29 · Ecophysiology of photosynthesis in semi–arid environments

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29.1. CHARACTERISTIC FEATURES OF SEMI-ARID ENVIRONMENTS

29.1.1. Introduction

Arid and semi-arid environments currently cover a third of terrestrial Earth surface. By definition, 'semi-arid' refers to environments where insufficient water is available for vegetation growth. Semi-arid regions are characterised by being intermediates between desert (arid) and humid climates (Fig. 29.1), with an annual precipitation (250–1000 mm year^{-1}) typically lower than the potential evapotranspiration (PET). Furthermore, precipitation is concentrated in specific periods of the year, inducing interruptions of the growing season when water availability reaches the threshold that dramatically limits ecosystem functioning. In addition to pronounced seasonality, a third component is the unpredictability of precipitation, resulting in short drought periods even during the humid season. This unpredictability also refers to high year-to-year variability, which increases with decreasing annual precipitation, often leading to alternation of dry and humid cycles lasting several years. The inter-annual variability is also mirrored in actual evapotranspiration (AET).

The availability of precipitation and the topography of the site are the major factors determining the amount of water available for plants. However, a more detailed division of semi-arid biomes should also consider other components of climate. Temperature is a major climatic element differentiating semi-arid ecosystems. Aside from water, low temperatures become a limiting factor for plant productivity and growth in the coolest semi-arid zones, whereas heat stress can limit plant production in savannas and Mediterranean environments. According to Köppen (1936) classical classification, major biomes in semi-arid climates are savannas (Aw according to Köppen), steppes (BS) and Mediterranean-type ecosystems (Cs). Oceanic and tropical influences

prevent low temperatures in Mediterranean regions and especially in savannas. Steppes are characterised by continental influences with wide seasonal and daily ranges in temperature.

In addition to climatic factors, a common feature of semi-arid ecosystems is a reduced nutrient availability in the soil and an important disturbance regime mainly owing to fire and grazing (Section 29.4.5).

29.1.2. Main environmental limits in savannas, steppes and Mediterranean ecosystems

The largest savanna areas spread over sub-tropical regions of South America, Africa and Australia. Savannas are characterised by the absence of freezing temperatures and by a relatively high annual precipitation (Köppen, 1936). In some cases, actual precipitation exceeds evapotranspiration (Baldocchi *et al.*, 2004; Fig. 29.1). These climatic characteristics, along with other features such as deep and well-drained soils, permit the establishment of relatively complex and structured communities.

Steppes have a lower annual precipitation than savannas and are characteristic transition zones between savannas and deserts, with typical examples being the Sahel fringing the Sahara in Africa and similar semi-arid areas around the Thar Desert in the Indian subcontinent. Other boundary steppes represent gradients between Mediterranean-type ecosystems to deserts, such as Tijuana (Baja California, Mexico). The world's largest steppes are in temperate Eurasia (part of Ukraine, southwest Russia and neighbouring countries in Central Asia) and North America (Great Plains). While all steppes are characterised by the virtual absence of tall woody vegetation, this ample geographical distribution involves largely different climates. Steppes are divergent in terms of co-occurrence of high temperatures and seasonal precipitation. For instance,
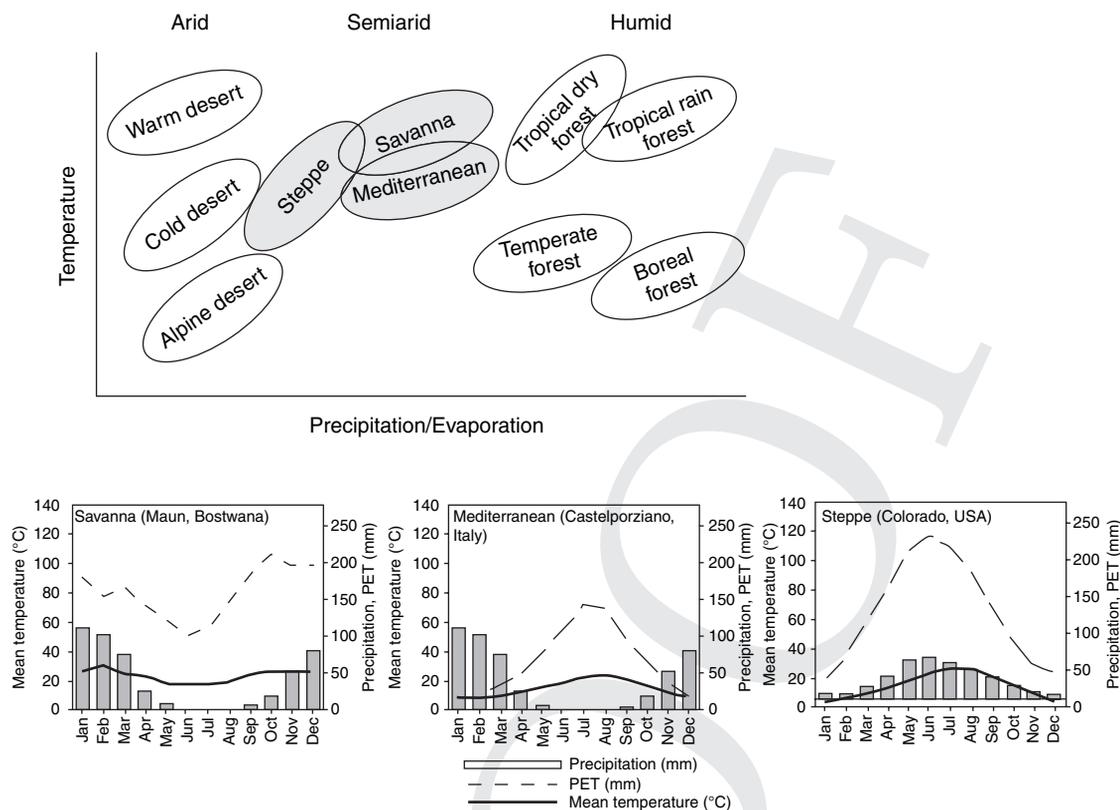
Fig. 29.1. A plot of the ecosystem types that are expected to occur along a climate gradient of temperature and the ratio of the incoming precipitation and potential evapotranspiration. The three semi-arid ecosystems included in the present chapter are shown in grey. Representative ombrothermic diagrams for each of these semi-arid ecosystems are shown below.

in Patagonian steppes the dry season coincides with hot temperatures during summer, whereas in the steppes of Great Plains and in Asian steppes optimal temperature and precipitation can co-exist in some places but not in the others. Freezing winter temperatures can significantly limit vegetation growth in continental steppes in lowlands of temperate zones in Great Plains, Mongolia, Patagonia and Russia.

The Mediterranean climate (or dry summer subtropical climate) is characterised by a hot and dry period in summer and a cool and wet period in winter. One of the most distinctive traits of this climate is the lack of any period of the year when optimal temperature and precipitation co-exist (Fig. 29.1). This type of climate occupies less than 5% of the global land surface and includes specific areas in North and South America, Europe, Australia and Africa, all of them located on the western or south-western coasts of these continents.

29.2. PLANT FUNCTIONAL AND PHOTOSYNTHETIC TYPES INHABITING SEMI-ARID AREAS

29.2.1. Major plant functional types and species co-existence

Vegetation in semi-arid ecosystems has characteristic adaptations to limited water and nutrient availabilities, spanning from physiological (photosynthesis, stomatal regulation) to structural (plant stature, leaf morphology, foliage aggregation and inclination, rooting systems) and phenological (evergreenness, period of physiological activity) features. Ecosystem formations in semi-arid regions differ substantially in species composition, but these ecosystems share some characteristic plant functional types. Although there can be a high diversity of growth forms and leaf habits in semi-arid ecosystems, the dominant growth forms are, however, low-stature woody plants and herbaceous forbs and

grasses. The proportions among these major functional types depend on water and nutrient availabilities.

Although the combinations of specific micro and meso-climatic factors can be more favourable to certain plant functional types, several plant functional types with their unique adaptive responses to environmental constraints (e.g., rooting system, photosynthetic pathway type) and phenologies can successfully co-exist in the same habitat. Unique adaptive responses and exploitation of resources in different canopy and root-zone layers and at different times during the season reduce the competition for limiting resources, permitting the coexistence of contrasting plant functional types (Noy Meir, 1973). For instance, grasses and forbs rely on the water in upper soil layers that is highly variable, while shrubs and trees rely on more stable deep-soil-water stores. This conceptual explanation of the coexistence of functional types is supported by evidence from studies in steppe communities (Sala et al., 1988), savannas (Knoop and Walker, 1985) and Mediterranean ecosystems (Gordon et al., 1989). Direct competition for the same resources by different functional types does occur in semi-arid ecosystems, but this is exceptional (McCarron et al., 2001).

29.2.2. Characteristics of major plant functional types

Herbaceous species have a relatively shallow root system, and are unable to tap deep water sources. Main adaptations to seasonally low water availability in herbaceous species are phenological, with plant growth being activated during the periods of high water availability in upper soil layers, and being arrested when water becomes scarcer. Annuals or therophytes allocate a very large proportion of their net biomass production to the growth of leaves and reproductive organs. Their success is directly related to the capacity to grow quickly during the wettest season, circumventing drought by early completion of lifecycle and releasing a large number of seeds before the onset of the dry period.

Perennial forbs and grasses differ from annuals in their bigger nutrient and carbohydrate reserves. Greater allocation to storage results in lower growth rates, but permits faster and earlier leaf and root development during the wet parts of the year. In semi-arid ecosystems, perennial herbs usually resist the unfavourable season as underground bulbs or tubers (geophytes) or buds near the soil surface (hemicryptophytes).

Among herbaceous species, C_3 is by far the dominant photosynthetic type in semi-arid ecosystems (Flexas et al.,

2003), especially in those areas located at higher altitudes, in steppes and under Mediterranean climates. C_4 species tend to be favoured over C_3 plants in warmer and more humid climates and thus dominate savannas (Grace et al., 1998). North- and South-American and Asian steppes also have a relatively low C_3/C_4 ratio (Suyker and Verma, 2001). Among C_4 subtypes, C_4 grasses are characterised by NAD-malic enzyme and PEPCk subtypes in most steppes (Pyankov et al., 2000).

Woody species or phanerophytes are represented by shrubs and trees. Shrubs and trees with extensive and deep-root systems are less limited by seasonal variations in soil-water availability than herbs. Depending on winter minimum temperatures, phanerophytes are either evergreen or winter-deciduous, although depending on water availability phanerophytes can become drought-deciduous or semi-deciduous.

Evergreen species tolerate stress conditions by retaining green leaves throughout the year. Evergreen leaf habit allows retention of nutrients from season to season and has been described as a more conservative water and nutrient-use strategy than the drought-deciduous strategy (Lloyd and Farquhar, 1994). Several studies have demonstrated that evergreen species dominate sites where resources are in short supply, like semi-arid environments (Beadle, 1966). Overall, the share of drought-deciduous or evergreen leaf habits in savannas and Mediterranean ecosystems depends on the availability of groundwater. Shrubs and trees able to tap water stored in deep soil profiles experience less seasonality in moisture and are evergreen, whereas woody species without access to groundwater during the drought period are commonly drought-deciduous.

Drought- or semi-deciduous phanerophytes are best adapted to the driest conditions of semi-arid environments, where they replace the evergreen communities. A special subtype of drought-deciduous xerophytes is the 'leafless non-succulent switch shrubs' (Oppenheimer, 1960). This subgroup consists of perennial species that shed mesophytic leaves during drought, but keep green stems and thereby maintain photosynthetic activity during the dry season (Yiotis et al., 2006). Typically, the drought-deciduous species in semi-arid environments possess relatively mesophytic leaves. However, some semi-deciduous species have seasonal leaf dimorphism, forming sclerophyllous leaves in summer and mesophytic leaves in winter (Aronne and De Micco, 2001). Seasonal dimorphism in semi-deciduous species avoids excessive water loss with
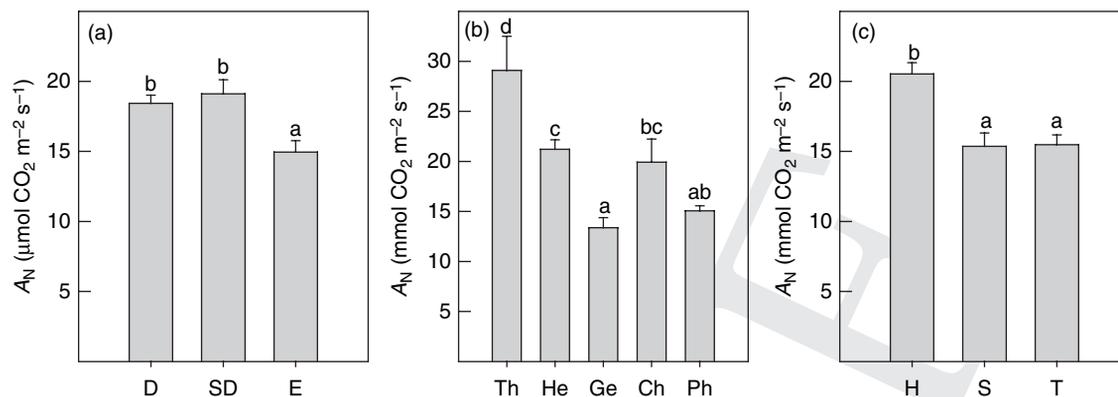
Fig. 29.2. Mean (±SE) photosynthetic rates per unit area of well-watered, non-stressed semi-arid species. Photosynthetic capacities are separately plotted according to **(A)** leaf habit (D, deciduous, *n*=223; SD, semi-deciduous, *n*=34; E, evergreen, *n*=71); **(B)** life form (Th, therophytes; *n*=6; He, hemicryptophytes, *n*=123; Ge, geophytes, *n*=19; Ch, chamaephytes, *n*=15 for Ch; Ph, phanerophytes, *n*=165); and **(C)** growth form (H, herbaceous, *n*=150; S, shrubs, *n*=115 for S; T, trees, *n*=63). For the leaf habit, both annuals and perennials with deciduous leaves have been included in group D. Values were taken from previous studies performed in the field and in controlled environments. When different estimates were reported for the same species, the highest value was considered. Varieties or cultivars of the same species were considered as a unique entry. Only the measurements performed at mid-morning were considered. Different letters denote significant differences among the means according to Duncan's test (*P*>0.05).

a reduction of transpiring surface through partial fall of leaves during the dry period.

Winter deciduousness is a typical feature of cold climates, but clearly disadvantageous in semi-arid regions where precipitation occurs during the winter, such as the Mediterranean climate. In these areas, the combination of winter deciduousness and dry summers would lead to a very short carbon-assimilation period that in some cases is insufficient to pay off the costs of leaf construction and maintenance (Flexas *et al.*, 2003). In fact, woody vegetation is essentially lacking in some environments, such as continental steppes, where winter temperatures are not compatible with wintergreenness, and foliage cannot also be supported during the entire summer owing to excessively low water availabilities.

Most woody species in semi-arid environments possess C_3 metabolism, with only few C_4 shrubs such as *Atriplex* species growing in ecotones between semi-arid environments and deserts (e.g., Akhani *et al.*, 1997).

Succulents with CAM photosynthetic type are relatively abundant in the ecotones between semi-arid ecosystems and deserts, but they are usually characteristic to more continental inner locations. In the Mediterranean Basin, suitable conditions for CAM species are only found in rocky, coastal areas (Flexas *et al.*, 2003). Most of the CAM species found in semi-arid areas are better defined as facultative CAM,

with the C_3-photosynthetic pathway dominating during most of the year, and CAM being expressed only under water and salt stress.

29.2.3. Differences in photosynthetic potentials among plant functional types

A revision of maximum photosynthesis rates per unit leaf area (A_{Nmax}) for 328 different species found in semi-arid environments demonstrates that A_{Nmax} is similar among species with annual (including deciduous) and semi-deciduous leaves, and significantly lower in species with evergreen leaves (Fig. 29.2A). This species ranking is in agreement with previous reports showing lower photosynthetic capacities for evergreens (e.g., Reich *et al.*, 1997; Flexas *et al.*, 2003). The higher leaf lifespan of evergreen leaves is achieved by rigidifying photosynthetic tissues, which results in a lower fraction of photosynthetic biomass within the leaves and reduced internal CO_2-diffusion conductance from substomatal cavities to the site of carboxylation (Niinemets and Sack, 2006, Section 29.2.4).

Among the lifeform groups, geophytes and phanerophytes had the lowest A_{Nmax}, whereas therophytes and hemicryptophytes had the highest (Fig. 29.2B). Low A_{Nmax} for semi-arid geophytes has been confirmed in several surveys (Forseth and Ehleringer, 1983; Gulías *et al.*, 2003).

Among growth forms, shrubs and trees had similar values for A_{Nmax} and significantly lower values than the herbaceous species (Fig. 29.2C) in agreement with previous reports (e.g., Jiang *et al.*, 1999). The main differences among the lifeforms and growth forms are driven by differences in foliage longevity among these species groups (Fig. 29.2A). Although herbaceous species are characterised by fast turnover of foliage, leaf longevity is significantly larger in woody perennials, especially in woody evergreens (Diemer and Körner, 1996).

29.2.4. Leaf structural adaptations to semi-arid environments that influence photosynthesis

In stressful environments, a variety of selection pressures operate on leaf morphological and anatomical design with important consequences for foliage photosynthetic activity. Plant photosynthetic activity adjusts to semi-arid environments by physiological photoprotection to avoid excess light intensities (Section 29.2.5) and by leaf and crown morphological adaptations to reduce transpiration and/or light interception and improve tolerance of low leaf-water potentials. Structural avoidance of excess radiation absorption is important in protecting against photoinhibition and in avoiding excessively high leaf temperatures and transpiration rates (Valladares and Niinemets, 2007). Thus, structural adjustments permit the plants to achieve an efficient compromise between maximisation of carbon gain and minimisation of exposure to high solar radiation.

Apart from evolutionary adaptations to limiting water availability and to other associated stresses, plants in semi-arid environments have large phenotypic plasticity in leaf and shoot architecture (Valladares *et al.*, 2005). High capacity for foliage adjustment in response to environmental stresses is present in all major functional types dominating semi-arid ecosystems – sclerophyll evergreen shrubs, malacophyll summer-deciduous shrubs and herbaceous species. At the extreme, plant species with dimorphic leaves possess foliage with completely different structure during the dry season in summer (crimped and partially rolled lamina with crypts in the abaxial surface where stomata are located, higher pubescence, smaller tightly packed mesophyll cells forming palisade parenchyma on both sides of the lamina in summer leaves) than during the wet season in winter when the leaves have more mesophytic in appearance (Aronne and De Micco, 2001).

In the following, we examine the key evolutionary and phenotypic modifications in foliage architecture in semi-arid environments.

29.2.4.1 LEAF MASS PER AREA AND RELATED MORPHOLOGICAL TRAITS

A vast number of studies have shown that LMA is larger in hotter and drier sites (e.g., Nobel, 1977; Wright *et al.*, 2005, Fig. 29.3). Such increases in LMA, both within species and across species, are well documented for key plant functional types in Mediterranean ecosystems (Salleo and Lo Gullo, 1990), steppe communities (Vendramini *et al.*, 2001) and savannas (Read *et al.*, 2006). High LMA has been classically related to sclerophylly, a plant trait in semi-arid ecosystems improving foliage longevity and resistance to low water availabilities (Scholes *et al.*, 2004). Although more robust foliage structure of semi-arid species is often associated with greater foliage longevity in such environments, both evergreen and deciduous species in semi-arid biomes have larger LMA than those in tropical or temperate biomes (Fig. 29.3).

LMA (g m^{-2}) is a product of leaf density (D, g cm^{-3}) and thickness (T, μm) that can vary independently (Niinemets, 1999; Fig. 29.3). Separation between these components of LMA is relevant as L_D and T can vary independently, and foliage photosynthetic potentials per area commonly increase with thickness owing to accumulation of mesophyll tissue, while photosynthetic potentials per mass decrease with density owing to accumulation of non-photosynthetic biomass (Niinemets, 1999). LMA increases with site aridity mainly because of modifications in leaf density (Niinemets, 2001, Fig. 29.3). Increases in leaf density in drier sites are commonly associated with thickening of cuticle and epidermis, with increased fractional sclerenchyma investments and smaller and more tightly packed mesophyll cells that also have thicker cell walls and greater pubescence (Niinemets and Sack, 2006).

Biome contrasts suggest that leaves are also commonly thicker in semi-arid environments than either in temperate or in tropical biomes (Fig. 29.3). In particular, a larger LMA of drought-deciduous species in semi-arid biomes than those in drought-deciduous species in tropics or winter-deciduous species in temperate ecosystems is associated with greater foliage thickness not with greater density (Fig. 29.3). Global-scale relationships between foliage structure and climate suggest that greater thickness in such ecosystems is not necessarily linked to water availability, but may result from enhanced radiation loads in semi-arid environments (Niinemets, 2001).
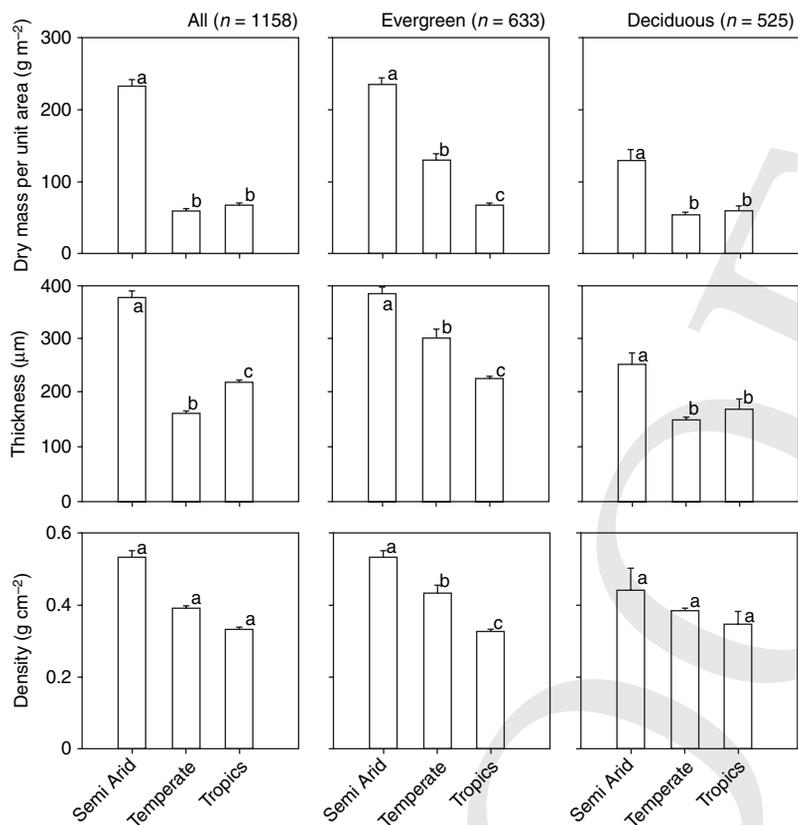
Fig. 29.3. Average (±SE) leaf dry mass per unit area (LMA) and its components, leaf thickness (*T*) and density (*D*) (LMA=*TD*), for a large number of angiosperm species from semi-arid (*n* =367), temperate (*n*=523) and tropical (*n*=268) biomes (database of Niinemets, 1999). The values of foliage morphological traits are separately given for evergreen (*n*=344 for semi-arid, *n*=35 for temperate and *n*=254 for tropical biomes) and deciduous (*n*=23 for semi-arid, *n*=488 for temperate and *n*=14 for tropical biomes) species. In all cases, foliage projected area has been used. Bars with the same letter are not significantly different according to ANOVA (*P*>0.05).

Benefits of high LMA

The main benefits of high LMA in semi-arid environments are as follows.

1. Larger leaf lifespan (Reich *et al*., 1997), probably as the result of enhanced tolerance of mechanical injures and herbivory by more robust leaves (Wright and Cannon, 2001).
2. Leaf rigidification that renders the leaves more resistant to pressure-driven changes in leaf volume and water content (Salleo *et al*., 1997). High LMA reduces tissue compression in dehydrating leaves and favours leaf recovery after drought-induced cavitation (Salleo *et al*., 1997). Furthermore, less-elastic leaves lose less water for common change in leaf-water potential. Thus, these leaves can extract water from drier soil than more mesophytic leaves (Niinemets, 2001).

3. Greater degree of mesophyll stacking (Smith *et al*., 1998) resulting in lower surface-to-volume ratio (1/thickness in broad-leaved species). Lower surface-to-volume ratio is associated with reduced transpiration rates and higher photosynthetic WUE as observed in perennial herbaceous steppe species (Voronin *et al*., 2003), savanna trees (Hoffman *et al*., 2005) and woody Mediterranean species (Paula and Pausas, 2006).

Negative consequences of high LMA

Although positive effects of high LMA in semi-arid ecosystems are mainly associated with adaptations to limited water

availability, the consequence of high LMA is typically low photosynthetic capacity per dry mass (Wright and Cannon, 2001). Negative relationships between LMA and photosynthetic capacity have been postulated to result from the following.

1. Higher resistance to CO_2 internal diffusion (i.e., lower g_m) owing to denser packing of mesophyll cells and thicker cell walls (Niinemets and Sack, 2006).
2. Lower leaf nitrogen (N) concentration and higher investment of N in non-photosynthetic components (Niinemets, 1999).
3. Lower chl. content and lower foliage light capture per mass (Wright and Cannon, 2001).

The last two negative effects of high LMA likely result from greater proportion of support tissue relative to physiologically active biomass.

29.2.4.2 LEAF SIZE AND SHAPE

Leaf energy balance significantly depends on leaf size and shape. In high radiation loads, large entire leaves have a thicker boundary layer for heat and water exchange, and thus require greater transpiratory cooling to maintain leaf temperatures within the optimal limits for photosynthesis than smaller leaves or leaves with dissected lamina (Givnish, 1979). This may not be possible in semi-arid environments where latent heat loss via transpiration is impeded by drought-driven stomatal closure. Consequently, there is a general trend of decreasing leaf size with increasing site aridity (Scholes *et al.*, 2004), and plants typical of semi-arid habitats commonly possess relatively small leaves (Tenhunen *et al.*, 1987).

Apart from direct influences of leaf size and shape on leaf temperature, thermal optima of photosynthesis may be different in leaves of various habits. In a comparison among eight species of *Pelargonium* from South-African semi-arid ecosystems, Nicotra *et al.* (2008) showed that the species with more dissected leaves had higher thermal optima of photosynthesis and greater rates of carbon gain and water loss. Higher thermal optima may reflect selection pressure to protect photosynthetic machinery against excessive leaf temperatures when stomata close in response to water stress.

29.2.4.3 LEAF PUBESCENCE

Leaf pubescence has been considered to be an adaptive trait in water-limited environments. A hairy surface acts as a spectrally neutral reflector for the UV, visible and IR parts of the spectrum, reducing the radiant energy absorbed by the leaf (Karabourniotis and Bornman, 1999). In consequence, presence of trichomes on leaf surface reduces heat load, and thus the reliance on transpiratory cooling to avoid high leaf temperatures (Ehleringer and Mooney, 1978). This permits maintenance of photosynthetic activity longer into the drought period. Moreover, reduced absorption of visible and UV-B radiation results in a lower degree of photosynthetic inhibition (Karabourniotis and Bornman, 1999). Further possible benefits associated with pubescence are reduced herbivory (Levin, 1973) and increased probability of water uptake by leaves (Savé *et al.*, 2000).

Although pubescence enhances plant performance in stressful environments, there are trade-offs associated with it. These include the additional costs for construction of pubescent leaves and lower rates of photosynthesis at common light intensity, especially when water availability is higher (Sandquist and Ehleringer, 2003). Overall, positive or negative effects associated with leaf trichomes on productivity and fitness depend on the level of environmental stresses, such as the degree of drought.

29.2.4.4 STOMATAL CHARACTERISTICS

Stomatal traits, such as density and size of stomata, largely influence stomatal conductance to gaseous transport (g_s). Therefore, modifications in stomatal number and dimensions can importantly alter leaf-water loss and photosynthetic rates. In a range of Mediterranean species belonging to different plant functional types, maximal g_s was highly correlated with stomatal area index (i.e., stomatal density × stomatal size) (Galmés *et al.*, 2007c) and photosynthetic capacity (Galmés *et al.*, 2007a). Small and abundant stomata enhance fine regulation of plant water use (Pearce *et al.*, 2006). Hence, species from semi-arid environments typically have leaves with higher density and smaller stomata than species from humid sites (Sundberg, 1986). However, exceptions to this rule exist, with some species well-adapted to highly stressed conditions having low stomatal densities (Galmés *et al.*, 2007c) and/or stomata with large pore sizes (Rhizopoulou and Psaras, 2003).

Although the plant species dominating semi-arid habitats are generally hypostomatous, possessing stomata commonly on the lower leaf surface only, amphistomatousness becomes more common with further reductions in water availability (James and Bell, 2000). Characteristically, amphistomatous species in xeric habitats have thick foliage elements, and accordingly, amphistomatousness is an adaptive feature

shortening the distance of CO_2 diffusion to mesophyll cells in these species (Parkhurst *et al*., 1988).

Specialised modifications in semi-arid species are sunken stomata and stomatal location in crypts (Fahn and Cutler, 1992). Compared with leaves having stomata on leaf surface, leaves with stomata embedded within mesophyll have vastly reduced boundary layer conductance for water, significantly curbing plant water loss.

29.2.4.5 CUTICULAR CONDUCTANCE TO WATER

The ability of plants to survive severe drought periods is affected by the ability to restrict residual water loss through the cuticula after stomata have closed. Low cuticular conductances to water have been reported as an adaptive trait in high water- and light-stressed semi-arid environments, and corresponds well with the degree of xeromorphism (Bolhàr-Nordenkampf and Draxler, 1993). In Mediterranean sclerophylls, low cuticular and stomatal conductances commonly co-occur (Levitt, 1980).

Although being beneficial in limiting the non-stomatal transpiration, the disadvantage of impermeable cuticula can be the constrained leaf water-absorption capacity. High capacity to adsorb water from fog, dew and infrequent precipitation has been proposed as an advantageous trait for species from arid and semi-arid ecosystems (Monk, 1966). Munné-Bosch *et al*. (1999) found improvements in water relations of drought-stressed Mediterranean plants after dew formation on the leaf surface. In these plants, the photosynthesis rate increased as the result of water uptake from the leaf surface. In species from semi-arid ecosystems of Venezuela, Díaz and Granadillo (2005) showed that productivity of canopy irrigated trees was even greater than that of soil-irrigated trees. However, foliar water uptake may rely more strongly on uptake through stomata than through cuticula (Peschel *et al*., 2003). Thus, the capacity of foliar water uptake will more strongly depend on plant ability for rapid stomatal opening in response to humid conditions rather than on cuticular water permeability.

29.2.5. Leaf physiological traits that influence photosynthesis

In addition to structural alterations, species inhabiting semi-arid ecosystems have developed a number of physiological adaptations to cope with co-occurring high-temperature and solar-irradiance stresses. These physiological modifications either serve to minimise the capture and processing of light or directly influence carbon assimilation. In addition,

structural adaptation to semi-arid conditions leads to changes in internal CO_2-diffusion conductance thereby further altering leaf-assimilation characteristics.

29.2.5.1 LEAF PHYSIOLOGICAL TRAITS CONTROLLING THE CAPTURE AND PROCESSING OF LIGHT

Under conditions of high PPFD and limited CO_2 entry through the stomata, the amount of light absorbed by leaves rapidly exceeds the capacity of cells to use the photochemical energy for photosynthesis and photorespiration. Under such conditions, foliage photosynthetic apparatus is prone to photoinhibition. To cope with enhanced risk of photoinhibition, plants in semi-arid ecosystems display a number of physiological adaptations: (1) reduction of light-harvesting pigment-binding complexes; (2) increased alternative electron transport capacity; (3) increased thermal dissipation of absorbed light energy; (4) increased antioxidant defence systems; and (5) enhanced synthesis of VOCs.

A reduction of the content of light-harvesting pigment-protein complexes relative to the rest of photosynthetic machinery is an effective way of diminishing the absorption of excess light. Such a reduction of an effective cross-section of photosystems is manifested in decreased chl. and carotenoid contents, frequently observed during drought periods in a series of semi-deciduous (Kyparissis *et al*., 1995) and evergreen (Munné-Bosch and Alegre, 2000) species in semi-arid environments.

In addition to avoidance of light capture, plants have also evolved other mechanisms to cope with the excess of absorbed light. In drought-adapted species, the photosynthetic electron transport rate is reduced by drought to a lesser extent than CO_2 assimilation (Gulías *et al*., 2002). Lower sensitivity of electron transport to drought is associated with enhanced electron transport to alternative electron sinks, mostly to photorespiration and the Mehler reaction. Increased engagement of these alternative electron sinks reduces the fraction of excess excitation energy and thus provides photoprotection against excess light (Flexas and Medrano, 2002b).

The rate of thermal dissipation of absorbed light energy is also enhanced in semi-arid species (Galmés *et al*., 2007b). The capacity for thermal dissipation of excitation energy is commonly explained on the basis of xanthophyll cycle – light-dependent conversion of violaxanthin to zeaxanthin through antheraxanthin – resulting in changes in conformation of pigment-binding proteins (Demmig-Adams and Adams, 2006). Enhanced capacity for thermal excitation-energy quenching is typically linked to higher content of

xanthophyll-cycle carotenoids (violaxanthin, antheraxanthin and zeaxanthin) per A_{leaf}, chl. and total carotenoids and a greater de-epoxidation state of xanthophyll-cycle carotenoids (greater fraction of zeaxanthin) (Demmig-Adams and Adams, 2006). The need for greater capacity of thermal energy dissipation is not only constrained to drought periods in the summer, but can also be relevant on winter days with freezing temperatures (García-Plazaola et al., 2003b). Under such conditions, low temperatures limit CO_2 assimilation and the fraction of excess light can be large.

Increased thermal-energy dissipation and reduced quantum efficiency under excess light generally imply increased foliage photoprotection ('dynamic photoinhibition', sensu Osmond, 1994). Under extreme conditions, the capacity for foliage electron transport is also reduced manifesting photodamage ('chronic photoinhibition', sensu Osmond, 1994). In semi-arid plants, drought and low temperatures generally result in 'dynamic photoinhibition' and, to a lesser extent – at least in well-acclimated leaves developed under high irradiances – 'in chronic photoinhibition' (Werner et al., 2002).

Other photoprotective mechanisms observed in semi-arid species are increased antioxidant activity (Munné-Bosch and Peñuelas, 2003) and synthesis of volatile compounds (Loreto and Sharkey, 1993). Lipid-soluble antioxidants such as tocopherol quench free radicals and lipid peroxides formed in membranes, while water-soluble antioxidants such as glutathione and ascorbate quench active oxygen species formed in the leaf liquid phase in response to excess energy driven oxidative stress (Havaux and Niyogi, 1999). Several lipid-soluble volatile compounds such as monoterpenes also function as antioxidants in the leaf lipid phase (Loreto et al., 2004a). Enhanced volatile-compound synthesis has been hypothesised to lessen the possible over-reduction of photosynthetic apparatus under stress conditions, functioning thus as a sort of metabolic safety valve (Rosenstiel et al., 2004). Yet only a relatively small fraction of electrons enter volatile-compound synthesis, and thus the contribution of emission of volatile organics to photoprotection is likely to be minor (Niinemets et al., 2002).

29.2.5.2 LEAF PHYSIOLOGICAL TRAITS INFLUENCING CARBON DIFFUSION AND ASSIMILATION

Two main barriers limit the diffusion of CO_2 from the ambient atmosphere to the site of carboxylation in the chloroplast: stomata and leaf mesophyll. Apart from morphological adaptations of stomata described in the previous section, stomatal closure in response to soil-water shortage is a common response among plants, but the extent
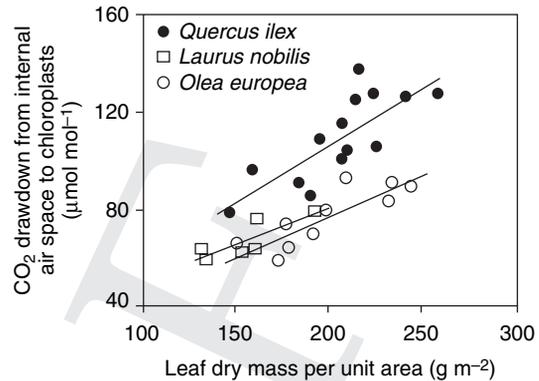

Fig. 29.4. Scaling of the CO_2 drawdown from internal air space to chloroplasts (ΔC) with leaf dry mass per unit area (LMA) in three Mediterranean sclerophyllous species (modified from Niinemets et al., 2005). Within-species variation in LMA was mainly owing to variation in leaf age. ΔC is the difference between CO_2 concentrations in internal air space (C_i) and chloroplasts (C_c). Given that net assimilation, A_N, is given as $A_N=g_m(C_i-C_c)=g_m\Delta C$, ΔC provides a measure of the extent to which photosynthesis is limited by g_m for leaves with a given photosynthetic capacity ($\Delta C=A_N/g_m$). All measurements were conducted at a leaf temperature of 25°C and ambient CO_2 concentration (ca. 350 μmol mol^{-1}).

and velocity of this response differ among species, resulting in widely varying efficiencies of water use. The species from semi-arid ecosystems typically have higher stomatal responsiveness to water deficit, resulting in greater WUE that allows them to use water longer into the drought period (Galmés et al., 2007c).

Once CO_2 has entered into the leaf, it must overcome a series of gas-, liquid- and lipid-phase resistances from the sub-stomatal cavities to the chloroplast stroma. Mesophyll internal diffusion conductance (g_m) accounts for these constraints on the diffusion pathway. The internal diffusion conductance depends on leaf anatomy, with long-lived leaves having lower values of g_m than deciduous species or annuals (Warren et al., 2007; Flexas et al., 2008, see also Section 29.2.4). Stronger limitation of diffusion in leaves with a more robust structure is mainly associated with thicker cell walls and a lower internal gas-phase volume than those in more mesophytic leaves (Syvertsen et al., 1995). The degree to which photosynthesis is limited by g_m (drawdown of CO_2 concentration from sub-stomatal cavities to chloroplasts) is positively associated with LMA in semi-arid species (Fig. 29.4). Lower g_m of these species is the cost these leaves 'pay' for greater longevity, cavitation resistance and capacity to extract water from drying soil.

In addition to leaf anatomy, g_m can also relatively rapidly acclimate to a variety of environmental conditions (see Chapter 4 for a detailed explanation). In semi-arid environments, short-term low water availability and high temperatures can induce large reductions in g_m. As a result, semi-arid species temporarily suffer from noticeably low CO_2 concentrations at the carboxylation sites (Galmés *et al.*, 2007a), strongly limiting CO_2 assimilation rates during water stress. This is especially significant in species with high LMA where already anatomical constraints seriously limit g_m (Galmés *et al.*, 2007a) for which these species can experience a larger advantage than mesic species of increased CO_2 concentration in the atmosphere in terms of both photosynthesis and WUE (Niinemets *et al.*, 2011).

Although low chloroplastic CO_2 concentrations limit carboxylation, low CO_2 stimulates oxygenation (photorespiration), further reducing net carbon fixation. Under these conditions, a higher Rubisco specificity towards CO_2 than to O_2 that competes for the same enzyme active site could importantly increase a species' competitive potential in semi-arid habitats. So far, the evidence of greater Rubisco specificity in ecosystems with high temperature and low water is limited (Galmés *et al.*, 2005), but the number of species screened so far is also clearly insufficient.

Alternatively, CO_2-concentration mechanisms present in several species in semi-arid ecosystems (C_4 and CAM pathway) can importantly increase the ratio of carboxylation to oxygenation and thereby significantly enhance photosynthesis during dry and hot periods (Sage, 2001). C_4 and CAM photosynthesis types are energetically more expensive and require more light quanta per mole fixed CO_2. However, in relatively open semi-arid environments with high solar-energy input, this high energetic cost is vastly outweighed by improved carbon gain during dry periods.

29.3. SEASONAL VARIATIONS AND RESPONSES OF PHOTOSYNTHESIS TO SINGLE ENVIRONMENTAL FACTORS

In addition to differences in the photosynthetic capacity among plant functional types (Section 29.2.3), annual carbon gain also depends on functional type-specific seasonal modifications in photosynthesis. In semi-arid environments (Mediterranean and savanna-type ecosystems) with similar annual amounts and variation in precipitation, there is a vast variation in seasonal timecourses of A_N among annual, drought-deciduous, semi-deciduous, winter-deciduous and evergreen species (Fig. 29.5). Clearly, the annuals have the
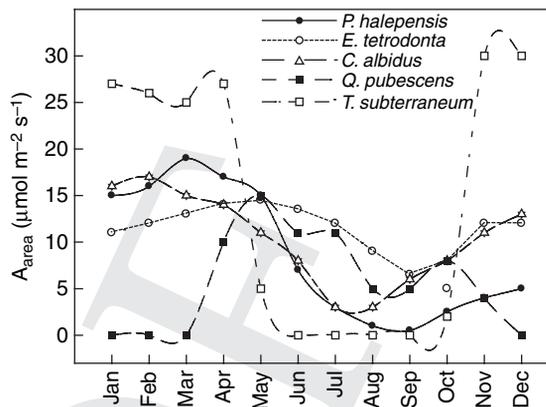

Fig. 29.5. Seasonal time courses of net CO_2 assimilation rate (A_{area}) for semi-arid species belonging to different plant functional types: evergreen conifer *Pinus halepensis* (data of Klein *et al.*, 2005, sampled in Israel, mean annual precipitation 270 mm and mean annual temperature 15°C); broad-leaved evergreen tree *Eucalyptus tetrodonta* (Prior *et al.*, 1997, savanna in Australia, 1300 mm and 26°C); semi-deciduous shrub *Cistus albidus* (Gulías *et al.*, 2009, Mediterranean macchia in Spain, 470 mm and 17°C); winter-deciduous tree *Quercus pubescens* (Damesin and Rambal, 1995, deciduous oak forest in southern France, 1100 mm and 13°C); and summer-deciduous perennial herb *Trifolium subterraneum* (Flexas *et al.*, 2003, Mediterranean grassland in Spain, 500 mm and 17°C). In the semi-deciduous species, the values of A_{area} only correspond to retained leaves.

highest maximum A_N, but they photosynthesise for only a few weeks/months a year. Winter-deciduous woody species have lower maximum rates, but maintain positive net photosynthesis (A_N) for 6–9 months per year (Fig. 29.5). In contrast, evergreen species exhibit lower maximum photosynthesis rates, but photosynthesise all year round with a significant fraction of annual carbon fixation performed in the winter months (Tenhunen *et al.*, 1987). This indicates that a type of compensatory relationship between maximum photosynthetic capacity, leaf lifespan and seasonal duration of photosynthetic activity is evident.

In semi-arid environments, leaf photosynthesis always exhibits a marked depression during dry months regardless of the functional group and site. However, the relative importance of this depression depends on both the functional type and the climate (Fig. 29.5). The lowest reduction in A_N can be observed in savanna ecosystems with deep soils, and relatively high annual precipitation, allowing species with deep root systems to reach the soil-water table (e.g., *E. tetrodonta* in Fig. 29.5).

Although winter depression of photosynthesis is generally considered as a major limitation in Mediterranean ecosystems, the reductions in photosynthetic potentials (A_N) *per se* are relatively moderate (Fig. 29.5). However, reduced light intensities and lower than optimum temperatures still reduce the realised carbon gain (Tenhunen *et al.*, 1987). Nevertheless, in semi-arid ecosystems that can support evergreen vegetation, summer drought is generally a more important limitation of annual carbon gain than winter temperatures (Flexas *et al.*, 2001). In colder semi-arid regions, particularly in steppes with temperate continental climates, low winter temperatures limit photosynthesis more strongly and can curb annual productivity more than summer drought (Méthy, 2000b). In semi-arid environments, chilling and freezing sensitivity of photosynthesis is higher for tropical and sub-tropical flora components than for species typical of temperate climates (Gulías *et al.*, 2009). Sensitivity to photoinhibition is another cause for decreased photosynthesis during winter (García-Plazaola *et al.*, 2003b), although semi-deciduous species seem to be more vulnerable to winter photoinhibition than evergreens (Werner *et al.*, 2002).

Some semi-arid environments such as Mediterranean ecosystems are often associated with complex site topography. To understand the responses of species groups to climate, it is further important to consider that local climatic differences can be highly variable within short distances in complex terrains. Such local climatic differences can affect annual photosynthesis of a single species by the same order of magnitude as the within-site variation in annual photosynthesis among species of different plant functional type (Flexas *et al.*, 2003). These between-site differences likely translate into large variation of the annual carbon balance between local populations of the same species.

29.4. WHOLE-PLANT FEATURES AND ECOSYSTEM GAS EXCHANGE

The consequences of variations in crown architectural traits for light interception and photosynthetic efficiency have been traditionally analysed in terms of total leaf LAI, leaf-inclination-angle distribution and leaf aggregation (spatial clumping) (Valladares and Pearcy, 1998; Cescatti and Niinemets, 2004).

A series of architectural traits at leaf, shoot and whole-canopy scale affect these three key sets of traits. In particular branching pattern, leaf-insertion angle, leaf rolling and phyllotaxis can importantly modify angular distributions and spatial clumping of foliage and thereby alter light-harvesting efficiency. Especially in ecosystems where LAI is small, foliage geometry strongly affects the diurnal and seasonal patterns of light capture and potential carbon gain (Valladares and Pugnaire, 1999).

29.4.1. Leaf-area index

Whole-community LAI is typically low in semi-arid environments owing to low water availability. However, LAI in semi-arid environments is highly non-uniformly distributed in space with areas exhibiting very low plant cover or even bare ground during drought periods intermixed with areas having high LAI (Asner and Wessman, 1997). High spatial heterogeneity in LAI can be found in savannas and Mediterranean shrublands with sparsely distributed evergreen woody species (Asner *et al.*, 2000). Evergreenness is the primary reason for accumulation of large leaf area within the canopy of semi-arid species (Rambal, 2001). Deciduous counterparts have significantly lower LAI in such environments (Damesin *et al.*, 1998).

Typically, whole-community LAI between 1–6 m^2 m^{-2} are found in Mediterranean macchia and forest ecosystems with values of 2–3 m^2 m^{-2} being most common (Rambal, 2001), 0.8–1.7 m^2 m^{-2} in savannas (Scholes *et al.*, 2004) and between 1–4 m^2 m^{-2} for semi-arid steppes and grasslands (Xu and Baldocchi, 2004). However, LAI within any community type increases with increasing precipitation, with the transition zones to humid biomes having the highest LAI values (Damesin *et al.*, 1998).

Apart from spatial heterogeneity, semi-arid environments also exhibit large temporal heterogeneity in LAI. Species from semi-arid ecosystems often partly shed leaves in response to drought and co-occurring high light stress (Werner *et al.*, 1999). Although instantaneous canopy photosynthesis can be linearly related to LAI in semi-arid species until relatively high values of LAI (Goulden, 1996), dropping some but not all leaves allows the plants to diminish the overall transpiratory water loss and continue photosynthesis longer into the dry season. Thus, having lower LAI during drought periods potentially maximising photosynthesis when enough water was available, results in larger annual carbon gain than temporally invariable LAI (Tenhunen *et al.*, 1990).

Partial leaf loss has been described in all semi-arid ecosystems in a variety of plant functional types such as perennial grasses (Balaguer *et al.*, 2002) and evergreen sclerophylls and conifers (Werner *et al.*, 1999). Many Mediterranean

semi-deciduous species have seasonal crown dimorphism, characterised by different types of branches and leaves during different seasons (Aronne and De Micco, 2001), but also reduced leaf area and size during the dry season (Gratani and Bombelli, 2000). Some drought-deciduous species retain green stems (see Chapter 7) after shedding leaves during a dry summer (Gibson, 1983). Reductions of LAI and increased reliance on the use of drought-specialised photosynthetic stems lead to water conservation and persistent photosynthesis during drought in semi-arid species (Comstock and Ehleringer, 1988).

At extremes, drought can result in complete loss of photosynthesising surface in drought-deciduous species (Werner *et al.*, 1999). However, drought-deciduous species from savannas, where multiple severe drought cycles can occur during a year, have been shown to be very opportunistic in their water use by retaining non-dormant buds. This fact results in very fast bud-break and leaf flush after significant rainfall events (Díaz and Granadillo, 2005).

Some authors have argued that all these long-term changes in LAI, and not physiological parameters, are actually the main response of many species well adapted to semi-arid conditions. In this sense, the ecological optimal theory given by Eagleson (1982) has been contrasted by modelling LAI in semi-arid environments, showing that this parameter is finelly tuned depending on the soil-water availability (Hoff and Rambal, 2003).

29.4.2. Leaf-inclination angle distributions

Modification of leaf-inclination-angle distributions is a powerful way to alter the total light interception and temporal variation of the occurrence of peak irradiances on the leaf surface. Horizontally exposed leaves represent an effective strategy for light interception, but horizontal leaves have their highest irradiances on the leaf surface at midday when other co-occurring stresses, such as drought and heat stress, are most severe. Thus, horizontal leaf-inclination angles in semi-arid environments can result in irreversible photodamage and pigment destruction (Valladares and Pugnaire, 1999). In dry and high-light environments, steep leaf-inclination angles provide a viable solution to enhance whole-plant carbon gain and reduce overheating and photoinhibition (Niinemets *et al.*, 2006a,b).

Leaf-inclination angle is generally considered a static trait as it cannot be strongly modified after petiolar and lamina tissues have been rigidified by lignification. Nevertheless, there are seasonal and daily modifications in leaf-inclination

angle in several species (Forseth and Ehleringer, 1982). Such modifications have been mainly assigned to drought-deciduous plants (Werner *et al.*, 1999), but can actually occur in evergreen sclerophylls (e.g., Gratani and Ghia, 2002), semi-arid grasses (Ryel and Beyschlag, 1995) and savanna deciduous trees (Scholes *et al.*, 2004). In species with strongly lignified foliage elements, such modifications in inclination-angle distributions can be partly ascribed to preferential shedding of leaves that have a less favourable exposure. In semi-deciduous dimorphic species, summer leaves have steeper leaf angles (Gratani and Bombelli, 2000), and the angles of the photosynthetic surface also become steeper during dry season in drought-deciduous species retaining green stems (Gibson, 1983).

Apart from the dry season, the structural photoprotection by vertical leaf orientation has also been shown to be an efficient photoprotective mechanism during winter when foliage photosynthetic activity is decreased by low temperatures (Oliveira and Peñuelas, 2002).

Although a steep inclination angle is a beneficial feature for high-light exposed foliage, significant within-canopy light gradients also exist in the canopies of semi-arid species. In low light, where most of the light arrives from high solar-inclination angles, vertical foliage orientation is clearly disadvantageous. In fact, there is large phenotypic plasticity in foliage-inclination angles with foliage orientation gradually shifting from vertical in high-light exposed shoots to horizontal in low-light exposed shoots (Valladares and Pearcy, 1998).

29.4.3. Leaf aggregation

Foliage in species dominating semi-arid environments is generally more densely packed and more strongly aggregated in space than in mesic species (Falster and Westoby, 2003). Such modifications result in reduction of mean irradiance on the leaf surface (Cescatti and Niinemets, 2004), and thus in a lower risk of photoinhibition both during the dry and cold seasons. The degree of foliage aggregation (spatial clumping) can be increased by several structural modifications. Leaf rolling or folding is a common response to stresses in semi-arid ecosystems, and has been observed in herbaceous (Haase *et al.*, 1999b) and woody perennials (Kyparissis and Manetas, 1993). Rolling protects leaves from high irradiance levels by decreasing the area exposed to light (Pereira and Chaves, 1993). Rolling also results in concealing stomata in perennial grasses (Haase *et al.*, 1999b) and drought-deciduous species (Aronne and De Micco,

2001), thus minimising water loss at the times photosynthesis is severely restricted. The degree of leaf rolling is proportional to the RWC of leaves (Pugnaire *et al.*, 1996), and thuerefore this mechanism is a potent way of regulating light interception and water use.

A high degree of foliage aggregation also results from smaller and more tightly packed leaves in semi-arid species (Givnish, 1984). Self-shading (and the degree of aggregation) by shoot axis inevitably increases with decreasing the length of foliage elements (Takenaka, 1994). High frequency of branching, short internodes and spiral phyllotaxis can further enhance the degree of foliage aggregation in the canopies of semi-arid species (Niinemets *et al.*, 2006a,b). Such characteristic architectural features observed among a variety of semi-arid species, such as tussock grass (*Stipa tenacissima*), leafless shrub (*Retama sphaerocarpa*) and evergreen shrub (*Quercus coccifera*), result in high self-shading and significantly reduced mean leaf irradiance (Valladares and Pugnaire, 1999).

Structural photoprotection through enhanced foliage aggregation and steeper inclination has an opportunity cost in terms of reduced carbon gain during periods when the environmental conditions are favourable. Nevertheless, characteristic high light stress in combination with drought and extreme temperatures makes such photoprotective strategies highly adaptive in semi-arid environments (Valladares and Pugnaire, 1999).

29.4.4. Ecosystem productivity and its seasonal and inter-annual variability

Semi-arid ecosystems have intermediate NPP among world biomes (see Grace *et al.*, 2006 and references therein). Only tropical and some temperate forests have higher productivity than semi-arid biomes (Grace *et al.*, 2006). Among semi-arid biomes, savannas exhibit the highest annual NPP of 720 g C m^{-2} year^{-1}, Mediterranean-type ecosystems are intermediate with 500 g C m^{-2} year^{-1}, and steppes the lowest with 380 g C m^{-2} year^{-1}. All semi-arid ecosystems together are responsible for 40% of world annual NPP (Grace *et al.*, 2006).

Net ecosystem productivity for CO_2 (NEP) results from the difference between gross primary productivity (GPP) and ecosystem respiration (R_{eco}). Typically, semi-arid ecosystems exhibit a GPP peak during late spring, when high temperatures co-exist with available water (Fig. 29.6). In summer, water deficits, high light and elevated temperatures lead to reduced photosynthetic rates of evergreen trees and
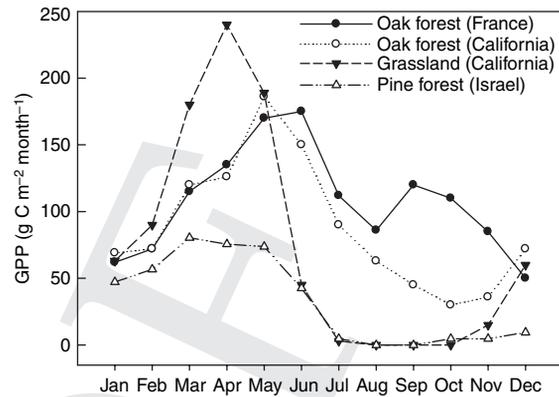

Fig. 29.6. Seasonal variation in gross primary productivity (GPP) in four semi-arid Mediterranean ecosystems. Data are from Ma *et al.* (2007) for Californian oak forest and grassland (with an annual precipitation of 560 mm), Allard *et al.* (2008) for French oak forest (900 mm) and Grünzweig *et al.* (2003) for Israeli pine forest (270 mm).

shrubs and to leaf senescence in shallow-rooted herbaceous annuals and perennials and in drought-deciduous shrubs and trees. This explains a general summer decrease in GPP in various semi-arid ecosystems dominated by different plant functional groups (Fig. 29.6).

Seasonal variability of R_{eco} is more complex than that of GPP, though both parameters are usually highly correlated (Ma *et al.*, 2007). This is partially owing to the limitation imposed by summer conditions on R_{eco}, which nevertheless does not counterbalance for the typically higher decrease in GPP, resulting in semi-arid ecosystems acting as net carbon source (i.e., negative NEP) during summer and early autumn (Pereira *et al.*, 2007). Upon soil re-watering in autumn, vegetation gradually recovers towards winter. For instance, French oak forest exhibited a secondary peak in GPP after the onset of autumn rainfall events (Fig. 29.6). Such a trend for an increased GPP after first rain events in autumn is related to the ability of semi-arid ecosystems to recover from drought effects if the length of drought is not excessive (Luo *et al.*, 2007). This is also related to high rain-use efficiency of several Mediterranean-type ecosystems, especially after the driest periods (Pereira *et al.*, 2007).

The degree of autumn and winter recovery of GPP depends on the amount of rainfall during this season as well as on winter temperatures. In some ecosystems autumn/winter recovery may be lacking, such as in the pine forest in Fig. 29.6, where there was no enhancement of precipitation in the autumn. Autumn recovery was also missing in

the grassland ecosystem, where the grasses were dormant after summer drought (Fig. 29.6). Furthermore, there is a clear depression in GPP during late autumn and early winter in the French oakland (Fig. 29.6), reflecting inhibition of photosynthesis by low temperatures.

Similarly to annual GPP, seasonal trends in GPP of semi-arid ecosystems depend on the capacity of plants to reach groundwater reserves, and therefore, on soil texture and plant functional-type-specific rooting systems. Ecosystems dominated by deep-rooted species sustain drought-induced reductions in GPP later than shallow rooted species (e.g., oak forest versus grassland in Fig. 29.6). Inability of steppe and savanna grasses to reach the soil-water table enhances and accelerates summer drought-induced GPP limitations (Suyker and Verma, 2001; Veenendaal *et al.*, 2004).

Inter-annual variability in NEP is extreme for semi-arid ecosystems, especially for semi-arid grasslands (Knapp and Smith, 2001). This is owing to the intrinsic variability of the precipitation patterns in semi-arid environments, and their differential effects on GPP and R_eco. For instance, after small pulses of rain, NEP is a source of carbon because R_eco is reactivated, but not GPP. Whereas for a big pulse of precipitation, GPP is reactivated and finally leads NEP into being a sink (Knapp and Smith, 2001). Extremely dry years can result in semi-arid ecosystems acting as carbon sources (Xu and Baldocchi, 2004). Such negative effects of unusually severe drought on NEP can even extend into the following years (Luo *et al.*, 2007).

29.4.5. Effects of disturbance on ecosystem productivity

Fire and grazing are the main disturbances in Mediterranean, savanna and steppe ecosystems (e.g., LeCain *et al.*, 2002; Grace *et al.*, 2006). Both fire and grazing exert profound influences on ecosystem structure, in particular on the composition of dominant plant functional types. For instance, grazing and fire reduce the abundance of C_3 woody species in steppe ecosystems (LeCain *et al.*, 2002). Such profound modifications in dominance of plant functional groups can cause dramatic changes in NPP.

The primary consequence of fire and grazing stress is the reduction in aboveground plant biomass. Initially, the decrease in LAI results in a temporary decline in ecosystem photosynthesis, leading to reduced CO_2-sequestration capacity (Grace *et al.*, 2006). Reduction in LAI also results in decreases in ecosystem annual evapotranspiration (AET) (Bremer *et al.*, 2001) and increases in soil-water stores that

can partly compensate for the effects of reduced LAI on productivity (Fleck *et al.*, 1998).

As a secondary response, the decrease in LAI stimulates re-growth in tolerant species. Grazing- and fire-tolerant species have a large tillering capacity, allowing them to quickly recover after grazing (McNaughton *et al.*, 1996). Apart from the immediate response after the disturbance, greater plant turnover and more numerous non-dormant buds in grazed ecosystems are associated with earlier 'green-up' after winter and summer stresses. Such an early onset of growth enhances early and late-season photosynthesis (LeCain *et al.*, 2000).

Young resprouts also often have higher A_N (Nowak and Candwell, 1984). Such a compensatory increase in A_N during the first season after fire or grazing is associated with reduced intra- and interspecific competition, resulting in higher light, water (De Souza *et al.*, 1986) and nutrient (Hulbert, 1988) (especially nitrogen (Hastings *et al.*, 1989)) availabilities for resprouts. For instance, improved water availability after fire was associated with higher g_s and g_m, greater A_N and reduced degree of summer photoinhibition in resprouts of Mediterranean evergreen species (Fleck *et al.*, 1998). In addition to immediate increases in photosynthetic capacity by improved nutrition, larger nutrient availability has also been shown to delay leaf senescence (Bremer *et al.*, 2001), thereby further increasing ecosystem carbon gain.

Both enhanced water and nutrient availabilities are necessarily short-lived with the effects becoming gradually less with increasing canopy leaf area and increasing competition. For instance, with increasing LAI the benefits of resprouts are lost as increased evapotranspiration owing to larger canopy conductance of resprouts leading to depletion of soil-water stores (Bremer *et al.*, 2001).

29.5. WATER-USE EFFICIENCY AND CLIMATE-CHANGE PERSPECTIVES

Global climate change associatied with elevated CO_2 concentrations results in increased temperature and altered precipitation patterns, which can profoundly affect the productivity of semi-arid ecosystems. Trends of increased temperature and decreased soil moisture have been predicted and documented globally (Jung *et al.*, 2010) and specifically for semi-arid regions (Osborne *et al.*, 2000). As a consequence of climate change, arid and semi-arid areas are expected to increase in worldwide coverage, but there are still large uncertainties in understanding how semi-arid ecosystems

will respond to this global change, although most evidences suggest negative effects. For instance, climate-change-induced increased drought has been reported to decrease the global terrestrial NPP from 2000 through 2009 (Zhao and Running, 2000) and to increase defoliation and mortality in trees from 1990 to 2007, particularly in Southern Europe (Carnicer et al., 2011).

29.5.1. Water-use efficiency

The long standing soil-water shortage and high leaf-to-atmosphere VPD have exerted an important evolutionary pressure for improved carbon assimilation over water losses in species typical of semiarid environments (Tsialtas et al., 2001). Improved WUE is achieved by a reduced stomatal aperture for a given carbon assimilation rate, which can occur as a result of both adaptation and acclimation processes (Flexas et al., 2003).

With respect to adaptation, as explained in Section 29.2.4, species of semi-arid environments typically possess a number of structural features in the stomatal apparatus that result in a relatively low intrinsic g_s. The negative effect of reduced g_s on conductance to CO_2 is overcountered by the positive effect on leaf-water losses. Hence, when compared with species from other biomes, in-situ measurements of the intrinsic WUE (A_N/g_s) under non-stressing conditions showed that most of the Mediterranean species lay in the region with the highest WUE (Gulías et al., 2003). Additionally, there are many other leaf structural and biochemical features that can indirectly affect WUE by limiting A_N. For instance, Medrano et al. (2009) showed that those Mediterranean species with the highest drought-induced increases in LMA presented the lowest increase in A_N/g_s, probably owing to increased internal leaf resistances to CO_2 transfer towards the active sites of carboxylation.

Regarding acclimation processes, stomatal closure is well-known as a common response to drought. In spite of such a general trend, there are important differences among species in their stomatal responsiveness to decreases in soil or plant water status. Historically, these differences have been referred as two different strategies, with drought-avoidant species presenting high stomatal responsiveness to increasing drought, and drought-tolerant species with low stomatal responsiveness to increasing drought. Both strategies are certainly found in semi-arid environments and work in tight coordination with other plant traits, such as xylem hydraulic conductivities, root-system extension or capacity for osmotic adjustments (Galmés et al., 2007c). In some cases, these different strategies are related to growth forms and leaf habits. For instance, for Mediterranean species there is a trend for an increased A_N/g_s from herbaceous species, through shrubs to trees (Medrano et al., 2009). Within shrubs and trees, there is also a trend related to leaf habits, with evergreen species presenting higher A_N/g_s than deciduous ones. The lowest values of A_N/g_s for herbs and semi-deciduous shrubs under well-watered conditions may be attributable to their high g_s. Under drought conditions, all growth forms increase A_N/g_s except herbs, with semi-deciduous shrubs and deciduous trees presenting the highest relative increase (Medrano et al., 2009). This is related to the drought-escape strategy of herbaceous species. However, Medrano et al. (2009) showed that herbaceous species typical of Mediterranean coastal environments presented the highest relative increase in A_N/g_s as drought progressed, and suggested that the capacity of withstanding water limitation may be an adaptation of all Mediterranean plants regardless of their growth form and leaf habit.

At the ecosystem scale, an important aspect in semi-arid biomes is ecosystem WUE (EWUE), defined as the ratio of net carbon flux to evapotranspiration. Decrease in EWUE with increasing VPD has been reported in Mediterranean ecosystems (Reichstein et al., 2002) and savannas along a precipitation gradient (Scanlon and Albertson, 2004). Again, differences in a plant functional type's composition among studied ecosystems may be the cause for the observed differences in EWUE along the aridity gradient.

29.5.2. Elevated CO_2 effects on plant water use

Arid and semi-arid ecosystems are believed to be among the most responsive to elevated CO_2, and there is evidence that rising CO_2 has already led to significant increases of NPP in semi-arid biomes during the last century (Osborne et al., 2000). This large CO_2-sensitivity is associated with the circumstance that these strongly water-limited ecosystems potentially benefit the most from CO_2-driven enhancements in plant WUE (Melillo et al., 1993). Numerous studies demonstrate that stomata close under elevated CO_2 resulting in reduced water use, while photosynthesis is stimulated and relatively more carbon can be assimilated with a given water loss, resulting in increased WUE and improved plant water availability (Nelson et al., 2004).

Improved WUE is believed to be the primary factor explaining the positive effects of elevated CO_2 on NPP. As less water is used for assimilation of a given amount of carbon, more water is potentially left in the soil (Nelson

et al., 2004). In Mediterranean-type ecosystems, actual evapotranspiration of a community is significantly reduced under elevated CO_2 (Grünzweig and Körner, 2001). This remaining water will permit for an extended period of water extraction into the dry season. The extension of the growing season increases summer canopy photosynthesis and therefore annual NPP and community biomass (Joel *et al.*, 2001).

No acclimation has been found in the stomatal sensitivity to elevated CO_2 in semi-arid species (Scarascia-Mugnozza *et al.*, 1996), suggesting that the reduced stomatal openness is maintained over long term. However, the improved soil-water storage is not always observed. In fact, larger soil-water availability has resulted in increased g_s in some semi-arid grasslands (LeCain *et al.*, 2003) and shrublands (Pataki *et al.*, 2000). Also, the sensitivity to *water-vapour* pressure was reduced at high CO_2 (Tognetti *et al.*, 2000). It is important to consider that stomatal responses to CO_2 involve both direct effects leading to stomatal closure and indirect responses mediated by long-term changes in soil-water availability. Such long-term effects can result in reversal of the closure responses (Morgan *et al.*, 2004). Although these responses are general for most plants, overall stomatal and mesophyll conductance limitations are greater in evergreen sclerophyll species than in deciduous species. Therefore evergreens have been suggested to improve their photosynthesis and WUE in response to increased CO_2 much more than deciduous, which is supported by meta-analysis data on doubling CO_2 experiments (Niinemets *et al.*, 2011). These differences could lead to shifts in the vegetation boundaries within semi-arid ecosystems, and indeed some evergeen species like *Quercus ilex*, *Ilex aquifolium*, *Hedera helix*, *Rhododendron ponticum* and *Prunus lauroceraus* have experienced northwards-expanded distribution in Europe in the recent decades (Niinemets *et al.*, 2011).

Photosynthetic downregulation or acclimation to high CO_2 and changes in carbon allocation patterns will also reduce potential gains in NPP (Poorter, 1993). Photosynthetic acclimation is often related to decreased leaf N content and photosynthetic enzyme activity (Moore *et al.*, 1999). Decline in foliage N content under CO_2 enrichment is common in semi-arid ecosystems (King *et al.*, 2004). Reduced N can limit the production of new sink tissues when assimilation rates are improved (Lee *et al.*, 2001c). This source/sink imbalance causes accumulation of carbohydrates, leading to feedback-limited photosynthesis

(Causin *et al.*, 2004). Available evidence demonstrates that photosynthetic apparatus does acclimate to elevated CO_2 in semi-arid species, but the extent of this acclimation is not entirely known. In Mediterranean species, photosynthetic capacity is commonly lower under elevated CO_2 (Niinemets *et al.*, 1999c; Tognetti *et al.*, 2000), although in steppe species some studies have found (LeCain *et al.*, 2003), but others have not (Anderson *et al.*, 2001) the reduction in the photosynthetic capacity.

29.5.3. Elevated CO_2 influences on LAI and plant functional types

Improved NPP can also be explained by enhanced LAI under elevated CO_2 (Osborne *et al.*, 2000). High whole-season LAI is associated with larger soil-water storage as well as delayed leaf senescence at elevated CO_2 (Zavaleta, 2001). However, larger LAI can offset the reduction in water use per A_{leaf} under elevated CO_2. Over the long term this can lead to reductions in soil-water content under elevated CO_2 (Ham *et al.*, 1995). This in turn will alter LAI until a new equilibrium between soil water and community LAI is achieved.

CO_2 enrichment can importantly alter plant-community structure and composition of key plant functional types in semi-arid environments. For instance, the growth and expansion of woody vegetation is accelerated in steppe ecosystems, possibly as the result of positive effects of increased soil-water stores on species with tap roots (Nelson *et al.*, 2004). Significant changes in plant-functional-type spectra can have major consequences on NPP of semi-arid ecosystems (Lloret *et al.*, 2004).

Among species with different photosynthetic pathways there is abundant evidence that productivity of C_3 species responds more to increased CO_2 than that of C_4 species (e.g., Morgan *et al.*, 2007). Substantial reduction of the area occupied by C_4 grasses is expected to occur under elevated CO_2 (Owensby *et al.*, 1999). Nevertheless, growth of C_4 species is also enhanced by CO_2, with the sensitivity often being similar to C_3 species (Morgan *et al.*, 2001).

In addition, low N concentration in semi-arid ecosystems may limit the photosynthetic advantage of C_3 grasses under elevated CO_2 (LeCain *et al.*, 2003). However, N-fixing C_3 species are expected to become more competitive under enhanced N limitations. CO_2 enrichment in several Mediterranean grasslands has resulted in increased coverage of legumes (Grünzweig and Körner, 2001).

29.5.4. Warming and reduced precipitation

While elevated CO_2 is expected to preferentially affect productivity of semi-arid ecosystems, predicted warming and reductions in precipitation can negatively affect GPP, offsetting the positive effects of increased atmospheric CO_2 (Allard *et al.*, 2008). For instance, in the Mediterranean basin a large decrease of April–September total rainfall is predicted, increasing the duration and severity of drought (Christensen *et al.*, 2007). Abnormally hot years that occurred recently in the Mediterranean basin led to negative NEP (Peñuelas *et al.*, 2007), challenging the hypothesis that future climate change will result in an enhancement of plant growth and carbon sequestration in semi-arid environments. Desertification of semi-arid ecosystems during the past decades is estimated to have contributed to approximately 20% of the global anthropogenic CO_2 effect on the atmosphere over the same period (Rotenberg and Yakir, 2010).

Alternatively, higher temperatures can enhance photosynthetic activity during winter and can promote early spring enhancement in NPP, especially at low latitudes. In semi-arid environments, the main growing season is expected to move towards winter months. This will affect canopy photosynthetic potentials over the seasons and alter the transitions from carbon sink to source, and *vice versa* (Ham and Knapp, 1998).

Higher temperatures in winter/spring may also increase the available thermal budget for growth and reproduction of insect herbivores. The increase of herbivory pressure on the vegetation will impact semi-arid ecosystems through reductions in LAI and whole-canopy carbon assimilation (Allard *et al.*, 2008). Alternatively, higher concentrations of carbon-based protective compounds in plants under elevated CO_2 may reduce herbivory pressure (McDonald *et al.*, 1999).

Increases in temperature may also alter the dominance of plant functional and photosynthetic types with profound influences on NPP of semi-arid environments. For instance, an increase of 2°C in mean annual temperature in Great Plains is expected to reduce the coverage of C_3 grasses by 50% (Epstein *et al.*, 1997).

Overall, global change (i.e., not only climate change but also changes in land use, perturbation regime, habitat degradation etc.) in semi-arid environments includes a wide array of factors influencing NPP at various spatial and temporal scales. Intricate interactions between these drivers complicate the prediction of global-change effects on NPP of semi-arid ecosystems, so more experimental and modelling work is needed to understand the complex interplay between the key climatic and global-change drivers on semi-arid ecosystems.

29.6. CONCLUDING REMARKS

Semi-arid refers to a heterogeneous collection of ecosystems with unique precipitation and temperature regimes. Although the term embraces a wide range of environments, seasonal water limitation and excess irradiance are the main limitations in all these environments, while heat and cold stress may also affect productivity in some of the semi-arid ecosystems. Key structural adaptations to cope with these stressful environments include sclerophylly, deep root systems, pubescence, vertical foliage-inclination angles and stronger foliage aggregation, while key physiological modifications include advanced stomatal regulation of water use, modifications in photosynthesis type and effective photoprotection and antioxidative capacity. As photosynthesis is strongly limited by water in these ecosystems, semi-arid ecosystems are expected to respond particularly strongly to elevated atmospheric CO_2 concentrations. However, the positive effects of elevated CO_2 can be offset by concurrent increases in temperature and reductions in precipitation.