 140	133	32.3	25.7	0.96	0.41	23	0.78	8	13	113	0.24	0.19	7

d, tree diameter at 1.3 m stem height; h, total tree height; v, tree volume; $CAI_{d\,max}$, $CAI_{h\,max}$, and $CAI_{v\,max}$ and corresponding ages report the maximum annual increment and the tree age when the maximum is achieved; MAI_d, MAI_h, and MAI_v represent mean annual increment of tree diameter, height, and volume.

Table 2.2 Effect of competition on size (d, h, and v), maximum current annual increment ($CAI_{d\,max}$, $CAI_{h\,max}$, and $CAI_{h\,max}$), and mean annual increment of diameter, height, and volume (MAI) of various tree species. The details result from stem analysis of one dominant tree (max) and one suppressed tree (min) on experimental plots with medium stand density. The quotient max:min represents the degree of superiority of dominant trees due to their privileged position and resource supply

Species	d cm	h m	v liter	$CAI_{d\,max}$ cm yr^{-1}	$CAI_{h\,max}$ m yr^{-1}	$CAI_{v\,max}$ l yr^{-1}	MAI_d cm yr^{-1}	MAI_h m yr^{-1}	MAI_v l yr^{-1}
Norway spruce	ZUS 603-3	Age 42							
min	13.4	17.7	139	1.0	0.84	8	0.3	0.42	3
max	28.3	25.2	733	1.3	1.20	42	0.7	0.60	18
max : min	2.1	1.4	5.3	1.3	1.40	5.3	2.1	1.40	5.3
Scots pine	BOD 610-3	Age 50							
min	10.0	12.8	41.1	0.2	0.37	2	0.2	0.26	1
max	29.8	19.7	641	0.8	0.70	31	0.6	0.39	13
max : min	3.0	1.5	15.6	4.0	1.90	20.9	3.0	1.50	16.0
Douglas fir	HEI 608-1	Age 35							
min	15.6	17.5	175	0.6	0.66	13	0.5	0.50	5
max	45.7	25.6	1,729	1.5	1.00	119	1.3	0.73	49
max : min	2.9	1.5	9.9	2.6	1.50	9.5	2.9	1.50	9.9
European beech	STA 91-3	Age 78							
min	9.3	13.3	37	0.1	0.09	1	0.1	0.17	1
max	46.7	29.4	2,727	1.0	0.74	124	0.6	0.38	35
max : min	5.0	2.2	73.7	10.4	8.20	103.3	5.0	2.20	35.0
Sessile oak	ROH 90-3	Age 142							
min	28	25.8	826	0.2	0.11	11	0.2	0.18	6
max	66	33.4	6,098	0.7	0.20	131	0.5	0.24	43
max : min	2.4	1.3	7.4	3.7	1.80	12.0	2.3	1.30	7.4

diameter and volume growth of the remaining trees. Height growth responds less to stand density. Light-demanding tree species (cherry, ash, birch) achieve the highest maximum increment rates ($CAI_{d\,max}$, $CAI_{h\,max}$, $CAI_{v\,max}$). Although the maximum CAI values of the shade-tolerant tree species (Norway spruce, Silver fir, and European beech) are lower, these species achieve high average MAI_d, MAI_h, MAI_v values in the later growth stages.

The values presented in Table 2.2 represent typical tree dimensions in central European forests at harvesting age. They are considered mature for harvest or old growth, even though they are still young in years in relation to their potential maximum age and size. The notable veneer oaks in 350- to 400-year-old stands in the Spessart attain diameters of 2 m and volumes of $>50\,m^3$. Norway spruce, Silver fir, and European beech trees in untouched relict forests in the Bavarian Forest National Park have 1–2 m diameters with $40\,m^3$ merchantable wood volume.

von Carlowitz (1713, p. 138) describes trees in Germany with diameters of almost 4 m and estimated volumes of $>150\,m^3$.

As such giants have been felled systematically in Europe since the Middle Ages, remnants demonstrating the true potential of really old trees here cannot be found. For this, we have to look in Germany at old-growth forests such as the preserved coastal rainforest stands along the Pacific west coast of North America where a single tree can reach 9 m diameter, 100 m height, and 1,500 m^3 volume at an age that may well exceed 2,000 years. From a list of the largest trees in these forests (Pelt 2001), some of the most impressive tree dimensions were found for the following species: Giant sequoia, *Sequoiadendron giganteum* (General Sherman: $d_{max} = 8.25\,m$, $h_{max} = 83.5\,m$, $v_{max} = 1{,}489\,m^3$); Coast redwood, *Sequoia sempervirens* (Del Norte Titan: $d_{max} = 7.23\,m$, $h_{max} = 93.6\,m$, $v_{max} = 1{,}045\,m^3$); Western red cedar, *Thuja plicata* (Quinault Lake Cedar: $d_{max} = 5.94\,m$, $h_{max} = 53.0\,m$, $v_{max} = 500\,m^3$); Douglas fir, *Pseudotsuga menziesii* (Red Creek tree: $d_{max} = 4.23\,m$, $h_{max} = 73.8\,m$, $v_{max} = 349\,m^3$); and Sitka spruce, *Picea sitchensis* (Queets Spruce: $d_{max} = 4.55\,m$, $h_{max} = 75.6\,m$, $v_{max} = 337\,m^3$).

2.3.2 *Growth and Yield at the Stand Level*

Growth and yield characteristics at the stand level are derived from periodic inventories, typically at 5- to 10-year intervals. For numerous research plots in Bavaria, time series of >100 years are available (cf. Chap. 3). Unlike on individual tree level on the stand level growth and yield parameters are given relative to a unit area (e.g. hectare, acre), and the tree number per unit area is given as a new separate measure. Tree number decreases with stand development due to self-thinning, silvicultural treatment, or disturbances. In contrast to the tree level, the turnover of merchantable or stem volume at the stand level caused by loss or removal of whole trees is significant.

2.3.2.1 Definitions for Standing Volume, Growth, and Yield

For periodic inventories, the diameter and tree height of all living trees on an area at a point in time t_1 are recorded. From both these parameters and the form factors, the standing volume of the stand $V_{1\,remain}$ at the time of the inventory t_1 can be determined (cf. $V_{1\,remain}$ in Fig. 2.5). In a repeated inventory at time t_2, e.g. 5 or 10 years later, the trees that survived and those that had died or were removed since the previous survey are recorded separately. Consequently, the total volume $V_{2\,total}$ can be divided into the standing volume $V_{2\,remain}$ and the volume turned over $V_{removed}$ $(V_{2\,total} = V_{2\,remain} + V_{removed})$. Although the mortality or removal of trees $(V_{removed})$ is an ongoing process, it is recorded as at the end of an inventory period, resulting in a saw-tooth yield curve of $V_{n\,remain}$ as shown by the solid line in Fig. 2.5. If the inventories were carried out each year, so that the exact time of a tree's death or removal was known, the curve would be much smoother, and the teeth smaller.

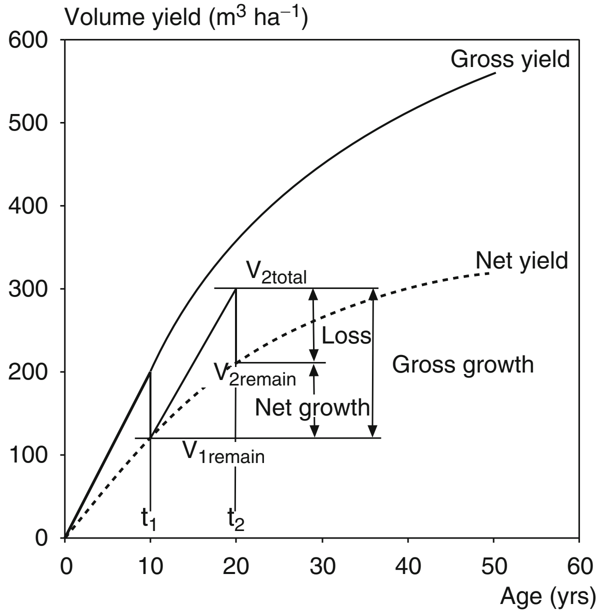

Fig. 2.5 Derivation of growth and yield characteristics by periodical stand inventories presented schematically. Gross and net volume yield (GY_V and NY_V, respectively) are represented by the *upper solid* and the *lower dashed curve*, respectively. $V_{1\,remain}$, $V_{2\,total}$, and $V_{2\,remain}$ represent the live standing volume at time t_1, total standing volume at time t_2, and remaining standing volume at time t_2. Difference $V_{2\,total} - V_{1\,remain}$ = gross growth. Gross growth is based on the two components: $V_{2\,remain} - V_{1\,remain}$ = net growth and $V_{2\,total} - V_{2\,remain}$ = losses due to whole tree turnover

Repeated inventories of whole stands are carried out in a periodic cycle of several years, and produces PAI values rather than CAI values; i.e. the mean annual growth rates over longer time intervals. Between two surveys at time t_1 and t_2, the PAI is

$$PAI = (V_{2\,remain} - V_{1\,remain} + V_{removed})/(t_2 - t_1). \tag{2.17}$$

The gross yield in volume is calculated from the integral of PAI,

$$\text{Gross volume yield } Y_{V\,gross} = \int_{t=t_0}^{t_n} PAI\,dt \tag{2.18}$$

and standing volume, equivalent to the net volume yield, is obtained from,

$$\text{Standing volume } Y_{V\,net} = \int_{t=t_0}^{t_n} PAI\,dt - \int_{t=t_0}^{t_n} V_{removed}\,dt. \tag{2.19}$$

As for individual trees, the mean annual increment MAI is defined as the gross yield at time n divided by the stand age in years,

$$MAI_n = \text{gross yield}_n / t_n. \tag{2.20}$$

Figure 2.6 shows (a) the volume yield curve for individual tree No. 4 at the long-term experimental plot Denklingen 5, trial plot 2 and (b–d) the yield and growth curves at the stand level. The increase in the gross and net stem yield or merchantable volume yield at the tree level is almost identical and monotone because virtually no turnover in stem volume or merchantable volume occurs (Fig. 2.6a). In contrast, tree removals at the stand level (self-thinning, damage, thinning) result in a

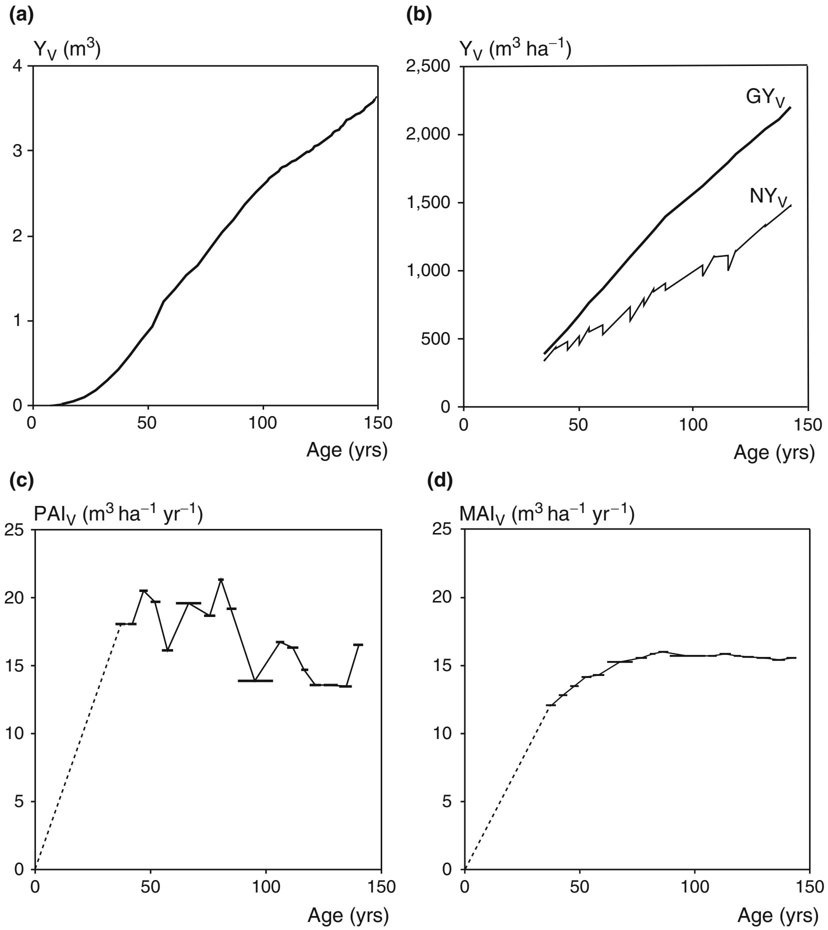

Fig. 2.6 Growth and yield curves of stem volume for long-term experimental plot Denklingen 5, plot 2. (**a**) Net and gross volume yield curve for tree No. 4, derived by stem analysis, (**b**) development of gross volume yield (GY_V) and net volume yield (NY_V) at the stand level, (**c**) periodical annual volume increment PAI_V, and (**d**) mean annual volume increment MAI_V derived from 18 successive surveys since establishment of the experiment in spring 1883

saw-tooth shaped curve for net yield NY_V (Fig. 2.6b, bottom line). One obtains the gross yield (GY_V) by adding the volumes of the remaining and removed trees (Fig. 2.6b, top line). As the stand ages, a continually larger proportion of the gross yield is removed, and hence no longer present. These intermediate yields can be determined from the long-term measurement of removals on long-term experimental plots. Under steady state conditions, the ageing process of PAI and MAI follow a unimodal optimum curve (Fig. 2.6c, d). MAI culminates later and at a lower level than PAI (cf. Chap. 10, Sect. 10.3).

2.3.2.2 Reference Values for Growth and Yield of Pure and Mixed Stands

The following tables present some characteristic growth and yield values for evenaged pure stands (Table 2.3), evenaged mixed stands (Table 2.4) and unevenaged mixed stands (Table 2.5) at experimental sites in Southern Germany. The average growth and yield data collated for up to 130 years, provided for trees and stands, represent moderately thinned and otherwise largely undisturbed stands from experimental research plots with moderate to good site conditions. The volume data refer to merchantable volume (>7 cm at the smaller end) for broadleaved trees and to stem volume for conifers.

In the evenaged pure stands (Table 2.3), the quadratic mean diameter attains 43.3–55.6 cm, stand basal area 28.2–88.4 $m^2 ha^{-1}$, and standing wood volumes 428–1,480 $m^3 ha^{-1}$ at age 93–178 years. Norway spruce and Douglas fir rank highest, whereas European larch and Sessile oak rank lowest. Maximum PAI values lie between 10.4 and 33.4 $m^3 ha^{-1} yr^{-1}$, MAI between 5.4 and 17.2 $m^3 ha^{-1} yr^{-1}$ and gross yield between 953 and 2,199 $m^3 ha^{-1} yr^{-1}$. Of this gross yield, 33–55% died or were removed during the stand lifetime (IY_V (%) = intermediate volume yield in percent), giving net yield values of 428–1,480 $m^3 ha^{-1}$ standing volume.

The values for the evenaged mixed stands (Table 2.4) are based on artificial time series comprising up to ten adjacent plots of different ages, which cover the stand life span (Pretzsch and Schiitze 2005, 2008) (cf. Chap. 9). The stands were inventoried between 1992 and 2008 to derive growth and yield characteristics for the most relevant types of mixed forest in South Germany. The mean height and quadratic mean diameter for the two species present in the stand are listed separately. The first species mentioned generally exceeds the second in height and diameter, introducing a certain horizontal stratification. At 100–146 years of age, the standing volume ranged from 580–921 $m^3 ha^{-1}$. Evenaged mixed stands, with MAI values of 11.8–18.5 $m^3 ha^{-1} yr^{-1}$ and gross yields of 1,281–2,112 $m^3 ha^{-1}$ at 100–146 years of age, do not fall behind the pure stands. However, the percentage intermediate yields (IY_V in %) in mixed stands of 50–81% are clearly higher than in pure stands, which means the final standing volume of 580–921 $m^3 ha^{-1}$, which is equivalent to the net yield, is lower than that of the pure stands.

The unevenaged mixed stands (Table 2.5) represent selection forests and moderately thinned mountain forests, consisting mainly of Norway spruce, Silver fir and European beech. On the research plots, trees range from seedling to almost

Table 2.3 Stand characteristics of evenaged pure stands of various tree species in central Europe after long-term inventory. Several inventories date back to 1870

Tree species	Experiment	Age years	d cm	h m	st. basal area $m^2\,ha^{-1}$	st. volume $m^3\,ha^{-1}$	$PAI_{V\,max}$ $m^3\,ha^{-1}\,yr^{-1}$	MAI_V $m^3\,ha^{-1}\,yr^{-1}$	GY_V $m^3\,ha^{-1}$	IY_V %
Norway spruce	DEN 05	143	54.4	40.3	88.4	1,480	21.3	15.4	2,199	32.7
Scots pine	BAY 52	131	43.3	36.3	44.0	700	12.1	10.5	1,370	48.9
Silver fir	WOL 97	134	53.9	34.0	45.1	637	12.0	9.5	1,268	49.8
European larch	MIS 47	178	55.6	36.7	28.2	428	10.4	5.4	953	55.1
Douglas fir	FRE 85	93	44.6	39.3	61.9	1,012	33.4	17.2	1,603	36.9
Sessile oak	LOH 59	168	50.3	33.0	37.4	605	10.6	7.7	1,301	53.5
European beech	FAB 15	178	51.5	38.0	48.0	950	15.9	8.7	1,551	38.7

d and h mean stand diameter and height; stand basal area; standing stem or merchantable volume, respectively; $PAI_{V\,max}$, maximum periodic annual volume increment since the beginning of the inventory; MAI_V, mean annual volume increment; GY_V, gross volume yield since stand establishment; IY_V, intermediate volume yield [$IY_V = 1-(\text{standing volume/gross volume yield}) \times 100$].

Table 2.4 Stand characteristics of evenaged mixed stands in Bavaria. The evaluation is based on artificial time series of mixed stands with up to 10 plots per time series and 2–3 successive inventories per plot. Mean annual volume increment (MAI_V), gross yield of volume (GY_V), and percentage of intermediate yield (IY_V) from stand establishment to the age of the oldest plot (age 110, 100, 136, 109, and 146, respectively)

Tree species	Experiment	Age years	d cm	h m	V $m^2 ha^{-1}$	MAI_V $m^3 ha^{-1} yr^{-1}$	GY_V $m^3 ha^{-1}$	IY_V %
Norway spruce-	SON 814	110	50.3	38.0	562	11.5	1,267	55.6
European beech			37.4	33.5	359	6.9	764	53.0
Total					921	18.5	2,031	54.8
Scots pine-	NEU 841	100	39.4	30.0	496	9.7	969	48.8
Norway spruce			24.9	25.1	380	7.9	786	51.7
Total					876	17.6	1,755	50.1
Scots pine-	GEI 832	136	59.1	32.3	144	5.4	732	80.3
European beech			23.0	26.1	250	10.1	1,380	81.9
Total					394	15.5	2,112	81.0
European larch-	GEM 871	109	53.6	38.1	197	4.3	467	57.8
European beech			45.9	35.3	383	7.5	814	52.9
Total					580	11.8	1,281	54.7
Sessile oak-	KEH 804	146	48.8	33.6	548	8.8	1,288	57.5
European beech			27.6	26.5	140	3.6	519	73.0
Total					688	12.4	1,807	61.9

300 years old. The quadratic mean diameter of the dominant species (mostly Norway spruce, sometimes Silver fir) attains 39.2–58.1 cm, height 29.4–37.4 m and basal area 29.7–66.9 $m^2 ha^{-1}$. The standing volume lies between 477 and 1,028 $m^3 ha^{-1}$. In contrast to the previous, comparably unstratified pure and mixed stands, the standing volumes do not show the final net yield values reached near the end of the rotation cycle, but give continuous averages that vary little due to the periodic removal of individual trees. The mean PAI and maximum PAI attain values of 4.7–15.9 and 5.5–19.6 $m^3 ha^{-1} yr^{-1}$ respectively. In these unevenaged forests, the long-term PAI averages compare best with the MAI values of evenaged rotation forests. A comparison shows that the PAI of unevenaged stands are of the same order as the MAI values in evenaged stands (Table 2.3), and slightly lower than the MAI values in the evenaged mixed stands (Table 2.4), which are highest.

2.3.2.3 Factor for Intermediate Yield or Whole Tree Turnover t_{ind}

At the stand level, the turnover of merchantable wood is considerable due to the loss of entire trees through self-thinning, tree removal and calamities. The spatial and temporal scale of forest stand dynamics makes this turnover easier to measure than in herbaceous communities. We can enter forest stands to measure the living and dead individuals without damaging them conspicuously, or impairing their ongoing development. To undertake similar surveys in herbaceous stands to document whole

Table 2.5 Stand characteristics of unevenaged mixed stands of Norway spruce, Silver fir, and European beech in the temperate mountain forests of Bavaria. Inventories date back to the year 1950

Tree species	Experiment	Age	d_{max}	h_{max}	st. basal area	V	$PAI_{V\,mean}$	$PAI_{V\,max}$
		years	cm	m	$m^2\,ha^{-1}$	$m^2\,ha^{-1}$	$m^3\,ha^{-1}\,yr^{-1}$	$m^3\,ha^{-1}\,yr^{-1}$
N. spruce-Silver fir-European beech	FRY 129/32	2 – 239	42.9	31.0	42.6	663	10.7	13.8
N. spruce-Silver fir-European beech	BOM 130/22	2 – 286	41.2	30.8	44.5	610	10.2	11.3
N. spruce-Silver fir-European beech	PAR 115/1	2 – 203	44.6	32.8	57.2	871	8.1	9.8
N. spruce-Silver fir-European beech	KRE 120/3	2 – 158	39.2	29.4	40.1	502	4.7	5.5
N. spruce-Silver fir-European beech	MAR 108/1	2 – 142	58.1	37.4	66.9	1,028	15.9	19.6
N. spruce-Silver fir-European beech	RUH 110/2	25 – 165	55.3	36.1	29.7	477	7.9	10.4
N. spruce-Silver fir-European beech	RUH 116/1	2 – 183	45.3	33.7	52.6	784	9.8	11.4

d_{max} and h_{max} mean stand diameter and height of the species with maximum size; st., basal area; V, total standing volume; $PAI_{V\,mean}$ and $PAI_{V\,max}$, mean and maximum periodic annual volume growth since start of the survey.

plant turnover, i.e. the mortality of whole plants, the surveyor would need to shrink to one-tenth his size (cf. Chap. 1, Sect. 1.1). Only then could one undertake comparable, spatially explicit measurements of growth and removal of individual plants without damaging the remaining stand, and thereby having an impact on further stand development. Consequently, the amount of turnover of plants in herbaceous stands is largely unknown. Maybe the following values from forests give some idea of the values in herbaceous stands that follow similar self-thinning processes to woody plants (Pretzsch 2002, 2005c).

Table 2.6 shows that, based on yield tables commonly used in Germany, the turnover of merchantable wood volume resulting from whole tree removal (IY (%) = whole tree turnover/total yield ×100) may be as much as 60.7% of the total volume produced (Sessile oak at age 200). For the experimental plots introduced above, the percentage turnover lies between 32.7% and 55.1% in evenaged stands, and 50.1–81.0% in unevenaged stands (cf. Tables 2.3 and 2.4). Hence, a substantial part of the entire stand production is simply absent at the end of the rotation period, and, if not entirely removed, is partially incorporated in the remaining stand in form of carbon, hydrogen and oxygen (C, H, O) or mineral nutrient elements. Long-term experiments on unthinned or lightly thinned (A grade) stands reveal that, during

Table 2.6 Percentage of intermediate yield IY [$IY_V = 1-$(standing volume/gross volume yield)$\times 100$] from age 20 to 200 years according to frequently used yield tables for tree species in Europe. The portion of removed volume decreases from stands with excellent site conditions to poor sites. The values presented apply for moderate thinning, and were derived from the yield tables quoted in the second column. In case of Norway spruce, the values refer to total stem wood; all other values refer to merchantable stem wood >7 cm at the smaller end. The last two columns present the factor t_{ind} for estimation of gross volume yield on the basis of net yield for the stand age 60 and 100 years ($GY_V = NY_V \times t_{ind}$)

Tree species	Yield table	Site class	Intermediate yield IY (%) at stand age							Multiplier t_{ind} at stand age	
			20	40	60	80	100	150	200	60	100
Norway spruce	Assmann and Franz (1965)	O40	15.3	33.2	36.2	37.5	39.4			1.57	1.60
		O20			17.1	21.6	26.2			1.21	1.28
Scots pine	Wiedemann (1943a)	I.		18.4	31.0	39.1	44.9			1.45	1.64
		VI.				7.4	22.0				1.08
Silver fir	Hausser (1956)	I.		16.0	30.0	41.0	47.0	56.0		1.43	1.69
		IV.			4.0	20.0	33.0	48.0		1.04	1.25
European larch	Schober (1946)	I.	7.4	29.2	34.5	37.2	39.7			1.53	1.59
		III.		16.9	27.0	33.1	37.0			1.37	1.49
Douglas fir	Bergel (1969)	I.	9.3	36.5	42.5	43.6				1.74	1.77
		III.		29.4	36.9	39.1				1.58	1.64
Sessile oak	Jüttner (1955)	I.		18.4	32.9	41.1	47.6	56.7	60.7	1.49	1.70
		IV.			6.5	11.3	18.2	32.8		1.07	1.13
European beech	Schober (1967)	I.		5.3	21.5	32.4	39.6	50.1		1.27	1.48
		IV.			7.4	19.5	27.6	41.3		1.08	1.24

the juvenile development phase, i.e. before canopy closure, only little merchantable wood is lost through self-thinning. The main turnover occurs from the early-mature stage onwards, where the percentage of the lost volume amounts to about 30%, a value that is remarkably stable among the tree species (Pretzsch 2005b).

Based on the reported proportions of gross and net yield, we introduce a first-order estimation of the total produced volume (=gross yield GY_V) from the remaining stand volume (=net yield NY_V). We assume a tree loss of 33% between stand establishment and harvesting under light to moderate thinning. This means 67% of the stand volume remains, and the factor for deriving total volume from standing volume, which includes the turnover owing to the removal of individual trees $t_{ind} = 1.5$ at age 100, is:

$$GY_V = NY_V \times t_{ind}, \tag{2.21}$$

with $t_{ind} = 1.5$ (1.04–1.77) at age 100.

The estimate $t_{ind} = 1.5$ is merely an approximation that serves for early-mature and mature stands in rotation forests (Table 2.6). Depending on age, silvicultural treatment and species, this value easily may vary between 1.04 and 1.77 (cf. Table 2.6).

The definitions and datasets introduced so far consider the entire standing stem or merchantable wood volume and do not distinguish dead and living wood. With increasing age and size, heartwood development progresses, and hence the ratio of living: dead tissue decreases. It can be assumed that the net growth of living wood volume in old stands and primary forests is static or even decreases while the total wood volume continues to accumulate. To differentiate living and dead wood volume, we refer to living wood volume as the "true" standing volume, and to the "true" growth and yield. The distinction becomes important when comparing the yield or production of woody and herbaceous stands. Large standing volumes of $>10{,}000\,\mathrm{m^3\,ha^{-1}}$, such as found in North American temperate rainforests could never consist entirely of physiologically active tissue (as in herbaceous stands), but mainly of dead, physiologically inactive tissue.

2.4 Stem and Merchantable Volume Growth as a Percentage of Gross Primary Production

The growth and yield measures, stem and merchantable wood volume, are standard forestry variables. In this chapter, we introduce values and rules of thumb for converting this wood volume to wood biomass, to total tree or stand biomass (including leaves, brushwood, and roots), and then into net primary production (NPP, including turnover) and gross primary production (GPP, including respiration). The intention is to bridge the gap between the forestry wood volume standards and the ecological primary productivity standards.

As Kimmins (1996), Landsberg (1986), and Larcher (1994) point out, biomass allocation, turnover, and respiration all depend on the following factors: growing conditions, species, treatment, and age. The quantities and relationships between them express the adaptability of a species to certain growing conditions, and, in this sense, are of major ecological interest. However, to obtain a rough estimate of primary productivity from forestry growth and yield values, the influence of each of these factors is given in relation to their potential deviation from a specific average value.

Despite the broad range in variation in the individual biomass compartments, and the turnover and respiration rates, the conversion from volume-based forestry growth and yield values to biomass, or carbon-based parameters of primary production should become transparent. We provide an insight into the average size of the relative percentages and losses. This insight and this classification of the forestry growth and yield parameters as a part of the whole primary production should not be lost in the plethora of studies about specific elements or new models.

Table 2.7 gives an overview of the descriptions, approximate values and range in variation of the multipliers used in this chapter. R expresses the basic specific wood density; i.e. the wood density defined in relation to green volume (Simpson 1993). The expansion factors e_{br}, e_l and e_r are used in the step-by-step conversion of merchantable volume to aboveground and belowground total volume. The factors e_{br},

Table 2.7 Estimates and range of the specific wood density R, expansion factors e_{br}, e_l, e_r, turnover factors t_{org}, t_{ind}, harvest loss factors l_s, l_b, factor for estimation of sapwood f_{sw}, and respiration f_{re}. The factors provide a rough estimate of standing total biomass, NPP, and GPP in relation to standing merchantable volume and mean annual volume increment. The reciprocal values, 1/R, $1/e_{br}$, etc., assist the estimation of standing merchantable volume from standing total biomass. They can be applied, e.g. for partitioning GPP and NPP into ephemeral and long-lasting components, aboveground and belowground components, stem wood and brushwood biomass. The estimates are based on references mentioned in the text

Conversion from	To	Factor	Thumb value (e.g. R)	Range	Reciprocal thumb value (e.g. 1/R)	Range
tree volume	tree weight	R ($t\,m^{-3}$)	0.50	0.38–0.56	2.00	2.63–1.79
stem volume over bark	tree volume above ground	e_{br}	1.50	1.15–3.00	0.67	0.33–0.87
tree volume above ground	tree volume above ground + leaves	e_l	1.05	1.03–1.12	0.95	0.89–0.97
tree volume above ground + leaves	total tree volume	e_r	1.25	1.11–2.00	0.80	0.50–0.90
stem volume over bark	total tree volume	$e_{br}\,e_l\,e_r$	2.00	1.48–6.72	0.50	0.15–0.68
net biomass growth	net biomass growth + organ turnover	t_{org}	1.30	1.27–9.13	0.77	0.11–0.79
net biomass growth + organ turnover	net biomass growth + organ + tree turnover	t_{ind}	1.50	1.08–1.77	0.67	0.57–0.96
standing stem volume over bark	harvested volume over bark	l_s	0.90	0.90	1.11	1.11
harvested volume over bark	harvested stem volume under bark	l_b	0.91	0.80–0.94	1.10	1.06–1.25
standing stem volume over bark	harvested stem volume under bark	$l_b\,l_s$	0.80		1.25	
total tree biomass	living tree biomass	f_{sw}	–	0.22–1.00	–	1.00–4.55
net primary productivity	net primary productivity + respiration = GPP	f_{re}	2.00	1.18 – 20.00	0.50	0.05–0.85

e_l and e_r are used to determine the proportion of branch wood, the foliage mass and the root biomass respectively. Given net biomass growth, the factors t_{org} and t_{ind}, representing the turnover from the loss of plant organs and whole trees respectively, are used to estimate gross growth. Harvesting losses from leaving the stump in the forest and from bark removal are estimated by l_s and l_b respectively. The factor f_{sw} is used to calculate the proportion of sapwood in the standing volume. Factor f_r is used to extrapolate GPP from NPP, i.e. by increasing the NPP by the respiration amount.

The factors in Table 2.7 facilitate the approximate conversion of known forestry parameters to production ecology measures. As these factors are not closely dependent on age or size, the approximate values (characteristic values) and range in variation are given. The reciprocal values (last column in Table 2.7) are used, when necessary, to derive forestry volume values from GPP or NPP.

2.4.1 From Standing Volume or Stem or Merchantable Wood Volume to Total Biomass

For this, conversion factors or estimate functions are used, which estimate the successive stem and merchantable biomass (in t), the aboveground total biomass and, finally, the total biomass from the volume of the aboveground stem or merchantable wood (in m^3). In particular, the estimate of the belowground components of stem volume, or merchantable volume, is inaccurate because the ratio of aboveground to belowground biomass is heavily dependent on moisture, nutrient and light status, which are determined by site conditions and stand density (Kimmins 1993, p. 13).

2.4.1.1 From Wood Volume to Wood Biomass by Specific Wood Density R

Wood volume v is converted to wood biomass w by the specific wood density R

$$w = v \times R. \tag{2.22}$$

Wood density is a unit of weight per volume and is mostly given in $kg\,m^{-3}$. Wood density R, given in $t\ m^{-3}$, represents the reduction factor from m^3 to t. Of the various possible density measures, we use the specific density, which converts fresh volume, with 100% water saturation and full hydration of cell walls, into dry weight with only 0.5–1% water saturation (Knigge and Schulz 1966, p. 132). In practise, this density is determined by extracting the humidity of the wood in an oven until the point of constant weight. The decomposition and volatilisation of organic compounds must be avoided. Wood density varies between 120.8 $kg\ m^{-3}$ for balsa wood to 1,045.5 $kg\ m^{-3}$ for pockwood. The commercial tree species in central Europe have specific densities of 350–550 $kg\ m^{-3}$ (cf. Table 2.8). As specific density varies

Table 2.8 Specific wood density R of selected tree species (R defined on the basis of the green volume). In central Europe tree species with wood densities of 350–550 kg m^{-3}, equivalent to transformation factors of R = 0.35–0.55 (t m^3), dominate (Knigge and Schulz 1966, p. 135)

Tree species		Specific wood density (kg m^{-3})
Balsawood	Ochroma lagopus	120.8
Grand fir	Abies grandis	332.0
White pine	Pinus strobus	338.6
Poplar	Populus spec.	376.8
Norway spruce	Picea abies	377.1
Sitka spruce	Picea sitchensis	401.7
Douglas fir	Pseudotsuga menziesii	412.4
Pine	Pinus spec.	430.7
Larch	Larix spec.	487.3
Maple	Acer spec.	522.2
European beech	Fagus sylvatica	554.3
Elm	Ulmus spec.	555.5
Sessile/Common oak	Quercus petraea/robur	561.1
Ash	Fraxinus spec.	564.2
False acacia	Robinia pseudoacacia	646.8
Bongossi	Lophira procera	890.2
Pockwood	Guaiacum officinale	1,045.5

with stand density (Bues 1984), species composition (Kennel 1965), stand treatment (Seibt 1965) and tree age (Knigge and Schulz 1966), the reference values in Table 2.8 represent average values from Knigge and Schulz (1966, p. 135). It is easiest to calculate a first-order approximation with a density of 500 kg m^{-3}, which is equivalent to the density factor R

$$R(\text{approximate}) = 0.5\,\text{t}\,\text{m}^{-3}. \tag{2.23}$$

In their Forest Resource Assessment, the FAO also applies a generalised density factor of 0.5 t m^{-3} for conifer and 0.6–0.7 t m^{-3} for broadleaved forests (FAO 2001; Brown 1997).

2.4.1.2 Brushwood Factor e_{br}: From Stem Volume to Aboveground Wood Volume

In addition to stem wood, the aboveground wood volume also includes brushwood (cf. Fig. 2.2, b_1 and b_2). The yield tables from Grundner and Schwappach (1952) assist the estimation of brushwood volume. Based on more than 70,000 trees, Grundner and Schwappach measured merchantable volume, stem volume, and total volume, including branches, for Silver birch, European beech, Red alder, Norway spruce, Scots pine, European larch, Austrian pine, and Silver fir. Thus, brushwood volume can be calculated from the difference between total aboveground volume and merchantable volume. Grundner and Schwappach provide brushwood volume values for broadleaved species, and both brushwood and needles for conifers. In the tables, the brushwood percentages (=brushwood volume/merchantable stem volume $\times 100$) are listed in relation to tree age, diameter and height.

Burschel et al. (1993) condensed these tables of brushwood percentages to species-specific, age-dependent brushwood factors e_{br}. For early-mature stands brushwood comprises an estimated 40% of the merchantable wood volume, and in old stands about 20%. Thus, to estimate total aboveground wood volume in relation to merchantable volume, a factor of $e_{br} = 1.4$ and 1.20 needs to be applied for early-mature and mature trees respectively. The factor e_{br} ranges from 2.0 for young trees to 1.20 for old growth trees. For very young stands with virtually no merchantable wood volume, Burschel et al. (1993) propose a constant value be derived from the merchantable wood volume of trees aged from 1–20 years, multiplied by a factor of $e_{br} = 3$ (Table 2.7).

Jacobsen et al. (2003) come to similar results in their biomass study. They employed age-dependent biomass functions for the calculation of aboveground biomass (incl. leaves) from merchantable wood biomass. For comparison, the e_{br} factors at age 20, 50 and 120 for the following species are: Norway spruce $e_{br} =$ 1.84, 1.41, 1.15; Scots pine $e_{br} = 1.71, 1.44, 1.23$; European beech $e_{br} = 1.51, 1.45,$ 1.28; and Sessile oak 1.45, 1.45, 1.45.

Thus,

$$\begin{aligned} &\text{v(aboveground wood volume)} = \text{v(merchantable wood volume)} \times e_{br} \\ &\text{with } e_{br} = 3.00 - 1.20. \end{aligned} \tag{2.24}$$

For the less frequent extrapolations based on stem volume, the extrapolation factors e_{br} are adjusted variously. For young stands the factors are reduced by a small percentage as the trees in these stands contribute stem volume but little merchantable volume >7 cm. For early-mature and mature conifers with a minimal amount of merchantable branch wood, the extrapolation factor e_{br} is reduced also due to the higher percentage of stem volume compared to merchantable volume. In contrast, in broadleaved stands, the factors increase because the stem-wood volume is smaller than the merchantable volume due to the high proportion of merchantable branch volume >7 cm. The difference between an extrapolation based on stem wood and on merchantable wood declines with age (or the size of the tree), and is ignored here.

For approximate extrapolations in early-mature stands, one can obtain the total volume, or the aboveground biomass by multiplying the merchantable volume, or the merchantable biomass by 1.5 respectively. For a first-order estimation of aboveground volume from merchantable volume, we propose a factor of,

$$e_{br}\,(\text{approximate}) = 1.5. \tag{2.25}$$

For simplicity, we assume that, for all tree organs, $w = v \times R$ applies, so that the expansion factor e_{br} can be used for volume v (2.24) and for biomass weight w.

2.4.1.3 The Leaf Factor e_l: From Aboveground Woody Biomass to Aboveground Total Biomass

The brushwood factor e_{br} derived from the tables by Grundner and Schwappach (1952) already contains the needle biomass for conifers (leaf factor $e_l = 1$). Therefore, a leaf factor needs to be added only for broadleaves:

$$\mathrm{w}(\text{total above ground biomass}) = \mathrm{w}(\text{above ground wood biomass}) \times e_l. \tag{2.26}$$

In the first approach, leaf biomass is modelled as a function of aboveground woody biomass. The leaf biomass functions from Jacobsen et al. (2003) model the declining leaf fraction of the total aboveground biomass with age. At ages 20, 50 and 120 the percentage of foliage biomass in relation to total aboveground biomass is: 18, 11 and 3% for Norway spruce; 32, 7 and 5% for Scots pine; 3, 3 and 1% for European beech; and 8, 5 and 2% for Sessile oak. This leads, in all cases, to decreasing leaf factors e_l: from $e_l = 1.22$–1.03 for Norway spruce, $e_l = 1.47$–1.05 for Scots pine, $e_l = 1.03$–1.01 for European beech, and $e_l = 1.09$–1.02 for Sessile oak.

In a second approach, the estimate of leaf biomass is independent of wood biomass. Assuming a constant assimilation surface and weight of the leaves in old and uneven-aged stands, the leaf biomass can be estimated from the annual litter fall and the average length of leaf life. For Norway spruce, Ellenberg (1986) measured a constant litter fall of 0.2–0.5 kg $m^{-2}\,yr^{-1}$, or 2–5 t $ha^{-1}\,yr^{-1}$, which corresponds to a needle biomass of 6–15 t ha^{-1} (assuming an average needle life of 3 years). Similarly, Scots pine stands reach 4 t ha^{-1} needle biomass (Ellenberg 1986, average needle life 2.5 years); European larch and Douglas fir stands, a maximum of 12–14 t ha^{-1} (Lyr et al. 1967); European beech stands, 3 t ha^{-1} (Assmann 1961; Ellenberg 1986) to 8 t ha^{-1} (Lyr et al. 1967); Sessile oak and European ash 2–3 t ha^{-1} (Assmann 1961); and Silver birch up to 5 t ha^{-1} (Lyr et al. 1967). For a 50- and 120-year-old European beech stand, a constant leaf biomass of 3–8 t ha^{-1} (mean 5 t ha^{-1}) conforms with the 3% and 1% leaf biomass listed above, when total aboveground biomass is 200 and 600 t ha^{-1}, respectively.

All in all, the orientation value of $e_l = 1.05$ serves as a good estimation of the leaf biomass for broadleaves (early-mature to mature stands), while the needle biomass for conifers is already included in the brushwood factor:

$$\begin{aligned} e_l\,(\text{thumb, broadleaf}) &= 1.05, \\ e_l\,(\text{conifer}) &= 1.00. \end{aligned} \tag{2.27}$$

2.4.1.4 Root Factor e_r: From Aboveground Biomass to Total Plant Biomass

Santantonio et al. (1977) and Fogel (1983) found that the percentage of roots in the total tree biomass ranges from 10–45% approximately depending on the growth conditions, corresponding to a root factor e_r of

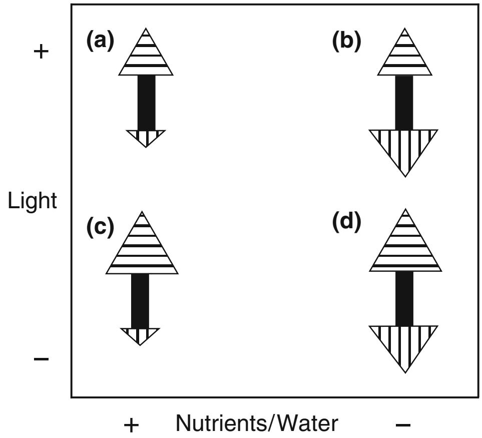

Fig. 2.7 Partitioning of total plant biomass on shoot and root organs in relation to supply of nutrients and water (x-axis) and supply of light (y-axis). Limitation of nutrient and water supply causes a partitioning in favour of roots. Limitation of energy supply raises the investment of biomass into shoots (by courtesy of Kimmins 1993, p. 13.)

$$\begin{aligned} &\mathrm{w(total)} = \mathrm{w(above)} \times \mathrm{e_r}, \\ &\text{with } \mathrm{e_r} = 1.11\text{–}1.81. \end{aligned} \tag{2.28}$$

Instead of the root factor, the literature mostly refers to the root to shoot ratio, which for the above-mentioned values, lies between 10:90 and 45:55. The large variation in the root to shoot ratio can be explained by the theory that the limitation of a resource leads to the promotion of growth of the plant organ responsible for supplying that critical resource (Comeau and Kimmins 1989; Keyes and Grier 1981).

In Fig. 2.7, four examples indicate the complexity of the root to shoot ratio. In the first example, where light, water and nutrient conditions are favourable (Fig. 2.7a), the tree shown develops a root to shoot ratio of 10:90 ($e_r = 1.11$). Under adequate light conditions, but with a water or a nutrient deficiency (Fig. 2.7b), the tree invests more into root growth, especially fine roots. Thus the root to shoot ratio increases in favour of roots to 45:55, with $e_r = 1.82$. With an adequate water and nutrient supply, yet critical light conditions, e.g. on nutrient-rich soils or for understorey trees (Fig. 2.7c), shoot growth is enhanced, so that the tree root to shoot ratio becomes 30:70, resulting in $e_r = 1.43$. In the case of rich soils, trees in the upper storey tend to allocate growth resources to extensive crown development, whereas trees in the understorey often invest in height growth to escape the shade (Oliver and Larson 1996). If light, water and nutrient supply is limited (Fig. 2.7d), the root to shoot ratio may resemble the example in Fig. 2.7a of 10:90, where $e_r = 1.11$. However, usually, the total biomass comprises a higher proportion of brushwood and fine roots and less stem wood.

Aside from the large variation in the root to shoot ratio caused by different site conditions, Burschel et al. (1993) identified an age-dependent change in root to shoot ratios in several studies from 10:10 for young to 10:30–10:40 for older trees, corresponding to root factors of $e_r = 2.0\text{–}1.25$. In the absence of additional information, we recommend an approximate value for e_r of

$$\mathrm{e_r(approximate)} = 1.25. \tag{2.29}$$

When tree biomass is extrapolated from the stem wood, merchantable volume, or the aboveground biomass without taking the site-specific root to shoot ratio into account, the root biomass is underestimated, especially on sites where growth is limited by the soil conditions.

2.4.1.5 Examples for Upscaling Merchantable Wood Volume to Total Plant Biomass

Figure 2.8a shows an example of a European beech stand (site class I, Schober 1971, moderate thinning). The biomass development is divided into the compartments stem wood, bark, brushwood, leaves, coarse and fine roots as derived with the biomass equations from Jacobsen et al. (2003). Similar equations for estimating various biomass components in relation to stem size have been developed, e.g. by Pretzsch (2005c), Pretzsch and Mette (2008), Seifert and Müller-Starck (2008) and Wirth et al. (2004). Based on the yield volume of 28–552 $m^3 ha^{-1}$ at age 30–120 from the tables, the biomass equations and expansion factors predict the biomass of stems, bark, brushwood, leaves, coarse roots and fine roots to be 16–306, 1–8, 6–64, 1–6, 3–53 and 1–4 t ha^{-1} respectively. This produces a total plant biomass of 27–447 t ha^{-1}. The stem wood accounts for 58–68% of the total biomass, which, despite all the uncertainties associated this estimate, is an important percentage for scaling up the total biomass (Fig. 2.8b).

An overall upscaling factor $e_{br,l,r}$ for the direct conversion of merchantable wood volume or biomass into total tree volume or tree biomass can be calculated:

$$e_{br,l,r} = e_{br} \times e_l \times e_r = 1.50 \times 1.05 \times 1.25 \cong 2.0 \quad (2.30)$$

(cf. Table 2.7).

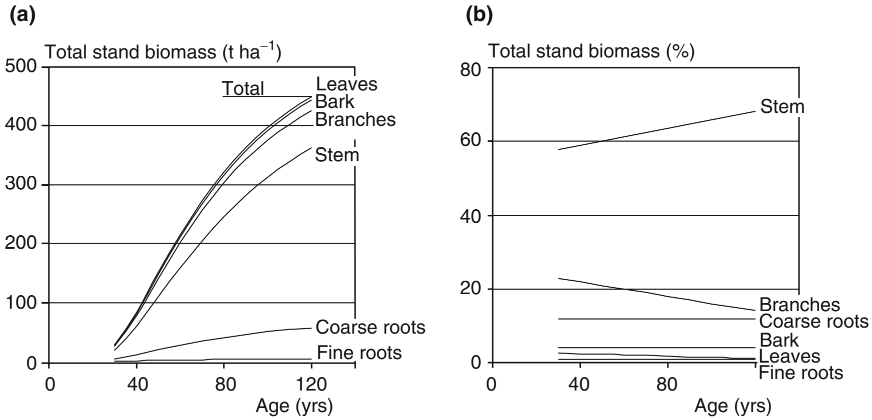

Fig. 2.8 Biomass development of an European beech stand, site index I (Schober 1972, mod. th.), and the fractions of leaves, bark, branches, stem wood, coarse roots, and fine roots: (**a**) stand biomass in t ha^{-1} and (**b**) relative portion of the various tree organs (%)

The second example in Table 2.9 is based on the standing merchantable wood volume in Germany taken from the BWI[2] inventory results (Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz, 2005). In 2002, the average standing merchantable volume ranged from 274 $m^3\,ha^{-1}$ in Douglas fir to 480 $m^3\,ha^{-1}$ in Silver fir stands. These values were extrapolated using the specific wood density R and the expansion factors e_{br}, e_l, and e_r to obtain total stand biomass values between 205 and 365 t ha^{-1}. For broadleaved species, the values of merchantable volume in $m^3\,ha^{-1}$ and total plant biomass in t ha^{-1} are approximately equal because the reduction factor for wood density R and the expansion factors e_{br}, e_l, and e_r are almost equal. For conifers, the biomass values are 10–30% lower than the merchantable wood volume due to the lower specific wood density.

In Table 2.10 the merchantable wood volume of the long-term experimental plots in Tables 2.3–2.5 are converted into biomass. The range in standing volume of the evenaged pure stands, 428–1,480 $m^3\,ha^{-1}$, is equivalent to a total biomass range of 378 t ha^{-1} (European larch) and 1,012 t ha^{-1} (Norway spruce) (cf. Table 2.10, above). For the evenaged mixed stands, the total biomass calculated from merchantable wood volumes of 394–918 $m^3\,ha^{-1}$ ranges from 371 t ha^{-1} (Scots pine – European beech) to 756 t ha^{-1} (Norway spruce – European beech) (Table 2.10, centre). For the unevenaged mixed stands, the merchantable wood volumes of 477–1,028 $m^3\,ha^{-1}$ correspond to a total biomass of 351–721 t ha^{-1} (Table 2.10, below). In comparison with the wood volume values, the total biomass values of conifers and broadleaved species lie closer together. Often the higher wood density of broadleaved species compensates for the lower packing density of the trees in the stand compared to conifer species.

2.4.2 *Ephemeral Turnover Factor t_{org} for Estimation of NPP*

Net primary productivity of forest stands is defined as the increase in biomass per unit area over a given time period (e.g. year, decade) plus the turnover of short-lived plant organs (bark, branches, leaves, roots) and entire trees that are lost between inventories. These two components constitute the biomass turnover and are introduced as short-term or ephemeral turnover, which often follows an annual cycle, and the long-term turnover of entire trees through self-thinning, thinning or calamities.

The turnover factor t_{ind} (approximate) = 1.50 (1.08–1.77) was introduced to estimate total merchantable wood volume produced from the volume of the remaining stand (Sect. 2.3.2); in other words the standing volume must be multiplied by $t_{ind} = 1.50$ to obtain the total volume production. The standard variables CAI, PAI, and MAI already include whole tree turnover. Thus, for the calculation of the NPP, only the factor t_{org} for the ephemeral turnover of plant organs (e.g. foliage, roots, branches) is absent. Of course, as with the above factors, the short-term turnover depends on site conditions, stand age, species and stand treatment.

The quantification of ephemeral turnover essentially is accompanied by considerable uncertainty; aboveground litter fall, belowground turnover of fine root biomass,

Table 2.9 Mean standing volume ($m^3\,ha^{-1}$) and mean periodic annual increment ($m^3\,ha^{-1}\,yr^{-1}$) for dominant tree species in Germany according to the Second National Forest Inventory BWI^2 (Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz, BWI^2, Der Inventurbericht, pp. 75 and 167), approximate standing biomass ($t\,ha^{-1}$) and NPP ($t\,ha^{-1}\,yr^{-1}$)

Tree species	Mean standing volume $m^3\,ha^{-1}$	PAI $m^3 ha^{-1}\,yr^{-1}$	Specific wood density R $kg\,m^{-3}$	Expansion factor e_{br}	Expansion factor e_l	Expansion factor e_r	Turnover factor t_{org}	Total biomass $t\,ha^{-1}$	NPP $t\,ha^{-1} yr^{-1}$	NPP $kg\,m^{-2}\,yr^{-1}$
Norway spruce	404.1	16.37	377.1	1.45	1.00	1.25	1.30	276.2	14.55	1.45
Scots pine	281.7	9.12	430.7	1.45	1.00	1.25	1.30	219.9	9.26	0.93
Silver fir	480.4	15.95	377.1	1.45	1.00	1.25	1.30	328.4	14.17	1.42
European larch	300.7	12.75	487.3	1.45	1.00	1.25	1.30	265.6	14.64	1.46
Douglas fir	273.6	19.41	412.4	1.45	1.00	1.25	1.30	204.5	18.86	1.89
Sessile oak	285.9	8.25	561.1	1.45	1.05	1.25	1.30	305.3	11.45	1.15
European beech	352.4	11.74	554.3	1.45	1.03	1.25	1.30	364.6	15.79	1.58
Total min	273.6	8.25	377.1	1.45	1.00	1.25	1.30	204.5	9.26	0.93
Total max	480.4	19.41	561.1	1.45	1.05	1.25	1.30	364.6	18.86	1.89

Total standing biomass ($t\,ha^{-1}$) was estimated on the basis of standing volume ($m^3\,ha^{-1}$) using specific wood density R and expansion factors e_{br}, e_l, and e_r. Net primary productivity was estimated on the basis of mean PAI ($m^3\,ha^{-1}\,yr^{-1}$) using specific wood density R, expansion factors e_{br}, e_l, and e_r, and turnover factor t_{org}.

Table 2.10 Upscaling from standing merchantable volume to total standing biomass and from mean annual increment of merchantable volume to NPP on selected long-term experimental plots in Southern Germany (cf. Tables 2.2–2.4). Total standing biomass ($t\,ha^{-1}$) was estimated on the basis of standing merchantable volume using specific wood density R and expansion factors e_{br}, e_l, e_r. Net primary productivity was estimated based on MAI ($m^3\,ha^{-1}\,yr^{-1}$) in the case of pure evenaged and mixed evenaged stands and based on PAI ($m^3\,ha^{-1}\,yr^{-1}$) in the case of mixed unevenaged stands. For the upscaling we applied specific wood density R; expansion factors e_{br}, e_l, and e_r; and turnover factor t_{org} (cf. Tables 2.7–2.9)

Tree species	Experimental plot	Standing volume m^3ha^{-1}	Total st. biomass $t\,ha^{-1}$	MAI (PAI) $m^3ha^{-1}yr^{-1}$	NPP $t\,ha^{-1}yr^{-1}$	NPP $kg\,m^{-2}yr^{-1}$
pure even-aged						
Norway spruce	DEN 05	1,480	1,012	15.4	13.7	1.4
Scots pine	BAY 52	700	546	10.5	10.6	1.1
Silver fir	WOL97	637	435	9.5	8.4	0.8
European larch	MIS 47	428	378	5.4	6.1	0.6
Douglas fir	FRE 85	1,012	756	17.2	16.7	1.7
Sessile oak	LOH 59	605	646	7.7	10.8	1.1
European beech	FAB 15	950	983	8.7	11.7	1.2
Total min		428	378	5.4	6.1	0.6
Total max		1,480	1,012	17.2	16.7	1.7
mixed even-aged						
Norway spruce-European beech	SON 814	918	756	18.5	19.7	2.0
Scots pine-Norway spruce	NEU 841	876	647	8.8	8.4	0.8
Scots pine-European beech	GEI 832	394	371	15.5	19.0	1.9
European larch-European beech	GEM 871	580	570	11.8	15.0	1.5
Sessile oak-European beech	KEH 804	688	730	12.4	17.1	1.7
Total min		394	371	8.8	8.4	0.8
Total max		918	756	18.5	19.7	2.0
mixed uneven-aged				PAI		
N. spruce-S. fir-E. beech	FRY 129/32	663	500	10.7	10.5	1.0
N. spruce-S. fir-E. beech	BOM 130/22	610	481	10.2	10.5	1.0
N. spruce-S. fir-E. beech	PAR 115/1	871	626	8.1	7.6	0.8
N. spruce-S. fir-E. beech	KRE 120/3	502	414	4.7	5.0	0.5
N. spruce-S. fir-E. beech	MAR 108/1	1,028	721	15.9	14.5	1.4
N. spruce-S. fir-E. beech	RUH 110/2	477	351	7.9	7.6	0.8
N. spruce-S. fir-E. beech	RUH 116/1	784	591	9.8	9.6	1.0
Total min		477	351	4.7	5.0	0.5
Total max		1,028	721	15.9	14.5	1.4

loss of primary production to microbial symbionts or defoliation by herbivores can account for a very significant, yet rarely quantified proportion of NPP. For example, carbon allocation to mycorrhizal fungi or for symbiontic N-fixation can be an energy demanding process that consumes part of the net primary production. A good estimation of the quantity of ephemeral turnover in relation to site is provided in Comeau and Kimmins (1989) investigation of Lodgepole pine stands (*Pinus contorta*) in the Rocky Mountains, in Southeast British Columbia. The turnover of fine roots is between 50 and 62% of the total NPP on dry soils, yet only between 31 and 40% on soils of medium humidity. On the dry soils, fine and small root production is 3.2–4.9 times as high as needle production, while, on the humid soils, it is only 1.3–2.5 times higher. Obviously, on dry sites, the tree invests in fine root production for the uptake of the more limited resource, water. Keyes and Grier (1981) obtain similar results for Douglas fir stands along the North American west coast. They show that, although stem-wood production was nearly twice as high on good sites as on poor sites, in total, NPP was only 13% higher on the good sites. On the poor sites, 53% of NPP was allocated to the root, primarily to fine root production with a rapid turnover, whereas only 23% of the NPP was invested in belowground biomass growth on good sites. These results confirm that the percentage of ephemeral turnover increases as nutrients and water supply become less favourable. The highest turnover appears to occur for those plant organs that ensure the supply of the most limiting resource.

Keeping in mind site dependency, some typical values for ephemeral turnover from the literature are summarised. These values typically are given as a turnover factor t_{org}, which can be used to estimate mean NPP in relation to volume growth MAI, PAI, or CAI as follows:

$$\text{NPP} = \text{MAI(total biomass)} \times t_{org}. \tag{2.31}$$

Ellenberg (1986, p. 122–128, 332) found values of $t_{org} = 1.27$–1.45 for Norway spruce, and 1.40–1.83 for European beech, which increased with age. Brünig (1971) obtained values of $t_{org} = 1.69$–2.15, which increased from trees with light–heavy crowns. From von Droste (1969, p. 193), we can derive values of $t_{org} = 1.69$ for Norway spruce only for the aboveground compartments. Assmann (1961, p. 34), who refers to Boysen-Jensen (1932) and Mar-Möller (1945), derives values of $t_{org} = 2.0$–2.17 in European ash stands for the aboveground compartments only. For European beech stands, Mar-Möller (1945) identifies a $t_{org} = 1.40$–1.54, and Larcher (1994, p. 134) a $t_{org} = 1.56$. For tropical rainforests in Thailand, Larcher (1994, p. 134) assumes an ephemeral turnover of $t_{org} = 9.13$, i.e. the turnover exceeds the biomass production by a factor of 9. In the following calculations for temperate forests in central Europe, we assume an ephemeral turnover factor of

$$t_{org}\,\text{(approximate)} = 1.3. \tag{2.32}$$

To reduce age dependency, and attain a long-term average for ephemeral turnover, the MAI should be used to upscale to NPP. By adopting MAI, the long-term average NPP also becomes comparable to the NPP of the annual or periodic cycles of herbaceous stands.

2.4.2.1 Examples for Upscaling from Merchantable Volume Growth or Increment to NPP

Table 2.9 lists, in column 3, the mean periodic annual volume increment ($m^3\,ha^{-1}\,yr^{-1}$) for the most important forestry species in Germany from 1987 to 2002 (Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz, 2005). The growth in merchantable wood volume ranges from $8.25\,m^3\,ha^{-1}\,yr^{-1}$ for Sessile oak stands to $19.41\,m^3\,ha^{-1}\,yr^{-1}$ for Douglas fir stands. The values represent the average across all possible site conditions and age classes. Consequently, they represent very stable average PAI values (15 years interval), and provide a good indication of the productivity of central European forests. The conversion to NPP using the appropriate wood density R (t m^3), expansion factors e_{br}, e_l, e_r, and ephemeral turnover factor t_{org} (cf. Table 2.9) results in NPP values between 9.26 t $ha^{-1}\,yr^{-1}$ for Scots pine stands and 18.86 t $ha^{-1}\,yr^{-1}$ for Douglas fir stands, which corresponds to the NPP range of 10–15 t $ha^{-1}\,yr^{-1}$ for woody and herbaceous vegetation in the temperate latitudes given by Körner (2002, p. 945).

The NPP also can be calculated for the long-term experimental plots presented in Tables 2.3–2.5 (Table 2.10). For evenaged pure stands with an MAI of $5.4–17.2\,m^3\,ha^{-1}\,yr^{-1}$, the NPP ranges from 6.1–16.7 t $ha^{-1}\,yr^{-1}$ (maximum for Douglas fir and Norway spruce, minimum for European larch). The evenaged mixed stands, with an MAI of $8.8–18.5\,m^3\,ha^{-1}\,yr^{-1}$, assume an NPP of 8.4–19.7 t $ha^{-1}\,yr^{-1}$. For the unevenaged mixed stands with a PAI of $4.7–15.9\,m^3\,ha^{-1}\,yr^{-1}$, the rough estimate of NPP is 5.0–14.5 t $ha^{-1}\,yr^{-1}$; all these estimates are obtained from the approximate wood density values R (t m^3), expansion factors e_{br}, e_l, e_r, and ephemeral turnover factor t_{org}.

2.4.3 Deriving Harvested Volume Under Bark from Standing Volume over Bark

Standing volume over bark v(standing o.b.) is the volume measure commonly used in forest inventory (stem volume or merchantable volume). It indicates the volume of the standing stem including bark and the later harvesting losses (stump volume). To obtain the harvested volume from this measure of volume over bark, the v(standing o. b.) is reduced by a factor $l_s = 0.90$, which represents the 10% volume of the tree stump (cf. factor l_s, Table 2.11). This factors accounts for the fact that the trunk base s_0 in Fig. 2.2 is not extracted from the forest in conventional harvesting methods.

An additional factor $l_b = 0.80–0.94$ allows for a 6–20% bark volume loss, which is species-dependent (cf. factor l_b, Table 2.11). This result in a harvest loss factor l_s and bark loss factor l_b of:

$$l_s\,(\text{approximate}) = 0.9, \tag{2.33}$$

$$l_b\,(\text{approximate}) = 0.9\,(0.80\ldots0.94). \tag{2.34}$$

Table 2.11 Species-specific relationships between standing stem volume over bark and harvested volume under bark (Bayerisches Staatsministerium für Ernährung, Landwirtschaft und Forsten, 1981, p. 306). For example, in stands of European beech, 1 m^3 standing stem volume over bark results in 0.9 m^3 harvested volume over bark and 0.85 m^3 harvested volume under bark. The losses due to harvest are 10% for all species ($l_s = 0.90$), while the losses due to debarking range from 6% to 20% ($l_b = 0.80$ to $l_b = 0.94$). The last column represents the reciprocal value of the loss factors l_s and l_b, i.e. the expansion factors for converting harvested volume under bark to standing volume over bark (all factors are rounded to two decimal places)

Species resp. Genus	from: standing volume over bark to: harvested volume o. b. l_s	from: harvested volume over bark to: harvested volume u. b. l_b	from: standing volume over bark to: harvested volume u. b. $l_b l_s$	from: harvested volume under bark to: harvested volume o. b. $1/l_b$	from: harvested volume over bark to: standing volume o. b. $1/l_s$	from: harvested volume under bark to: standing volume o. bark $1/(l_b l_s)$
Norway spruce	0.90	0.90	0.81	1.11	1.11	1.23
Scots pine	0.90	0.88	0.79	1.14	1.11	1.27
Silver fir	0.90	0.90	0.81	1.11	1.11	1.23
European larch	0.90	0.80	0.72	1.25	1.11	1.39
Douglas fir	0.90	0.88	0.79	1.14	1.11	1.27
Sessile and Common oak	0.90	0.88	0.79	1.14	1.11	1.27
European beech	0.90	0.94	0.85	1.06	1.11	1.18

Therefore, the actual harvested volume amounts to 72–85% of the standing volume over bark or, conversely, the standing stem volume is 118–139% of the harvested volume under bark (cf. Table 2.11, right column). In Germany, different states, regions and districts use different conversion factors with only minor differences that reflect the various provenances grown, and silvicultural practices and harvesting techniques applied. When wood volume over bark needs to be converted to harvested volume under bark, the reduction factors of 0.72–0.846 are used ($l_s \times l_b$). As an approximate value, $l_s \times l_b$ (approximate) = 0.8 can be used:

$$\begin{aligned} &\mathrm{v(harvested\ u.\ b.)} = \mathrm{v(standing\ o.\ b.)} \times l_s \times l_b, \\ &\mathrm{v(harvested\ u.\ b.)} \cong \mathrm{v(standing\ o.\ b.)} \times 0.8. \end{aligned} \tag{2.35}$$

Alternatively, if the harvested volume under bark is known, then the corresponding reciprocal multipliers, of $1/(l_b \times l_s) = 1.18$ for European beech, which has a thin bark, to 1.39 for European larch, whose bark is extremely thick, are used (Table 2.11).

Finally, a conversion factor may be needed that converts stacked cubic volume (st. c. m) to solid volume in m^3, since 1 st. c. m $\cong 0.7$ solid m^3. Conversely, the reciprocal is 1 m^3 solid wood = 1.43 st. c.m.

$$\mathrm{v(solid\ m^3)} = \mathrm{v(stacked\ m^3)} \times 0.7, \tag{2.36}$$

or

$$\mathrm{v(stacked\ m^3)} = \mathrm{v(solid\ m^3)} \times 1.43. \tag{2.37}$$

2.4.4 Conversion of Merchantable Wood Volume to GPP

Equipped with the basic specific wood density R and the expansion and conversion factors in Table 2.7, we can estimate roughly the net and gross primary production associated with a given volume growth and yield. Conversely, we can assess how the GPP is partitioned into respiration, turnover and growth of merchantable wood (including harvest losses, if desired). The following two examples summarise the derivation of wood volume from gross primary production.

In the first example, the steps for deriving GPP from the harvested volume (merchantable, under bark) are given in formulae (2.38a)–(2.38g).

Given that the harvest of a 150-year-old European beech stand results in V(merchantable, harvested u. b.) = $850\,m^3\,ha^{-1}$, which indicates excellent site fertility, this value can be transformed into standing merchantable volume over bark;

$$\begin{aligned} \mathrm{V(merch.,\ standing\ o.\ b.)} &= \mathrm{V(merch.,\ harvested\ u.\ b.)} \times 1/(l_s \times l_b) \\ &= 850\,m^3\,ha^{-1} \times 1.177 = 1{,}000\,m^3\,ha^{-1}. \end{aligned} \tag{2.38a}$$

(consider that all factors in Table 2.11 are rounded to two decimal places)

In the next step, we determine the total volume of the stand including all above and belowground biomass by applying the expansion factors

$$\begin{aligned} V(\text{standing}) &= V(\text{merch., standing o. b.}) \times e_{br} \times e_l \times e_r \\ &= 1{,}000\,m^3\,ha^{-1} \times 2.00 = 2{,}000\,m^3\,ha^{-1}. \end{aligned} \tag{2.38b}$$

Total volume yield including the intermediate thinnings V(total), i.e. including the turnover of all individual trees is

$$\begin{aligned} V(\text{total}, t_{ind}) &= V(\text{standing}) \times t_{ind} \\ &= 2{,}000\,m^3\,ha^{-1} \times 1.5 = 3{,}000\,m^3\,ha^{-1}. \end{aligned} \tag{2.38c}$$

Total gross volume yield, which includes the intermediate thinnings and plant organ turnover

$$\begin{aligned} V(\text{total}) &= V(\text{total}, t_{ind}) \times t_{org} \\ &= 3{,}000\,m^3\,ha^{-1} \times 1.3 = 3{,}900\,m^3\,ha^{-1}. \end{aligned} \tag{2.38d}$$

By multiplying this value by specific density R, we convert volume to biomass weight

$$W(\text{total}) = V(\text{total}) \times R = 3{,}900\,m^3\,ha^{-1} \times 0.5 = 1{,}950\,t\,ha^{-1}. \tag{2.38e}$$

Mean annual NPP of the 150-year-old European beech stand is obtained when this value is divided by the age of the stand, i.e. by 150 years

$$\begin{aligned} NPP &= W(\text{total})/\text{age} = 1{,}950\,t\,ha^{-1}/150\ \text{years} \\ &= 13.00\,t\,ha^{-1}\,yr^{-1}\ \text{or}\ 1.30\,kg\,m^2\,yr^{-1}. \end{aligned} \tag{2.38f}$$

Finally, we apply $f_{re} = 2.0$ to obtain a rough estimate of GPP

$$\begin{aligned} GPP &= NPP \times f_{re} = 13.00\,t\,ha^{-1}\,yr^{-1} \times 2 \\ &= 26\,t\,ha^{-1}\,yr^{-1}\ \text{or}\ 2.6\,kg\,m^2\,yr^{-1}. \end{aligned} \tag{2.38g}$$

In the reverse calculation, the reciprocal values of the expansion and turnover factors (cf. Table 2.7) enable one to partition the GPP (set 100%) roughly into NPP, total net growth, net growth standing, and net growth harvested (2.39a)–(2.39d). Figure 2.9 shows the reverse calculation of net stem growth harvested from NPP, indicating the various proportional volume losses in percent.

$$NPP = GPP \times (1/f_{re}) = 100\% \times 0.5 \cong 50\%, \tag{2.39a}$$

$$\begin{aligned} \text{Net growth total} &= NPP \times (1/t_{org}) \times (1/t_{ind}) \\ &= 50\% \times 0.77 \times 0.67 \cong 25\%, \end{aligned} \tag{2.39b}$$

$$\begin{aligned} \text{Net growth standing} &= \text{Net total biomass growth} \times (1/e_{br}) \times (1/e_l) \times (1/e_r) \\ &= 25\% \times 0.67 \times 0.95 \times 0.80 \cong 12.5\%, \end{aligned} \tag{2.39c}$$

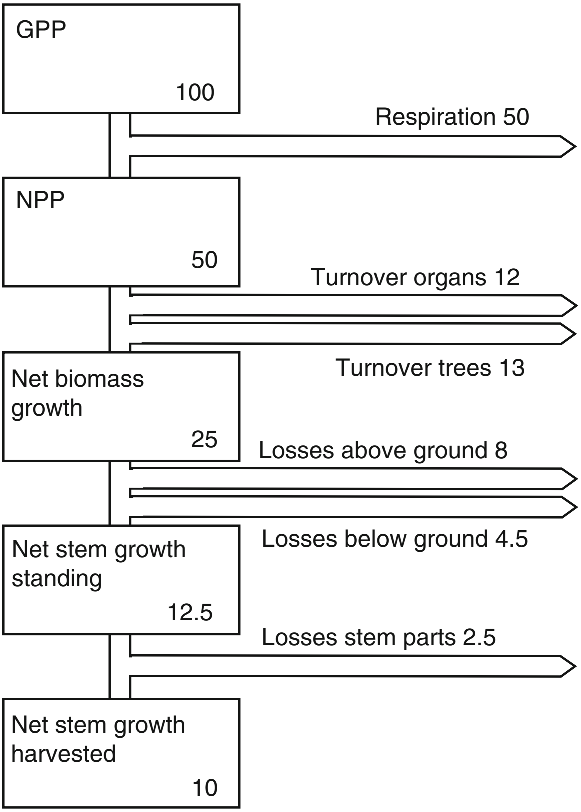

Fig. 2.9 Partitioning of a stand's total synthesised GPP (100%) in respiration, turnover of organs, turnover of whole trees, and losses due to harvest. During a stand development only about one tenth of the GPP and one fifth of the NPP are harvested as merchantable net stem growth

$$\begin{aligned}\text{Net growth harvested} &= \text{Net stem growth standing} \times (1/l_s) \times (1/l_b) \\ &= 12.5\% \times 0.90 \times 0.91 \cong 10\%.\end{aligned} \tag{2.39d}$$

It can be seen that only 10% of the GPP or 20% of the NPP is merchantable and actually harvested in conventional forestry practices. The percentages rise to about 15% and 30% respectively if the trees, which die as a result of self-thinning or which are harvested in intermediate thinnings, are included. Based on these calculations, it is now possible to compare the harvest index HI, commonly applied in agriculture, to the wood harvest in forests. HI is defined as the ratio of harvested biomass to net primary production:

$$\text{HI} = \text{Biomass extracted/NPP}. \tag{2.40}$$

In forestry, the biomass extracted corresponds to the harvested merchantable biomass, which was calculated to be 0.20 of the NPP and 0.30 when the turnover of previous intermediate harvests is included. If the total aboveground biomass was actually harvested (without harvest loss), the HI may rise to about 0.60 of NPP. Thus, in comparison with the HI of agricultural grass crops (HI up to 0.85), root crops (up to 0.86), or fast growing tree plantations such as willows, poplars or eucalypts (up to 0.70), the harvest index of the conventional wood harvest is much lower (cf. Larcher 1994, p. 128). In agriculture and fuelwood plantations, the high HI also reflects the considerable nutrient removal. As long as the conventional stem-wood harvest in forestry discards the crown in the forest, the majority of the nutrient minerals remain in the ecosystem.

2.5 Dead Inner Xylem

Unlike herbaceous plants, many tree species develop heartwood in the course of ontogenesis (Fig. 2.10, dark grey). For the comparison of growth and yield of woody and herbaceous plants, it is interesting to distinguish the living, or active tree biomass, i.e., the sapwood, from the dead biomass, i.e., the heartwood. We have specified the growth and yield of living, or active biomass as "true" growth and yield. The heartwood falls into the category of turnover, and has to be subtracted from the standing volume or biomass.

In a first approach, the true biomass can be estimated from the total biomass by a simple factor. Of course, the sapwood portion f_{sw} changes with age and size, but for regional or long-term averages, we can say;

$$\text{Biomass (living)} = \text{biomass} \times f_{sw}. \qquad (2.41)$$

The heartwood development usually begins when the physiological activity of the inner xylem, i.e. water conduction, has ceased. At a macroscopic scale, the

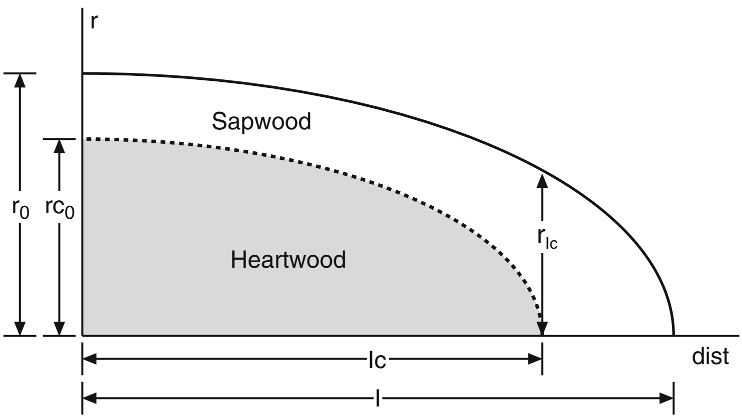

Fig. 2.10 Stem form (*continuous black line*) and border between sapwood and heartwood (*dashed line*) are approximated by a paraboloid. r_0 stem radius at ground level; l stem length; rc_0 radius of dead heartwood at ground level; lc length of core wood zone; r_{lc} stem radius at position lc where sapwood portion is 1.0

heartwood can often be recognised by a transition in colour from the lighter sapwood to the darker heartwood. The heartwood tissue is dead and less permeable to water-based solutions (Knigge and Schulz 1996, p. 104). The sapwood contains the functional, yet dead water-conducting tracheids and xylem vessels, living xylem parenchyma and, towards the outer edge, also the living cambium and phloem tissue. The heartwood development proceeds slowly, and is by no means circular (in year rings), but rather resembles amoeboid proliferations of heartwood into the sapwood (Fig. 2.11).

The proportion of heartwood usually increases with tree size and may be considerable. Trendelenburg and Mayer-Wegelin (1955, pp. 472–474) found

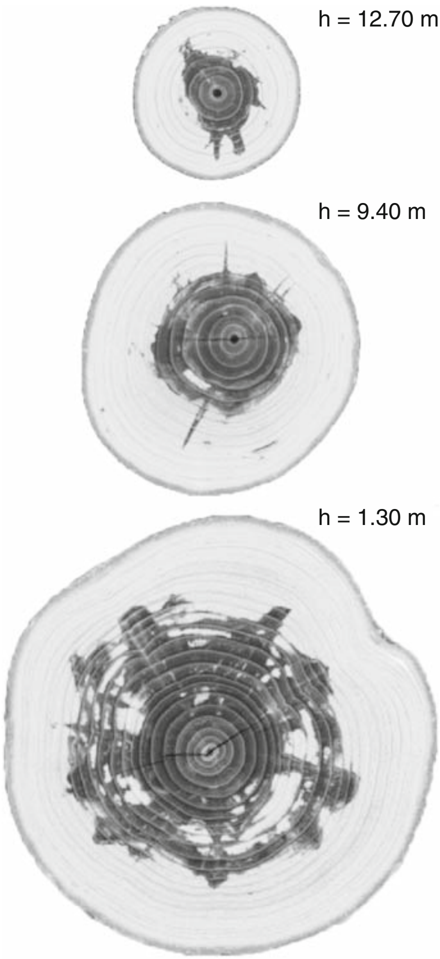

Fig. 2.11 Differentiation between sapwood (*light grey*) and dead heartwood (*dark grey*) via CT scanning. Stem disks of Norway spruce No. 22 from long-term plot TRA 639 near Traunstein/South Bavaria (age 40, $d_{1.3} = 29.1$ cm, $h = 18.9$ m). In the disks from heights of 1.3 m, 9.4 m, and 12.7 m, the portion of dead heartwood amounts to 39%, 26%, and 25%, respectively

percentage volumes of dead heartwood up to 36, 60, 53 and 74% for European beech, Norway spruce, Scots pine and Sessile oak respectively. Knigge and Schulz (1966, p. 109) report 50 and 75% for Scots pine and Sessile oak. According to Lohmann (1992, p. 46), the inert heartwood can comprise up to 78% in Norway spruce. We summarise the results into f_{sw} values ($f_{sw} = 1 -$ heartwood portion) for Norway spruce $f_{sw} = 0.22$–0.40, Scots pine $f_{sw} = 0.47$–0.50, Sessile oak $f_{sw} = 0.25$–0.26, and European beech $f_{sw} = 0.64$.

An efficient method for distinguishing sapwood and heartwood makes use of computer tomography (CT). In Fig. 2.11, we show the example of a 40 year-old Norway spruce tree from Traunstein (TRA 639) with $d_{1.3} = 29.10\,\mathrm{cm}, h = 18.90\,\mathrm{m}$ and a crown base height of $h_{cb} = 7.20\,\mathrm{m}$. The tree was cut into segments, and three sections at heights of 1.30, 9.40, and 12.70 m were inserted into a computer tomograph type SIEMENS Somatom AR.HP. At each height, three cross-sections 1 mm thick were obtained within close proximity applying an acceleration voltage of 130 kV. With the different intensity in the CT images resulting, the moist sapwood and the dry heartwood can be separated with commercial image software (here: Photoshop$^{\mathrm{TM}}$ 7.0). The percentage heartwood in Fig. 2.11 is 39% at 1.30 m height, 26% at 9.40 m height and 25% at 12.70 m height. Unlike conventional staining methods, which react to the starch content or ph-value, the CT method is based on water content, which is closely correlated to physiological activity (Vötter 2005).

Similar analyses of Norway spruce, Scots pine, Sessile oak, and European beech show a species-specific decrease in the proportion of sapwood from $f_{sw} = 1.0$ in the juvenile phase to 0.25–0.50 in the mature phase. The 3D computer tomography model of the proportion of sapwood and heartwood (Fig. 2.10) yields heartwood volume percentages (f_{sw} factors in brackets) of 0% in the juvenile phase of the tree ($f_{sw} = 1$), 1−35% at $d_{1.30} = 10$–$15\,\mathrm{cm}$ ($f_{sw} = 0.99$–0.65) and 3–56% at $d_{1.30} = 30$–$50\,\mathrm{cm}$ ($f_{sw} = 0.97$–0.44) (Pretzsch 2005c). The trees analysed were extracted from pure stands with aboveground biomasses 96–342 t ha^{-1} for Norway spruce, 45–153 t ha^{-1} for Scots pine stands, 109–433 t ha^{-1} for European beech and 93–171 t ha^{-1} for Sessile oak. The corresponding biomass of the dead inner xylem comprised 13–192 t ha^{-1}.

In forest inventories and measures, the differentiation between sapwood and heartwood is of little practical relevance and is disregarded (Oliver and Larson 1996, p. 332). Yet, scientifically, it enables some interesting connections to be made between woody and herbaceous growth and yield behaviour. If the "turnover" in form of increasing heartwood is included in the estimation of net growth, then the actual net growth is smaller than calculated, and turnover would equate with biomass production at a much earlier phase in stand life. Although general correction factors are still lacking, Pretzsch (2005c) outlines a preliminary approach for distinguishing between living sapwood and heartwood where it was possible to link self-thinning and maximum density rules for herbaceous plant communities (Yoda et al. 1963) and forests (Reineke 1933) (cf. Chap. 10, Sect. 10.4). When investigating the ecophysiological capacity or maximum density of an ecosystem, it makes sense to regard only the living, and therefore metabolically active biomass.

2.6 Growth and Yield and Nutrient Content

The immense amount of biomass stored in a forest is composed mainly of carbon, hydrogen and oxygen (C, H, O), but also of the nutrient minerals N, P, S, K, Ca, Mg, K and some trace elements. Unlike herbaceous vegetation with its annual or perennial cycles, this means that a tremendous pool of nutrient minerals is stored in the vegetation and temporarily withdrawn from the soil. These nutrients become available through the decomposition of the organic turnover, which, in some ecosystems such as the tropical rainforests, represents the main source. According to Fink (1969), dry organic biomass from vegetation consists of 90–95% C, H, O in the proportions 44–59% C, 42–46% O and 5–7% H. The remaining 5–10% consists of N, K (1–5%), Ca, Mg, P, S, Cl (0.1–2.0%), Fe, Mn, Zn, Cu, B (5–200 ppm) and Mo (0.2–5 ppm).

Table 2.12 lists the mean percentages of the macronutrients according to Jacobsen et al. (2003). Leaves contain the highest concentration of N, P, K, and Mg, bark the highest Ca concentration. The nutrient store in stems is minimal, on average 5–10% of the leaf concentrations. Broadleaved trees have higher nutrient concentrations than conifers in almost all tree compartments.

Table 2.12 Nutrient concentration in stem wood, bark, branches, leaves and/or needles, coarse roots, and fine roots (results for Norway spruce, Scots pine, Sessile oak and European beech according to Jacobsen et al. (2003))

Tree species	Nutrient	Stem wood mg g^{-1}	Bark mg g^{-1}	Branches mg g^{-1}	Leaves mg g^{-1}	Coarse roots mg g^{-1}	Fine roots mg g^{-1}
Norway spruce	N	0.83	5.17	5.24	13.36	4.14	10.77
	P	0.06	0.65	0.65	1.33	0.37	0.98
	K	0.46	2.83	2.39	5.70	1.38	2.18
	Ca	0.70	8.17	3.33	6.03	1.59	2.61
	Mg	0.11	0.77	0.53	0.79	0.30	0.55
Scots pine	N	0.76	3.85	3.61	14.46	1.77	7.44
	P	0.05	0.46	0.34	1.32	0.21	0.62
	K	0.42	2.08	1.67	5.03	1.08	1.47
	Ca	0.62	5.03	2.07	4.08	0.97	2.83
	Mg	0.18	0.61	0.43	0.87	0.30	0.45
Sessile oak Common oak	N	1.56	5.16	6.19	26.15	3.71	8.94
	P	0.08	0.30	0.43	1.74	0.27	0.74
	K	0.95	2.00	2.00	7.38	2.16	3.40
	Ca	0.46	21.49	4.41	11.43	4.07	6.18
	Mg	0.09	0.65	0.44	2.27	0.40	1.06
European beech	N	1.21	7.35	4.27	26.01	3.03	7.15
	P	0.10	0.50	0.48	1.46	0.35	0.60
	K	0.93	2.34	1.50	8.66	1.34	2.18
	Ca	0.95	20.52	4.02	8.88	2.69	5.29
	Mg	0.25	0.59	0.36	1.25	0.43	0.74

Nitrogen N attains concentrations between 13.36 mg g^{-1} (Norway spruce) and 26.15 mg g^{-1} (Sessile oak). The N concentration in tree compartments decreases in the following order: leaves > fine roots > brushwood ≅ bark > coarse roots > merchantable stem wood.

The amount of phosphorus P stored in the leaves is only approximately one-tenth the N content: between 1.32 mg g^{-1} (Scots pine) and 1.74 mg g^{-1} (Sessile oak). In the tree compartments, the phosphorus concentration decreases in the same order as for nitrogen: leaves > fine roots > brushwood ≅ bark > coarse roots > merchantable stem wood.

Potassium K, with leaf concentrations between 5.03 mg g^{-1} (Scots pine) and 8.66 mg g^{-1} (European beech), and magnesium Mg with leaf concentrations between 0.79 mg g^{-1} (Norway spruce) and 2.27 mg g^{-1} (Sessile oak) show the same distribution pattern as N and P.

Only for Calcium Ca, with bark-concentrations between 5.03 mg g^{-1} (Scots pine) and 21.49 mg g^{-1} (Sessile oak), does the order differ: rough bark > leaves > brushwood ≅ fine roots > coarse roots > merchantable stem wood.

2.6.1 From Total Biomass to the Carbon Pool

The C content is almost similar in all plant organs, and the lower concentration of carbon in leaves is negligible for the tree, so, generally, one can assume that carbon accounts for 50% of the total plant biomass.

$$\text{Biomass(C)} = \text{Biomass(total)} \times 0.5. \tag{2.42}$$

For a more differentiated C allocation pattern in relation to species, position in the stand, and so on, see Körner (2002). Taking the mean values of the standing wood volume from the BWI[2] (Table 2.9, Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz, 2005), the carbon pool of the stand biomass ranges from 102 t C ha^{-1} (Douglas fir) to 182 t C ha^{-1} (European beech). The average NPP values calculated range from 4.6 t C ha^{-1} yr^{-1} (Scots pine) to 9.4 t C ha^{-1} yr^{-1} (Douglas fir), and the biomass values for the almost 100-year-old evenaged central European forests in Table 2.10, (upper section) are equivalent to 189 t C ha^{-1} (European larch) to 506 t C ha^{-1} (Norway spruce). The NPP values for the stands in Table 2.10 range from 2.5 t C ha^{-1} yr^{-1} in mixed Norway spruce-Silver fir-European beech mountain forests, to 9.9 t C ha^{-1} yr^{-1} in mixed lowland Norway spruce-European beech forests.

2.6.2 Nutrient Minerals

While the C concentration is relatively stable among the tree compartments, the mineral nutrients N, P, K, Mg, Ca, S and the trace elements are concentrated in the

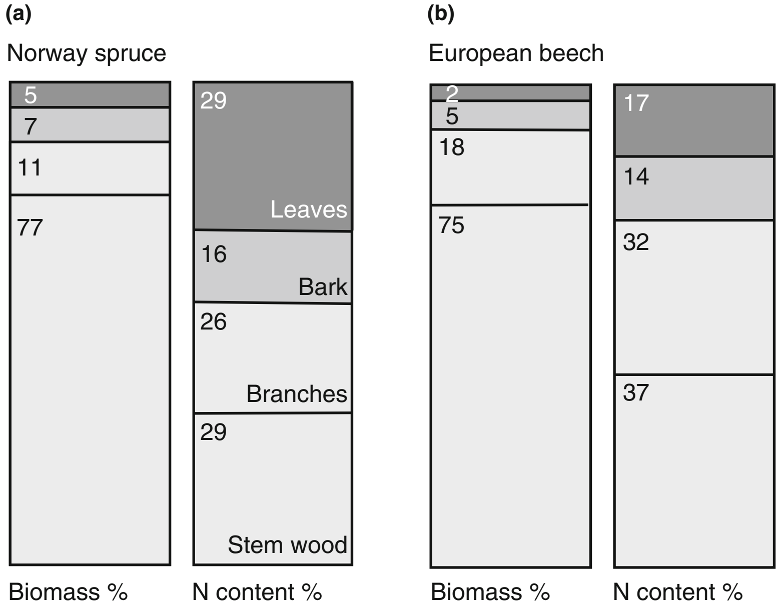

Fig. 2.12 Fraction of aboveground biomass and nitrogen in leaves, bark, branches, and stem wood at age 100 years. (**a**) For Norway spruce, the total above ground biomass at age 100 years amounts to 527 t ha^{-1} and the nitrogen content to 1.2 t ha^{-1}. (**b**) In European beech stands of the same age, the aboveground biomass is 347 t ha^{-1} and the nitrogen content 0.9 t ha^{-1}

leaves and the rough bark. Figure 2.12 depicts the mineral distribution for a 100 year-old (a) Norway spruce stand with 527 t ha^{-1}, and (b) European beech stand with 347 t ha^{-1} aboveground biomass respectively. In each case the left bar shows the distribution of the total aboveground biomass on the different tree organs stem wood, branches, bark and leaves. Although leaves, bark and branches make up only a minor part of the total biomass, they comprise a major portion of the total nitrogen content and other nutrient minerals.

For example, the total amount of nitrogen N stored in the aboveground biomass adds up to 1.2 t ha^{-1} for Norway spruce and 0.9 t ha^{-1} for European beech. Of this amount, 71% and 63% are stored in leaves, bark and branch wood of the Norway spruce and European beech stands, which contribute merely 23% and 25% to the total aboveground biomass respectively. The remaining 29% and 37% in each stand is present in the merchantable wood and is removed in the harvest. Since the distribution of the other macronutrients P, K, Ca, and Mg is more or less equal, it is estimated that the harvest of merchantable wood extracts one third of these minerals as well. Any additional harvesting of the crown, bark or brushwood leads to an over-proportional reduction in the mineral nutrients, which becomes especially critical on nutrient-limited sites.

By applying the biomass equations and the estimations of nutrients contents by Jacobsen et al. (2003) to standard yield table data for Norway spruce and European

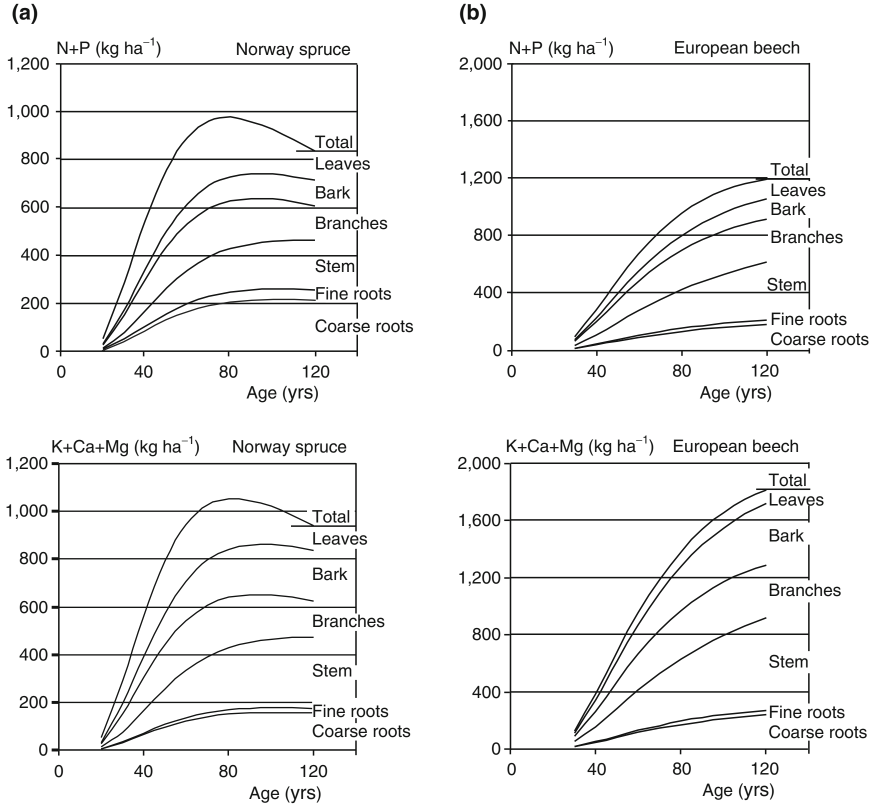

Fig. 2.13 Accumulation of N + P and K + Ca + Mg (kg ha^{-1}) in the total stand biomass, and in the separate compartments leaves, bark, branches, stem wood, fine and coarse roots. (**a**) For Norway spruce, we assumed site index II (Wiedemann, 1936/42, mod. th.). (**b**) For European beech, we applied Schober's yield table and site index I (Schober, 1972, mod. th.). For partitioning of biomass to tree organs and estimations of nutrients contents, we applied functions from Jacobsen et al. (2003)

beech, we now model the mineral nutrient distribution between the tree compartments during stand development. Again, the results are merely approximations. A particular stand may deviate significantly due to its site-specific nutrient constraints. As can be seen in Fig. 2.13, at age 120, Norway spruce stands (left) have accumulated about 1 t ha^{-1} N + P ($\sim$10:1), and an amount of 1 t ha^{-1} K + Ca + Mg. European beech stands accumulate more: 1.2 t ha^{-1} N + P and 1.8 t ha^{-1} K + Ca + Mg. In addition, the figure shows the distribution of N + P and K + Ca + Mg over the different plant organs. Whereas Norway spruce reduces the needle and branch wood biomass after 60–80 years of age, and thus the amount of minerals as well, European beech continues to increase leaf biomass and brushwood, and, consequently, also accumulates more minerals. Of course, in the short-term turnover of these organs, a certain amount of the minerals is constantly recycled and reused.

Table 2.13 Nutrient contents of forest stands of medium site quality at age 100 years. Estimation of standing volume is based on common yield tables from Wiedemann (1936/1942) for Norway spruce, Wiedemann (1943a) for Scots pine, Jüttner (1955) for Sessile oak (1972) for European beech. Nutrients content was estimated according to Jacobsen et al. (2003)

Tree species	Nutrient	Stem wood kg ha^{-1}	Bark kg ha^{-1}	Branches kg ha^{-1}	Leaves-needles kg ha^{-1}	Coarse roots kg ha^{-1}	Fine roots kg ha^{-1}	Total kg ha^{-1}
Norway spruce	N+P	201	106	174	187	218	41	927
Scots pine		125	61	84	98	80	51	498
Sessile/ Common oak		321	136	322	189	260	55	1,283
European beech		343	128	301	155	158	27	1,111
Norway spruce	K+Ca+Mg	287	214	185	159	158	19	1,022
Scots pine		188	108	89	39	60	24	508
Sessile/ Common oak		294	92	333	142	434	61	1,356
European beech		557	381	373	106	208	28	1,654

Table 2.13 summarises the assumed mineral pool, calculated in the same way as in the previous example, in forest stands aged 100 years (medium site quality). Together nitrogen and phosphorus range from 0.498 t ha^{-1} (Scots pine) to 1.283 t ha^{-1} (Sessile/Common oak). The amount of K, Ca and Mg ranges from 0.508 t ha^{-1} (Scots pine) to 1.654 t ha^{-1} (European beech). The N:P ratio is 10:1, and the K:Ca:Mg ratio is 30:60:10. Although thinning measures always recycle part of the minerals in the vegetation, at the end of the rotation period the soils have lost an estimated 1–3 t ha^{-1} minerals to the trees. In selection forests, which typically possess less standing biomass, the minerals stored in the vegetation are probably a little less, and the recycling is more even and not so concentrated at the time of harvest.

Table 2.14, above, gives a range for organic C and the mineral nutrient content stored in forest soils in central Europe (Ziegler 1991; Rehfuess 1981; Burschel et al. 1993). These values do not reflect the actual amount of minerals available to plants, but serve as rough comparisons with organic C and nutrient in the standing biomass (Table 2.14, below). With an organic C content in the soils of 35–362 t ha^{-1} (Ziegler, 1991) or 51–213 t ha^{-1} (Rehfuess 1981), the amount is equal in order of magnitude to the C content in the mean standing biomass in forests in Germany (Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz, BWI^2, Der Inventurbericht, p. 75) (cf. Table 2.9). A significant amount of nitrogen also can be stored in the ground vegetation. It can be seen, for instance, that on poor nutrient sites the ground vegetation contains one third of the total ecosystem nitrogen content in extreme cases.

Table 2.14 Range of organic carbon content C_{org} and nutrient content N, P, K, and C in soils in Southern Germany according to Rehfuess (1981) and (Ziegler, 1991), and nutrient content in standing biomass at age 100 years. For the estimation of nutrient content in standing biomass at age 100 years, compare Table 2.13

Compartment	C_{org} $t\,ha^{-1}$	N $kg\,ha^{-1}$	P $kg\,ha^{-1}$	K $t\,ha^{-1}$	Ca $t\,ha^{-1}$
Nutrients in soil					
min	35.00	4,260	2,890	79.0	6.0
max	362.00	21,420	9,895	766.0	578.0
Nutrients in standing biomass at age 100					
Norway spruce	138.10	844	83	0.373	0.568
Scots pine	109.95	456	42	0.150	0.293
Sessile and Common oak	152.65	1,205	78	0.520	0,745
European beech	182.30	1,019	92	0.495	1.031

The 100-year-old Norway spruce and European beech stand (Table 2.14) had accumulated 844, and 1,019 $kg\,ha^{-1}$ N respectively, as opposed to the 4,260–21,420 $kg\,ha^{-1}$ in the soil (Rehfuess 1981). The amount of phosphorus in the soil ranges from 2,890 to 9,895 $kg\,ha^{-1}$, compared to the 83 $kg\,ha^{-1}$ P in the Norway spruce and 92 $kg\,ha^{-1}$ P in European beech stand. Potassium accumulation amounted to 79–766 t ha^{-1} in the soil compared to 0.373 t ha^{-1} in the Norway spruce, and 0.495 t ha^{-1} in the European beech stand, and calcium accumulation to 6–578 t ha^{-1} in the soil compared to 0.568 and 1.031 t ha^{-1} in each stand.

2.7 Efficiency of Energy, Nitrogen, and Water Use

The energy, nitrogen, and water use efficiency (EUE, NUE, and WUE, respectively) specifies the production per resource demand. In the literature, we find a number of different parameters for the numerator, such as the photosynthetic activity in $\mu mol\,CO_2\,m^{-2}\,s^{-1}$, the NPP in t biomass $ha^{-1}\,yr^{-1}$ or the growth of aboveground dry matter in kg biomass $m^{-2}\,yr^{-1}$ (cf. Kimmins 1993; Landsberg 1986; Larcher 1994). In addition, various parameters are used for the denominator; e.g. for water use efficiency (WUE) can refer to annual precipitation, annual evapotranspiration or annual transpiration. The lack of convention creates difficulties in comparing different studies. Körner (2002) even questions the significance of efficiency quotients in general. Nevertheless, this chapter aims to give a rough idea of the resources needed per unit of wood production. For the production unit (numerator), we distinguish productivity of merchantable wood volume per unit area ($m^3\,ha^{-1}\,yr^{-1}$), annual NPP per unit area (total or aboveground) ($t\,ha^{-1}\,yr^{-1}$) and calorific value of net primary production ($GJ\,ha^{-1}\,yr^{-1}$). For the denominator, we refer to annual sum of global radiation per unit area ($GJ\,ha^{-1}\,yr^{-1}$) for EUE, average annual content of foliage nitrogen per unit area ($t\,N\,ha^{-1}\,yr^{-1}$) for NUE, and the annual sum of stand transpiration per unit area ($l\,m^{-2}\,yr^{-1}$) for WUE.

Therefore the efficiency quotients resulting are: EUE = productivity unit/global radiation; NUE = productivity unit/foliage nitrogen; and WUE = productivity unit/transpiration. We occasionally apply units such as litres of wood volume, and g or kg of biomass instead of cubic metres or tons to illustrate the relationships more clearly.

These efficiency parameters are especially relevant for forest production and management, and can be used as input for efficiency-driven hybrid growth models (cf. Chaps. 1 and 11). Furthermore, they also may reveal species-specific advantages in certain environments, for example a higher competitiveness under constrained water availability. It is often amazing that, on the one hand, large quantities of water and energy are needed to produce one unit of wood, e.g. approximately 1 J wood per 100–200 J global radiation, or 1 g wood per 500 g H_2O. On the other hand, for nitrogen, the relationship is reversed, e.g. 100–500 g wood per 1 g N. Simply put, if water and energy form the basis of your "soup", nitrogen and other nutrient minerals represent the "salt".

2.7.1 Energy Use Efficiency (EUE)

The calorific value of dry matter for European conifer and broadleaved species is 20.45 and 19.78 $kJ\,g^{-1}$, respectively (Runge, 1973). Ellenberg (1986, p. 331) determined the calorific values of each tree compartment for Norway spruce and European beech. For Norway spruce he obtained values of 20.36–20.79 $kJ\,g^{-1}$ for wood in stems, branches and roots, 20.34–21.14 $kJ\,g^{-1}$ in bark, 20.74–20.79 $kJ\,g^{-1}$ in the needles and fine roots, 21.25 $kJ\,g^{-1}$ in needle litter, and 36.87 $kJ\,g^{-1}$ in resin. The calorific values for European beech were 19.72–20.10 $kJ\,g^{-1}$ for stem, branch and root wood, 20.78–23.13 $kJ\,g^{-1}$ for bark, 20.30–21.63 $kJ\,g^{-1}$ for leaves and fine roots, 21.07 $kJ\,g^{-1}$ for leaf litter and 23.08 $kJ\,g^{-1}$ for beechnuts. Thus the merchantable wood, which comprises the largest portion of the long-term fixed biomass, has the lowest calorific value. Bark, with its protection and defence functions and its resin content, has a much higher calorific value. In general, the calorific value of herbaceous plants is lower than woody plants, of broadleaves lower than conifers, and of aquatic plants lower than terrestrial plants. Larcher (1994, p. 138) assumes that, in many cases, lower calorific values can be an evolutionary advantage as less energy needs to be invested.

The unit of the calorific value is $1\,J = 2.78 \times 10^{-7}\,kWh = 0.239 \times 10^{-3}\,kcal$. In the following discussion, we use units of kJ, MJ or GJ, which correspond to $J \times 10^3, J \times 10^6$ and $J \times 10^9$, respectively. For simplicity, we round the calorific value of broadleaved and conifer wood equally to $20\,kJ\,g^{-1}$ ($1\,g\,biomass \mathrel{\hat{=}} 20\,kJ \mathrel{\hat{=}} 0.0056$ $kWh = 4.78\,kcal$). The bark and resin, with their protection and defence functions, have higher values, but this does not affect the result significantly because they only

Table 2.15 Calorific value of various tree species per solid cubic metre stem wood (s. c. m, left) and stacked cubic metres (st. c. m, right). We apply the conversion factor st. c. m ≙ 0.7 × s. c. m. R represents the specific wood density defined on the basis of the green volume ($kg\,m^{-3}$). The biomass is given as $10^6\,g\,m^3$ (Mega g), calorific value in 10^9 Joule (GJ), and 10^6 Watt hours (Mega Wh)

Tree species	R $kg\,m^{-3}$	Biomass per m^3 Mega g	Calorific value per m^3 GJ	Calorific value per m^3 Mega Wh	Biomass per st. m^3 Mega g	Calorific value per st. m^3 GJ	Calorific value per st. m^3 Mega Wh
Balsawood	121	0.121	2.416	0.672	0.085	1.691	0.470
Grand fir	332	0.332	6.640	1.846	0.232	4.648	1.292
White pine	339	0.339	6.772	1.883	0.237	4.740	1.318
Poplar	377	0.377	7.536	2.095	0.264	5.275	1.467
Norway spruce	377	0.377	7.542	2.097	0.264	5.279	1.468
Sitka spruce	402	0.402	8.034	2.233	0.281	5.624	1.563
Douglas fir	412	0.412	8.248	2.293	0.289	5.774	1.605
Pine	431	0.431	8.614	2.395	0.301	6.030	1.676
Larch	487	0.487	9.746	2.709	0.341	6.822	1.897
Maple	522	0.522	10.444	2.903	0.366	7.311	2.032
European beech	554	0.554	11.086	3.082	0.388	7.760	2.157
Elm	556	0.556	11.110	3.089	0.389	7.777	2.162
Sessile-Common oak	561	0.561	11.222	3.120	0.393	7.855	2.184
Ash	564	0.564	11.284	3.137	0.395	7.899	2.196
False acacia	647	0.647	12.936	3.596	0.453	9.055	2.517
Bongossi	890	0.890	17.804	4.950	0.623	12.463	3.465
Pockwood	1,046	1.046	20.910	5.813	0.732	14.637	4.069

make up a small portion. By multiplying biomass, in tonnes, by 20, its calorific value can be converted to GJ. Tons of carbon, which makes up 50% of the biomass, must be multiplied by 40 to obtain the calorific value in GJ. The species-specific calorific values for wood volume in m^3 and stacked cubic metres st. c. m ($1\,m^3 \sim 0.7$ st. c. m) are summarised in Table 2.15.

For the denominator in the energy use efficiency quotient, we assume an annual sum of global radiation of 36,000 $GJ\,ha^{-1}\,yr^{-1}$ for central Europe between 47° and 57° N. For the period 1961–1990, the Bavarian climate stations reported the average value of 36,719 $GJ\,ha^{-1}\,yr^{-1}$, the Bavarian climate atlas 35,421 $GJ\,ha^{-1}\,yr^{-1}$ (Rötzer et al. 1997), the German climate atlas 36,000 $GJ\,ha^{-1}\,yr^{-1}$ and long-term climate stations determinations in the different regions in Germany a range between 33,600 and 40,799 $GJ\,ha^{-1}\,yr^{-1}$ (Ellenberg 1986). In the calculation of the energy use efficiency below, we assume an annual global energy sum of 36,000 $GJ\,ha^{-1}\,yr^{-1}$.

Table 2.16 summarises the EUE for the periodic annual merchantable volume increment ($m^3\,ha^{-1}\,yr^{-1}$) based on the national inventory (BWI^2, Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz, 2005). The values for the periodic annual merchantable volume increment (9.12–$16.37\,m^3\,ha^{-1}\,yr^{-1}$) were translated into NPP with the conversion factors introduced in this chapter (9.26–$15.80\,t\,ha^{-1}\,yr^{-1} = 185$–$316\,GJ\,ha^{-1}\,yr^{-1}$). The quotient EUE_V relates the growth of merchantable wood volume (volume in litre $ha^{-1}\,yr^{-1}$) to the annual sum of global radiation ($GJ\,ha^{-1}\,yr^{-1}$)

$$EUE_V = \frac{\text{PAI}}{\text{Global radiation}} (l\,GJ^{-1}). \tag{2.43}$$

The EUE_{NPP} uses NPP as a productivity unit ($kg\,ha^{-1}\,yr^{-1}$)

$$EUE_{NPP} = \frac{\text{NPP}}{\text{Global radiation}} (kg\,GJ^{-1}). \tag{2.44}$$

Finally, the $EUE_{cal\,NPP}$ is based on the calorific value of the NPP ($GJ\,ha^{-1}\,yr^{-1}$):

$$EUE_{cal\,NPP} = \frac{\text{calorific value NPP}}{\text{Global radiation}} (GJ\,ha^{-1}\,GJ^{-1}\,ha). \tag{2.45}$$

As can be seen in Table 2.16, the energy use efficiency in relation to merchantable wood volume lies between $EUE_V = 0.231\,GJ^{-1}$ for European oak, and $0.451\,GJ^{-1}$ for Norway spruce. EUE_{NPP}, the EUE in relation to NPP, amounts to $0.26\,kg\,GJ^{-1}$ for Scots pine and $0.44\,kg\,GJ^{-1}$ for European beech. The $EUE_{cal\,NPP}$ values of 0.005–0.009 reveal, that the efficiency ratio for the conversion of sun energy into biomass production only reaches $<1\%$. Most of the incoming radiation energy

Table 2.16 Energy use efficiency of various tree species in Germany. Estimate of productivity is based on mean periodic annual increment PAI according to Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz (2005, p. 167) and expansion and conversion factors reported in Sect. 2.4. Estimate of the corresponding sum of mean global radiation in $GJ\,ha^{-1}\,yr^{-1}$ is based on Rötzer et al. (1997)

Components	Norway spruce	European beech	Scots pine	Sessile and Common oak
Productivity				
PAI merch. volume ($m^3\,ha^{-1}\,yr^{-1}$)	16.37	9.12	11.74	8.25
NPP ($t\,ha^{-1}\,yr^{-1}$)	14.55	9.26	15.80	11.45
Calorific value of NPP ($GJ\,ha^{-1}\,yr^{-1}$)	291.00	185.20	316.00	229.00
Resource				
Global radiation ($GJ\,ha^{-1}\,yr^{-1}$)	36,000	36,000	36,000	36,000
Efficiency				
EUE_V (l merch. volume GJ^{-1})	0.45	0.25	0.33	0.23
EUE_{NPP} ($kg\,GJ^{-1}$)	0.40	0.26	0.44	0.32
$EUE_{cal\,NPP}$ ($GJ\,ha^{-1}\,GJ^{-1}\,ha$)	0.008	0.005	0.009	0.006

EUE_V refers to the litre of merchantable volume per GJ global radiation. EUE_{NPP} represents kg total net primary production per GJ global radiation. $EUE_{cal\,NPP}$ reflects efficiency ratio for the conversion of sun energy into biomass production.

(50–60%) does not fall within the photosynthetically useful spectrum; another 10–20% is reflected or transmitted, and most of the remainder is lost in the process of photosynthesis itself (cf. Larcher 1994, p. 118 and Körner 2002, p. 943).

The energy use efficiency EUE is an important parameter for the estimation of the potential productivity in a certain region, and can be used to initialise simple top-down models (e.g. Landsberg 1986, p. 173; cf. Chap. 11). It is clear that the global radiation solely cannot explain productivity, and to avoid errors caused by such a mono-causal approach, or to obtain a higher spatial resolution, additional limiting factors need to be included in estimation approaches, or in growth models.

2.7.2 Nitrogen Use Efficiency (NUE)

To derive rough estimates for NUE in European forests we apply the productivity values from the BWI^2 (Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz, BWI^2, Der Inventurbericht, p. 167). The estimation is based on the species-specific periodic annual volume increments (PAI) of stands in the age class 81–100. The foliage nitrogen content, estimated from the standing volume by using the scaling methods introduced in this chapter, revealed leaf nitrogen pools of 48.9–167.4 $kg\,ha^{-1}$. Table 2.17 provides an overview of nitrogen use efficiency values (NUE) in relation to the measures of productivity, stem volume growth in litres, aboveground biomass growth in kg, and NPP in kg. This results in NUE_V values of 108.7–293.51 of merchantable wood volume per kg foliage

Table 2.17 Nitrogen use efficiency of foliage of various tree species in Germany. Estimate of productivity is based on mean periodic annual increment of stands in age class 81–100 years according to Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz (2005, p. 167) and expansion and conversion factors reported in Sect. 2.4. The foliage nitrogen content is estimated according to Jacobsen et al. (2003)

Components	Norway spruce	European beech	Scots pine	Sessile and Common oak
Productivity				
PAI merch. volume ($m^3\,ha^{-1}yr^{-1}$)	18.2	8.4	14.4	8.6
above g. biomass ($t\,ha^{-1}yr^{-1}$)	10.0	5.2	11.9	7.4
NPP ($t\,ha^{-1}yr^{-1}$)	16.2	8.5	19.3	12.0
Resource				
Foliage nitrogen ($kg\,ha^{-1}$)	167.4	55.1	48.9	74.4
Efficiency				
NUE_V (l stem volume $kg^{-1}N$)	108.7	151.9	293.5	115.7
NUE_B (kg above g. biomass $kg^{-1}N$)	59.5	94.8	243.0	98.9
NUE_{NPP} (kg NPP $kg^{-1}N$)	96.6	154.1	394.9	160.6

NUE_V indicates how many litres of merchantable stem volume are produced in one year per kg foliage nitrogen available during the same year. NUE_B refers to the aboveground biomass in kg per kg foliage nitrogen. NUE_{NPP} stands for kg NPP per kg N.

nitrogen. Related to the aboveground biomass production, the efficiencies assume values of $NUE_B = 59.5–243.0$ kg aboveground biomass per kg leaf N, and, finally, of $NUE_{NPP} = 96.6–394.9$ kg NPP per kg foliage nitrogen (Table 2.17).

The latter nitrogen use efficiencies agree with values from Jørgensen and Schelde (2001) who determined a range of $NUE_{NPP} = 104–370$ kg NPP per kg foliage N from measurements of poplar, willow and pine. Comeau and Kimmins (1986) found a foliage nitrogen efficiency of 35–75 kg NPP per kg foliage N in *Pinus contorta* stands.

2.7.3 Water Use Efficiency (WUE)

The studies by Menzel and Rötzer (2007), Peck (2004), Rötzer et al. (1997), and Wohlrab et al. (1992) provide average transpiration values and an upper and lower limit for the most common tree species in central Europe (Table 2.18). They produce annual transpiration averages of 285–363 $mm\,yr^{-1}$ ($= l\,m^{-2}\,yr^{-1}$) and a minimum and maximum of 119 and 765 $mm\,yr^{-1}$, respectively.

As for EUE and NUE, the WUE is estimated for the tree species Norway spruce, Scots pine, European beech, and Sessile oak based on the average volume increment data PAI from the BWI[2] (Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz, 2005). As shown in Table 2.18, the PAI of 9.1–16.4 $m^3\,ha^{-1}\,yr^{-1}$

Table 2.18 Water use efficiency of various tree species in Germany. Estimate of productivity is based on mean periodic annual increment PAI according to Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz (2005, p. 167) and expansion and conversion factors reported in Sect. 2.4. Consumption of water for transpiration is estimated according to Menzel and Rötzer (2007), Rötzer et al. (1997), and Wohlrab et al. (1992)

Components	Norway spruce	Scots pine	European beech	Sessile and Common oak
Productivity				
PAI merch. volume ($m^3\,ha^{-1} yr^{-1}$)	16.40	9.10	11.70	8.30
above g. biomass ($t\,ha^{-1} yr^{-1}$)	8.95	5.70	9.72	7.05
NPP ($t\,ha^{-1} yr^{-1}$)	14.50	9.30	15.80	11.50
Resource				
Transpiration ($l\,m^{-2} yr^{-1}$)	287	342	363	285
min	119	173	268	171
max	516	765	601	327
Efficiency				
WUE_V (cm^3 merch. V $kg^{-1} H_2O$)	5.7	2.7	3.2	2.9
WUE_B (g above g. biomass $kg^{-1} H_2O$)	3.1	1.7	2.7	2.5
WUE_{NPP} (g NPP $kg^{-1} H_2O$)	5.1	2.7	4.4	4.0

WUE_V indicates how many cm^3 of merchantable volume can be associated with the transpiration of 1 l of water. WUE_B refers to g of aboveground biomass production per kg water. WUE_{NPP} represents the NPP in g per kg H_2O.

merchantable wood volume and 5.7–9.7 t $ha^{-1} yr^{-1}$ aboveground biomass results in water use efficiencies of $WUE_V = 2.7–5.7 cm^3$ wood volume per kg H_2O and $WUE_B = 1.7–3.1$ g aboveground biomass growth per kg H_2O, respectively. The calculation of the water use efficiency of NPP

$$WUE_{NPP} = \frac{NPP}{transpiration} (g\,NPP\,kg^{-1}\,H_2O) \qquad (2.46)$$

is based on 9.3–15.8 t $ha^{-1} yr^{-1}$ NPP, and yields 2.7–5.1 g NPP per kg H_2O, respectively.

Even though the expansion factors employed in the estimation of aboveground biomass and NPP are only first-order approximations, the water use efficiencies determined correspond well with literature values. Lyr et al. (1967, p. 181) and Assmann (1961, pp. 26–28) report values of 169 and 300 g transpired H_2O needed per 1 g biomass in Douglas fir and Sessile oak stands, respectively. Translated into WUE_B, this means 2.9–5.9 g biomass per kg H_2O. Larcher (1994, p. 107) indicates water use efficiencies in the order of 1.3–3.6 g biomass per kg H_2O for herbaceous plants, 1–2 g kg^{-1} H_2O for tropical woody plants, 3–5 g kg^{-1} H_2O for temperate conifer and broadleaf trees, and 3–6 g kg^{-1} H_2O for sclerophyllous shrubs. Landsberg (1986, p. 158) assigns the WUE a highly indicative value for production prognoses and models. Until now, the WUE is more widely used in agriculture, mainly because transpiration measurements are comparably difficult to obtain in forest vegetation.

2.7.3.1 Efficiency Parameters and Hybrid Models

The translation of traditional wood volume measures from forestry into NPP and the derivation of efficiency parameters, as shown in this chapter, are essential for understanding of hybrid models. Hybrid models are used for the prediction of NPP and stand development (Kimmins 1985; Kimmins et al. 1999). They integrate the knowledge of both forest and ecological sciences in much the same way as was done here. Readily available time series for the development of stand volumes are combined with intensive physiological measurements of biomass allocations available for limited sites and turnover rates to derive site-specific light, water or nutrient use efficiencies. These parameters are applied in hybrid models for estimating NPP, stand dynamics, and yield on a given site, e.g. in relation to silvicultural prescriptions, changing climate conditions, or other disturbance factors (cf. Chaps. 1 and 11).

Summary

This chapter draws a link between the volume-oriented forestry measures and the biomass measures used in production ecology. Tools and rules of thumb will be provided to convert the forestry growth and yield values into primary productivity

and production efficiencies, and vice versa. In ecological studies in the temperate zone of central Europe, direct physiological measurements of the gas exchange in plants and indirect estimations based on energy balances, litter production, or evaporation rates provide approximate values for gross primary production (GPP) of 20–40 t ha^{-1} yr^{-1} or 2–4 kg $m^{-2}yr^{-1}$ and net primary production (NPP) of 10–20 t ha^{-1} yr^{-1} or 1–2 kg m^{-2} yr^{-1}, respectively. Forest inventories and long-term experimental plots, on the other hand, report an average growth of merchantable wood volume of 10–20 m^3 ha^{-1} yr^{-1}. This chapter explains how to convert wood volume growth data to NPP through multiplication with the specific wood density, biomass expansion factors, and turnover rates and to GPP by adding respiration.

(1) The gross primary production (GPP) (in t ha^{-1} yr^{-1}) refers to the total biomass in a certain time period and area synthesised through photosynthesis. The net primary production (NPP) (in t ha^{-1} yr^{-1}) is defined as the biomass that remains after subtraction of the continuous losses through respiration. Growth is defined as the total biomass produced by a plant or a stand within a defined period (e.g. day, year, 5-year period). Depending on whether the biomass that was lost and turned over within this period (i.e. leaves, fine roots, branches or entire plant individuals) is included or not, we refer to gross or net growth. Yield is defined as the entire produced and accumulated biomass since the establishment of a stand. We distinguish gross and net yield, in analogy to the differentiation between gross and net growth. Gross yield includes the entire above and below ground ephemeral biomass losses like leaf litter, fine root turnover, and loss of entire tree individuals through mortality and/or thinning.

(2) In conventional forestry, which aims to produce stem wood, the approximate relative proportions of NPP, net biomass growth, and net stem growth harvested to 100% GPP are 50%, 25%, and 10%, respectively. This means that only 10% of GPP, or 20% of NPP, is merchantable and actually harvested in traditional forestry practice. The harvest index (HI = biomass extracted/NPP) is 0.2, or 0.3 when the intermediate thinning is included. Thus, compared to HI for agricultural grass crops (up to 0.85), root crops (up to 0.86), or fast growing tree plantations such as willows, poplars, and eucalypts (up to 0.60), HI for traditional multifunctional forest management is much lower.

(3) A list of the most important forestry parameters and their values is provided for temperate stands of central Europe. Growth or increment describes the rate at which the volume or coverage of a plant or a stand changes in a given time period current annual increment (CAI) expresses growth over one year, whereas periodic annual increment (PAI) expresses the mean growth over a period of more than one year. Yield is the entire biomass produced and accumulated since the stand establishment. Gross yield includes the accumulated turnover from the time of stand establishment, whereas net yield does not. The long-term productivity of a plant or a stand on a given site is expressed best by the mean annual increment MAI (synonym mean annual growth), obtained by dividing the yield at a given time n by the age t: $MAI = yield_n/t_n$. These terms are equally valid at the tree or stand level. For the main tree species in the temperate forests of central Europe maximum

PAI_V values typically lie in the order of $8-20\,m^3\,ha^{-1}\,yr^{-1}$, MAI_V values $5-19\,m^3\,ha^{-1}\,yr^{-1}$. While old stands on good sites may hold $1000\,m^3\,ha^{-1}$ and more, the German national forest inventory comes up with average stand volumes between $274–480\,m^3\,ha^{-1}$.

(4) To convert standing stem volume or merchantable volume to total biomass, the following factors are applied ("$\cong$" indicates thumb values): wood volume v (m^3) is converted to wood biomass w(t) by the specific wood density R ($w = v \times R$ with $R \cong 0.5\,t\,m^{-3}$); the merchantable volume, or merchantable biomass is multiplied by the brushwood factor $e_{br} \cong 1.5$ to obtain total volume, or aboveground total woody biomass respectively. In general, the reference value $e_l = 1.05$ provides a good estimation of leaf biomass for broadleaves (early mature to mature stands), whereas the conifer needle biomass is already included in the brushwood factor. As roots make up approximately 10–45% of the total tree biomass, we recommend using $e_r \cong 1.25$. The overall scaling factor $e_{br,l,r}$ for the direct conversion of merchantable wood volume, or biomass to total tree volume, or tree biomass, respectively can be calculated by $e_{br,l,r} = e_{br}e_le_r = 1.50 \times 1.05 \times 1.25 \cong 2.0$.

(5) The turnover during stand development incorporates the turnover of short-lived plant organs (bark, branches, leaves, roots), and entire trees that are removed through self-thinning or harvesting. For temperate forests in central Europe, we assume an ephemeral turnover factor of $t_{org} \cong 1.3$; volume or biomass growth MAI, PAI, or CAI is multiplied by t_{org} to obtain total primary production [e.g. $NPP = MAI(\text{total biomass})\,t_{org}$]. The turnover factor $t_{ind} \cong 1.50$ (1.08–1.77) estimates the total volume production (i.e. including removed trees) from the volume of the remaining stand; in other words the standing volume is multiplied by $t_{ind} = 1.50$ to obtain total volume production. The turnover depends on site conditions, stand age, species, and stand treatment, and estimated turnover is associated with considerable uncertainty.

(6) To determine harvested volume from the standing volume of stem wood including stump and bark, v(standing o.b.), the standing volume is multiplied by a reduction factor $l_s = 0.90$ due to the loss of the tree stump, which remains in the forest in conventional forestry harvesting practices. An additional loss factor $l_b = 0.80$ to $l_b = 0.94$ accounts for 6–20% bark loss, which is species-dependent. Therefore, the actual harvested volume comprises 72–85% of the standing volume over bark.

(7) Many tree species develop dead heartwood during their ontogenesis. In the comparison of growth and yield of woody and herbaceous plants, it makes sense to distinguish the living or active tree biomass, i.e. the sapwood, and the dead biomass, i.e. the heartwood. We specify the growth and yield of the living, or active, biomass as "true" growth and yield, while the dead heartwood falls into the category of the turnover. The true biomass can be estimated from the total biomass with a simple factor f_{sw} [$\text{biomass(living)} = \text{biomass} \times f_{sw}$], which presents the proportion of sapwood of the total wood. For Norway spruce, Scots Pine, Sessile oak, and European beech, the factor f_{sw} displays a species-specific decrease from $f_{sw} = 1.0$ in the juvenile phase to 0.25–0.50 in the mature phase.

(8) The biomass stored in a forest consists of 90–95% carbon, hydrogen, and oxygen (44–59% C, 42–46% O, 5–7% H) and the remaining 5–10% is comprised of N (1–5%), K, Ca, Mg, P, S, Cl (0.1–2.0%), Fe, Mn, Zn, Cu, B (5–200 ppm), and Mo (0.2–5 ppm). The C content is almost similar in all plant organs and lower in leaves. Since this difference is negligible at the whole-tree level, carbon is generally assumed to make up 50% of total plant biomass. The total biomass of evenaged central European forests about 100 years old ranges from 189 $t\,C\,ha^{-1}$ (European larch) to 506 $t\,C\,ha^{-1}$ (Norway spruce). A biomass value of 300 $t\ ha^{-1}$ or 30 $kg\ m^{-2}$, equivalent to 150 $t\,C\,ha^{-1}$ or 15 $kg\,C\,m^{-2}$, serves as an approximation of the average standing biomass of managed forests in central Europe.

(9) While leaves, bark, and branches constitute only a minor part of the total biomass, they contain a major fraction of the total nitrogen and other nutrient minerals. Although nutrients in the vegetation are always recycled, at the end of the rotation period, the forests have temporarily stored an estimated 1–3 $t\ ha^{-1}$ minerals in the vegetation. In a sample calculation for different stands at age 100 (medium site quality), the sum of nitrogen and phosphorus ranged from 0.498 $t\,ha^{-1}$ (Scots pine) to 1.283 $t\ ha^{-1}$ (Sessile oak) and the amount of K, Ca, and Mg from 0.508 $t\,ha^{-1}$ (Scots pine) to 1.654 $t\ ha^{-1}$ (European beech). On nutrient-poor sites, in extreme cases, the vegetation may contain one third of the total ecosystem nitrogen. Harvesting crown, bark, or brushwood significantly enhances the loss of mineral nutrients, which becomes especially critical on sites with limited nutrient availability.

(10) Energy, nitrogen, and water use efficiency (EUE, NUE, and WUE) specify productivity per resource demand (e.g. EUE = productivity/global radiation). For EUE, we assume an annual sum of global radiation in the denominator of 36,000 $GJ\,ha^{-1}\,yr^{-1}$ for central Europe between 47° and 57° N. The EUE_V relates the growth of merchantable wood volume ($m^3\,ha^{-1}\,yr^{-1}$) to the annual sum of global radiation ($GJ\,ha^{-1}\,yr^{-1}$) and ranges from 0.23 l GJ^{-1} for European oak to 0.46 l GJ^{-1} for Norway spruce. Using NPP as the productivity measure, the EUE_{NPP} amounts to 0.26 $kg\,GJ^{-1}$ for Scots pine and 0.44 $kg\,GJ^{-1}$ for European beech. When measuring productivity in terms of calorific value, $EUE_{cal\ NPP}$, we assume an equal calorific value for broadleaved and conifer wood of 20 $kJ\,g^{-1}$ (1 g biomass $\hat{=}$ 20 kJ $\hat{=}$ 0.0056 kWh = 4.78 kcal). Relating the calorific value to the global radiation, the resulting $EUE_{cal\,NPP}$ values of 0.005–0.009 reveal that the efficiency of the conversion of sun energy to biomass production is only $<1\%$.

(11) Nitrogen use efficiency (NUE) relates the stand productivity to the foliage nitrogen content, which was estimated to vary between 48.9 and 167.4 $kg\,ha^{-1}$ in temperate forests (calculated from averages of species-specific stand volumes for the class of 81–100 years of age). This results in NUE_V values of 108.7–293.5 litres of merchantable wood volume per kg foliage nitrogen. When related to the aboveground biomass production, the efficiencies assume values of NUE_B as 59.5–243 kg aboveground biomass per kg leaf N and NUE_{NPP} as 96.6–394.9 kg NPP per kg foliage nitrogen.

(12) Water use efficiency (WUE) relates stand productivity to annual stand transpiration. The latter lies between 285 and 363 $mm\,yr^{-1}$ (=litres $m^{-2}\,yr^{-1}$) in temperate forests. In relation to the annual growth of merchantable wood volume, WUE_V amounts to 2.7–5.7 cm^3 wood volume per kg H_2O; for aboveground biomass growth, WUE_B is 1.5–3.3 g per kg H_2O and for NPP is 2.7–5.1 g per kg H_2O, respectively.

(13) Hence, large quantities of water and energy are necessary to produce one unit of wood, e.g. approximately 1 J of energy fixed in wood for 100–200 J global radiation, 1 g wood for 500 g H_2O transpirated. In contrast, for nitrogen, the relation is reversed, e.g. 100–400 g wood production for 1 g N stored in the leaves. In simple words, when water and energy form the basis of your "soup", nitrogen and other nutrient minerals constitute the "salt".

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