Chapter 6
Overstory–Understory Relationships

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Frontispiece Chapter 6. Holm oak dehesa managed for a grassland understory using periodic cultivation. Some shrubs have begun to invade. (Photograph by G. Moreno)

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Abstract A key issue for sustainable management of oak woodlands is understanding the complex overstory-understory relationships that influence ecosystem productivity and stability. Oak removal is traditionally practiced in Californian ranches and Spanish oak dehesas to increase forage for grazing, but the response of the understory, and subsequently of the trees, is not fully understood. Existing knowledge of the effects of trees on understory forage production and the effects of the understory on tree production and recruitment is reviewed to synthesize from what is known and to identify knowledge gaps. Emphasizing the few published manipulative experiments to clarify the importance of facilitation and competition, plant to plant interactions are analyzed to examine three aspects of the relationship between trees and the understory: understory production, tree growth and production, and tree regeneration. First, we find that understory production is related to canopy-caused gradients of aboveground and belowground resources such as light, nutrients, and water. Second, the consequences of tree density and understory structure on oaks are analyzed, including competitive use of belowground resources. Third, the importance of the understory for oak seedling survival is discussed for its effect on the stability and sustainability of Spanish and Californian oak woodlands. While dehesa shrub encroachment is certainly favorable for oak seedling regeneration, it does not maintain longer-term stand functions and profitability from livestock, wildlife, and cork production. We conclude by proposing a future research agenda for the study of plant-to-plant relationships.

Keywords Canopy-caused gradients · Competition · Facilitation · Tree production · Seedling recruitment · Shrub encroachment

6.1 Introduction

Californian oak woodlands and Spanish dehesas are formed of evergreen and deciduous oaks within a grassland matrix dominated by annual grasses and forbs, where livestock production is integrated with oak and, on occasion, grain crop production (Huntsinger and Bartolome 1992; Campos et al. 2007; Marañón et al. 2009). In both Spain and California, oak woodland soils used for grazing tend to be shallow and infertile, unsuitable for intensive crop production. A mix of differing understory species and tree canopy densities provides a high degree of landscape structural diversity.

On the Iberian Peninsula, this diversity has been fostered by centuries, even millennia, of human influence and a combination of agricultural, pastoral, and forestry

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uses, where different vegetation structures depend on land use (Joffre et al. 1999; Marañón et al. 2009). Californian oak woodlands reflect a history of several thousand years of human influence, mostly through the use of fire as an element of management by indigenous peoples (Bartolome 1989), but with the addition since 1769 of European land use practices, including grazing, and wide-scale cultivation (Chap. 2). In addition, the California woodland has been hugely influenced and continues to be shaped by the introduction of non-native species that began with European–American colonization. In both systems, human impacts likely resulted in more open tree canopies and more of an herb-dominated understory (Marañón et al. 2009).

Currently, the Californian oak savanna type is considered a stable community that, in the absence of human intervention, changes slowly or not at all (Huntsinger et al. 1991) while Spanish dehesa, sometimes considered a natural part of the landscape in Southwestern Iberian Peninsula, has an unstable understory assemblage carefully maintained by land managers (Marañon 1988). Indeed, without direct human intervention, dehesas are rapidly invaded by aggressive shrubs (Campos et al. 2007) while a shrub understory is not common in Californian oak savanna (Table 6.1).

Table 6.1 Common vegetation in Californian oak woodland and Spanish dehesa

	California oak woodland	Spanish dehesa
Common oaks		
Evergreen	Coast live oak (*Quercus agrifolia*); interior live oak (*Q. wislizenii*)	Holm oak (*Q. ilex*) and cork oak (*Q. suber*) are the most common oaks in dehesa
Deciduous	Blue oak (*Q. douglasii*) and valley oak (*Q. lobata*). Blue oak is most widespread	Pyrenean oak (*Q. pyrenaica*) at higher elevations
Semi-deciduous	Englemann oak (*Q. engelmannii*)	Lusitanian oak (*Q. faginea*) and Algerian oak (*Q. canariensis*)
Soils	Varied volcanic, metamorphic, and sedimentary origins	Developed over acid slates and granites. Low contents of organic matter, mineral N and available P
Understory	Native perennial bunchgrasses invaded (emigrated from other Mediterranean regions) by non-natives such as annual grasses *Avena*, *Bromus*, and *Festuca* spp., and other herbaceous species	Annual grasses and other herbaceous species, subject to rapid invasion by rockrose (*Cistus* spp.) and leguminous brooms (*Retama, Genista* and *Cytisus* sp.), and less commonly by gorse (*Ulex* spp.) and heather (*Erica* spp.)
Tree management	Relictual, heterogenous spacing, extensive	Deliberate spacing, pruning, intensive

Trees intercept solar radiation and rainfall and usually compete more efficiently for belowground water and nutrients than understory plants. As a result, in most agroforestry systems the net effect of trees on herbaceous plant productivity is negative (Jose et al. 2004). In the mid-twentieth century, oak removal was promoted to increase forage production on oak woodlands in California (George 1987), and in the latter half of the twentieth century to facilitate mechanization in intercropped Spanish dehesas. Millions of oaks were lost (Elena et al. 1987; Fernández-Alés et al. 1992).

However, tree cover has been maintained because of the multiple positive benefits from oaks. For instance, in Spain and Portugal, acorns are of high value for feeding pigs, oak leaves provide a forage reserve during the dry season and during droughts, and trees protect livestock from extreme weather conditions. In California, acorns and leaves support wildlife, the trees shelter livestock, wood can be sold for firewood or chips, and most landowners prefer the look of a woodland to an undifferentiated open plain. Moreover, in both Spain and California the net effect of tree overstory on pasture understory varies depending on the site (Moreno 2008; Marañón et al. 2009) and is often neutral or positive, resulting in interest in replanting of oaks in formerly cleared Californian woodlands (Alagona 2008; UC-OWCW 2012). The relationship between oaks and forage production varies with abiotic factors and with the size and age of trees, and changes as the trees grow. For example, shrubs may enhance oak seedling recruitment, but later negatively affect tree growth and productivity. These temporal changes should be taken into account when defining structural goals for management practices for each specific site.

Reviewed here is how tree, shrub, and herb interactions affect ecosystem productivity and stability in Californian oak woodland and Spanish dehesa, in order to pull out integrative and comparative conclusions that can contribute to future management decisions. There is a lack of literature in some areas, especially for Californian oak woodlands, and suggestions for future research are included in the conclusions. An extensive recent review of Mediterranean-type savanna systems by Marañón et al. (2009) provides an excellent summary of species-environment interactions in the understory, with numerous examples from both Spain and California, so the precise details of understory species composition is not addressed comprehensively here (Fig. 6.1).

6.2 Tree Effects on Understory Production

Deciduous and evergreen oaks affect the production, species composition, chemical quality and phenology of the understory in Iberian dehesas (González Bernáldez et al. 1969; Alonso et al. 1979; Puerto et al. 1987; Calabuig and Gómez 1992; Moreno 2008; Gea-Izquierdo et al. 2009; Fernández-Moya et al. 2011; Rivest et al. 2011a) and Californian oak woodlands (Parker and Muller 1982; McClaran and Bartolome 1989; Marañón and Bartolome 1993; Callaway and Davis 1998).

Fig. 6.1 Matched photos taken in an un-grazed coast live oak woodland in 1982 and 1992 at Mt. Diablo State Park near San Francisco. Only the graduate student presence has changed. (Photographs by L. Huntsinger and J. Bartolome)

Fig. 6.2 The multiple colors of the grassy understory of a *blue* oak woodland near Hopland, California, reflect the interaction of soil, water, light, and species composition. (Photograph by L. Huntsinger)

This is a common feature of oak woodland and savanna communities worldwide (Rice and Nagy 2000; Marañón et al. 2009) and effects on understory can be explained by the spatial heterogeneity of resources created by the presence of scattered trees in these systems. Here, the canopy-caused resource gradients and the consequences for understory productivity and quality are analyzed (Fig. 6.2).

6.2.1 Canopy-Caused Resource Gradients

Evidence for the effects of trees on the spatial heterogeneity of light availability, microclimate affects, soil moisture, and nutrient distribution comes from comparing areas beneath and outside of the tree canopy (Dahlgren et al. 1997; Young 1997). Isolated oaks strongly reduce light availability for the plants beneath them. Montero et al. (2008) reported a 75 % reduction in light close to the trunks of evergreen holm oaks in Spanish dehesa. Light availability increased rapidly with distance from the trunk, with 70 % of the full sunshine reaching plants at the edge of the canopy, and 100 % out beyond about four times the canopy radius (Fig. 6.3a). As a consequence of tree shade and interception of long-wave radiation at night, daily and seasonal variations of temperature are buffered under the canopy (Moreno et al. 2007a). Researchers in California found similar results, with reductions in radiant energy under the evergreen coast live oak and deciduous blue oak ranging from 25 to 90 % (Jackson et al. 1990; Callaway et al. 1991). Marañón and Bartolome (1994) reported that light levels under coast live oaks were only 2 % of that in the open in mid-summer (Fig. 6.3b).

Oaks are long-lived trees, frequently more than 100 years old, and often over 300 years of age (McClaran and Bartolome 1989; Plieninger et al. 2003). Over an

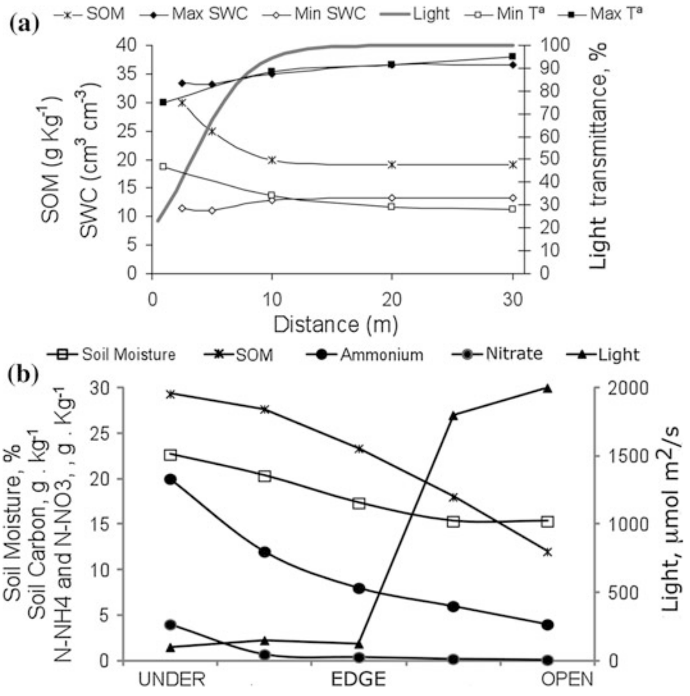

Fig. 6.3 Oak effects on resources. **a** Distribution of resources under and around isolated holm oaks (distances refer to from tree trunks), adapted from Moreno et al. (2007a). Soil organic matter (SOM; 0–30 cm depth); Maximum and minimum soil water content (SWC; measured over 3 years at 0–100 cm depth); Light (Percentage of light transmitted measured by fish eye photograph method); Min Tª and Max Tª (Mean values of daily minimum temperature measured in coldest month and mean values of daily maximum temperatures measured in hottest month, July). **b** Distribution of resources under and around coast live oaks, adapted from Marañón and Bartolome (1994) and Dahlgren et al. (2003). Light was measured at noon July 30; soil moisture was average from autumn to spring; organic carbon (0–15 cm depth); soil nitrogen (0–30 cm depth) was measured in March as ammonia and nitrate

extended period, trees significantly affect the fertility of the soil, mostly by recycling leaf litter and by the turnover of nutrients that are pumped through the root systems from deep in the soil and out beyond the canopy. In addition, trees are effective at retaining atmospheric solutes due to their high surface area and aerodynamic resistance (Moreno and Gallardo 2003), and throughfall and stem-flow may contribute to soil nutrient inputs (McPherson 1997; Dahlgren et al. 1997, 2003). Moreover, trees reduce possible losses of nutrients by erosion and leaching (Young 1997). As a result, nutrients show higher values beneath oaks than in adjacent open areas (Dahlgren et al. 1997). Soil nutrient content generally decreases rapidly with distance and the influence of the trees disappears only a few meters beyond the canopy projection. In addition, part of the nutrient accumulation in the sub-canopy soil could occur at the expense of the adjacent area (McPherson 1997) given that animals tend to concentrate below the tree canopies and the wide lateral root system of trees in dehesas (Moreno et al. 2005) can bring nutrients from the interstitial area.

The positive effect of trees on soil fertility has been quantified for many dehesas (e.g., Vacher 1984; Puerto and Rico 1988; Escudero 1992; Gallardo et al. 2000; Gallardo 2003; Moreno et al. 2007b; Gea-Izquierdo et al. 2010) and Californian oak woodlands (Parker and Muller 1982; Marañón and Bartolome 1994; Dahlgren et al. 2003). The nutrient content in these savannoid soils depends largely on the build-up of soil organic matter (SOM) near the trees (Chap. 4). Although soil organic matter values are highly variable among and within sites, available data suggest that in general soil organic matter is higher in Californian oak woodlands, where carbon contents above 20 g/kg in the open and above 40 g/kg beneath oaks are frequent (Dahlgren et al. 2003). In Spanish dehesa values below 10 g/kg in the open and 20 g/kg beneath the canopy are frequent (Moreno et al. 2007b; Fernández-Moya et al. 2011). A common pattern is for soil organic matter to measure up to two times higher beneath the canopy (Fig. 6.3a). Nutrients determined by biological mechanisms, such as available nitrogen, reflect spatial distribution of soil organic matter. The same is true for other nutrients; but phosphorus, which is mostly determined by geochemical mechanisms, shows a highly variable spatial pattern more closely linked to physical variations in soils and parent material (Gallardo 2003).

Oaks significantly modify soil physical properties beneath the canopy in Spanish dehesas and Californian oak woodlands, increasing soil water-holding capacity, macroporosity and infiltration rates compared to open areas (Joffre and Rambal 1988; Puerto and Rico 1989; Frost and Edinger 1991). These changes are mostly explained by the increase in soil organic matter and the decreased bulk density near the trees (Cubera and Moreno 2007a). Changes in physical properties explain much of the observed increases in soil water content (SWC) under tree cover found by Puerto and Rico (1989) and Joffre and Rambal (1993) in subhumid (about 700 mm of annual rainfall) holm oak dehesa.

For California, Parker and Muller (1982), Marañón and Bartolome (1994), and Moody and Jones (2000) all found that in open coast live oak woodlands soil water content was lower and decreased more rapidly (Fig. 6.3b) outside the canopy, although the situation was reversed during extended droughts. Baldochi et al. (2004)

reported a positive effect of deciduous blue oaks on soil moisture, although other authors have reported no significant effect of this oak species on soil moisture in the rooting zone of annual understory plants during the time of year when these plants were phenologically most active (Jackson et al. 1990; Callaway et al. 1991).

In contrast, Cubera and Moreno (2007a), Gea-Izquierdo et al. (2009), and Moreno and Rolo (2011) found decreased soil water content near dehesa evergreen oaks, especially on the driest sites and/or during the driest years, similar what has been found for many other agroforestry systems (Young 1997; Jose et al. 2000). This phenomenon is attributed to decreased water input because of interception, and an increase in water loss through transpiration under the canopy, which could outweigh the positive effects of trees on water-holding capacity (Cubera and Moreno 2007a). Evergreen oaks intercept rainfall, in one holm oak example 30 % of rainfall (Mateos and Schnabel 2002), and absorb water from the soil continuously throughout the year with moderately high transpiration rates in winter and summer (Infante et al. 2003; David et al. 2004). The reasons for differences among sites, especially in Californian savanna and Spanish dehesa, are not yet clear. Jackson et al. (1990) reported much higher values of pasture root biomass outside the canopy in a California pasture than for an understory pasture from October to April, hampering the soil recharge in open areas because more water is transpired in that period. Only in May was root biomass higher beneath the canopy. A higher abundance of graminoid species in Californian savannas could partially explain the differences. Annuals tend to concentrate root growth and soil–water utilization in the upper soil profile, while the native perennial bunchgrasses of Californian savannas allocate a high proportion of their biomass to the development of a deep root system, allowing them to continue soil–water utilization well into the dry season and to contribute to the formation of a very dry soil profile (Holmes and Rice 1996). While soil water recharge is limited beneath trees in dehesas, in Californian oak savannas perennial grasses may limit this recharge.

6.2.2 Understory Composition, Nutrient Quality and Phenology

Savannas worldwide have proved similar in the way the tree canopy affects understory species composition, nutrient quality and phenology (Fig. 6.4). In dehesa, grasses are dominant beneath the canopy, while legumes and forbs become more abundant in the less fertile interspaces (Marañón 1986; Puerto 1992). This difference may be explained by the increased content of soil nitrogen and the nitrogen mineralization rate beneath oak canopy (Gallardo et al. 2000), which favors grasses as they need more soil nitrogen to thrive, while legumes and forbs are less dependent on soil nitrogen (Joffre 1990). The higher resistance of grasses to shading compared to legumes might explain this pattern (Nunes et al. 2005). Marañón and Bartolome (1993) demonstrated the importance of shade to the spatial location of species in a Californian example. They switched around intact

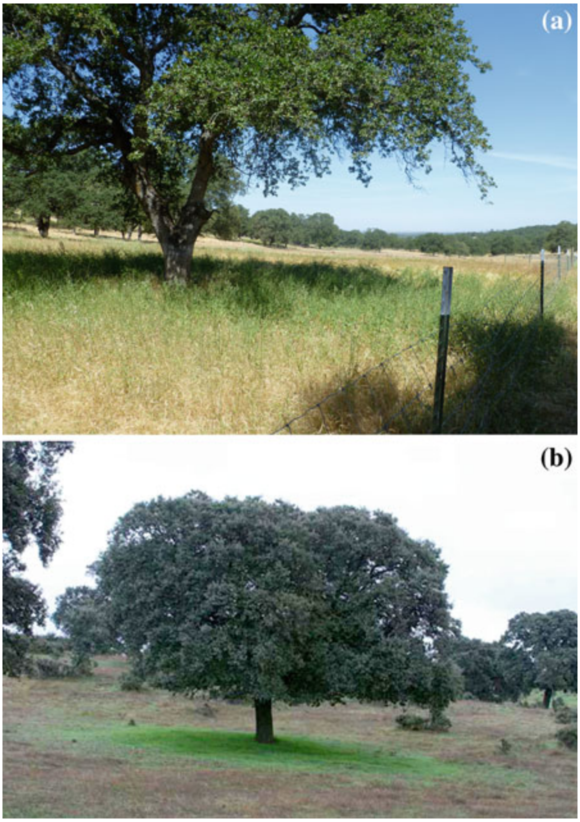

Fig. 6.4 Species composition, duration of *green* growth, and production may all differ under the oak canopy as compared to outside the canopy, as in these examples from California's central Sierra foothills in early summer (**a**) and from North Extremadura in Spain in mid-winter (**b**). (Photographs by L. Huntsinger and D.S. Howlett, respectively)

blocks of soil from under the canopy, at the edge, and in the open in a *Quercus agrifolia* savanna and found that shading caused high mortality of the herbaceous species that came from open areas (Fig. 6.5). Many other studies document changes in species composition for herbaceous communities depending on whether or not they are under the oak canopy in dehesa and woodland (Marañon et al. 2009). In regions with usually high plant α diversity or species diversity in habitats, the presence of a high number of species influenced by a tree canopy gradient of light, nutrients, and soil structure results in very high habitat diversity (β diversity or diversity of habitats) and total species diversity in a landscape (γ diversity or total species diversity; Chap. 8).

The herbaceous understory has a higher content of some nutrients (mainly N and K) in plants beneath than outside the canopy (González-Bernáldez et al. 1969; Puerto 1992; Moreno et al. 2007a, b). Herbaceous plants uptake nutrients located in the uppermost soil layer more easily than oaks, as Rivest et al. (2011b) demonstrated through experimental fertilizations in dehesa on different soil types. This helps explain why the chemical qualities of the understory reflect the heterogenous patterns of soil fertility around trees (Moreno et al. 2007b). However, the

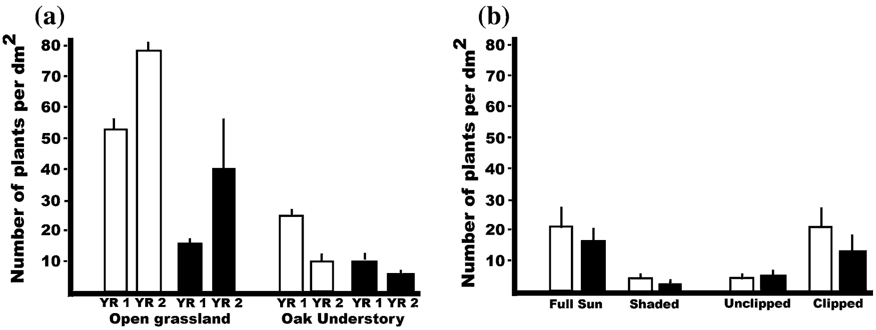

Fig. 6.5 Differences in density of understory plants in open grassland and under coast live oak canopy over 2 years. **a** Blocks of soil were transplanted from understory to open grassland (*shaded bars*) and vice versa (*unshaded bars*) and **b** subjected to *clipping* and *shading*. Adapted from Marañón and Bartolome (1993)

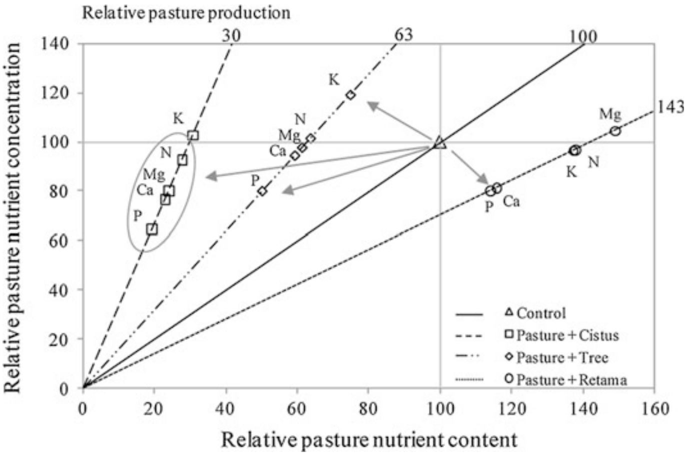

Fig. 6.6 This vector analysis of relative response in pasture production shows nutrient concentration and content (*N*, *P*, *K*, *Mg* and *Ca*) of vegetation under holm oak or shrubs (broom—*Retama*—or rockrose—*Cistus*–). Data for pasture growing in open areas was used as a reference (100 value for pasture production, nutrient content and concentration). Diagonal lines indicate pasture production (g m^2). *Arrows* and *circles* depict significant vector shifts. From Rolo et al. (2012)

understory responds to increased nutrient availability mostly though increased growth and changes in botanical composition and not less so to increases in plant nutrient concentrations (Gea-Izquierdo et al. 2010; Rolo et al. 2012; Fig. 6.6).

A longer growing season beneath the tree canopy, with an earlier start in winter and later drying in summer, is reported (Alonso et al. 1979; Puerto et al. 1987, 1990; Calabuig y Gómez 1992) (Fig. 6.4 and 6.7). Warmer temperatures beneath canopy would allow continued understory growth in winter compared to in open pasture

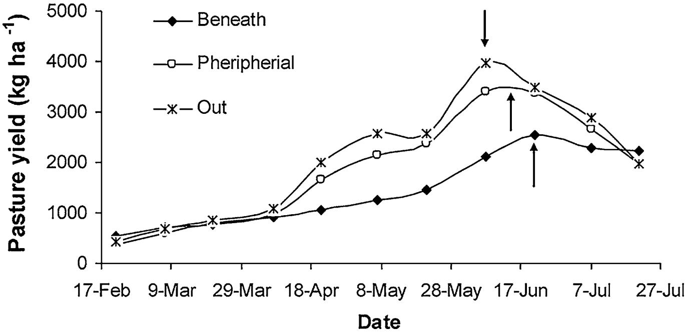

Fig. 6.7 Temporal evolution of forage yield at three distances from holm oak trees. Note the decrease of pasture yield beneath the canopy, and the temporal difference for the maximum yield. Adapted from Puerto (1992)

(Moreno et al. 2007a). Dominant grasses beneath a dehesa canopy dry out later in summer than forbs and legumes that are dominant outside of the canopy because grasses are capable of using water from deeper soil layers (Joffre et al. 1987).

6.2.3 Understory Production

The net effect of trees on understory production depends on the balance of positive, or facilitative effects and negative, or competitive effects (Marañón et al. 2009). Studies reveal that the effect of trees on the understory in open oak woodlands is highly variable, ranging from decreased to increased production (see examples in Callaway et al. 1991; Puerto 1992; Allen-Diaz et al. 1999). The direction and magnitude of these effects depends on environmental factors like precipitation, soil type and fertility as well as biological factors like the species in the understory and the kind of oaks, amount of canopy cover, tree age and the root architecture of the interacting plants in the community (Quilchano et al. 2007; Tyler et al. 2007). For instance, Frost and McDougald (1989) reported that herbaceous production was up to 115–200 % greater under scattered blue oak than on open grassland in California (Battles et al. 2008). Like this deciduous oak, evergreen oaks can increase pasture yield beneath their canopies, as reported for holm oak in Spain (Puerto 1992).

The positive response of understory production to moderate tree cover is generally attributed to, as reported above, more favorable physical and chemical soil properties and soil and air temperatures under the tree (Moreno et al. 2007a). In a manipulative experiment conducted in three dehesas, Moreno (2008) found that pasture yield was higher beneath the canopy. But in fertilized and watered plots pasture yield was significantly higher under artificial shade (50 % full-sunlight) than under the canopy (Fig. 6.8), showing that shade, despite the negative influence of reducing light for photosynthesis, probably played a greater positive

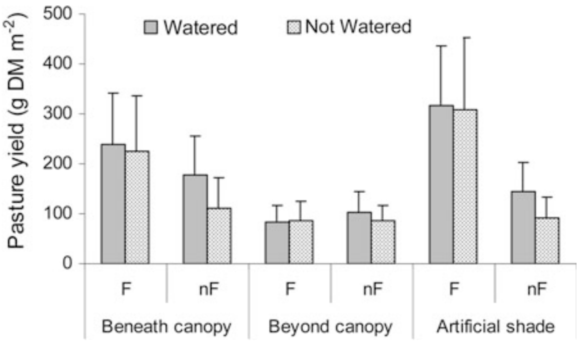

Fig. 6.8 Effects of artificial and natural shade, fertilization and watering on pasture yield (g m^{-2} ± S.D.) in Iberian dehesas. The treatments were: artificial shade (50 % of full sunlight), fertilization (200 g m^{-2} of NPK 15/15/15 in February), and watering (90 l m^{-2}, applied as 10 l m^{-2} every week from 1st April–31st May). Adapted from (Moreno 2008)

role by reducing damage to photosynthetic apparatus from too much light (photoinhibition, Valladares and Pugnaire 1999). In California, Frost and McDougald (1989) concluded that increased forage production under the canopy during drought conditions was, in large part, due to shading, which reduced moisture loss via evapotranspiration. Indeed, it has been pointed out that in a Mediterranean climate, maximum production of dehesa understory is obtained with around 30 % of overstory cover (Etienne 2005), and Allen-Diaz et al. (1999) reported that in Californian savannas evergreen oaks only inhibited production when canopies exceeded 25 %, whereas deciduous oaks did not consistently inhibit understory production until cover exceeded 60 %.

Although a sparse canopy can produce more understory growth, trees do intercept a certain proportion of solar radiation that could be used for photosynthesis (PAR; photosynthetically active radiation) and take up water and nutrients, making them unavailable for understory plants. As a consequence, many cases of significant reduction of pasture yield beneath oak canopy compared to open pasture have been reported, especially with evergreen oaks (Marañón and Bartolome 1993) for coast live oak; Puerto 1992; Nunes et al. 2005; Rivest et al. 2011a for holm oak), and under deciduous oaks with canopy cover of about 40–50 % (McClaran and Bartolome 1989; Battles et al. 2008).

These studies confirm that trees compete for resources with the understory. In the three dehesa experiments conducted by Moreno (2008), when the main nutrient (N, P, K) limitations were removed through fertilization, artificial shade produced a higher understory yield than tree shade, suggesting that negative effects, such as competition for soil water, limited production under the canopy (Fig. 6.8 and 6.9). By contrast, soil moisture does not seem to have a major role in net balance of effects of Californian oaks on pasture understory production (Callaway et al. 1991). The higher proportion of dehesa studies reporting a negative effect of oaks on understory production is understandable because soil moisture frequently is

Fig. 6.9 Livestock redistribute nutrients on rangelands. For example, they like to spend time in the shade, as shown by these Merino sheep and Spanish horses under cork and holm oaks in dehesas of Extremadura, Spain. They enrich the soils under trees with their manure. (Photograph by A. Hummer (**a**) and G. Moreno (**b**))

higher beneath oak canopy there than in the open in California, while it is often higher in open pasture than under the canopy in dehesa (Fig. 6.3).

Standiford and Howitt (1993) noted the contrasting effects of tree canopy on understory production in areas of higher and lower rainfall in California. McClaran and Bartolome (1989) found a rainfall-dependent tree/understory relationship, showing that canopy depresses forage yield more in higher rainfall areas (Fig. 6.10) and that tree facilitation, or benefits to understory production, increased with aridity and plant water stress. This fits the stress-gradient hypothesis, which posits that interactions among plants are context dependent, shifting from competition to facilitation as environmental stress decreases (Bertnes and Callaway 1994). Forage production was higher under the trees than in open areas where annual rainfall was below 500 L m^{-2} while the reverse is found in areas receiving more than 500 L m^{-2}.

By contrast, the stress gradient hypothesis has not been confirmed for dehesa. In fact, Moreno's (2008) experiment indicated the opposite. Understory yield beneath the canopy was higher than in the adjacent open grassland, but differences decreased with the aridity of the sites, with increases of 16.8, 34.0, and 33.4 % beneath canopy compared to open pasture in dehesas with annual rainfall around 450, 550 and 650 L m^{-2}, respectively. Similarly, Gea-Izquierdo et al. (2009) reported a positive effect of oak canopy on dehesa pasture yield in average climatic years, but the interaction changed with increasing abiotic water stress. In a dry year, the higher fertility beneath the canopy could not be used for plant growth because of the lack of moisture and the effect of the oak canopy was neutral. The decreased positive effect of trees with aridity in Spanish dehesas indicates that competition for soil water is an outstanding factor in the balance of positive and negative effects of trees on pasture. This kind of exception to the soil gradient hypothesis is common in Mediterranean ecosystems (Maestre et al. 2006, 2009), especially when the abiotic stress gradient is driven by a resource such as soil water in arid and semiarid ecosystems. The reasons for the differential behavior of

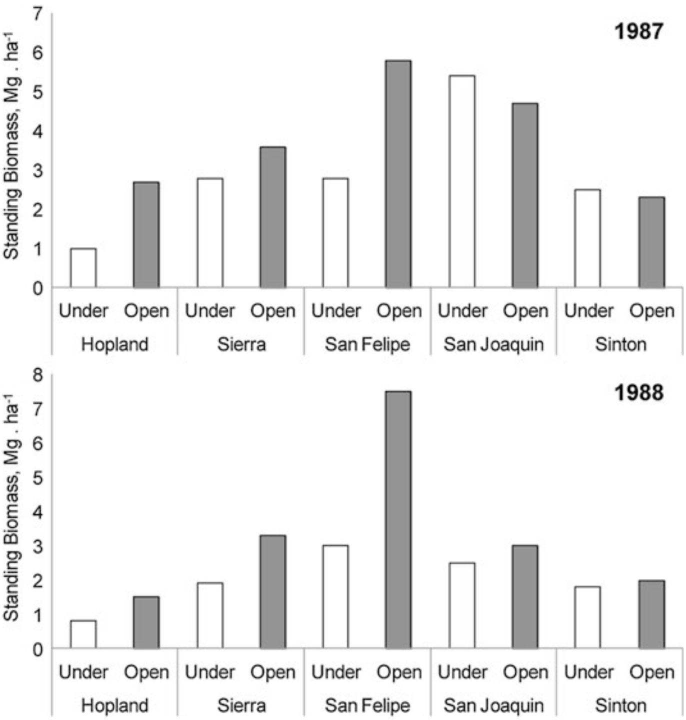

Fig. 6.10 Mean understory and open grassland peak aboveground biomass in 1986 and 1987 at five locations in Californian blue oak savanna. Annual rainfall in 1986 and 1987 was above and below average, respectively. The x-axis sites represent an annual rainfall gradient from 100 cm/year (Hopland) to 25 cm/year (Sinton). Adapted from McClaran and Bartolome (1989)

Californian oak woodlands and Spanish dehesas with respect to the stress gradient hypothesis need to be explored with consideration of the differences in pasture species life-forms and soil fertility and depth between the two systems.

6.3 Interactions Affecting Trees

6.3.1 Tree-Tree Competition: The Importance of Widely-Spaced Trees

Precipitation in Mediterranean systems is highly variable from year to year, and there is a summer drought of varying severity each year. The low tree density of oak woodlands and dehesas allows trees to survive and continue to produce even in severe drought conditions. Wider spacing between trees implies greater water availability for each tree, resulting in a reduction of the duration and intensity of tree water stress compared to trees growing in more closed forests of the same regions. Numerous authors report higher water potential and photosynthetic and transpiration rates at leaf and tree scales during the summer for holm and cork oaks in the dehesa, as compared to closed stands (Joffre and Rambal 1993; Infante et al. 2003; David et al. 2004; Moreno and Cubera 2008).

When trees are spaced further apart their roots can exploit a larger soil area and obtain more water and nutrients, explaining the improved physiological status of dehesa oaks. Oak tree roots expand outwards up to 7 times the projection of the canopy and as much as 25 times the canopy volume into the soil, allowing trees to meet their water needs during the dry Mediterranean summers (Moreno et al. 2005). In general, larger lateral root spread has been found in plants and trees growing at low densities in dry environments (Eastham et al. 1990; Schenk and Jackson 2002). Cubera and Moreno (2007a) showed during the summer, when herbaceous dehesa plants are dry and senescent, and unable to use water, soil water content continues decreasing as far as 20 m beyond the tree trunk and 200–300 cm in depth, indicating that holm oak trees were consuming the water accumulated there from winter rains. Similarly, for Californian savannas Baldochi and Xu (2007) conclude that Mediterranean oaks must meet their limited water supply by, among other mechanisms, constraining the leaf area index of the landscape by establishing a canopy with widely spaced trees. A strong relationship among tree density, water availability, and tree productivity is a common feature of semiarid savannas (e.g., Smith 1986). However, Battles et al. (2008) found that in a Californian oak woodland [blue oak (*Quercus douglasii*), interior live oak (*Quercus wislizenii*) and foothill pine (*Pinus sabiniana*)], with overall mean annual rainfall of 775 mm, tree productivity increased linearly with oak cover, while the total productivity (trees and understory) increased linearly with increasing canopy cover until it leveled off at approximately 55 % cover.

The spacing of trees is more critical in the driest open woodlands. Moreno and Cubera (2008) reported that in dry dehesas (annual rainfall <500 L m^{-2}), both predawn and midday water potentials, CO_2 accumulation, and sap flow density proportional to transpiration rates were significantly higher in trees growing in low tree density areas ($\sim$20 trees ha^{-1}) compared to those in high tree density areas ($\sim$100 trees ha^{-1}). By contrast, in humid dehesas (annual rainfall >700 L m^{-2}), differences in both water potentials and CO_2 accumulation among tree densities were very small and emerged only at the end of the dry season (Fig. 6.11). Indeed, Joffre et al. (1999) reported for Spanish dehesas that mean oak density increases with rainfall at a large geographical scale. This pattern seems a common feature for stable savannas as revealed by Sankaran et al. (2005) for African savannas.

Joffre and colleagues pointed out in 1999 that the dehesa structure follows an *ecohydrological equilibrium*, explained in the work of Eagleson and Segarra (1985) who hypothesized that water availability limits natural vegetation systems, resulting in a canopy density that produces both minimum water stress and maximum biomass. Natural savannas were defined as a biotic response to alternating wet and dry seasons, because the density of trees and grasses is controlled by the amount of soil water available during the vegetative season (Eagleson and Segarra 1985).

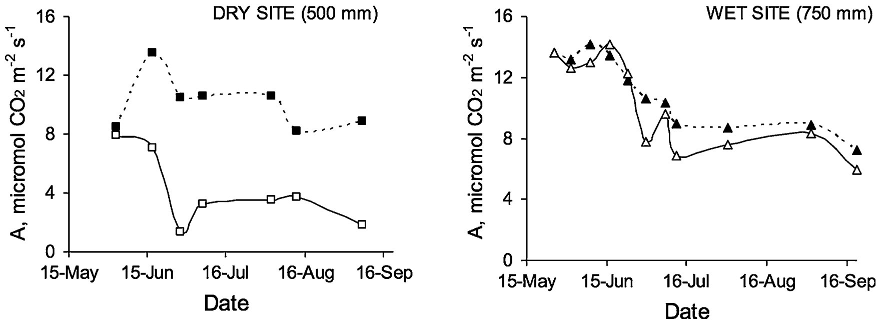

Fig. 6.11 Mean values for CO_2 accumulation rates in mature holm oak growing in dehesa with a canopy cover below 20 % (*black square* or *triangle*) and dense coppice with canopy cover above 90 % (*open square* or *triangle*). Adapted from Moreno and Cubera (2008)

Maximum woody cover in savannas with mean annual rainfall of less than ~650 mm is constrained by, and increases linearly with, mean annual rainfall. These arid and semi-arid savannas may be considered "stable" systems in which water constrains woody cover and permits grasses to coexist. Above an annual rainfall average of ~650 mm, savannas are "unstable" systems in which rainfall is sufficient for woody canopy closure, and disturbance such as fire and herbivory is required for the coexistence of trees and grass (Sankaran et al. 2005). While an ecohydrological equilibrium might play a role in the vegetative stability in most Californian open oak woodland (Marañón et al. 2009), it does not stabilize oak woodland dehesas, where if human intervention and grazing pressure is excluded, an immediate woody encroachment starts (Marañón et al. 2009; Rolo and Moreno 2011). The ecohydrological equilibrium noted in dehesa by Joffre et al. (1999) is an ecoystem "mimic", and reflects a management target of maximizing forage as well as tree production in the unnatural dehesa. More research is needed in this area to understand the diverse interactions of trees, shrubs, and water availability in California and Spain (Figs. 6.12, 6.13).

Apart from the direct positive effect of low tree density on tree water status, Úbeda et al. (2004) reported a clear benefit of forest clearance on the leaf nutrient content in cork oak. As a result of the improved hydric and nutritional status of trees in dehesas the production of acorns was 10 times higher in a managed holm oak dehesa compared to a dense holm oak forest (Pulido and Díaz 2005; Chap. 7).

6.3.2 *Trees and Shrubs: Competitive Use of Soil Resources in the Dehesa*

Very few studies concerning the effects of the shrub layer on trees are available in the dehesa, and there are even fewer for the California oak woodland, although shrubby infilling occur in both systems (Allen-Diaz et al. 2007; Plieninger et al. 2010).

Fig. 6.12 In California, the distribution of trees and shrubs in this blue and coast live oak woodland near San Francisco is largely a function of soil type, water, and past management and fire regimes. The flat area in the foreground was probably cultivated sometime in the twentieth century. The crisp lines between shrubs and grasslands reveal the underlying geology rather than a property or management border, and the trees are denser in the swales where soils are moister, as well as on the northern aspects of slopes (looking north). California oak woodlands occur on highly heterogenous soils. (Photograph by L. Huntsinger)

This section refers only to data compiled from studies conducted in Spanish and Portuguese dehesas.

It is to be expected that many shrub species compete with oaks for belowground resources, given that shrubs and oaks have similar root system structures (Canadell et al. 1996; Schenk and Jackson 2002; Rolo and Moreno 2012). The scanty information on the root systems of shrubs growing in dehesas has shown both shallow and deep root profiles, with roots reaching several meters in depth for heather, gorse, and broom (*Retama*), and less than 1 m for rockrose (Silva et al. 2002; Silva and Rego 2003; Rolo and Moreno 2012).

Regardless of the specific root profile, a shrub understory can decrease soil moisture, water potential, CO_2 assimilation rate, tree growth and the acorn production of evergreen oaks (Moreno et al. 2007a; Cubera and Moreno 2007b; Moreno and Rolo 2011; Rolo and Moreno 2011; Rivest et al. 2011a). Shrub encroachment influences the nutritional status of the trees with lower N, Ca and Mg leaf contents in trees growing with shrubs than in trees growing with native grasses (Moreno and Obrador, 2007; Rolo et al. 2012). By contrast, trees showed significantly higher values of foliar P in trees with shrubs than in trees with grasses. The increase of foliar P in trees with dehesa encroachment could indicate some level of positive interaction (facilitation) between trees and shrubs. Although beneficial interactions between woody plants are widely recognized (Scholes and

Fig. 6.13 In Spain, the distribution of trees and shrubs in this holm and cork oak woodland in Monfragüe National Park is largely a function of topography, land use history and fire. The flat area in the middle was cultivated for decades in the twentieth century, resulting in a very low tree density. Further up, a typical dehesa landscape resulted from deliberate tree clearing and continuous grazing. Below, in steeper areas, trees have almost been eliminated by periodic fires, and shrubs now dominate. (Photograph by G. Moreno)

Archer 1997; Barnes and Archer 1999; Marañón et al. 2009), possible facilitation in dehesas remains unexplained and unconfirmed, and requires further research given that P is commonly seen as one of the most limiting factors for many Mediterranean ecosystems (Vallejo et al. 2006).

Overall, studies indicate that shrubs have more negative (competition for water) than neutral (complementary use of water), or positive (facilitation for some nutrients) effects on tree growth and acorn production. Annual shoot elongation and acorn production per tree were significantly higher in dehesas with a pasture understory than in those with a shrub understory (Moreno et al. 2007a; Rivest et al. 2011a). Such belowground competition is known in other tree-shrub ecosystems (subtropical savanna parklands; Barnes and Archer 1999).

Nevertheless, leaf water potential of holm oak remains relatively high (> -1 MPa at dawn) even in shrub encroached dehesa plots during the summer (Cubera and Moreno, 2007b; Rolo and Moreno 2011) (Fig. 6.14), while holm oak leaf water potential in dense forests usually reaches under -4 MPa in semiarid regions (Moreno and Cubera 2008). In sum, the relative competitive effects are the following: dense forests >shrub-invaded plots >savannas. The maintenance of a relatively favorable water status for oaks in shrub encroached stands is essential for satisfactory acorn development in summer (Carevic et al. 2010). The limited negative effect of shrub understory is explained by the plasticity of the holm oak

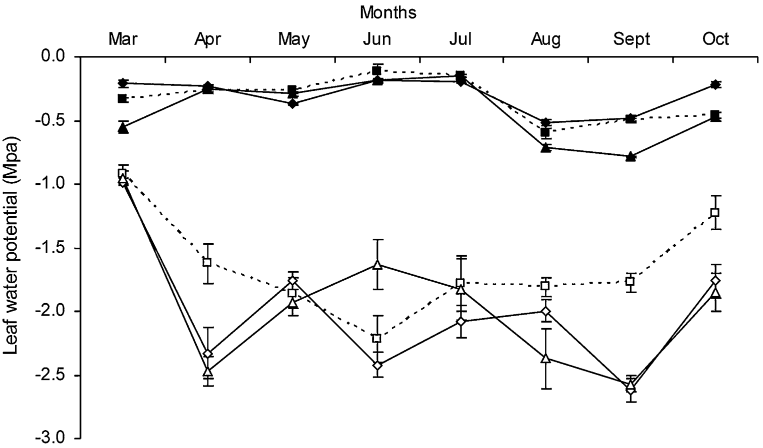

Fig. 6.14 Daily maximum (*filled symbol*) and minimum (*open symbol*) values of leaf water potential of mature holm oak measured through the summer in 2003. The understory consisted of cereal crop (*circles*), native grasses (*squares*) and shrubs (*triangles*). Adapted from Cubera and Moreno (2007b)

root system, allowing it to escape competition for soil water—holm oak has a deeper rooting system when growing with a shrub understory than when growing with a pasture understory (Rolo and Moreno 2012).

6.3.3 Tree and Pasture: Tree Dependence on Deep Soil Water

Spatial separation between herbaceous plants and tree root systems has been described in Californian blue oak savannas (Callaway et al. 1991) and in dehesas (Joffre et al. 1987; Gómez-Gutiérrez et al. 1989; Moreno et al. 2005). The latter authors found that roots of native grasses were located mostly in the upper 30 cm, and root length density (RLD) decreased exponentially with depth up to 70 cm (Fig. 6.15). In the same plots, holm oak had a lower root density in the first 10 cm of the soil, and oak root density remained almost uniform with depth at a given distance from the tree.

The limited vertical overlap of herb and oak root profiles suggests that competitive effects of understory herbs are unimportant for tree water uptake in dehesa. Several studies focusing on water dynamics in different agroforestry systems have shown different spatial partitioning of water resources between trees and the understory. Cubera and Moreno (2007a) reported spatial separation between herbaceous plants and trees in relation to soil water uptake. Soil dried uniformly beneath and outside the canopy only for the uppermost 50 cm of the soil, while at deeper layers soil water content increased with the distance from the tree trunk,

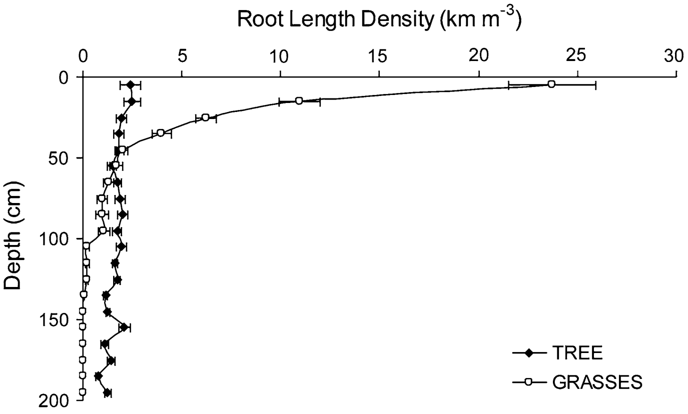

Fig. 6.15 Rooting profiles of trees and native grasses in holm oak dehesa. Adapted from Moreno et al. (2005)

indicating that herbaceous plants did not use water below 50 cm depth, as is consistent with their root system. Joffre et al. (1987) reported similar values, with annual and perennial grasses absorbing water from the uppermost 40 and 60 cm of the soil, respectively.

By contrast, during summer drought holm oak trees show a high dependence on water below 3 m depth (Cubera and Moreno 2007a). The low dependence of trees on water in the uppermost soil layer was shown in an experimental irrigation trial, where holm oak did not respond to irrigation in terms of fecundity, acorn production or shoot elongation (García-López 2005). Thus, while water limitation is an important feature in most dehesas, water consumed by grasses (and cereal crops) probably does not cause significant water stress to mature dehesa trees if tree roots can reach deep soil layers (Cubera and Moreno 2007a). Baldocchi et al. (2004) have demonstrated how oaks in California depend on the absorption of deep water, below the maximum rooting depth for understory grasses (Fig. 6.16).

6.4 Interactions Affecting Tree Seedling Performance and Recruitment

Seedling establishment and juvenile growth often limit recruitment of oaks, and morphological and physiological attributes during these periods are regarded as key factors for the recruitment and survival of tree populations. Adaptability to water stress at the seedling stage can be important because of high mortality and the need to survive in competition with understory grasses, shrubs and mature overstory trees for belowground resources (Mediavilla and Escudero 2004). Under the competitive conditions that the seedlings grow in, a non-conservative use of resources favors the quick root growth needed for establishment (Mediavilla and

Escudero 2003). The set of adaptive traits of oak seedlings determines differential recruitment success across the characteristic habitat and microhabitat heterogeneity of Iberian dehesas and Californian oak woodlands (Huntsinger et al. 2004).

6.4.1 Pasture and Oak Seedling Relationships

The intensity of competition for water and nutrients between understory plants and oak seedlings determines the survival of seedlings and thus oak recruitment. The negative effect of understory herbaceous plants on oak recruitment is well documented in Californian oak woodlands (Gordon and Rice 1993; McCreary 2001), but studies for dehesas are scant. Navarro-Cerrillo et al. (2005) found that holm oak survival increased 2.5 fold in the first summer after the transplanting of 1-year-old seedlings when the herbaceous plants were mechanically or chemically surpressed (Fig. 6.16 and 6.17). Enhancement of oak seedling survival and growth by the removal of competing understory grasses and forbs has proved successful with both natural and artificial regeneration in Californian oak woodlands and savannas (McCreary et al. 2011).

Pulido and Díaz (2005) have reported that most of the seedlings in dehesas (86 %) die during the first summer of life from desiccation due to lack of water. This pattern of seedling mortality has been repeatedly observed in Mediterranean

Fig. 6.16 Removing herbaceous vegetation from around an oak seedling can increase survival during the first year, as in the California example. This effect has been found in California and Spain

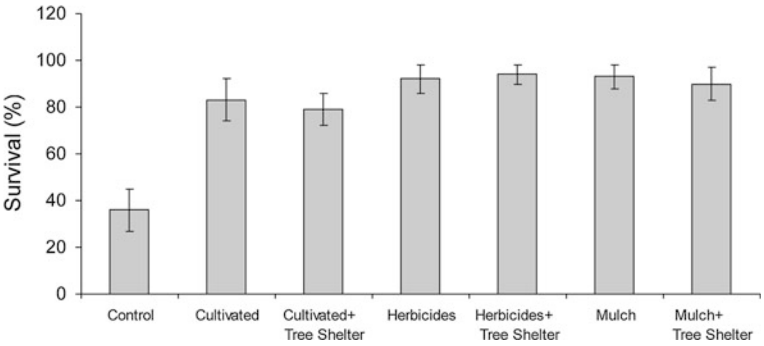

Fig. 6.17 Holm oak seedling survival with different methods of weed control. In the control treatment, where seedlings grew with competing weeds, there was significantly higher seedling mortality. Adapted from Navarro-Cerrillo et al. (2005)

climate regions, including California (Allen-Diaz and Bartolome 1992). In contrast, Pulido and Díaz (2005) found mortality in the second summer was negligible, indicating that presumably seedlings were using water too deep to be consumed by herbaceous plants. Hence, it seems that a noticeable proportion of the seedlings in dehesa can survive competition with native pasture plants, although perhaps not browsing by livestock and wildlife (Pulido et al. 2010). Survival may be lower when the herb layer is improved through seed sowing and/or fertilization (Olea and San Miguel 2006), affording the pasture understory a competitive advantage (Cubera et al. 2012).

The suppression of oak seedling growth by herbaceous species competition seems more acute in Californian oak woodlands. Collet et al. (2006) grew downy oak seedlings (*Q. pubescens*) for 4 years in bare soil or with grass competition and found that root system size was considerably reduced by grass competition. Gordon et al. (1989), examining the competitive effects of two annual species on Californian blue oak seedling growth in 1 m deep boxes, found that the type and density of grasses significantly effected seedling emergence and growth rate.

A high density of annual plants suppressed oak root growth and shoot emergence. Fibrous grass roots had a greater competitive effect than did tap-rooted forbs. Only 20 % of the acorns planted in high density smooth bromegrass (*Bromus hordeaceous)* neighborhoods showed aboveground shoot growth, 56 % of those planted in low density smooth bromegrass or the annual forb broad leaf filaree (*Erodium botrys*) emerged, while 19 % emerged in the control box with no forbs or grasses. The results suggested that competition for soil water with introduced annual species contributes to the high rate of blue oak seedling mortality observed in Californian woodland systems. Although the genetically determined strategy of oak seedlings to rapidly develop a deep taproot helps them escape the strong competition for soil water from herbaceous plants (Mediavilla and Escudero 2003), when seedlings grow in a dense herbaceous understory, the effectiveness of this strategy is limited, and the vertical root growth of the seedlings can be suppressed by neighboring pasture species (Gordon and Rice 1993).

6.4.2 Shrub and Oak Seedling Relationships

A shrubby understory is found in both dehesas and Californian oak woodlands (Marañón et al. 2009; Allen Diaz et al. 2007), but is much more common in Iberia. The extensive work on shrub-oak seedling relationships in dehesa contrasts with a meager published record in California. The higher interest shown by dehesa researchers is probably due to the worrying lack of oak regeneration that affects most managed and grazed dehesas, and the fact that without intensive management, most Spanish dehesa converts to a shrubland (Plieninger et al. 2010). Shrubs can use more resources than grasses, and what is more important, use both nutrients from the uppermost soil layer and water from deeper soil layers because of the dual (horizontal and vertical) rooting systems of many Mediterranean shrub species (Rolo and Moreno 2012). Indeed, as commented earlier shrub-encroached dehesas in general show lower soil resources than savanoid dehesas.

Although shrubs seem to use soil resources more exhaustively than herbaceous plants, shrub encroachment predictably results in a significant increase in oak seedling recruitment in dehesas (Pulido and Díaz 2005; Smit et al. 2008; Plieninger et al. 2010; Pulido et al. 2010) (Fig. 6.18). This happens for several reasons, including the attraction of acorn dispersers such as rodents and jays to shrubby areas, protection against browsing herbivores, improvement of soil fertility, and softening of the harmful effects of the Mediterranean summer drought (Retana et al. 1999; Gómez 2003; Gómez-Aparicio et al. 2004, 2005a, b; Puerta-Piñero et al. 2006; Plieninger et al. 2010), although acorn predation under some shrub species can limit regeneration (Callaway and Pugnaire 2007). Indeed, dispersers as rodents are acorn consumers that act as accidental dispersers (Muñoz and Bonal 2011). Pulido et al. (2010) conducted a controlled experiment where acorns were seeded into an enclosure to prevent acorn depredation, showing a direct positive effect of shrubs on acorn germination and holm oak seedling survival in Central-Spain dehesas (Fig. 6.19). This facilitative phenomenon, called the "nurse plant effect", is widespread among Mediterranean oak species seedlings (Castro et al. 2004, 2006; Gómez-Aparicio et al. 2005a; Marañón et al. 2009), although it is a species specific-dependent process (Rolo et al. 2013).

One question that arises is whether the facilitative effect of nurse shrubs on early recruitment of trees is caused by a "canopy effect" that creates a more favorable microclimate and protects the seedling from herbivores, or a "soil effect" because shrubs modify the soil properties, or both. Physical protection against wildlife and livestock has been described as the major mechanism that facilitates oak regeneration when highly competitive shrub species are present in managed dehesas (Puerta-Piñero et al. 2006; Smit et al. 2008; Plieninger et al. 2010). In addition, the provision of natural or artificial shade invariably results in a dramatic increase in seedling survival in dehesas and Californian woodlands (see Callaway 1992; Marañón et al. 2009). The effects of light limitation are negligible when compared with the increased survival and reduced photo-inhibition resulting from moderate shade (Gómez-Aparicio et al. 2004; Castro et al. 2006). After all,

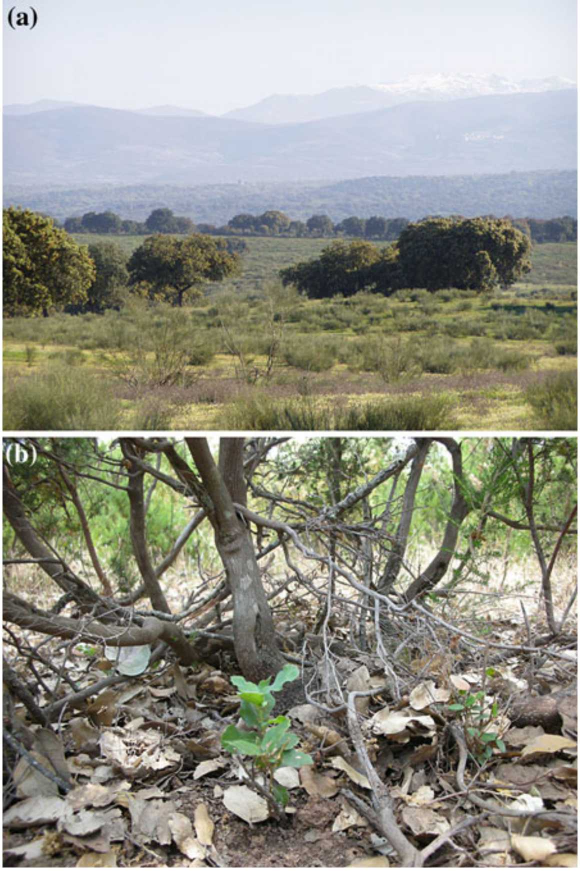

Fig. 6.18 **a**, **b** Shrubs will encroach on dehesa within a few years if the understory is not intensively managed. Some species of shrubs have been shown to act as “nurse plants,” fostering the recruitment of oak seedlings. (Photograph by G. Moreno)

seedling (1–3 years old) growth of Mediterranean oaks has been shown to be only moderately reduced even in 20 % sunlight (evergreen oaks; Cardillo and Bernal 2006) and 13 % sunlight (deciduous oaks; Gómez-Aparicio et al. 2006), which is comparable to the natural shade found in many managed Mediterranean climate forests characterized by an open structure (Gómez-Aparicio et al. 2006). Quero et al. (2006) demonstrated that shade ameliorated, or at least did not aggravate, drought impact on seedlings of four oak species (holm, cork, Pyrenean and Algerian oaks). Under drought conditions, deep-shaded seedlings were able to achieve higher photosynthetic rates, stomatal conductance, and N concentration than seedlings under full light. This apparent alleviation of drought impacts for seedlings growing in shade could explain the pattern of higher survival under shade of shrubs and trees commonly observed in Mediterranean systems.

An improvement in soil conditions under some shrub canopy is reported as positive for oak seedlings (Moro et al. 1997; Puerta-Piñero et al. 2006; Rolo et al. 2012, 2013). A reduction of soil compaction has a positive effect on shrubs (Verdú

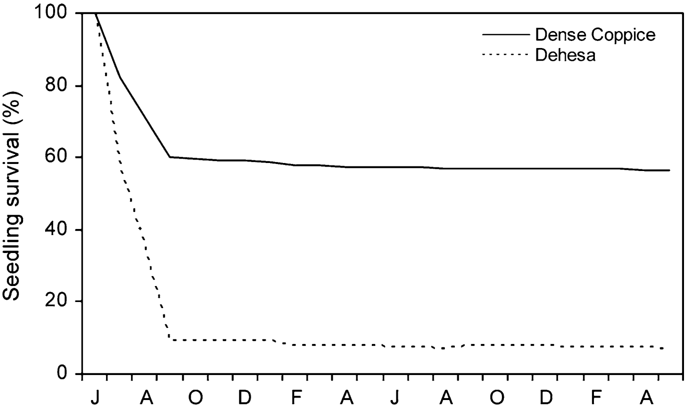

Fig. 6.19 A two year curve of seedling survival comparing a dehesa with a nearby shrub-encroached holm oak forest. Adapted from Pulido and Díaz (2005)

and García-Fayos, 1996). Gómez-Aparicio (2005a) found that shrub species significantly increased the depth at which maximum soil compaction was reached by 10 cm. With respect to soil moisture, results are less consistent, with one study reporting a significant increase in superficial soil moisture (Gómez-Aparicio et al. 2004; Moreno and Rolo 2011), but others failing to find this positive effect (Cubera and Moreno 2007b; Gómez-Aparicio et al. 2005a, b; Moreno and Rolo 2011). Nuñez et al. (2003) and Rolo et al. (2013), examined whether gum rockrose (*Cistus ladanifer*) has a nurse effect on holm oak seedlings, and found an overall neutral or negative effect on oak recruitment explained by the lower soil water content under gum rockroses.

In ecosystems characterized by a severe summer drought, pioneer shrubs represent a major safe site for early tree recruitment, improving seedling survival during summer by the modification of both the above and below-ground environment. Nevertheless, it is necessary to keep in mind that shrub-seedling interactions are species-specific and vary with the physical and biological environment (Marañón et al. 2009). In natural communities, only a subgroup of co-occurring species provides benefits, while the effects of the remaining species vary from competitive to neutral (Callaway and D’Antonio 1991; Puerta-Piñero et al. 2006; Callaway and Pugnaire 2007). Gómez-Aparicio et al. (2004), explored variation in the magnitude and direction of interactions along spatial gradients defined by altitude and aspect using 18,000 seedlings of 11 woody species planted under 16 different nurse shrubs. They found a consistent facilitative effect in all environmental situations explored, but with differences in the magnitude of the interaction, depending on the seedling species planted as well as the nurse shrub species involved. Additionally, shrub species can have an indirect effect on seedling recruitment through an increase or a reduction in pasture growth, with under-explored consequences for oak seedling survival.

6.5 Lessons Learned

A thorough understanding of the interactions among plants, soils, disturbance and other factors in dehesas and Californian oak woodlands is necessary to assess their sustainability. They share a Mediterranean climate, oaks, and many understory species. These shared characteristics are tempered by some significant differences in the amount of information available and some real differences in functional properties, especially those related to the roles of soil nutrients and water (Fig. 6.20).

Tree clearance as practiced in dehesa and Californian oak woodlands can positively affect the development of the understory and the remnant trees, which take advantage of the lower tree density. Tree roots can access a large volume of soil resources, especially water, unused by the understory layer. This allows the trees to maintain good water status over the summer and to grow more acorns, which is of importance for livestock rearing in dehesa and for wildlife in both places.

The limited overlap in the roots of the trees and the pasture together with the slow growth of many oak species and their capacity to thrive in poor soils make long-term management for livestock production, wildlife, and wood products in both Iberia and California possible. In the Iberian Peninsula oaks are actively managed as dehesa, without significant negative effects on pasture growth, and there is a growing interest in maintaining the trees. In California, the widespread thinning or clearing of oaks has been greatly reduced in the last few decades with the recognition of their limited impact on forage production at lower densities, and diverse oak conservation initiatives have been launched.

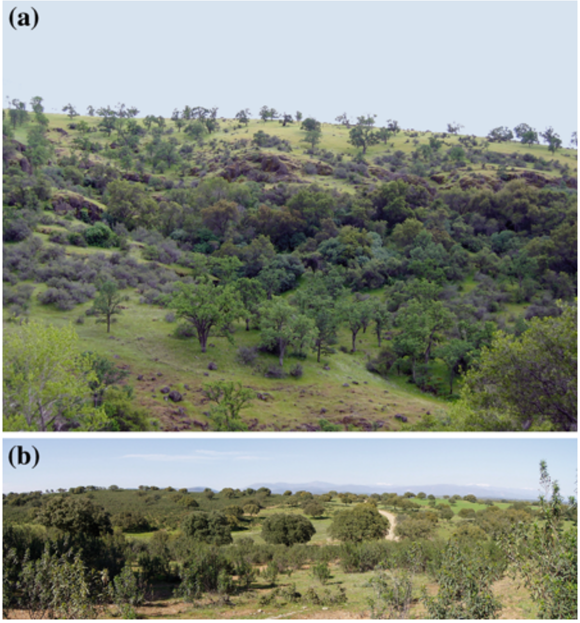

Fig. 6.20 **a**, **b** Shrub encroachment occurs distinctively in Californian and Spanish oak woodlands. Above, a shrub understory is comparatively uncommon in California but does occur, here on volcanic soils in the northern Sierra foothills. Blue and valley oaks intermix with various shrub species including buckbrush (*Ceanothus cuneatus*) (photo unattributed). Below, by contrast, shrub encroachment occurs quickly in Spanish dehesa unless shrubs are controlled by periodic cultivation and grazing. (Photographs by G. Moreno)

We have described how oak trees can facilitate understory forage production through the positive effect of shade and improved soil fertility. In Californian oak woodland pasture productivity increases up to as much as 60 % tree cover, especially for drier areas where rainfall is below 500 L m^{-2}. By contrast, in dehesa the effect of trees on pasture understory growth becomes more negative with aridity. This phenomenon in California oak woodlands needs to be confirmed taking into account different pasture taxa and soil types. To our knowledge, a conclusive study comparing the effect of evergreen and deciduous oaks on pasture understory yield is still missing, but from partial studies conducted in Californian oak woodlands, it can be said that positive effects are less evident with evergreen than with deciduous oaks.

The net effect of trees on understory yield varies considerably, with some studies reporting understory yield increased in the vicinity of the trees and others finding the opposite. More consistent is the positive effect of trees on understory nutrient content, landscape and habitat diversity, and phenology through the lengthening of the growing season, although evidence for this latter phenological effect is not as strong for Californian oak woodlands.

The two-layered dehesa system has been called unsustainable because of the absence of natural tree regeneration. Although oak seedlings have physiological adaptations for overcoming understory competition during summer drought, efforts made by managers to favor understory yield and reduce shrub understory could have a negative effect on oak seedling establishment. In addition, the current grazing pressure seems to be a definitive cause of a lack of oak regeneration in Spain, as presented in this volume (Chap. 5). Shrub encroachment in Californian oak woodlands has not been adequately researched and is poorly understood. In contrast, dehesa shrub encroachment has been extensively researched and shown as a way to potentially increase and sustain oak recruitment (Ramírez and Díaz 2008). Different Mediterranean shrubs seem to play multiple positive effects on microclimate and soil that favor tree establishment.

Although dehesa shrubs compete with trees for soil resources more strongly than herbaceous plants, the nutritional and hydric status of mature trees is not substantially affected by shrub unerstory. Hence, the rotation of grazing zones to generate a mosaic with some temporal ungrazed shrubby patches where oak can regenerate can be recommended as a mechanism to favor dehesa persistence without compromising the short-term productivity of trees. Although some practical methods for ensuring adequate oak recruitment have been developed, researched, and implemented in Californian oak woodlands, providing for natural oak regeneration is still a challenge in California because of the many influences on it, the numerous oak species involved, and inconsistent linkages to management activities including grazing.

6.6 Future Research

Explicit long-term strategies should be designed to promote management practices that ensure dehesa and Californian oak conservation. However, in order to convince landowners, administrators and policy-makers, better knowledge is needed.

For instance, although tree effects on soil and understory have been widely studied, studies focusing on the conditions and specific sites that result in positive or negative interactions are still needed. In this sense, the optimal tree density of dehesas under different uses and ecological constraints has not been adequately studied. The optimum tree density must be determined as a function of the effect of trees on understory and as a function of the tree–tree competition for soil resources, primarily for water. It would be useful to link these results to the specific characteristics of ecological sites such that they could guide management goals in both dehesas and Californian oak woodlands.

The nurse effect of shrubs is a species-specific phenomenon. For example, studies on the effects of gum rockrose on holm oak seedlings, the most common tree-shrub combination in the dehesa, have failed to show this effect. Further studies focusing on specific combinations of tree and shrub species on specific ecological sites will be needed. These studies should include developing a better knowledge of the root systems of shrubs. Similarly, the effects of changes in understory composition and production on seedling survival must be studied. And while dehesa shrub encroachment is certainly favorable for oak seedling regeneration, it does not maintain longer term stand functions and profitability from livestock, wildlife, and cork production. How to manage this temporal change in the relationships of shrubs and trees is an important topic (Ramírez and Díaz 2008). Finally, basic shrub studies in California are needed, with an emphasis on the effects of fire and grazing intensity on vegetation change (Fig. 6.21).

Finally, the stability of dehesa and Californian oak woodland systems in the face of long-term climatic change will need further study. The expected increase in the

Fig. 6.21 Once shrubs like gum rockrose have taken over a dehesa for the long term, it is no longer able to function for the production of multiple agricultural products, and is no longer really a dehesa woodland. As trees and shrubs get larger, the interrelationship between them changes too, towards stronger competition. (Photograph by G. Moreno)

probability of extreme events could have dramatic consequences in dehesa (Joffre et al. 1999) and oak woodlands (Allen-Diaz et al. 2007). Indeed, apparently higher oak tree mortality is presently occurring in dehesas (Sanchez et al. 2002) and in California (Rizzo and Garbelotto 2003), including mortality caused by invasive pathogens. The effect of global warming on this increased mortality is uncertain and it deserves more research, as do the consequences of global warning for many dehesas and Californian oak woodlands undergoing woody encroachment.

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