6 Water availability and productivity
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6.1 Introduction

Plant life and primary productivity depend on water availability. On Earth, nearly 20% of the global land surface is too dry to be cultivated. The quest for water and devising ways to use it efficiently for crop production has shaped civilisations around the world. When shortages in precipitation, often coupled to high evaporative demand, reduce moisture availability for an extended period in a way that will affect negatively the normal life in a region, a drought is said to occur. Drought, however, is not easy to define or to quantify objectively. In ecological terms, a drought will interfere negatively with ecosystem processes (productivity, biogeochemical cycles) or structure, whereas in agriculture, a drought is said to occur when soil water is not enough to meet the needs of the local crops.

Temporary drought, as a climatic anomaly, must be distinguished from the normal occurrence of seasonal low precipitation, which is a permanent feature of a given climate. For example, aridity refers to low moisture regions, such as those where the mean annual precipitation is less than half the value of potential evaporation. In semi-arid regions the interannual variability in water availability is larger than in humid regions and adequate rainfall may not occur every year (Ellis, 1994; Loik et al., 2004). In arid lands, the precipitation may come in well-separated events or ‘pulses’. The timing of rainfall, the extent of the dry season and the regime of rain pulses determine resource availability and shape ecosystem structure and function (Schwinning et al., 2004).

Droughts have affected human societies since the earliest times and had enormous impacts throughout history. For example, the invasion of Europe by the barbarian tribes from central Asia at the time of the fall of the Roman Empire may have been driven by the drying of pastures (Lamb, 1995). Later, by the beginning of the seventeenth century, the initial difficulties of British settlement in North America may have resulted from coincidental extreme droughts (Stahle et al., 1998).

Today, water is considered again a major issue in international politics. This is the case of highly populated countries, e.g., Egypt, Iraq or Syria, that use large amounts of water resources in irrigation but depend on river inflow from neighbouring countries (Araus, 2004). With the growth of human population, the improvement of the standards of living, especially in developing countries, the needs for water are expected to increase. Moreover, large areas of the globe will suffer the intensification of water deficits (IPCC, 2001; see also Chapter 1). At present approximately 7%
of the world’s population lives in areas where water is scarce but this may rise to 67% of the world’s population by 2050 (Wallace, 2000). The very dry areas of the globe have more than doubled since the 1970s (Dai \textit{et al.}, 2004). On the other hand, both natural vegetation and crops will be subjected to an increase in variability as the frequency and intensity of extreme events, such as droughts, may be a major consequence of climate change (Gutschick & BassiriRad, 2003).

In Portugal, for example, there has been a greater variability in the frequency and intensity of rainfall and a consistent increase in drought frequency in the last 25 years, resulting from warming and a significant reduction of precipitation in late winter and early spring (Miranda \textit{et al.}, 2006). In the Iberian Peninsula, almost all simulations with general circulation models suggest a future reduction in precipitation during spring and summer, i.e., an increase in the length of the dry season (Miranda \textit{et al.}, 2006).

In this chapter we will assess how plant productivity is determined in water-limited environments in the context of climate change scenarios. We will consider the impact of droughts in natural vegetation as well as in agriculture and forestry and the importance of spatial and temporal variability in water supply. Finally, we will discuss wildfires, as they are major environmental forces, closely linked to drought, that determine the structure and function of many ecosystems (Bond \textit{et al.}, 2005).

### 6.2 Water deficits and primary productivity

#### 6.2.1 Net primary productivity

Net primary productivity (NPP) may be quantified as a linear function of the photosynthetically active radiation absorbed by the canopy (APAR):

\[
NPP = \varepsilon \times APAR
\]

where \( \varepsilon \) the radiation conversion efficiency into biomass. The value of APAR depends on incident short-wave solar radiation, leaf area index (LAI) and the canopy structure, which affects the light extinction coefficient \((k)\). The slope of the relationship between plant productivity and APAR, i.e. \( \varepsilon \), varies with plant type and environmental conditions (Russell \textit{et al.}, 1989).

Water deficits affect NPP in two ways: (1) reducing APAR (mainly as a result of changes in LAI) and (2) reducing radiation conversion efficiency \( \varepsilon \) through changes in net photosynthesis and whole-plant carbon loss through respiration. Important interactions with nutrients, temperature and atmospheric CO\textsubscript{2} are expected. Reductions in APAR (associated with lower LAI) due to medium-term water deficits result mainly from restricted growth, leaf senescence and branch losses. Leaf expansion is one of the plant processes most sensitive to drought. With water deficits, not only fewer leaves are produced but also they are smaller and thicker, thus leading to low LAI (Chaves \textit{et al.}, 2003). On the other hand, as water potentials decrease, leaf shedding will increase through regulated senescence (Munné-Bosch & Alegre,
and/or branch and petiole xylem cavitation (Tyree & Sperry, 1989; Rood et al., 2000; Davis et al., 2002; Vilagrosa et al., 2003).

Differences in $\varepsilon$ gay result from differences in plant respiration. In general, long-term exposure to water deficits leads to a decline in plant respiration, as a result of decreased metabolism associated with lower photosynthesis, export of assimilates and growth. For example, this is what happens during the dry summer in Mediterranean ecosystems (Rambal et al., 2004). Differences observed among species in the response of respiration to drought, which are often reported in the literature, are apparently due to different growth sensitivity to drought (Lambers et al., 1998). There are also differences between mitochondrial respiration in the light that depends mostly on the amount of primary products directly derived from photosynthesis, and respiration in the dark that also depends on end products of metabolism (Haupt-Herting et al., 2001). On the other hand, the accumulation of osmolytes (e.g. sorbitol) under drought, implying less availability of sugars, may result in a further decrease of respiration, in particular in the alternative path, as was observed in wheat roots in drying soil (Lambers et al., 1998). Studies by Ghashghaie et al. (2001) in *Helianthus annuus* and *Nicotiana sylvestris* indicated a progressive decline in respiration with dehydration (from around $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ to less than $0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, accompanying the decline in relative water content from 95 to 60%). Although respiration rates decrease under water deficits, plant carbon balance may be negatively affected when the ratio of respiring biomass increases relative to assimilatory surface, because shoot growth is more sensitive to water stress than root growth (see also Chapter 5, this volume).

The value of $\varepsilon$ changes seasonally. For example, we calculated the monthly average $\varepsilon$, in terms of gross primary productivity (GPP) as GPP/APAR, from eddy-covariance data in an eucalypt plantation. As $\text{GPP} = (\text{NPP} + \text{R})$, with R standing for total plant respiration, $\varepsilon$ should mimic $\varepsilon$ even though not parallel, as the responses of GPP and R to temperature differ. The variation in $\varepsilon$ ranged from approximately 4 in winter to near 1 g MJ$^{-1}$PAR in the summer (Mateus, J., Pita, G. & Rodrigues, A., 2005, personal communication; Figure 6.1). The high monthly $\varepsilon$ in winter resulted from moderate temperatures, abundant water and a large number of overcast days. Diffuse light from overcast skies is photosynthetically more efficient than direct light and can account for increases in daily $\varepsilon$ up to 42% (Rosati & Dejong, 2003). The decline in $\varepsilon$ through the season is probably the result of increasing vapour pressure deficits and light saturation at high PAR (Ruimy et al., 1995) as the number of clear-sky and dry days increase from winter to summer. In summer, severe plant water deficits lead to declining carbon assimilation rates (Pereira et al., 1986) and even lower $\varepsilon$.

In crops, in addition to the decline in NPP, yield may be further decreased as a result of the negative effect of water deficits on harvest indices, i.e., the ratio between harvestable biomass and NPP. For example, Earl and Davis (2003) showed that water stress reduced substantially final grain yield in maize, but the reduction in APAR contributed much less to the yield loss than the decreases in $\varepsilon$ and in harvest indices.
Figure 6.1 Monthly averages of $\dot{\varepsilon}$ as GPP = $\dot{\varepsilon} \times$ APAR, measured with the eddy covariance method, in a Eucalyptus globulus plantation in Herdade de Espirra, central Portugal – Lat. 38° 38′ N, Long. 8° 36′ W; mean annual temperature, 16°C; mean annual precipitation, 709 mm; stem age, 9 years; leaf area index, 3 (Mateus, J., Pita, G. & Rodrigues, A., 2005, personal communication).

6.2.2 Water-use efficiency

The quantification of the dependence of plant productivity on water resources may be viewed as the slope of the relationship of net primary production and the amount of water actually lost by transpiration (T) over the year as

$$\text{NPP} = \text{WUE}_t \times \text{water supply} \times \text{proportion of water used by plants},$$

where the season-long water-use efficiency (WUE$_t$) or transpiration efficiency is the ratio of biomass produced to the correspondent plant transpiration [in g (dry matter) kg$^{-1}$ H$_2$O or mmol C mol$^{-1}$ H$_2$O] (Jones, 2004b). Water supply is precipitation plus irrigation, if appropriate, or precipitation during the growing season plus water in the soil at the moment of sowing for annual crops.

Short-term variability in transpiration efficiency is dominated by physiological – stomatal conductance and photosynthesis – and meteorological variables – vapour pressure deficit of the air, wind. The transpiration efficiency tends to increase under moderate water stress, as a result of greater stomatal restriction on transpiration and a relatively less sensitive response of the photosynthetic apparatus. On the contrary,
high vapour pressure deficit in the atmosphere imposes a decline in WUEt because transpiration increases without concomitant change in photosynthesis (Jones, 2004b). This sets an upper limit for WUEt in any given climate. Reduced transpiration under high irradiance raises the risk of leaf temperature increasing above the optimum for metabolic activity or at least above the threshold that leads to irreversible leaf tissue oxidative stress. Additionally, water-use efficiency (WUE) may decrease under severe water stress, or when water deficits combine with high temperature and high light, due to inhibition of photosynthesis (Chaves et al., 2004; Jones, 2004b). This is also apparent at the whole canopy level, as for example, under the Mediterranean summer drought, where WUEt decreased with severe water deficits accompanied by a strong decline in carbon assimilation (Reichstein et al., 2002).

At the scale of ecosystems we can integrate both hydrological and physiological components and ecosystem level WUE (WUEe; Gregory, 2004) is defined as:

\[
WUE_e = \frac{NPP}{E + T + R + D}
\]

where \(E\) is the direct evaporation from plant and soil surfaces, \(T\) is transpiration, \(R\) is the liquid water run-off and \(D\) is drainage below the rooting zone. Since in hydrological analysis it is common to separate liquid from vapour fluxes, the use of water for biomass production has been historically considered as the ratio of NPP to evapotranspiration \((T + E)\) (Rosenzweig, 1968; Lieth & Whittaker, 1975). While \(T\) represents the amount of water required for primary production, the other terms of the water balance are virtually non-productive. The proportion of water transpired in relation to evapotranspiration \([T/(T + E)]\) is a measure of water-supply efficiency (Rockström, 2003).

Reflecting roughly the impact of physiological controls, WUEe (or rain use efficiency) tends to be maximum under limiting water supply (Huxman et al., 2004), as suggested by Figure 6.2. The great variability in the data is mainly because of species differences and plant metabolism (e.g. C3/C4), differences in nutrition and soil properties and rainfall seasonality. The trend line shown for forests indicates that with high water supply the non-productive fluxes of water become more important. This trend was also shown in a eucalyptus plantation where irrigation and fertilisation treatments were applied (Table 6.1). The treatments were irrigation to satisfy the evapotranspiration demand in summer (I), irrigation as in I plus fertilisers added according to plant needs (IL), no irrigation but with fertilisers added (F) and control plots (C) (Madeira et al., 2003). WUEe decreased substantially (80%) in well-watered as compared to rainfed plots in the normal rainfall year as shown in Table 6.1 (precipitation close to the average, 607 mm). In a previous wet year (precipitation 1200 mm) the differences between well-watered and rainfed plots were negligible (unpublished results), but WUEe was approximately 12% greater in the fertilised plots than in the non-fertilised plots, both rainfed and irrigated.
6.3 Variability in water resources and plant productivity

6.3.1 Temporal variability in water resources

Some biomes are characterised by the strong seasonality of water availability. For plant productivity it is not indifferent if the water comes continuously in a regular fashion, or if it comes in widely separated instalments (Harper et al., 2005). In tropical savannas, grasslands and regions with Mediterranean climate, there are several months without rain, occasionally interrupted by sporadic rainfall events. In

<table>
<thead>
<tr>
<th>Water supply (mm)</th>
<th>Treatments</th>
<th>NPP (aboveground) (kg m(^{-2}) year(^{-1}))</th>
<th>WUE(_e) (g mm(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>613</td>
<td>C</td>
<td>2.08</td>
<td>3.39</td>
</tr>
<tr>
<td>613</td>
<td>F</td>
<td>2.39</td>
<td>3.89</td>
</tr>
<tr>
<td>1532</td>
<td>I</td>
<td>2.90</td>
<td>1.89</td>
</tr>
<tr>
<td>1532</td>
<td>IL</td>
<td>3.25</td>
<td>2.12</td>
</tr>
</tbody>
</table>

*See text for details.
these ecosystems, NPP is often more closely related with the length of wet or dry seasons than with annual rainfall per se (House & Hall, 2001).

The timing of the rainy seasons is also important. Ecosystems with winter rain (Mediterranean) and summer rain (monsoonal) differ in NPP and community composition, for example, in the distribution of plants with C4 and C3 photosynthesis metabolism. As C4 plants are favoured by drought and high temperatures during the growing season, the mixture of C3 and C4 species can be achieved in one of two ways: a temporal separation, with C3 grasses active in winter–spring and C4 grasses active in summer, or by growth-form separation as in the monsoonal system with C4 grasses and C3 woody vegetation (Ehleringer & Cerling, 2001). The Mediterranean type of ecosystems, which have an active winter–spring C3 herbaceous component, do not have a native group of C4 plants because the summer is too dry, even though C4 crops (such as maize) thrive there when irrigated.

C4 crops have intrinsic transpiration efficiency, roughly twice that of C3 crops, due to lower stomatal conductance and higher photosynthetic capacity. In rainfed crops, however, actual transpiration efficiency under the usual climatic conditions for the different photosynthetic types is rather conservative. This is because WUEt is also determined by the prevailing vapour pressure deficit, and so for temperate zone C3 crops a less efficient photosynthetic pathway is compensated for by a more humid atmosphere (Rockström, 2003).

In many arid and semi-arid environments, rainfall pulses are a major feature of the climate and the ecosystem goes through repeated cycles of drying and rewetting (Schwinning et al., 2004). During wet periods plant production may occur and reserves are stored for the continuation of ecosystem functioning between rain events (Reynolds et al., 2004). However, some plant groups (e.g. trees) may obtain resources from different depths in the soil (Walter, 1973), behaving in partial independence from specific rainfall events. Plant responses may be (1) increase in LAI due to germination of annuals and sprouting of perennials, (2) beginning of photosynthesis in perennials as plant water status improves and (3) mineralisation of soil organic matter and improvement of nutrient availability. But not all rainfall events trigger the same responses. The rain thresholds will vary with plant functional group and response type. For example, the amount of water delivered by a given ‘rainfall pulse’ may not be enough to allow the increase in grass LAI, but permit the mineralisation of soil organic matter. The biological meaning of rainfall pulses will be different for each component of the ecosystem (Reynolds et al., 2004).

Plant responses also depend upon the ‘memory’ of the system, i.e., the time between rain events will modify the response, and there is often a decoupling between resource availability and their use. For example, as soils dry during the prolonged rainless season, their biological activity declines. When soils are subsequently rewetted by small rain events, there is a sudden ‘burst’ of decomposition, nutrient mineralisation and CO₂ release – the Birch effect (Cui & Caldwell, 1997; Austin et al., 2004; Jarvis et al., in press) – but not plant activity (Pereira et al., 2003). At this time the herbaceous plants may not be there to utilise the released nutrients, and the deep-rooted perennials cannot use current rainfall until water is enough to
reach deeper soil horizons. In these circumstances, the loss of carbon and nitrogen from the soil is inevitable (Pereira et al., 2003; Schwinning & Sala, 2004; Jarvis et al., in press), and so summer rains often have no effect in plant growth. Climate changes towards greater aridity may decrease water and nutrients availability due to enhanced temporal heterogeneity and increased asynchrony of water availability and the growing season (Austin et al., 2004). Rain falling when plant cover is scarce leads to a decrease in the proportion of water that is used by the plants \( \frac{T}{(T + E)} \) and lower WUEe.

Severe droughts may have long-lasting effects on ecosystems. For example, during the severe drought of 1994 in Spain there was high mortality of *Quercus ilex* trees and other woody species (Peñuelas et al., 2001). Similar results have been reported for other regions as shown by tree-ring analyses, which allow a precise dating of tree deaths over decades. Episodes of massive tree mortality occurred in northern Patagonia and coincided with exceptionally dry springs and summers during the years 1910s, 1942–1943 and the 1950s (Villalba & Veblen, 1998). Different species may exhibit different sensitivities to drought. Those species that normally reach subsoil water, as *Q. ilex* ssp. *rotundifolia* (David et al., 2004), showed less variability in wood-ring patterns with climate than species that depend more on the use of current precipitation, e.g., *Pinus halepensis* (Ferrio et al., 2003).

In many cases there is not a simple short-term relationship between tree death and annual rainfall. Jenkins and Pallardy (1995) studied the effects of drought on growth and death of trees of the red oak group in Missouri Ozark Mountains and found that trees that were dead at the time of sampling had in all cases been severely affected by drought in the past. Likewise, ring variation could be used to predict the likelihood of tree death following a severe drought in *Pinus edulis* in arid northern Arizona (Ogle et al., 2000). In northeastern Spain Lloret et al. (2004) found that the response of *Q. ilex* to the 1994 drought was influenced by the effects of a drought 10 years earlier: plants that resprouted weakly after the previous drought were more likely to die in response to the recent event than the more vigorous plants. How vigorously a given plant recovers from stress will influence its hierarchy in the community and chances of survival. The resilience of ecosystems subjected to recurrent extreme droughts may be seriously affected by the loss of vigour and increasing difficulty of regeneration of surviving trees (Lloret et al., 2004).

### 6.3.2 Variability in space

Spatial variability in water resources may have a large effect on the landscape. In addition to micro-environment patterns the spatial variability in water can be affected by the plants themselves. Plant foliage intercepts rain before it reaches the soil, leading to evaporative losses and to the rearrangement of water input into the soil; roots and litter enhance water infiltration and reduce run-off, whereas roots may promote redistribution of moisture (Ryel et al., 2004). Work in evergreen oak Mediterranean savannas showed that more water was stored and was available in soils underneath tree crowns than in the open. This may result from better soil
properties (e.g. more organic matter; Joffre & Rambal, 1993) and increased rain capture by canopy interception and throughfall (David et al., 2005) as well as from hydraulic redistribution through roots (Ludwig et al., 2003).

An increasing number of studies have reiterated the crucial role of deep rooting for plant survival during the drought season (but see Section 6.3.3). In tropical and temperate zone savannas, the long dry seasons tend to select either for deep-rooting woody perennials that may use subsoil water (Schenk & Jackson, 2005) and/or for herbaceous plants that are strict drought avoiders with their life cycle tuned to the duration of the period with enough soil moisture (Walter, 1973). Although soil water may be exhausted up to the grass/shrub rooting depth during the dry season, enough water is usually available for woody plant transpiration, except in extremely dry sites or after severe droughts.

Deep rooting (> 1 m) is more likely to occur in sandy soils, as opposed to clayey or loamy soils (Schenk & Jackson, 2002a) and depends on plant type, increasing from annuals to trees (Schenk & Jackson, 2002b). In extreme arid environments, rooting depth is limited by the small infiltration depth that results from low-rainfall events on very dry soils (Schenk & Jackson, 2002b).

6.3.3 In situ water redistribution – hydraulic redistribution

Root architecture and distribution in the soil is of utmost importance as it determines plant access to water (Ryel et al., 2004). However, roots have also the role of water redistribution. The passive movement of water through roots from wetter, deeper soil layers into drier, shallower layers along a gradient of water potential (Caldwell et al., 1998; Horton & Hart, 1998) is known as hydraulic lift. A similar concept was developed to include the downward (Schulze et al., 1998) or even lateral transport of water by roots. Together they are called hydraulic redistribution (Burgess et al., 1998). These processes typically occur when stomatal aperture is minimal (e.g. at night), otherwise the atmospheric draw on water for transpiration is stronger than that provided by the water potential gradients in the soil. Hydraulic redistribution seems to be more effective in plants with dimorphic root distributions (e.g. shallow lateral and deep tap roots) and where soil water infiltration is limited as in more fine-textured soils (Ryel et al., 2004).

Hydraulic redistribution has been proposed as a mechanism that can buffer plants against water deficits during seasonal drought (Richards & Caldwell, 1987; Ryel, 2004). The downward water transport increases infiltration, reducing run-off losses and may help plants to use water in a more conservative way and may facilitate root growth through dry soil layers (Schulze et al., 1998), as well as allowing nutrient uptake from deep soil horizons (McCulley et al., 2004). In hydraulic lift, water absorbed by deep roots is redistributed back to shallow roots, enabling them to survive and absorb water and nutrients even when the soil is dry and to take advantage of precipitation pulses (Seyfried et al., 2005). The quantity of water redistributed by the upward movement of water may amount to 14–33% of plant daily transpiration (Richards & Caldwell, 1987). The movement of water to the shallower soil layers,
where most of the soil nutrients and microbes are, can improve plant water and nutrient status (Caldwell et al., 1998), as well as provide benefits to mycorrhizal mutualists (Querejeta et al., 2003) and neighbouring plants (Dawson, 1993) (but see Ludwig et al. (2004); see also Section 6.4).

6.4 Plant communities facing drought

Adaptation to semi-arid environments, namely in the Mediterranean, may be used as a paradigm of the range of plant traits adaptive to water scarcity. In Figure 6.3a, plants of group I have drought-avoiding behaviour without photosynthetic active parts during dry periods but survive in a resistant form. These are a majority in the flora of most semi-arid and arid environments (e.g. annuals, chamaephytes). Another extreme is plants of group II, which are water spenders without tolerance to dehydration, exploiting specific habitats that permit access to water during most of the year. The other groups in Figure 6.3 consist of ‘drought persistent’ (i.e. perennial plants that maintain some photosynthesis during the dry periods) according to Noy-Meir (1973). Some of these are true xerophytes, but others may be very vulnerable to climate change as the lauroid sclerophyllous (group V), which are relics from the Tertiary, such as Arbutus and Myrtus, that may be eradicated if rainfall becomes more irregular than in the present period (Figure 6.3b). Groups III and IV succeed either by avoiding dehydration through stomatal closure (group III) or by some dehydration avoidance (e.g. deep rooting) and a variable degree of tolerance to dehydration (Valladares et al., 2004b).

6.4.1 Species interactions with limiting water resources

Species coexistence in a situation of limiting water resources implies either avoiding interactions (niche segregation) or allowing some interaction (niche overlap). For example, the coexistence of different functional types regarding water resources enables plant communities to occupy a larger amount of physical space, exploring more resources (McConnaughay & Bazzaz, 1992). The exploitation of spatially and/or temporally distinct water resources by plants allows the coexistence of different species and life forms in environments where water is scarce (Noy-Meir, 1973; Reynolds et al., 2004).

Heterogeneity in hydrological conditions across topographic gradients may result in niche differentiation as has been observed in many plant communities (e.g. Dawson, 1990). Even in the absence of any obvious topographic variation, species segregation along a niche gradient of soil drying has been shown to occur (Silvertown et al., 1999). In water-limited environments successful competitors have root systems that are able to rapidly proliferate in resource-rich volumes of soil, depleting the resources before competing plants do (Passioura, 1982; Kroon et al., 2003). For example, Eissenstat and Caldwell (1988) showed that Agropyron desertorum, an invader bunchgrass of the Great Basin in the United States, exhibited root growth
Figure 6.3 (a) Distribution of the main functional groups of Mediterranean woody plants in relation to their strategies regarding water use (see text) and (b) the same functional groups according to their positioning in face of climate conditions and presumed tendencies with climate change. The arrow in (b) indicates the trend of climate change according to most scenarios (adapted from Valladares et al. (2004b)).
earlier in the season than *Pseudoroegneria spicata* (native bunchgrass), resulting in more rapid water extraction.

Competition is a relatively frequent plant–plant interaction in semi-arid and arid plant communities (Fowler, 1986). However, as water availability fluctuates temporally and spatially, it can be postulated that the intensity of competition also fluctuates. For example, trees and shrubs in semi-arid and arid systems can specialise in using deeper stores of water for drought survival, but they usually have an extensive and fairly dense horizontal root system in the sub-superficial layers (10–30 cm), augmented in wet periods by deciduous rootlets. There is strong competition for water in this layer between direct evaporation, ephemerals and shrubs (and shrub seedlings) and between different species within each plant group (Noy-Meir, 1973; LeRoux *et al.*, 1995). Nevertheless, the stratification of soil moisture and root systems tends to minimise competition for water and enables coexistence (Lin *et al.*, 1996). These contrasting results may arise from differences in the seasonality of precipitation, with stratification being most effective in environments with most precipitation falling when low-potential evapotranspiration or plant inactivity allows a surplus of water to infiltrate for later use by deep-rooted plants (Sankaran *et al.*, 2004; but see Section 6.3). As mentioned above, the downward redistribution of water (hydraulic redistribution) can be a mechanism for deep-rooted plants to store water below the reach of shallower rooting plants. Competition for water can be avoided by the asynchrony of biological activity, e.g., different phenologies or different growth responses to temperature (Reynolds *et al.*, 2000; Filella & Peñuelas, 2003), as is the case of trees and herbaceous plants in Mediterranean ecosystems.

Positive interactions, or facilitation, occur when one plant species enhances the survival, growth or fitness of another (Callaway, 1995). Neighbouring plant species may compete with one another for resources but they may also provide benefits for neighbours such as more available moisture, shade, higher nutrient levels and shared resources via mycorrhizae. Under water-stress conditions the shade provided by ‘nurse plants’ significantly increases seedling survival because of improved water relations. Hydraulic lifted water by deep-rooted plants can facilitate water use by shallow-rooted plants (Dawson, 1993), including tree seedlings (Brooks *et al.*, 2002). But this is not always the case because competition by roots of the dominant plants may eradicate the advantages (Ludwig *et al.*, 2003).

It is unlikely that species coexistence is determined by one mechanism alone. Net effects of one species on another may be the sum of both positive (niche differentiation, facilitation) and negative (competition) effects (Callaway, 1995). For example, nurse plants may facilitate the germination of seedlings of herbaceous plants by reducing soil temperature and increasing water content (Holzapfel & Mahall, 1999), but negatively affect seedling growth by reducing light. The combination of shade and drought may be especially meaningful for plant recruitment during ecological succession in environments with a long dry season. In such cases (dry-shade) seedling mortality may be higher in the shade rather than in the open, as shade not only decreases photosynthetic assimilation but also reduces the assimilate allocation to the roots more than the allocation to the shoots, rendering the plants less capable
of avoiding dehydration (Valladares et al., 2004a). The balance between negative and positive effects can also vary as productivity and resource availability increases (Pugnaire et al., 1996). This is supported by Briones et al. (1998), who found that competition between three dominant perennial desert species could be absent or reduced in low-precipitation years and be high in years with abundant precipitation.

Productivity of water-limited communities can be affected by species richness and identity. For example, water use and productivity of a community dominated by drought-avoiding species (group I) can be totally different from another dominated by water-spenders species (group II). In an extreme example with species substitution, Farley et al. (2005) showed that the afforestation of grasslands and shrublands could reduce the annual run-off on average by 44 and 31%, respectively. Run-off reduction can mirror higher community water use and productivity, although other factors can be involved (e.g. increased canopy interception losses).

Species- and functional-group rich communities can be more productive than poorer ones due to complementarity in resource use or positive interactions (but see Huston, 1997). For example, in a Mediterranean grassland, species-rich communities were more productive and used more available water than poorer ones (Caldeira, 2001). Also, asynchronous responses of different species to drought may lead to more stable primary productivity in diverse ecosystems than in less diverse communities (Yachi & Loreau, 1999). Several empirical studies showed that the temporal variability of ecosystems properties, e.g., productivity, decreased with increasing diversity (e.g. Tilman & Downing, 1994; Caldeira et al., 2005).

6.4.2 Vegetation change and drought: is there an arid zone ‘treeline’?

In the long-term, the mortality of woody plants may lead to changes in species geographical distribution. For example a simulation with the biogeochemistry–biogeography model BIOME4 (Kaplan et al., 2003) for Portugal, run with climate data from the Hadley Centre HadRM2 regional model, predicted that forest-dominated biomes might decrease from approximately 30 to 17%, whereas shrublands and grasslands might increase from 2 to 24% under a severe climate change scenario with atmospheric CO₂ concentration twice the present (Pereira et al., 2002). Changes would be more pronounced in the drier southern and interior regions where drought might become more severe and species are closer to the boundaries of their climatic distribution ranges. The simultaneous occurrence of severe droughts and wildfires might intensify this process.

Single drought events may also change plant community boundaries. For example, in northern New Mexico, United States, a severe drought during the 1950s shifted the ecotone between ponderosa pine forest and pinyon–juniper woodlands (Pinus edulis–Juniperus monosperma) by more than 2 km (Allen & Breshears, 1998). This change was rapid (less than 5 years), and occurred through the mortality of ponderosa pine, while the more drought resistant pinyon–juniper woodland was recruited into the new space.
In arid environments trees can be displaced and substituted by other plant growth-forms such as shrubs, establishing a dry land treeline (Stevens & Fox, 1991). When rains are infrequent and fail to fully saturate the soil, deep-rooted trees may be at a competitive disadvantage in comparison to shallower rooted functional groups (see Figure 6.3). In hot deserts, deep-rooted plants are largely restricted to habitats with deep-water infiltration such as washes, wadis or rock clefts (Schenk & Jackson, 2005). For example, in the Taklamakan desert the water-spending desert phreatophytes, such as *Populus euphratica*, have little tolerance to dehydration and their high water demand can only be met by ground water (Gries et al., 2003). Outside these specific habitats, rooting depth of desert plants is often restricted by shallow infiltration depths (Schenk & Jackson, 2002a).

Plant hydraulic failure as a result of water stress determines the limit of water deficits that a plant can withstand. It occurs when leaf and xylem water potentials fall below a species specific xylem cavitation threshold (Jackson et al., 2000) or if soil hydraulic conductance falls to zero due to high rates of plant water extraction or desiccation (Sperry et al., 1998). As water becomes scarcer, leaf water status is maintained above the threshold for xylem runaway cavitation by stomatal control and leaf area adjustments, avoiding loss of hydraulic continuity with soil water (Sperry et al., 2002). Other factors being equal, the hydraulic limits in the soil–leaf continuum depend on the branching structure, overall size of the continuum and root/shoot ratio (Sperry et al., 2002). As trees grow taller, increasing leaf water stress due to gravity and path length resistance may ultimately limit leaf expansion and photosynthesis so that further height growth can increase the risk of xylem cavitation (Koch et al., 2004). The partial dieback of peripheral branches and their attendant foliage may be a last-resort mechanism for whole-plant water conservation to survive drought (Davis et al., 2002). Under severe water deficits, trees, which have a single stem, may be more vulnerable to hydraulic failure than shrubs, typically with multiple stems. The hydraulic segmentation achieved by the multiple stems system can confine cavitation to the disposable organs that can thus be sacrificed, leaving still some viable elements (Rood et al., 2000), functioning as an insurance for long-term survival. On the other hand, repeated dieback of tree canopies with recurrent drought may induce a shrub habit in plants that would otherwise develop into a tree.

### 6.5 Droughts and wildfires

Fire is a natural component of many ecosystems. Often, it is the fire regime (frequency, intensity and timing) rather than drought that determines primary productivity as well as plant community (Pyne, 1997; Bond et al., 2005). Nevertheless, dry weather enhances the risk of biomass burning. For example, the severe drought of 1994 that damaged large amounts of woody plants in central and southern Spain (Peñuelas et al., 2001) also resulted in major forest fires, which burnt approximately 1.6% of the national forest area.
It is likely that wildfires will become more common in the future worldwide (Bond et al., 2005). The IPCC Third Assessment Report states that the higher the maximum temperatures, the more hot days and heat waves are very likely to occur over nearly all land areas, increasing the risk of forest fires (IPCC, 2001). Pereira et al. (2002) simulated the impact of future climate change on the meteorological risk of fire in Portugal. They found a significant increase in fire severity and length of fire season under the future climate, which resulted from a temperature increase and a decrease in precipitation in spring–summer. Likewise, Brown et al. (2004) found that prospective drying in the western United States created a future climate scenario with an increase in the number of days of high fire danger.

Vegetation fires are always possible because plant biomass is a good fuel in our oxygen-rich atmosphere. Live biomass, however, does not burn easily because it has a high moisture content. Drought interacts with fires, increasing dead branches and leaf shedding. These materials (dead biomass or necromass) represent the fine fuels, which once dehydrated in hot and dry weather, become highly inflammable and increase the risk of fire. Although drought and wildfires share common causes, it cannot be concluded that more or larger fires will occur in more arid regions. For fires to occur and expand, adequate amounts of fine fuel must be present. Wind, topography and human activities (often as the source of ignition) will also play a role (Pyne, 1997). The Iberian Peninsula may serve as a good case study. Fire frequency is highest in the hilly provinces of central and northern Portugal and Galicia (Spain), not in the more arid south (European Commission, 2003; Pereira & Santos, 2003). Wildfires occur where highly productive periods alternate with a hot dry weather, which facilitates ignitions. The Mediterranean vegetation ‘could . . . stand as a dictionary definition of a fire-prone environment. Annually, it undergoes a rhythm of winter wetting and summer drying, over which beats a cruder rhythm of drought. Almost always there is fuel in abundance – combustibles that lack only a properly timed spark to burst into flame’ (Pyne, 2005). Likewise, tropical savannas, where a highly productive rainy season alternates with a dry season, are the major contributors for biomass burning globally (Dwyer et al., 2000). In more arid climates, primary productivity is lower, decreasing the amount of fuel and fire incidence (Lloret, 2004).

Extreme events can override the climate tendency. For example, in 2003 Portugal experienced its worst fire season, with a total burnt area of about 5% of the countryside (~4000 km²; Pereira & Santos, 2003). But 2003 was not a very dry year as the annual precipitation exceeded the 1951–1980 30-year average. The exceptional fire season resulted from a heat wave, i.e., daily temperature maxima rising 5°C above the daily average (period of reference 1961–1990) for at least 6 consecutive days.

Droughts may have dramatic effects in ecosystems where water deficits are uncommon, as happened in the tropical rain forests of Southeast Asia in 1997/1998 where widespread wildfires were triggered by the droughts associated with the El Niño Southern Oscillation (ENSO) phenomenon (Roberts, 2001). Likewise, it was estimated that during the 2001 ENSO period of drought approximately one-third of Amazonian forests became susceptible to fire (Nepstad et al., 2004).
In regions where fire has been present for a long time, such as where the Mediterranean type of climate prevails, the vegetation has evolved under a strong fire influence (Lloret, 2004; Pausas et al., 2004; Bond et al., 2005). Plant traits responsible for post-fire persistence operate either at the level of the individual (resprouting) or by stimulating germination from the soil seed bank. Nevertheless, the regeneration depends largely upon environmental conditions before and after the fire as well as the fire regime (Lloret, 2004).

The post-fire persistence plant traits are often associated with differences in drought resistance. Morphological drought-avoiding traits (e.g. higher root/whole-plant biomass, deeper root systems) are more common in resprouters than in non-resprouters (Pausas et al., 2004). Furthermore, fire-induced sprouting does increase drastically the ratio of root to canopy biomass and will promote drought avoidance after fire (Lloret, 2004). On the contrary, woody non-resprouters (e.g., germination stimulated by fire) tend to be more drought-tolerant (e.g. higher xylem resistance to cavitation and embolism) and survive on drier sites than do resprouters. It appears that a greater drought resistance may be only coincidental and not causally related.

Fires may induce changes in soil hydraulic properties and nutrient availability, which may exacerbate the impacts of a drought. The effects depend largely on type of biomass burnt and on soil characteristics (type and moisture content), fire characteristics (intensity and duration), as well as on post-fire precipitation (Chandler et al., 1983). In general, low to moderate severity fires may promote a transient increase of pH and available nutrients as well as the enhancement of hydrophobicity, lowering the capability for the soil to soak up water (Certini, 2005). Severe fires, however, may have a much stronger impact. They may cause removal of organic matter, the creation of water-repellent layers, which may decrease markedly water infiltration rates, the deterioration of the soil structure and the increase in bulk density, which will result in further decreases in permeability and in water-holding capacity of the soil (Certini, 2005). One consequence of these changes in soil hydraulics is increased run-off and surface erosion, which, in turn, may induce a decline in nutrient availability, enhanced by volatilisation losses due to heating (Lloret, 2004; Certini, 2005). However, fire may improve nutrient availability, especially in cases where primary productivity is stagnant due to the immobilisation of nutrients in plant biomass or slow-decomposing litter and soil organic matter. In such cases fire may function as a rejuvenation factor at ecosystem level that will stimulate post-fire primary productivity, although this effect may be short-lived (Briggs & Knapp, 1995; Van de Vijver et al., 1999; Santos et al., 2003a).

6.6 Agricultural and forestry perspectives

6.6.1 Agriculture

The world cultivated land is 80% dedicated to rainfed agriculture, with the remaining 20% allocated to irrigation (Rockström, 2003). Nevertheless, irrigated agriculture is a major consumer of water resources and 40% of the food and agriculture
commodities are produced in irrigated areas. With the prospective growth of human population and climate change scenarios of increasing water scarcity, especially in the interior of continents and semi-arid regions, achieving a better efficiency of use of water in agriculture has become a major issue for farmers and researchers. Furthermore, land degradation reduces the soil water holding capacity and many irrigation systems waste large amounts of water. For example, more than 50% of the water allocated to irrigation in the southern and eastern Mediterranean may be wasted (Araus, 2004). One of the main aims of the 2000 World Water Council in the Hague was to increase water productivity for food production from rainfed and irrigated agriculture by 30% until 2015 (FAO, 2002). Additionally, increasing plant water use in agriculture is limited because sufficient run-off has to be guaranteed to sustain river ecology and other water uses, especially in drought-prone environments. It was suggested that globally only approximately 17% of the fresh water can be used for agricultural production (Rockström, 2003).

Many practices developed along the history of agriculture aimed at increasing the availability of water (such as irrigation, rainwater harvesting, mulching and contour ploughing) and enhancing the share of crop use in ecosystem water balance (such as ploughing, weeding, adjusting spacing to water availability). Plant selection and breeding for water-limited environments has resulted frequently in greater crop competitiveness with weeds and more thorough use of water resources (Blum, 1984). However, as mentioned above, especially in drought-prone environments, increasing plant water use in agriculture may be limited other social and ecological needs.

Concerns with a more efficient use of water resources led to the development of new management strategies that bring to the field agronomical and plant physiology concepts that may improve crop WUE while maintaining or even improving crop production and quality. New approaches may exploit plant sensing and physiological signalling of mild water deficits that coordinate plant adaptive responses to water shortage, as it is provided by controlled irrigation (Loveys et al., 2004). Attempts to manage crop source/sink balance by fine-tuning agricultural practices are also important (Goodwin & Boland, 2002) as harvest indices are often sensitive to water deficits. Plant breeding to develop genotypes with improved water uptake or better WUE without penalising yield is also taking place. Plant plasticity under water deficits is large, with some genotypes showing a high potential to deal with periods of water shortage (Centritto et al., 2004; Chaves & Oliveira, 2004).

Among the options to improve productivity in rainfed agriculture, is increasing the ratio between plant transpiration and non-productive evaporation losses through (1) avoiding the early season soil evaporation (or consumption by weeds or fallow) before full emergence of the crop and (2) maintaining high canopy cover throughout the growing season (Rockström, 2003). Increasing WUE, by increasing yields through improved agricultural management and plant breeding is possible and desirable (Wallace, 2000; Gregory, 2004). However, as discussed above, increasing WUE, has limitations. Moreover, constitutive high WUE, is sometimes associated with a low productivity syndrome that may limit the scope for breeding crops for higher transpiration efficiency.
Climate change may have contrasting impacts on rainfed agriculture according with geography and technology. While droughts may reduce crop production, warming and elevated atmospheric CO₂ may act positively on production potential. But even in water-limited environments, precipitation may not be the major determinant of crop productivity. In Australia, wheat seldom reaches the yield potential of 20 kg ha⁻¹ mm⁻¹ of water supply due to a combination of several limiting factors, such as low soil fertility or pests and diseases (Passioura, 2004). To come closer to the yield potential in rainfed crops in a changing climate, adaptation techniques should be adopted in the short-term and in the long-term (Pinto & Brandão, 2002). The former include the adequate choice of cultivars, timely planting, correct densities and harvest dates, as well as proper soil and nutrient management. Based on the Australian experience with dry land wheat, Passioura (2004) lists some practices that can ensure efficient water use (Table 6.2). On the other hand, land degradation may intensify the effects of drought to disaster levels.

The long-term measures will be the search for new genotypes with a higher adaptation to heat and drought and increased water- and nutrient-use efficiencies. Biotechnology may play a fundamental role in this context, although it must be acknowledged that a significant gestation time is still required before its impact is realised, as far as genetic modified crops are concerned (InterAcademy Council, 2004). There are, however, major breakthroughs utilising conventional breeding – good examples are the drought tolerant maize and wheat lines developed by CIMMYT through marker-selected breeding. Another example is the New Rice for Africa (NERICA), interspecific hybrid rice obtained by crossing *Oryza sativa* (Asian rice) with *Oryza glaberrima* (African rice), that gives 35% higher grain yields than the upland African rice varieties, when cultivated with traditional rainfed systems without fertilizer (InterAcademy Council, 2004). In addition to higher yields, the NERICA varieties are richer in protein and they are claimed to be more disease and drought resistant than local varieties of the West African savanna region.

In irrigated agriculture there is a strong need to increase efficiency, avoiding unnecessary water spending while improving product quality (Araus, 2004). These are the objectives of fine-tuning irrigation practices such as deficit irrigation, whereby water is supplied below the full plant demand, allowing a mild stress to develop

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**Table 6.2 Improving water economy in rainfed crops**

<table>
<thead>
<tr>
<th>Strategies</th>
<th>Tools</th>
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<tbody>
<tr>
<td>Optimising canopy development to increase the</td>
<td>Agronomic and breeding practices</td>
</tr>
<tr>
<td>ratio of crop transpiration/soil evaporation</td>
<td></td>
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<tr>
<td>Reducing water losses by drainage and</td>
<td>Early crop cover, deep root systems (genetic or nutrition)</td>
</tr>
<tr>
<td>increasing water capture</td>
<td></td>
</tr>
<tr>
<td>Improving WUE at the leaf level</td>
<td>Need to overcome pests and diseases and nutrient limitations, breeding</td>
</tr>
<tr>
<td>Improving harvest index per unit of water used</td>
<td>Adjusting crop phenology to the environment, specially flowering time</td>
</tr>
</tbody>
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*Adapted from Passioura (2004).*
with only small negative effects on yield (FAO, 2002). This strategy may lead to
greater economic gains than that by maximising yields. In general, deficit irrigation
has been more successfully applied to crops less sensitive to water deficits (as cot-
ton, maize, groundnut, grapevine, peach or pears) than to sensitive crops like potato
(Kirda et al., 1999).

Regulated deficit irrigation (RDI) is a type of deficit irrigation where the amount
of water applied is not constant throughout crop development, taking into consid-
eration the needs at each stage. This method is used in high-density orchards to
reduce excessive growth and to optimise fruit size and quality (Chalmers, 1986).
RDI may also improve the extent of soil water uptake as mild deficits during vegeta-
tive growth may have a favourable effect on root growth, improving water acquisition
from deeper soil layers, as observed in studies with groundnuts in India (FAO, 2002).

In the partial rootzone drying approach, each side of the root system is irrigated
during alternate periods. The plant water status is maintained by the wet part of the
root system and stomatal closure is promoted by the dehydrating roots of the other
half of the root system (Davies et al., 2000), using less water per plant. This type of
deficit irrigation will be efficient in canopies where stomatal control over shoot water
status through transpiration is important (Kang & Zhang, 2004). This is the case
of the crops with isohydric behaviour, where stomata do respond to root signalling,
most likely through ABA synthesised in the roots and modulated via xylem pH,
such as grapevines (Santos et al., 2003b; Loveys et al., 2004; Souza et al., 2005).

An efficient monitoring of plant performance is an essential component of the
water-saving strategy. Several techniques are available, although most of them
are time-consuming and demanding as far as equipment is concerned, such as
monitoring soil water or plant water relations (sap flow metres or leaf water po-
tential). Thermal imaging is emerging as a potential tool to monitor canopy water
status. The use of indices such as crop water stress index, calculated from canopy
temperatures in relation to references, can give us estimates of stomatal aperture
and therefore be used for irrigation scheduling (for a review see Jones, 2004a).

6.6.2 Forestry

As in agriculture, current trends in population growth and the improvement of the
standards of living lead to an increase in the global demand for forest products.
The consumption of wood-based products and paper increased four times faster
than the population during the twentieth century (FAO, 2000). Today these needs
are partly covered by cultivated forests, but natural forests will face an increasing
pressure for logging. Additionally, deforestation for agriculture and energy is likely
to proceed in tropical countries. On the other hand, the forest management paradigm
changed during the last decades, emphasising sustainable management and ecosys-
tem services, rather than wood production alone. As a consequence, forests must
provide raw materials, preserve biodiversity and provide other ecosystem services
such as the mitigation of greenhouse gas emissions through carbon sequestration.
Because natural forests are at risk and need to be preserved, there is little doubt that
managed forests – both tree plantations and ‘renaturalised’ forests – will continue to perform these essential roles in society.

In many regions, e.g., central Europe, forest production may have increased with global change due to the effects of increased CO₂ concentration in the atmosphere combined with nitrogen deposition (Bascietto et al., 2004; Kilpeläinen et al., 2005) and a longer growing season due to warming (Myneni et al., 1997). However, severe droughts can offset such gains (Raffalli-Delerce et al., 2004). That is the case of France and Portugal, where assessments of the impacts of climate change in forestry at the regional level have forecasted gains in productivity in the wetter northern regions and losses in the drier southern regions (Loustau et al., 2005; Pereira et al., 2005). In addition to the generalised drought effects on NPP, the change of carbon allocation towards roots will reduce the proportion of NPP available for stem growth, resulting in a greater decline in timber productivity than in NPP.

Changes in climate, e.g., increasing drought severity, will put trees under stress and may influence the distribution of other organisms, some of them essential for ecosystem function (mycorrhizae) as well as for the preservation of biodiversity. On the other hand, many observations suggest that plants subjected to drought stress may become more susceptible to insect attacks (Mattson & Haack, 1987). For example, plant water stress had a major role in promoting survival and growth of Phorachanta semipunctata larvae, an insect pest that attacks Eucalyptus globulus outside Australia (Caldeira et al., 2002). The consequent tree mortality may lead to this crop becoming unviable in drought-prone areas.

Maintaining forest productivity with increased aridity may imply diverting to the economically interesting species the largest possible proportion of water supply. This may be achieved using deep-rooting genotypes (if possible), site preparation techniques that can improve water availability (e.g. by removing hardpans that limit rooting depth) and increasing the ratio of transpiration/actual evapotranspiration (T/AET). The main non-productive portion of AET is the evaporation loss of rainfall intercepted by the canopies, which may account for 25–75% of overall evapotranspiration (McNaughton & Jarvis, 1983). Very little has been done to increase T/AET, except manipulating tree density. Yet, as mentioned above, the option of using more water for tree production is constrained by the need to allow enough run-off and drainage to maintain ecological and socioeconomic services such as river flows and aquifer recharge.

The reduction of stand density (thinning) may decrease the interception losses and increase the amount of water available per remaining tree, enhancing their survival and growth. Thinning, however, may produce changes in the physical environment below the canopy (e.g. increasing light, higher temperature, changes in soil organic matter decomposition rates), which favour the development of understorey vegetation. This will compete with canopy trees, thus offsetting the effects of water reallocation in the stand. Furthermore, in fire-prone environments, the development of understorey vegetation can pose an additional risk, as grasses, shrubs and juvenile trees are more quickly affected by droughts than deep-rooted mature trees, increasing the amount of highly inflammable biomass (see also Section 6.5). The
association of fires with frequent severe droughts and, eventually, with pests and diseases may bring about drastic changes in the environmental settings for forest development, requiring an adaptive approach to forest management.

During the last decades forest management has emphasised sustainability of resource use and ecosystem services. While the current practices are able to cope to some degree with the effects of climate fluctuations and its associated impacts, large gaps still persist in our knowledge of forest ecosystems functioning and their responses to multiple disturbances. Furthermore, given the long timescale of forest growth, the present climate change process may be too rapid for the natural adjustment of forests to the new environments. Improved ecosystem monitoring and research are therefore key steps in management under a rapidly changing climate, and should be incorporated into the management process itself (Dale et al., 2001). The adaptive management approach, which considers learning as a part of the management process, may be essential especially because greater climatic variability and increased frequency of extreme events are expected.

References


WATER AVAILABILITY AND PRODUCTIVITY


PLANT GROWTH AND CLIMATE CHANGE


PLANT GROWTH AND CLIMATE CHANGE


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