Chapter 3
Above Ground Processes: Anticipating Climate Change Influences

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Introduction

Over the past 250 years since the beginning of the industrial revolution the amount of CO_2 in the atmosphere has been gradually increasing from ca. 275 to 390 ppm, largely as a result of land-use change and anthropogenic emissions from the burning of fossil fuels. The atmospheric CO_2 concentration ($[CO_2]$), which is now higher than it was at any time in the past 20–25 million years (Pearson and Palmer, 2000), rose at the rate of 1.9 ppm $year^{-1}$ for the 1995–2005 decade (i.e. the largest average increase observed for any decade in at least the last 200 years) (IPCC 2007) and is expected to double during this century. The most important consequence of this rise in $[CO_2]$ is a change in the long wave radiation balance and warming of the surface temperature of the Earth. The total temperature increase over the past 150 years was

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0.76°C. Moreover, the steady increase in the concentration of tropospheric O_3 and other air pollutants, including various kinds of aerosols have caused other climate changes. The IPCC Fourth Assessment Report (IPCC 2007) suggests that changes in atmospheric constituents and in radiative forcing of the climate system are likely to continue. The global average surface warming following a doubling of carbon dioxide concentrations is likely to be in the range of 2–4.5°C by the end of the century. Increasing temperature and atmospheric [CO_2] along with associated changes in the hydrological cycle will most likely alter the structure and function of forest ecosystems.

The three most important climate features that influence forests are precipitation, atmospheric and soil dryness, and temperature. Climate classifications are usually based on these three features, and especially the ratio of precipitation to atmospheric dryness. Thus, decreases in precipitation and/or increased atmospheric dryness (which can also result from increased temperatures unaccompanied by increases in absolute humidity) can change climate from mesic to semi-arid or arid. Climate change is expected to exacerbate and reiterate regional drought events, especially mid-latitude aridity (Jentsch et al. 2007). Dieback of forest trees in response to extreme climate events can have long-term impacts on community dynamics and species interactions (Condit et al. 1995; Breshears et al. 2005; Gitlin et al. 2006; Allen and Breshears 2007), and may feed back upon atmospheric CO_2 and climate.

There are several lines of evidence that temperate and boreal forests influence the physical and chemical properties of the atmosphere through evapotranspiration, albedo and carbon exchange, which may have positive and negative forcings on regional and continental climate (Bonan 2008; Rotenberg and Yakir 2010). The carbon cycle is the most important of the biogeochemical cycles implicated in the greenhouse effect, accounting for more than 63% of greenhouse forcing (IPCC 2007). The natural biogeochemical movement of carbon to and from the terrestrial vegetation is larger than that from anthropogenic activities (fossil-fuel use and deforestation). Of the 762 Pg of carbon in the atmosphere, about 122 Pg C are annually exchanged between the atmosphere and terrestrial vegetation, i.e. removed from the atmosphere through photosynthesis, and returned to the atmosphere by plant respiration and organic mass decomposition (Denman et al. 2007). More than 16% of the atmospheric CO_2 each year reacts with Rubisco (ribulose bisphosphate carboxylase-oxygenase, the primary photosynthetic enzyme which converts inorganic carbon, as CO_2, into organic compounds in terrestrial plants with the C3 photosynthetic pathway) in more than 95% of earth's plant species, including all temperate and boreal tree species.

Worldwide, forests play an important role in the global carbon cycle (Fig. 3.1) because they cover about 30% of the Earth's land surface (Bonan 2008). Forests are estimated to comprise about 95% of all aboveground and 40% of belowground terrestrial pools of organic carbon. They therefore contribute significantly to the terrestrial carbon sink (Körner 2006; Denman et al. 2007). Forests also play a major role in regulating the global hydrologic cycle (Fig. 3.2). Together with carbon sequestration, evapotranspiration, through feedbacks with clouds and precipitation, exerts a negative "physiological" forcing on regional and continental climate (Bonan 2008; Rotenberg

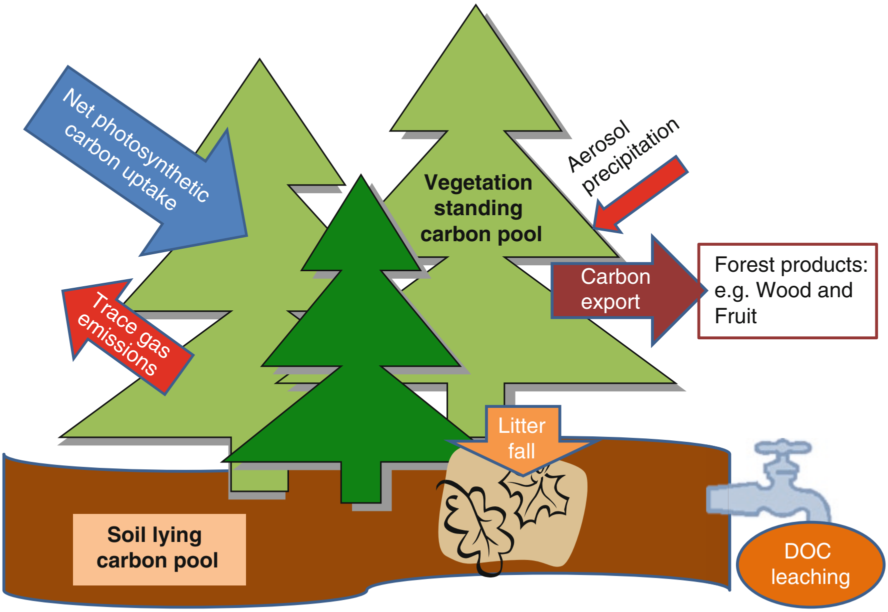

Fig. 3.1 Main components of the forest carbon cycle. The forest is a major factor in global carbon sequestration and represents a large standing pool of carbon. Changes in climate can lead to far reaching consequences for the forest carbon cycle and global CO_2 levels. Although carbon sequestration is a negative radiative forcing (blue), forest emission of isoprenoids and other greenhouse trace gases, and precipitation of aerosols in forest are positive forcings (red). Carbon leaves the forest in forest products or as dissolved organic carbon (DOC). Net photosynthetic uptake is described in the text

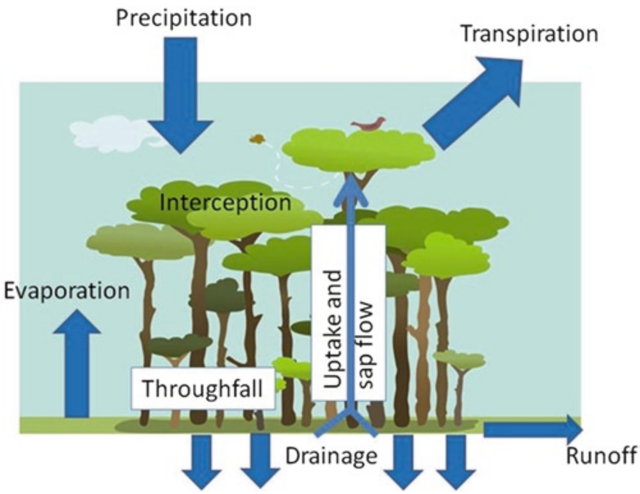

Fig. 3.2 Main components of the forest hydrological cycle. Small changes in any of the components of the forest hydrological cycle can have large influences outside the forest, e.g. changing flooding and water outflow, or groundwater and aquifer recharge. Quantifying these components is a major challenge

and Yakir 2010). Climate change may critically alter the biogeophysical and biogeochemical functioning of forests. Our current ability to predict when regional-scale plant stress will exceed a threshold that results in rapid and large-scale shifts in ecosystem structure and function is lacking. However, it is fundamentally needed to assess potential climate-change impacts (McDowell et al. 2008), including changes in vegetation and associated ecosystems and their feedbacks to the climate system (Keane et al. 2001; Scholze et al. 2006). Thus, understanding the effects of climate change on carbon assimilation and transpiration is critical to predict the future physiological feedbacks of forests on both the biosphere-atmosphere interactions (Bonan 2008; Rotenberg and Yakir 2010) and continental runoff (Betts et al. 2007).

This chapter discusses the interactive influences of climate change on forest processes at leaf (i.e. primary physiological and secondary metabolic responses), whole-plant (e.g. tertiary growth responses), and ecosystem levels (e.g. influences of forest on climate).

Elevated [CO_2] Influences on Leaf to Tree Level Processes

Along with land use transformation, changes in the chemical composition of the atmosphere, with increasing greenhouse gases, is the most important component of global change. Of the several anthropogenic greenhouse gases emitted globally, CO_2 is pre-eminent as an agent of potential future climate, as it accounts for about 63% of the gaseous radiative forcing responsible for anthropogenic climate change. Unlike temperature, precipitation and pollution concentrations, which have high spatial variations, rising [CO_2] is globally remarkably uniform and is likely to affect forest growth worldwide and, consequently, their “physiological” forcings on atmospheric temperature and hydrologic cycles. Therefore, studies on the effects of elevated [CO_2] on tree growth and resource use efficiency are crucial to understand the impact of rising [CO_2] on the biogeophysical and biogeochemical functioning of forests.

In the short-term, increasing levels of [CO_2] influence directly the physiology of terrestrial C3 plants via increased net photosynthesis (A) and decreased transpiration (E). Stomata modulate these primary physiological processes, because they act as control valves in the *pathways* of gaseous diffusion for the incoming CO_2 and the outgoing transpirational water vapour, enabling optimisation of CO_2 uptake per water loss. Notwithstanding this, A and E can themselves affect stomatal conductance (g_s) through several feedback loops (Wong et al. 1979). The implication of the complex direct or indirect feedback effects on g_s is that there are significant uncertainties about the physiological controls of stomatal behavior and it is not always apparent whether g_s controls gas exchange or vice versa. The first part of this section addresses the direct influence of rising [CO_2] on leaf gas exchange, by analysing the quantitative links between leaf biochemistry and gas exchange kinetics; the second part then reviews the main responses of forest trees to elevated [CO_2].

In C_3 species, short-term response of A to changes in intercellular CO_2 concentrations (C_i) are well known. In the model of Farquhar et al. (1980), A is given as:

$$A = v_c - 0.5v_o - R_d = v_c(1 - \Gamma^*/C_i) - R_d \tag{3.1}$$

where v_c and v_o are the carboxylation rate and the oxygenation rate of Rubisco, respectively, 0.5 is the stoichiometry between O_2 uptake by RubP (ribulose bisphosphate) oxygenase and photorespiratory efflux of CO_2 (Jordan and Ogren 1984), and Γ^* is the photosynthetic compensation point, i.e. the [CO_2] at which the photorespiratory CO_2 evolution equals the rate of photosynthetic CO_2 uptake. Using Fick's first law of diffusion, it is possible to measure E as:

$$E = g_{tw}(\chi_i - \chi_a) \tag{3.2}$$

where χ_i and χ_a are the water vapor concentrations inside the leaf and in the ambient air, respectively, and g_{tw} is the total leaf conductance to water vapour, which is given by:

$$g_{tw} = g_s \cdot g_{bl} / (g_s + g_{bl}) \tag{3.3}$$

where g_{bl} is the boundary layer conductance to water vapour. Stomatal conductance to water vapour can then be obtained from g_{tw} by removing the g_{bl} contribution:

$$g_s = 1/(1/g_{tw} - 1/g_{bl}) \tag{3.4}$$

Because CO_2 diffuses along the same pathway as water, and considering that the ratio of the binary molecular diffusivities of CO_2 and water vapor in air is taken as 1.6 in the stomata and 1.37 in the boundary layer, it is possible to calculate the combined boundary layer-stomatal conductance to CO_2 (g_{sc}) as:

$$g_{sc} = 1/(1.6/g_s - 1.37/g_{bl}) \tag{3.5}$$

Then net steady state A can be also expressed as:

$$A = g_{sc}(C_a - C_i) = g_m(C_i - C_c) = g_t(C_a - C_c) \tag{3.6}$$

where:

$$g_t = g_{sc} \cdot g_m / (g_{sc} + g_m) \tag{3.7}$$

g_m and g_t are the mesophyll conductance and the total conductance to CO_2 diffusion, respectively, while C_c is [CO_2] at the Rubisco binding sites in the chloroplast. C_c is proportional to the gradient between [CO_2] in the air (C_a) and in the chloroplasts. C_c is, therefore, inversely related to the total resistance to CO_2 diffusion from air through leaf boundary layer and stomata into both the substomatal cavities and the intercellular air spaces present in the mesophyll, i.e. boundary layer-stomatal resistance to CO_2 diffusion in the gas phase, and from the cell walls to the sites of carboxylation, i.e. mesophyll resistances to CO_2 diffusion in the gas and liquid phase (Centritto et al. 2003; Niinemets et al. 2009).

According to Eq. 3.1, A is dependent on the carboxylation-photorespiration balance and on respiration, and is ultimately driven by C_c (Eq. 3.6); whereas, assuming that the sub-stomatal cavity is saturated with water vapour, and that g_{bl} is not affected by growth in elevated [CO_2], leaf transpiration is controlled by g_s at any given absolute humidity of the outside atmosphere (Eqs. 3.2 and 3.4). Because respiration is not inhibited by growth in elevated [CO_2], contrary to what was reported in earlier studies as a result of an artefact of the way respiration measurements were made (Davey et al. 2004), Ainsworth and Rogers (2007) have recently pointed out that rising [CO_2] affects plants and ecosystems via two fundamental processes: enhanced A and reduced g_s. Because the kinetics sensitivity of these two physiological processes to climate change factors affects both the carbon and the hydrological cycles, they are becoming embedded in models of the biogeochemical and of land surface feedbacks on climate (Bonan 2008).

CO_2 may be directly sensed by the surface of the guard cells in response to variations in C_i. Mott (1988) showed that stomatal aperture responds to C_i, such that the C_i/C_a ratio remains approximately constant. This conservative ratio indicates that changes in C_a, by causing proportional changes in C_i, make responses to C_i effective sensors of changes of C_a (Mott 1988). However, conservative C_i/C_a ratios imply that stomatal conductance (Eq. 3.6) and, in turn, leaf-level transpiration (Eq. 3.2), decrease as [CO_2] increases.

At ambient [CO_2], the operating C_c is generally at the transition between the limitations to photosynthesis caused by Rubisco activity and RubP regeneration capacity (Farquhar et al. 1980). However, because g_t is usually lower in forest trees than in herbaceous and shrub species (Niinemets et al. 2009), C_c of non-stressed trees is well below the transition from Rubisco carboxylation-limitation to RuBP-regeneration limitation (Fig. 3.3). This implies that Rubisco is not CO_2-saturated at current atmospheric [CO_2] and, consequently, A is limited by substrate supply. Moreover, CO_2 is in competition with O_2 for the active sites of Rubisco, which consequently can react with either CO_2 or oxygen, the latter leading to photorespiration, which generally accounts for about 30% of carbon loss in C3 leaves at 25°C (von Caemmerer and Quick 2000). Despite the decline in stomatal conductance and, consequently, in total diffusional limitations to photosynthesis (Eq. 3.6), increases in [CO_2] will result in higher C_c which will not only reduce photorespiratory loss by decreasing the oxygenation rate of Rubisco (Stitt and Krapp 1999), but will also concomitantly increase its carboxylation reaction rate. Thus, C3 photosynthesis is stimulated in elevated [CO_2], although its marginal increment declines as [CO_2] increases (Fig. 3.3) (Körner 2006; Loreto and Centritto 2008). Decreased g_s associated with high C_i is an adaptive response to C_a, by which diffusional limitations to A are adjusted in response to changes in mesophyll demand for CO_2 (i.e. the biochemical limitations to A) resulting in an increase in instantaneous transpiration efficiency (ITE) (Centritto et al. 2002; Wullschleger et al. 2002; Hu et al. 2010).

The effects of growth in elevated [CO_2] on g_m have surprisingly received little attention, and the few published studies have reported either unaffected g_m, in *Betula pendula* (Eichelmann et al. 2004), in shade leaves of *Liquidambar styraciflua* and in *Populus tremuloides* (Singsaas et al. 2003), or increased g_m, in sun leaves of *Liquidambar styraciflua* (Singsaas et al. 2003), in response to elevated [CO_2]. On the

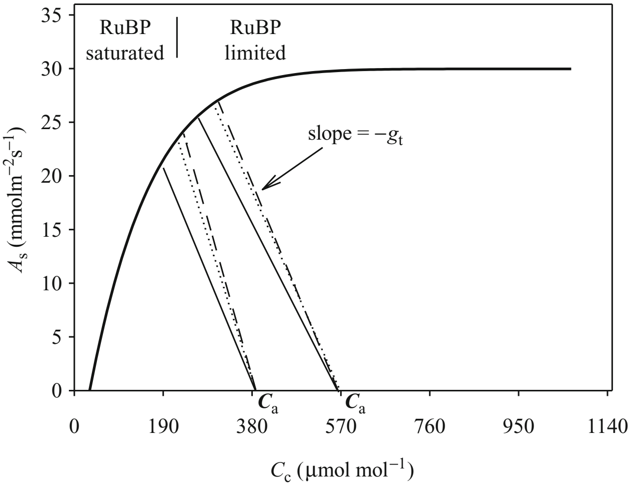

Fig. 3.3 Summary of A_s/C_c (ratio of assimilation to CO_2 concentration at the chloroplast) curves, plotted from average *J*, *V* and maximum *A* at saturating [CO_2] and PPFD, in plants of *Populus nigra* (Centritto et al. 2010 unpublished results). The initial slope of the curve is limited by Rubisco carboxylation efficiency, and is therefore ribulose-1,5-bisphosphate (RuBP) saturated. Beyond the inflection curve, A_s is assumed to be limited by the potential RuBP regeneration rate. The lines relating either ambient or elevated C_a (ambient CO_2) to A_s are the supply function for CO_2 in trees (—), crops and legumes (·······), and grasses (----), with the slopes of these lines equal to $-g_t$

contrary, the effects of elevated [CO_2] on *A*, g_s and ITE of forest species have been investigated in many studies (see for reviews: Curtis and Wang 1998; Ainsworth and Long 2005; Körner 2006). A meta-analysis of many FACE (Free Air Carbon dioxide Enrichment) experiments on forest trees (Ainsworth and Long 2005) showed that elevated [CO_2] resulted in a 47.4% increase in PPFD-saturated *A*, a 28.6% increase in the diurnal photosynthetic carbon assimilation, a 73.7% increase in ITE, and a 15.9% decrease in g_s (Fig. 3.4). It has been frequently reported that long-term growth in elevated [CO_2] may induce loss of photosynthetic capacity in C_3 species (Stitt and Krapp 1999). Downward acclimation of photosynthetic capacity may represent an optimisation of the distribution of the resources within the chloroplast to avoid the situation where either Rubisco or the apparatus for the regeneration of RuBP are in excess. Although some acclimation of photosynthesis capacity has been demonstrated in studies of trees grown in open-air field conditions, e.g. in fast growing poplar clones (Bernacchi et al. 2003) and in 1-year-old pine foliage (Crous et al. 2008), it is noteworthy that virtually no significant downward acclimation of photosynthesis of tree species, as expressed by maximum Rubisco carboxylation rate (*V*), maximum rate of electron transport (*J*) and *V*/*J* ratio (Fig. 3.4), was found by Ainsworth and Long (2005) in their literature review of FACE experiments. This is further evidence that when plants growing in elevated [CO_2] are rooted in the ground and adequate sinks are available so that N uptake keeps pace with carbon uptake and the source-sink functional balance is not altered,

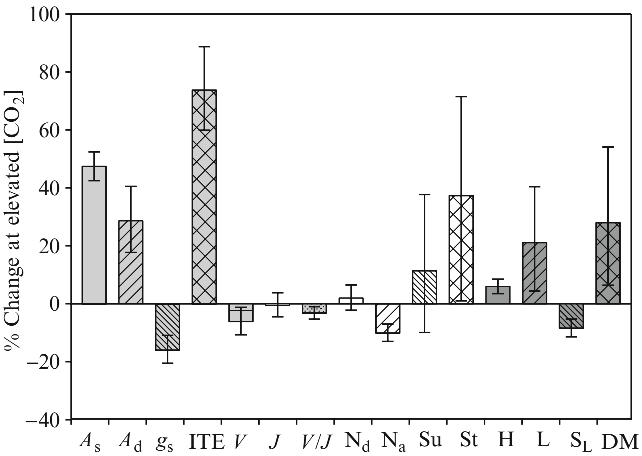

Fig. 3.4 Mean response (±95% confidence interval) of forest trees to elevated [CO_2] (data derived from the meta-analysis of many FACE experiments by Ainsworth and Long 2005): light saturated photosynthesis (A_s), diurnal carbon assimilation (A_d), stomatal conductance (g_s), instantaneous transpiration efficiency (ITE), maximum Rubisco carboxylation rate (V), maximum electron transport rate (J), V/J ratio, nitrogen content per unit of dry mass (N_d), nitrogen content on leaf area basis (N_a), sugar (Su) and starch (St) content on area basis, plant height (H), leaf-area index (L), specific leaf area (S_L), above-ground dry matter production (DM)

downward acclimation of photosynthetic capacity does not occur (Centritto et al. 2004; Springer et al. 2005).

The main tree responses to elevated [CO_2] are summarized in Fig. 3.4. In general, trees are more responsive to growth in elevated [CO_2] than plants belonging to other functional groups (Ainsworth and Long 2005; Körner 2006). In fact, despite the fact that height increased by only 6%, trees showed the largest response in terms of LAI (+21.1%) and aboveground dry mass (+28%) in response to growth under FACE (Fig. 3.4). Furthermore, Norby et al. (2005) found that the stimulation of forest net primary productivity in response to elevated [CO_2] is highly conserved across a broad range of productivity. The largest response of trees to elevated [CO_2] has been ascribed to a number of concomitant factors. First of all, g_{sc} and g_m are generally lower in forest trees than in other plants (Niinemets et al. 2009), resulting in lower g_t and, consequently, in lower C_c (Fig. 3.3). Because at current atmospheric [CO_2] the operating C_c of C3 plants lies in the curvilinear region of the photosynthetic-C_c response curve, the lower C_c of forest trees implies that as C_a increases the stimulation in A is higher than the increase for other functional groups (Fig. 3.3). In addition, for the most part, trees grown under FACE conditions were not only young and fast-growing, but were grown in either decoupled (in terms of nutrient supply, i.e. plants non depending on a natural nutrient cycle) or expanding (plants given ample space and time to access the available resources per unit land area) systems (see Körner 2006, for a thorough review). These trees could then accumulate "signals" (Körner 2006) propagating their effect over growing seasons

(Blackman 1919; Centritto et al. 1999b), resulting finally in their being more responsive to elevated [CO_2] than crops and grassland (Ainsworth and Long 2005). It is noteworthy that no lasting growth stimulation by CO_2 enrichment was found in 32-to 35-m-tall, mature trees in a near-natural deciduous forest (i.e. in a coupled systems': steady-state nutrient cycle and full canopy development - Körner 2006) in Switzerland after 4 years (Körner et al. 2005).

Drought, Rising Temperature, and Extreme Events Influences on Leaf to Tree Level Processes

Recent drought events, which are part of a widespread pattern of drying throughout the Northern Hemisphere, and which appear to be the worst since at least the middle of the fifteenth century, have the potential to become more frequent and exert an impact on larger mid-latitude areas, as projected by general circulation models. Warmer air temperature will exacerbate the impact of drought on plant water loss by elevating the vapour pressure deficit (VPD) in the atmosphere, thereby increasing the potential transpiration (see review by Mc Dowell et al. 2008). Mc Dowell et al. (2008) pointed out that elevated temperature may increase hydraulic failure and carbon starvation, and that changes in demographics of mortality agents (Thomas et al. 2002), such as insects and pathogens, may amplify carbon starvation, the main mechanism for drought driven mortality, when a species and site specific critical threshold of evapotranspiration is surpassed. The progressive massive dieback of woody plants, primarily Norway spruce (*Picea abies* L.) in the central Europe regions has recently become a well-known reality (Střelcová et al. 2009). Similar damaged stands are in boundary regions of Poland, in the Czech Republic, Germany and Italy. Furthermore warming is predicted to cause earlier snow melt and this is likely to increase the length and severity of summer droughts.

Drought influences plant growth in a number of different ways, i.e. through a decrease in the water potential of cambial cells, resulting in subsequent inhibition of cell growth, reduction of metabolic activity, inhibition of stomatal conductance and consequently of photosynthesis. Physiological processes are sensitive indicators of stress in plants, especially in extreme environmental conditions. However, it is difficult to identify all of the relevant factors influencing the water regime of forest stands, although Schwalm et al. (2010) have recently shown that assimilation is more sensitive to drought than respiration at the ecosystem level. To describe the water demands of tree species precisely it is important to know their response to various water stress levels and to characterise symptoms and consequences of the drought effect on forest trees and stands. At the tree level, sap flow measurements provide accurate estimates of the tree water supply and sap flow is also a good indicator for tree water stress (Nadezhdina 1999). Transpiration and consequently sap flow is controlled by atmospheric demand and soil water content. Air temperature, radiation, wind speed and air humidity are the main driving forces of the atmospheric demand, which is characterized by the potential evapotranspiration

(PET). PET can be calculated by using the FAO Penman-Monteith equation (Allen et al. 1998). A threshold for soil water deficit can be derived by using the definition of “relative extractable soil water” (R_{ew}) of Bréda et al. (1995):

$$R_{\mathrm{ew}} = \left(S_{\mathrm{act}} - S_{\mathrm{min}}\right) / W_{\mathrm{ext}} \tag{3.8}$$

where S_{act} is the actual soil water content; S_{min} is the minimum observed soil water content and W_{ext} is the maximum observed extractable water. A R_{ew} threshold between “control by demand” and “control by offer”of 0.4 indicates soil water deficit. Transpiration, photosynthesis and respiration are sharply decreased when the R_{ew} drops below this threshold (Granier et al. 2007). If sufficient soil water is available for the trees, transpiration is dominated by PET and the correlation between PET and sap flow is strong. As soil water reserves shrink due to drought, available soil water decreases and the correlation between PET and the transpiration weakens. Consequently, soil water content is the major determinant of transpiration. After soil water reserves are recharged the atmospheric demand returns to playing a major role in transpiration (Leitgeb et al. 2002).

Plant responses to [CO_2] can be either amplified or reduced by water and nutrient limitations (McCarthy et al. 2010) and by rising temperature, which is already increasing growing season length over Europe (Menzel and Fabian 1999). Curtis and Wang (1998) showed that growth of woody plants in elevated [CO_2] was halved under nutrient limitations. Ainsworth and Long’s synthesis (2005) of the results from FACE experiments supports these conclusions. Similarly, McCarthy et al. (2010) found that the absolute enhancements of net primary productivity of trees growing in elevated [CO_2] became progressively smaller as nitrogen availability decreased and were not observable when nitrogen availability was very low. In contrast, low water availability is often shown to amplify tree growth responses to elevated [CO_2] (Wullschleger et al. 2002; Seiler et al. 2009). Amplifications of CO_2 responses in water stressed conditions is caused by reduced g_s and, in turn, by decreased leaf level transpiration under elevated [CO_2], which may lead to an increase in plant water potential and water use efficiency (Centritto et al. 2002), a delay in the onset of drought (Centritto et al. 1999c), and a conservation of soil water (Wullschleger et al. 2002).

Many studies have addressed the interactions that arise between elevated [CO_2] and drought, and most have focused on one or more components of plant water relations (Tschaplinski et al. 1993; Tognetti et al. 1998, 2000b; Centritto et al. 1999c; Ellsworth 1999), addressing the potential interaction between elevated [CO_2] and drought by direct multifactor manipulations (Johnsen 1993; Centritto et al. 1999a), comparing drought-induced changes in plant water relations at natural CO_2 springs (Tognetti et al. 1999, 2000a) or inferring CO_2-drought interactions by observing seasonal patterns of response (Ellsworth 1999; Tognetti et al. 2000b; Domec et al. 2009; McCarthy et al. 2010). These studies attempted to interpret results in the context of the potential ameliorating effects that elevated [CO_2] may have on the drought response of trees. The most direct impact is the reduction in transpiration caused by lower stomatal conductance commonly found under elevated [CO_2], which may ameliorate drought tolerance by increasing leaf or whole-plant water-use efficiency, thus enabling plants to better exploit water-limited environments. Increased allocation of carbon to root growth and osmotic adjustment in plants exposed to elevated [CO_2] may, for example, alleviate the negative impacts of water stress by improving the capacity to extract soil water. Elevated [CO_2] may also influence water relations and plant responses to drought by altering developmental processes, including root and shoot architecture (Miao et al. 1992) and leaf morphology (Thomas and Harvey 1983). However, because elevated [CO_2] often increases leaf area index and its negative effect on g_s tend to be reduced under water stress (Centritto et al. 1999c; Tognetti et al. 1999; Centritto et al. 2002; Gunderson et al. 2002; Domec et al. 2009), the benefits of CO_2-improved conservation of soil water in terms of maintaining growth or carbon gain during drought appear relatively minor (Wullschleger et al. 2002). McCarthy et al. (2010), by re-assessing 10 years of data from the Duke FACE experiments, found that the amelioration of drought effects by increased [CO_2] was observed only in the presence of very high nitrogen availability.

Rising temperature will have contrasting influences on A and g_s with respect to elevated [CO_2], and may also affect respiration. Rising temperature will increase the solubility of O_2 and especially the specificity of Rubisco for O_2, relative to CO_2, and this will decrease the RuBP-saturated and the RuBP-limited rates of carboxylation, favouring oxygenation and thus increasing the ratio of photorespiration to A (Jordan and Ogren 1984). However, because carboxylation by Rubisco will be favoured in elevated [CO_2], the depression of the rate of oxygenation relative to carboxylation by elevated [CO_2] will produce an upward shift in the temperature optimum of A (Long and Drake 1992). Moreover, Ehleringer and Björkman (1977) have shown that the maximum quantum yield (φ) of C_3 species decreases with increase in temperature, since increasing amounts of the NADPH and ATP produced by electron transport are diverted into photorespiration. By decreasing photorespiration elevated [CO_2] will reduce the decline in φ at all temperatures (Ehleringer and Björkman 1977). Consequently, the compensation photon flux density of A is also depressed at all temperatures by elevated [CO_2], and, as for A and φ, the effect will be largest at higher temperatures (Long and Drake 1992). Eventually, the impact of elevated temperature on A is dependent on whether temperature will increase beyond the thermal optimum of photosynthesis (Long and Drake 1992). Respiration, like photosynthesis, follows a general temperature-response curve: increases exponentially with temperature in its low range, reaches a maximum at an optimal temperature, and then declines. In short-term studies, respiration is usually stimulated by rising temperature. However, long-term studies show that respiration acclimates to growth temperature (Atkin et al. 2005), resulting generally in a respiration to photosynthesis ratio remarkably insensitive to rising temperature (Gifford 1995; Arnone and Körner 1997).

The effect of lower g_s on transpiration under elevated [CO_2] may be partially offset by a rise in canopy temperature, actual transpiration and hence canopy vapour pressure. This effect may be offset by an increase in leaf area and hence absorption of radiation. Another direct impact of climate change on water use is the increase in transpiration caused by larger canopy–atmosphere vapour pressure gradients that develop under rising air temperatures. The increase in these gradients is believed to be only partially offset by rising atmospheric humidity caused by more rapid evapotranspiration. Thus, regional soil drying is a projected consequence of some climate change scenarios unless accompanied by substantial increases in precipitation. There is much uncertainty about the net effects of elevated [CO_2] and temperature on stand water requirements. During the day the plant is under a heavy energy load consisting mainly of the incident solar radiation and ambient air temperature. While some of this energy is important for photosynthesis, most of it is not utilized and must be dissipated. It is partly dissipated by thermal radiation emission and sensible heat transfer to the air, but most of it is dissipated by transpiration ('latent heat'). Transpiration causes leaves to cool relative to ambient temperature when the environmental energy load on the plant is high. The rate of transpiration is also directly related to the air VPD (which is negatively related to relative humidity) and wind speed.

Experimental evidence shows contrasting results with respect to tree responses to combined increases in [CO_2] and temperature. Norby et al. (1995) found that above-ground biomass of sugar maples was decreased in response to warming, whereas Teskey (1997) and Wang et al. (2003) found inconsistent responses in enhancement of photosynthesis to elevated CO_2 and temperature in pine trees. Thus, our recognition of the myriad of interactions between plant and environment, with various feedbacks, indicates that only with advanced modelling of tree processes will we be able to fully assess the influences of climate change scenarios.

Extreme events, which are likely to increase in frequency and magnitude, are predicted to have a significant impact on forests. High temperatures usually occurring in concert with drought can cause large-scale declines in productivity. In the temperate zone of Europe, the 2003 summer heat wave, with its exceptionally hot and dry spell, caused a 195 g C m^{-2} $year^{-1}$ decline in ecosystem photosynthesis and a reduction in ecosystem respiration of 77 g C m^{-2} $year^{-1}$, resulting in a net annual loss of 0.5 Pg of carbon across the continent (Ciais et al. 2005; Bréda et al. 2006), roughly corresponding to 4 years of net ecosystem carbon storage, and increased forest mortality (Bigler et al. 2006). It has been suggested that such a crash of about 30% in gross primary productivity over Europe was unprecedented during the last century. Battisti and Naylor (2009) recently pointed out that in temperate regions extreme seasonal heat, such as that during the 2003 heat wave in central Europe, could become the median seasonal temperature in many locations by the end of the twenty-first century. Thus, climate-change driven frequency of droughts, or climatic variability (IPCC 2007), can lead to vegetation failure (Swetnam and Betancourt 1998; Martínez-Vilalta et al. 2002). Warmer air temperature will exacerbate the impact of drought on plant water loss by elevating the VPD of the atmosphere, thereby increasing the atmospheric demand for transpiration. Altered net radiation associated with climate change could also increase transpiration (see discussion below). Given the potential risks of climate-induced forest dieback, increased management attention to adaptation options for enhancing forest resistance and resilience to projected climate stress can be expected (Allen et al. 2010).

Influences on Hydraulic Structure of Trees

Three main components affect the forest water system: *stock*, *flow*, and *service*. Each of these is influenced by the intensity and duration of water stress. The water-availability (*stock*) mechanism indicates that drought drives changes in the amount of water held in the soil. This flow of water (and nutrients) is processed through the root system to become the flow of transpired water. Trees function within a physical system consisting of the soil-plant-atmosphere continuum. Tree water deficit develops as the demand exceeds the amount of water available in the soil to the depth of the root system. The demand for water is set by potential evapotranspiration, which influences both plant transpiration and soil evaporation. The energy for transpiration is provided mainly by solar radiation. Adjustments in water supply and demand are influenced over decades in response to climate, plant size, edaphic properties such as soil texture and depth, and stand density (Mencuccini 2003; McDowell et al. 2006). Transpiration from canopy surfaces, as the cohesion-tension theory states (Dixon and Joly 1894), pulls water from soil to leaves, and causes a variable gradient of water potential (Ψ) within the plant. Thus, according to the Fick's first law of diffusion, water movement is a passive process occurring along a complex network of fine capillaries (vessels and tracheids), forming the xylem conducting system. Water flow through stems specifically conforms to Darcy's law, where volume flow rate (Q) is a function of the hydraulic conductance (k) and the pressure difference between the ends of the flow path ($\Delta\Psi$):

$$Q = k \cdot \Delta\Psi \tag{3.9}$$

In analysing the components of the soil-leaf continuum conductance may be distinguished from conductivity (K); k can be measured directly, or derived from the integration of K with respect to the distance (x) along the flow path. The k is thus a function of flow path length, whereas K is independent of length:

$$K = -Q / (\mathrm{d}\Psi / \mathrm{d}x) \tag{3.10}$$

Although osmotic forces contribute to water flow into the root xylem (Passioura 1988) and may influence water flow from leaf xylem to mesophyll cells (Canny 1993), longitudinal transport in mature stem xylem introduces symplastic barriers and osmotic potential does not participate in driving flow (Pickard 1981). As water transpires from the leaf, leaf Ψ is reduced. If water is available in the soil (high Ψ), water will flow into the leaf to replenish the evaporative loss with a small reduction in leaf Ψ. As soil Ψ declines, leaf Ψ must decrease further in order to create the necessary gradient differential to drive the water up from the drying soil to the transpiring leaf (Fig. 3.5a). The negative pressures (tension) that continuous columns of water through the xylem can withstand before breaking (cavitation) is critical to the ability of a plant to tolerate dry periods (Tyree and Sperry 1989).

The hydraulic-failure (*flow*) mechanism predicts that reduced soil water supply coupled with critically high evaporative demand causes xylem conduits and the

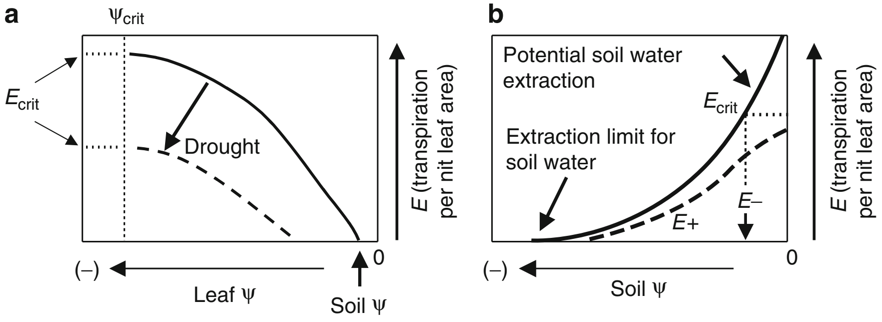

Fig. 3.5 (**a**) Draft of transpiration per unit leaf area as a function of leaf water potential (Ψ) for a plant with relatively abundant soil moisture (*solid line*) and the same plant with reduced soil moisture availability (*dashed line*). Evapotranspiration (E) exceeding critical rates (E_{crit}, maximum transpiration beyond which hydraulic failure occurs and soil-to-leaf hydraulic conductance falls to zero) results in xylem water potentials associated with hydraulic and symplastic failure (Ψ_{crit}). As bulk soil Ψ declines (drought), the relationship E/Ψ flattens and hydraulic limits become more severe. (**b**) Draft of transpiration per unit leaf area as a function of soil water potential. The *solid line* represents the transpiration threshold beyond which hydraulic failure occurs, and the *dashed line* represents realized transpiration, with the difference between the two lines representative of a hydraulic margin of safety. Regulation of E (E+) is necessary for the plant to stay within its hydraulic limits and fully exploit its potential for soil water uptake. Without regulation, (E-) once E surpasses E_{crit} there is no further water uptake, and the ability of the plant to extract water is compromised (extraction, – regulation). Redrawn from Sperry et al. (2002)

rhizosphere to cavitate (become air-filled), stopping the flow of water and desiccating plant tissues. The hydraulic-failure mechanism is based on the tenet that complete desiccation leads to cellular death. Hydraulic failure may be particularly likely if drought is sufficiently intense that plants run out of water before they run out of carbon. There is a complex relationship between stem-specific hydraulic conductivity and climate, related to life history (Maherali et al. 2004), which may bring to a virtual stasis in stem-specific hydraulic conductivity across sites with contrasting seasonality of rainfall. Bhaskar et al.'s (2007) global meta-analysis revealed that in deciduous angiosperms, evolution of increasing stem-specific hydraulic conductivity was correlated with decreasing precipitation, but water availability did not explain variation in stem-specific hydraulic conductivity in evergreen angiosperms or conifers. The evolution of stem-specific hydraulic conductivity within the evergreen angiosperms emerges as unrelated with climate parameters, including atmospheric demand and temperature. Under contrasting humidity conditions, intraspecific comparisons have found higher leaf-specific hydraulic conductivity in tree populations experiencing higher VPD (Maherali and De Lucia 2001). Higher leaf-specific hydraulic conductivity may be part of a hydraulic strategy to balance leaf water supply with the high evaporative demand during the dry season, when predawn Ψ is particularly negative (Fig. 3.5b). A highly conductive soil-leaf transport pathway can prevent excessive drops in late season leaf Ψ and allow continued carbon gain under high VPD (Addington et al. 2006). Leaf-specific hydraulic conductivity is determined by the interaction between stem-specific hydraulic conductivity and the leaf to sapwood area ratio; changes in leaf-specific hydraulic conductivity can be achieved through various combinations of change in the other two traits (Maherali and DeLucia 2000):

$$Q = (k_{\mathrm{s}} A_{\mathrm{s}} / h \eta A_{\mathrm{l}}) \Delta \Psi \tag{3.11}$$

where k_{s} is saturated permeability of the conducting path, A_{s} is sapwood area, A_{l} is leaf area, h is height, η is the viscosity of water, and $\Delta\Psi$ is $\Psi_{\mathrm{s}} - \Psi_{\mathrm{l}} - h\rho g$ (soil and leaf water potentials, respectively, and the gravitational pull on a water column of height h and density ρ). The complicated interplay among these traits may explain the varying direction of correlation: in some cases higher transport efficiency (stem-specific hydraulic conductivity) may allow maintenance of larger leaf deployment (higher leaf to sapwood area ratio), but the resulting leaf-specific hydraulic conductivity is dependent on their relative changes (Bhaskar et al. 2007).

The water-demand (*service*) mechanism predicts that stomata close to prevent hydraulic failure. Plants have to down-regulate their transpiration (through stomatal action) when soil Ψ decreases to stay within the hydraulic limits of the soil-to-leaf conducting system (Bond and Kavanagh 1999; Sperry et al. 2002; Buckley 2005), which decouples the canopy from the water-demanding atmosphere by increasing the resistance for water vapour leaving the crown (Meinzer et al. 1997):

$$\Psi_{\mathrm{l}} - \Psi_{\mathrm{s}} = -cDg_{\mathrm{s}} / k_{\mathrm{l}} \tag{3.12}$$

where D is defined as the imposed water VPD at the leaf surface, c is a constant (cDg_{s} equals the transpiration rate), and k_{l} is the leaf-specific hydraulic conductivity.

While reducing g_{s} reduces water loss, it also reduces CO_2 diffusion from the atmosphere to the site of carboxylation, thereby constraining photosynthetic CO_2 uptake (Eq. 3.6) (Wong et al. 1979). This may eventually lead to carbon starvation as a result of continued metabolic demand for carbohydrates. The lack of carbon may be particularly detrimental if drought is not intense enough to cause hydraulic failure, but lasts longer than the amount of time that the plant can survive with its existing carbon reserves. Down regulation of transpiration due to hydraulic constraints leads to 'isohydric' behaviour, i.e. regulation of transpiration in order to prevent leaf Ψ from decreasing to levels that endanger the integrity of the hydraulic system. This type of behaviour has been shown to result in a direct relationship between canopy resistance to water vapour and VPD (e.g. Bond and Kavanagh 1999; Sperry 2000; Cohen and Naor 2002). Since branches fix and store carbon, an established branch could be autonomous (i.e., not dependent on the tree) with respect to carbohydrates.

Branches usually cannot be autonomous with respect to water because water flows from the roots via the stem and is not recycled, unless branches are insulated from factors affecting other branches or if branches are insulated from each other (Sprugel et al. 1991). Schenk et al. (2008) showed that in contrast to shrubs in humid environments which tend to be hydraulically integrated, shrubs adapted to dry environments have modular hydraulic systems, achieved anatomically at the vessel-network scale or developmentally at the whole-plant scale. Hydraulic isolation of conduits allows independent stomatal regulation and, consequently, reduces the spread of runaway embolisms by allowing embolism repair while other parts of the xylem are under tension. Thus, branch autonomy with respect to water could benefit trees. Some isolation of individual branches might prevent a localized stress from decreasing plant Ψ as a whole (or decreasing it to some critical level), so that stomata of the affected branch would close while the rest of the tree would remain functional. In extreme cases, e.g. desert plants, branch dieback is a common behaviour for plant survival because the modular hydraulic systems allow isolated plant modules to be able to survive if these have access to small pockets of water in heterogeneous soil (Schenk et al. 2008). Thus, branch autonomy is a way to deal with the danger of runaway cavitation.

Influences on Tree Growth and Water Use Efficiency

There is evidence for a strong dependence of growth on ongoing tree water relations. In contrast to dry periods, wet periods may promote susceptibility to future drought via increased growth of leaf area and reduced growth of roots and sapwood, resulting in trees that have high ratios of hydraulic demand (leaf area) to supply (root area) (McDowell et al. 2006) (Fig. 3.6a). Stem tissues (bark, phloem, xylem) serve as a water reservoir for transpiration, and short-time oscillations in the stem dimensions reflect the water status of these tissues (Zweifel et al. 2000; Deslauriers et al. 2003), although Gall et al. (2002) found that in Norway spruce reversible variations of stem diameters did not reflect changes in internal water relations. Adaptations to water stress occur at several different temporal scales. In the short-term, water loss and leaf water status is controlled by g_s, keeping Ψ within the hydraulic limits necessary to maintain water transport through xylem (Tyree and Ewers 1991). Medium-term responses to water supply include osmotic adjustment to maintain gradients for water movement from the soil to leaves and changes to elasticity of leaf tissue to maintain turgor at low leaf water content (White 2000). Over longer time frames, plants may change growth rates in response to water supply, or there may be preferential allocation to roots so that capacity for water transport is maintained (Whitehead et al. 1984).

Diameter growth of woody species records plant-environment interactions throughout life span. Inter- and intra-annual variability of the diameter of tree trunks may be conveniently used to detect the seasonal growth patterns of trees as a result of changing environmental conditions, especially climate variation (Tatarinov and Cermák 1999; Deslauriers et al. 2003; Zweifel et al. 2006). At high elevation and latitude, the main factor controlling the seasonal pattern of diameter growth is temperature, although during dry years growth is limited even though high summer temperatures favour high growth potential. Strongly reduced radial growth during

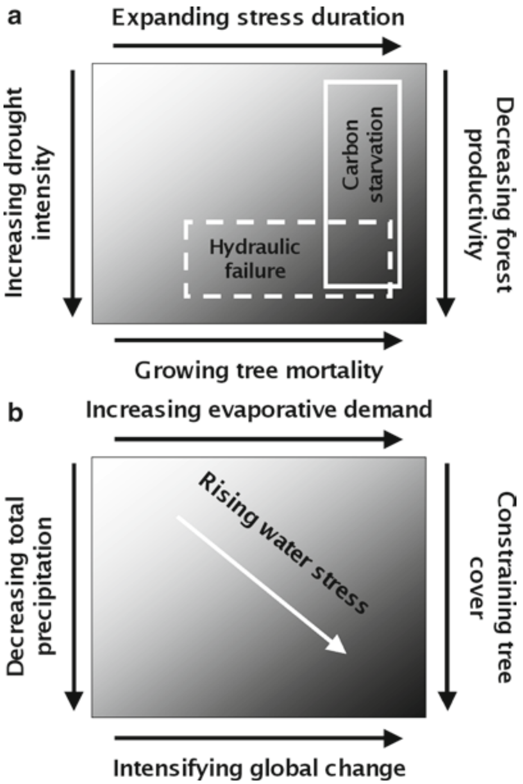

Fig. 3.6 (**a**) Theoretical relationship based on the hydraulic framework, between stress duration, drought intensity, forest productivity and tree mortality. Carbon starvation is hypothesized to occur when drought duration is long enough to curtail photosynthesis longer than the equivalent storage of carbon reserves for maintenance of metabolism. Hydraulic failure is hypothesized to occur if drought intensity is sufficient to push a plant past its threshold for irreversible desiccation before carbon starvation occurs. Inspired by McDowell et al. (2008). (**b**) Forest structure, water supply and water requirement network under varying climate change scenario

the extraordinary drought in 2003, in Europe, was registered in beech (Löw et al. 2006; Werf et al. 2007) and in oak, pine and spruce (Zweifel et al. 2006).

The hydraulic architecture of a tree shows three general qualitative properties: integration, compartmentalization and redundancy. The conducting system is built from a large number of integrated elements, tracheids and vessels, each being a unit of conduction, in communication with other elements by pits, which play a major role in protecting the conducting system from entrance of air. In all axes (trunk, branch, twig, petiole), at any given level, several xylem elements are present, like pipes in parallel, and a track of conducting elements is in close lateral contact with other tracks of vessels or tracheids. A correlation between wood density and cavitation resistance (Hacke et al. 2000) could mean that wood density is not only related to mechanical support requirements of the plant, but also to protecting the xylem pipeline from collapsing under large negative pressure. In a climate change scenario, the more drought-tolerant the plant, the more negative the xylem pressure can become without cavitation and the higher the wood density (Fig. 3.6b). Denser and stronger wood is necessary to balance the higher negative pressure within the xylem conduits (Hacke et al. 2001). Thus, although cavitation resistance is not always associated with reduced saturated xylem conductivity (Tyree et al. 1994), it would demand a price by reducing growth rate through higher xylem density (Enquist et al. 1999). The long-term structural adjustments that maintain homeostasis between water supply, water demand, and plant metabolism (Whitehead and Jarvis 1981; Katul et al. 2003; Bréda et al. 2006) may play a role in the survival or mortality of plants during drought.

Trees undergo seasonal and diurnal fluctuations in water content, as water goes into and out of storage. Water-storage capacity (or hydraulic capacitance of a plant tissue, C) is the mass of water that can be extracted, without irreversible wilting, per unit change in Ψ of the tissue:

$$C = \Delta R_{\mathrm{wc}} / \Delta \Psi \tag{3.13}$$

where R_{wc} is the relative water content of wood (stem, branches, etc.), calculated as $(W_{\mathrm{f}} - W_{\mathrm{d}})/(W_{\mathrm{s}} - W_{\mathrm{d}})$; W_{s} is the saturated weight determined after overnight hydration and blotting of excess water, W_{f} is the fresh weight, and W_{d} is the dry weight determined after oven-drying to constant weight.

The hydraulic conductance of a stem depends on stem length, transverse area of xylem, number and size distribution of xylem conduits, and extent of cavitation. In transpiring woody plants, most of the pressure drop in shoots occurs in the minor branches because leaf-specific conductance decreases as branch diameter decreases (Zimmermann 1978). When soil moisture declines, unrestrained and elevated midday transpiration rapidly leads to an exceedingly negative xylem Ψ inducing catastrophic embolism (Tyree and Sperry 1989) and reducing leaf-specific hydraulic conductivity to zero. The critical Ψ value causing full cavitation varies widely among species (Pockman et al. 1995; Pockman and Sperry 2000; Maherali et al. 2004) and is thought to be a function of interconduit pit structure (Pittermann et al. 2005), stems being more energetically costly and less vulnerable to cavitation than roots (Sperry et al. 2002). Hydraulic failure also occurs within soils and is functionally similar to xylem cavitation (McDowell et al. 2008). The hydraulic conductance of soils is a function of texture and structure, water content, hydraulic conductivity, and water table depth. Higher tension is required to pull water through fine-textured soils because of their small pore sizes, and thus fine-textured soils have lower conductance than sandy soils when water is abundant. However, fine-textured soils retain hydraulic conductance longer and at more negative Ψ than coarse-textured soils because the low conductance of fine soils results in slower water loss to transpiration and drainage (Sperry et al. 1998); besides, in coarse-textured soils hydraulic conductivity drops when water films become discontinuous (something like “soil embolism”).

Species Differences in Water Relations and Canopy Structure Across Europe

Transpiration equals approximately half of the total annual precipitation under temperate conditions in Europe (Denmead and Shaw 1962). The energetic equivalent of this amount of transpired water represents an important contribution to the energy balance of the Earth's surface. Soil drought may be a factor significantly affecting the transpiration rate via stomata and consequently the partitioning of energy in the energy budget of evaporating surfaces and, in turn, the energy exchange between vegetation and the atmosphere. Since this partitioning of energy determines the properties of the planetary boundary layer (Wilson and Baldocchi 2000), transpiration, reduced by water stress may have a significant influence on the climate (Shukla and Mintz 1982). For these reasons, research on transpiration has become important for understanding climate and climate change, especially in recent decades when the frequency of extreme weather phenomena has risen (Karl et al. 1995). VPD is an important environmental factor, which, together with low soil moisture, affects the gas exchange between vegetation and the atmosphere. A close statistical relationship exists between evaporative demand and canopy resistance for water vapour transfer to the atmosphere (Granier et al. 2000), which is related to the 'isohydric' behaviour discussed below. Consequently, evapotranspiration is not proportional to VPD (Bunce 1996).

Plants fall into two categories across the continuum of stomatal regulation of water status (Tardieu and Simonneau 1998). Isohydric plants reduce g_s as soil Ψ decreases and atmospheric conditions dry, maintaining relatively constant midday leaf Ψ regardless of drought conditions (Fig. 3.7). Isohydric behaviour has been observed in temperate hardwoods, Australasian and neotropical trees, and other species of gymnosperms (Loewenstein and Pallardy 1998a, b; Bonal and Guehl 2001; Fisher et al. 2006). Anisohydric species, by contrast, allow midday leaf Ψ to decline as soil Ψ declines with drought. Anisohydric species tend to occupy more drought-prone habitats compared with isohydric species and have xylem that is more resistant to negative Ψ (Franks et al. 2007).

Relating the hydraulic structure to the plant death is based on the premise that whole-plant hydraulic failure will be lethal. This premise may be false in cases of resprouting or xylem refilling. Resprouting has been observed following cavitation-induced shoot dieback in shrubs (Davis et al. 2002), mesic hardwoods (Tyree et al. 1993), and riparian trees (Horton et al. 2001). A benefit of reducing leaf area via shoot dieback is the resulting improvement in water status of the remaining foliage and subsequent survival of the individual (Tyree and Sperry 1989; Bréda et al. 2006). Refilling of cavitated elements may occur in some species when drought is relieved by precipitation, although the mechanisms and frequency of refilling remain a debated issue (e.g. Borghetti et al. 1991). Genetic differences could potentially play an important role in these mechanisms. The species-specific difference in regulation of the hydraulic safety margins occurs in part via differential relationships between leaf Ψ and g_s. Although isohydric species appear more vulnerable to

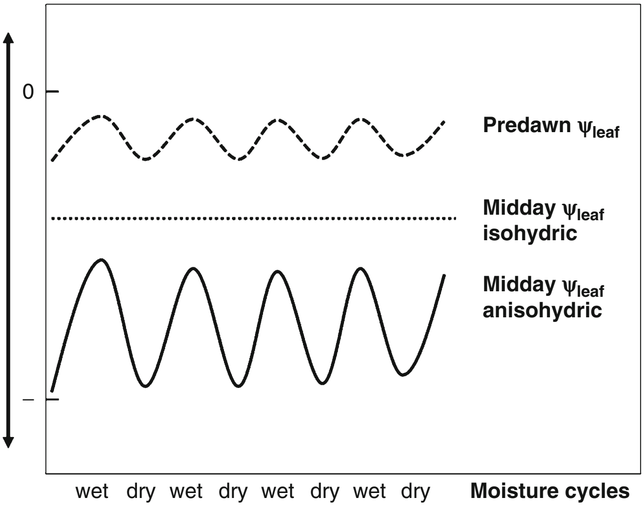

Fig. 3.7 Approximation of the two classical forms of water status control in vascular plants (isohydric and anisohydric). Midday leaf water potential (Ψ_{leaf}, *solid line*) relates to the same predawn water potential (*dashed line*). The vertical positioning of the midday water potential lines relative to each other is arbitrary. In isohydric plants, the midday Ψ_{leaf} is maintained relatively constant despite fluctuations in predawn leaf (and therefore soil) water potential. In anisohydric plants, the difference between predawn and midday Ψ_{leaf} is usually larger in drier periods because of a combination of moderate stomatal regulation of transpiration rate and the usually higher transpiration demand in drier periods. Redrawn from Franks et al. (2007)

embolism, they should actually be less likely to experience hydraulic failure because they close their stomata rather than risk cavitation. Anisohydric trees, instead, have higher rates of gas exchange during drought, but run a higher risk of cavitation as a consequence.

Leaf water availability limits plant productivity, and influences the adaptation of plants to environmental conditions. For a given size, angiosperms transport considerably larger quantities of water than conifers (Meinzer et al. 2005). The reduction in leaf-specific hydraulic conductance has been indicated amongst the mechanisms responsible for reduced growth in trees as they age and increase in height (Yoder et al. 1994), through reductions in g_s and therefore photosynthesis (Ryan and Yoder 1997). Hence, the ability to move water to the site of evaporation with a minimum investment is a major factor driving the architecture and physiology of trees, including the function of stomatal regulation. Stomatal regulation is a complex process as it depends on how microclimate, C_i, plant hormones, leaf Ψ and soil Ψ (Whitehead 1998) induce a variety of physiological responses that may regulate g_s (Dodd 2003). Besides other factors, leaf Ψ has been recognized as playing a key role in stomatal regulation (Bond and Kavanagh 1999). Studies of possible trade-offs between hydraulic conductivity and mechanical strength of wood (secondary xylem) indicate that as individual vessel water conduction is increased via larger vessel lumen area, mechanical strength of the wood may be reduced due to the reduced cross-sectional area of fibers (Wagner et al. 1998). However, other anatomical variables may confound the influence of the number and diameter of conduits. These variables include pith diameter, ray width, and fiber cell wall thickness.

The total volume (V, m^3) of a stem results from those of gaseous (V_g), liquid (V_l) and solid (V_s) spaces within the stem; $V_g + V_l$ represent the maximum available space for hydraulic networking (see Roderick and Berry 2001). The volumetric fraction of a stem, potentially available for the hydraulic network, can be derived from:

$$\left(V_g + V_l\right)/V = 1 - 0.97\left[D\right] \sim 1 - \left[D\right] \tag{3.14}$$

where [D, g m^{-3}] is the basic density of woody stems, defined as the ratio of dry mass to fresh volume.

Species differences in patterns of water use and response to soil water stress are two areas of uncertainty in determining tree transpiration (Pataki and Oren 2003), because of the spatial variability in species composition. This fact complicates scaling water use in mixed stands from tree to stand level. Tree specific transpiration under water stress is strongly influenced by root formation and stomatal closure, whereas tree specific root penetration depends on soil properties (review by Rewald et al., Chapter 2, this volume). In a limited rooting zone, decreasing soil water reduces sap flow significantly, including its response to VPD. Therefore shallow rooted tree species may show large reductions of sap flow in response to VPD, while deeply rooted species show only gradual reductions in transpirations as the soil dries (Oren and Pataki 2001). In addition, topography can play a major role in drought driven mortality (Guarin and Taylor 2005).

Much literature deals with the effect of water stress on tree transpiration, but the number of studies on species differences is still too limited to draw general conclusions for relating water use to tree species attributes (Hölscher et al. 2005). Gartner et al. (2009) compared the hydrological regime of Norway spruce and birch growing on heavy soils during a pronounced drought stress period. In spite of having significantly higher transpiration rates, birch trees could more easily adapt their transpiration to soil water stress. An internal redistribution of sap flow in the xylem under drought stress may be taken as an indication of water stress (Cermák and Nadezdhina 1998). Gartner et al. (2009) also found evidence of such an internal redistribution in spruce trees under soil water stress. They conclude that the reason for the better performance of birch trees in drought stress periods is due to the exploitation of soil water reserves in deeper soil layers and in a more efficient adsorption of soil water. Burk (2006) found that broadleaved trees in general could overcome high negative water potentials much better than conifers. Coners (2001) observed root water potentials of only −0,6 MPa in spruce roots, but −1,8 MPa in beech roots and −1,2 MPa in oak roots during drought stress periods. Remarkably, in warm and dry regions at low elevation, where Norway spruce was artificially planted far beyond its natural range, the fine roots of spruce are not supported by mycorrhizal communities, which play an important role in water uptake.

Hölscher et al. (2005) studied sap flow of broad leaved tree species during a seasonal drought and found a reduction of average daily sap flux during a dry period of 44% in *Tilia cordata*, 39% in *Fagus silvatica*, 37% in *Acer pseudoplatanus*, 31% in *Carpinus betulus* compared to the sap flow in a wet period. A higher influence of soil moisture in dry periods was detected for *Fagus silvatica* than in the other species, which were more effectively controlled by the VPD. However, they argue that the relative reduction of the sap flux density does not sufficiently characterize the drought sensitivity of broad leaved trees.

For forests in Europe, Granier et al. (2007) concluded that net ecosystem exchange is reduced by soil water depletion, but to a lesser extent than gross ecosystem production, due to the compensatory effect of the decreased ecosystem respiration and the fact that coniferous species in general seem to be less affected than broadleaved species. Drought impacts not only the annual growth; it also influences the growth and vitality in the following years (Dobbertin et al. 2010). Van Mantgem et al. (2009) found increased mortality rates in old growth forests in the Western United States. They conclude that regional warming and increases in water deficits are likely contributors to that phenomenon.

Canopy Atmosphere Interactions: Forest Influences on Climate

Forest influences on evapotranspiration and other factors (e.g. albedo and carbon storage) can exacerbate or mitigate anthropogenic climate change. While tropical forests might have a role in mitigating global warming through evaporative cooling, increased atmospheric water vapour (that does not increase cloudiness) leads to a positive radiative forcing, thus, even for tropical forests the influence on climate is not straightforward. The effect of temperate forests is unclear and that of boreal forests would be weak (Bonan 2008). Tropical forests have lower albedo, higher net radiation and higher evapotranspiration, compared with pasture, producing a shallow boundary layer, thus sustaining forest transpiration in the dry season (Da Rocha et al. 2004). In boreal forests, conifers have low summer latent heat flux (evaporative fraction) compared with broadleaved deciduous trees, producing large sensible heat fluxes and a deep boundary layer (Baldocchi et al. 2000) (Fig. 3.8). Competing factors from low albedo during winter and evapotranspiration during summer influence annual mean temperature, making the net climate forcing of temperate forests highly uncertain (Bonan 2008). However, Rotenberg and Yakir (2010) and Schiller (Chapter 9, this volume) have recently demonstrated that the Yatir forest, a planted pine forest at the dry timberline (285 mm mean precipitation) at the edge of the Negev desert in southern Israel, adjusted its metabolism to reduce the impact of severe temperature and water stress. This homeostatic-like ecosystem-level behaviour resulted in a high net ecosystem CO_2 exchange to gross primary productivity ratio and in displacement of the timing of biological activity (i.e. peak of carbon uptake) to early spring, leading to net carbon uptake slightly lower than mean global pine forests and slightly larger than average European pine forests, i.e. 2.3, 2.5 and

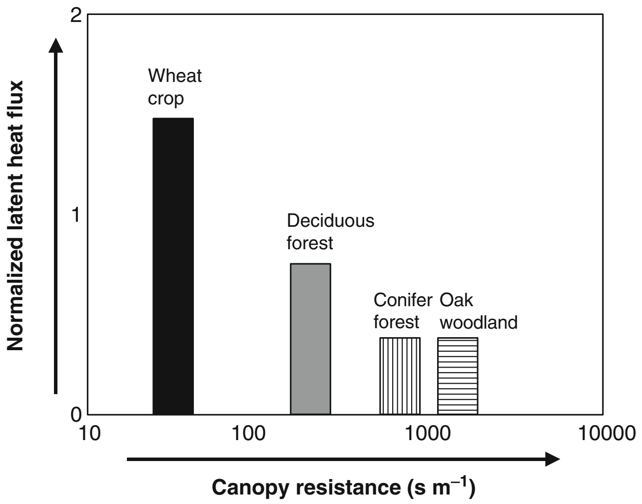

Fig. 3.8 Evapotranspiration normalized by its equilibrium rate in relation to canopy resistance for wheat crop, temperate deciduous forest, boreal conifer forest, and Mediterranean oak woodland. Latent heat exchange rates are normalized by the equilibrium *evaporation* rate ($\lambda E/\lambda E_{eq}$). Inspired by Bonan (2008)

2.0 metric tons per hectare, respectively. The substantial amount of carbon sequestered modified the surface energy balance: the plantation of the Yatir forest initially caused a regional warming because of the decreased albedo, but about 40 years after planting the balance between the albedo heating effect and the carbon sequestration driven cooling effect was reached. However, considering the positive radiative forcing caused by the observed suppression in longwave radiation, the time needed to reach a net cooling effect would be about 80 years after planting in the worst-case scenario (Rotenberg and Yakir 2010). These analyses focus on the influence of this type of forest on the energy budget of Earth's land surface, while it is clear that because of the decreased albedo this dry forest causes local warming.

The interactions between forest canopies and the atmosphere are in both directions since forests have a significant impact on the atmosphere. Recent reviews of forests, land use changes and climate targeted the influences on climate change (Betts 2007; Bonan 2008), which are important factors to consider as forest composition and extent change in the future. The basic interactions of forests with climate have been introduced into climate models (Sellers et al. 1997). Canopy atmosphere interactions can be viewed from several viewpoints, e.g. surface energy fluxes and radiative forcing (Fig. 3.9), the hydrological cycle (Fig. 3.2), and the carbon cycle (Fig. 3.1). Of course these are not independent of each other, but different viewpoints are necessary in order to focus on the relevant issues. Here we limit the discussion to aspects relevant to the water cycle and the European context, which ranges from Boreal Scandinavian forest through mid-latitude humid temperate forests and to semi-arid to arid Mediterranean, and excluding tropical forest.

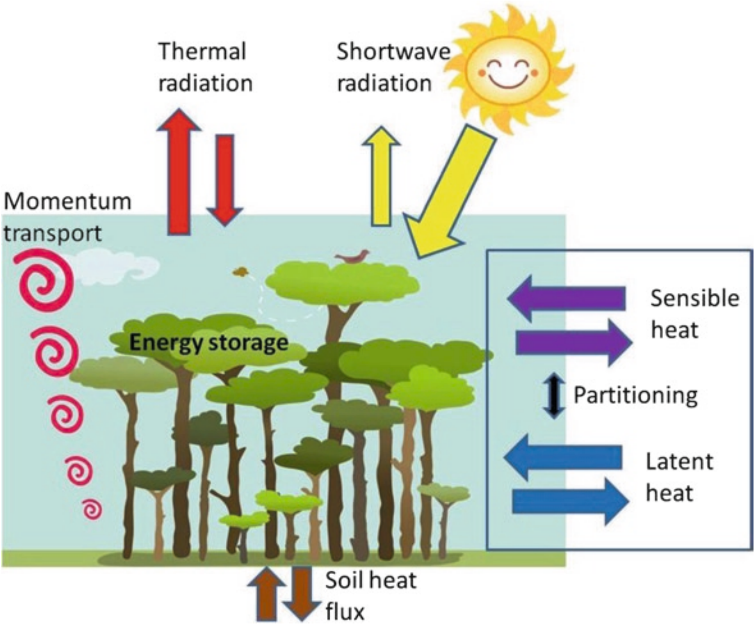

Fig. 3.9 Energy exchange of forest (inspired by Bonan 2008). Solar energy is the main input to the forest system and the fraction reflected is the albedo. A small amount of energy is stored in the forest, net thermal radiation and soil heat flux are responsible for some energy loss, while most energy is dissipated by sensible and latent (or evaporative) heat exchange with the atmosphere. Heat exchanges are facilitated by momentum transport in the surface boundary layer, which increases with wind speed and surface roughness

Climate always influences water issues through the hydrological cycle, i.e. precipitation patterns and evapotranspiration demand (Fig. 3.2). Soil drought accompanied by dry air can affect substantially the transpiration and consequently the soil water dynamics. High evaporative demands of the atmosphere can compensate partially for the reduction in transpiration rates caused by reduced soil water in the root zone (Střelcová et al. 2009). Large-scale impacts on the climate system include influences on the earth's radiation balance through influences on albedo, aerosols and CO_2 exchange, where aerosols include dust and smoke. Another impact is that on wind speed, which changes turbulence and momentum transport.

Solar energy drives climate processes, as well as photosynthesis, powering the biosphere. Net solar radiation depends on the albedo, or the ratio of reflected radiation to that reaching the earth (i.e. the solar constant). Albedo depends mostly on cloudiness, but also on land use. Planetary albedo has been relatively constant in recent decades, but a change of 1% can have a large impact on climate (Raval and Ramanathan 1989; Wielicki et al. 2005; Ramanathan 2008). Forests in general have lower surface albedo, due to the dark colour of leaves and trapping of radiation in the canopy; the latter explaining their lower albedo even when snow covered. This leads to increased temperatures relative to non-forested landscape. Values of albedo for different forest types and other land uses are presented in Table 3.1.

Table 3.1 Albedo of various forests and other land use types

Land use type	Albedo[a]	Albedo (Eurasia) February, 1995[b]	Albedo (Eurasia) July, 1995[b]
Deciduous forest	0.10–0.20		
Coniferous forest	0.05–0.15		
Boreal forest with snow	0.12–0.30		
Rain forest	0.12		
Grass (July, August)	0.25		
Lawns	0.18–0.23		
Not cultivated fields	0.26		
Fresh snow	0.80–0.90		
Old snow	0.45–0.70		
Free water surface and solar elevation > 45°	0.05		
Wet dark soil	0.08		
Dry dark soil	0.13		
Dry sand	0.35		
Evergreen needleleaf forest		0.30	0.14
Evergreen broadleaf forest		0.14	0.15
Deciduous needleleaf forest		0.23	0.14
Deciduous broadleaf forest		0.18	0.18
Mixed forest		0.20	0.15
Closed shrublands		0.27	0.23
Open shrublands		0.27	0.27
Woody savannas		0.20	0.17
Croplands		0.18	0.16
Urban and built-up		0.23	0.18

[a] Textbook values; Donatelli et al. (2005).

[b] AVHRR satellite measurements; from Strugnell et al. (2001).

Forests are very efficient radiators of long wave radiation and their emissivity, 0.96–0.98, is slightly higher than that of other land uses, which also improves their dissipation of excess absorbed energy (Jin and Liang 2006). Forests enhance turbulence and reduce wind speed near the ground. This enhances the dissipation of energy through convection (sensible heat transfer to the atmosphere), mixing in the lower atmosphere, but reduces wind erosion and dust accumulation in the atmosphere. In addition, dust and other aerosols are deposited in the forest, resulting in "cleaner" air.

Natural and anthropogenic aerosols are today recognized as playing a major role in radiative forcing both directly through reducing atmospheric transmissivity and indirectly through their role as cloud condensation nuclei (e.g. Cohen 2009). Some aerosols change cloud frequency and properties. The forest's role in reducing atmospheric aerosol load is therefore important. However, forest fires add large amounts of smoke to the atmosphere having the opposite effect. Even so, smoke has a short-term impact on climate when compared to the long-term reductions of aerosols by forests.

Two more general features of forests are their large standing carbon pool, which if released would significantly increase atmospheric CO_2 concentrations, their large uptake of CO_2 (equivalent to about a third of anthropogenic carbon emissions) and that they are relatively efficient in removing soil moisture.

Conclusions

Increasing [CO_2] along with associated changes in temperature will most likely alter the structure and function of forest ecosystems and thus will affect their productivity and their role as stable sinks to CO_2 sequestration and as regulators of the global hydrologic cycle. However, models predict that Earth's surface temperatures will increase along with shifts in precipitation that result in greater drought severity and frequency (IPCC 2007; Seager et al. 2007). As an example, maximum summer temperatures are likely to increase more than the average in southern and central Europe, whereas increasing water stress will dramatically affect mainly south-eastern Europe. Thus, forest ecosystems will experience a combination of numerous environmental stresses, which may significantly alter their physiological feedback on regional and continental climate. However, there is a great deal of uncertainty with regard to tree responses to interactive effects of global change scenarios. Models focusing on the interactions between climate change factors might help the scientific community to fill in the gaps in knowledge of how forest trees will respond to interacting effects. However, model accuracy depends to a large extent on our understanding of forest responses to climate changes. We conclude that there is an urgent need for multifactor climate change experimental studies examining the kinetic sensitivity of photosynthesis, stomatal conductance-transpiration, and respiration to the interactive effects of rising temperature, elevated [CO_2], and environmental stress, in order to improve our ability to predict the physiological forcing of forest ecosystems on climate change.

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