

Understory-Canopy Relationships in Oak Woodlands and Savannas¹

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Abstract: We summarize available information about the relationships between oak overstory and understory plants for major California rangeland types. Understory biomass, productivity, and plant species composition vary considerably because of geographic location, overstory species composition, and overstory density and distribution. Deciduous oak canopies in areas with less than 50 cm annual precipitation generally have either no effect or enhance understory productivity compared to adjacent grassland. Dense canopies in areas with more than 50 cm annual precipitation generally suppress understory productivity. Forage management implications are summarized for different woodland types around the State.

The five major hardwood rangeland habitat types used in the California Wildlife Habitat Relationships System, occupying nearly 4 million ha, have been defined and mapped in California (Standiford and Tinnin 1996). The types, with dominant species in parentheses, are: blue oak woodland (*Quercus douglasii*); blue oak-foothill pine woodland (*Q. douglasii* and *Pinus sabiniana*), valley oak woodland (*Q. lobata*), coastal oak woodlands (*Q. agrifolia*, with *Q. engelmannii* in the south), and montane hardwood (*Quercus chrysolepis*, *Q. wislizenii*, *Q. garryana*, and *Q. kelloggii*).

Cover of the understory of oak woodlands and savannas is predominately annual grasses native to the Old World. Species composition under the canopy differs from that in the adjacent open grassland. Productivity and chemical composition also show striking differences that are important considerations for management. We summarize published information about understory composition and productivity applicable to forage management in oak-dominated vegetation.

Species Composition

Studies in the North Coast Ranges and the Sacramento Valley foothills showed consistent differences in understory composition between blue oak canopy and open grassland. Murphy (1980) reported more forbs, fewer legumes, and more perennials under sheep-grazed blue oak canopy compared to adjacent grasslands. Jackson and others (1990) reported that species composition differed significantly, with ungrazed open grassland supporting *Bromus mollis*, *Hordeum hystrix*, *Avena barbata*, *Bromus madritensis*, *Lolium multiflorum*, *Cynosurus echinatus*, *Anagalis arvensis*, *Daucus pusillus*, *Geranium molle*, *Madia* spp., and *Trifolium* spp. The understory was primarily *Brachypodium distachyon*, *Bromus diandrus*, *Lolium multiflorum*, *Bromus mollis*, *Hordeum leporinum*, *Daucus pusillus*, *Geranium molle*, *Silene* sp., and *Silybum marianum*.

Jansen (1987) reported understory composition in cattle-grazed areas similar to that reported in the other northern studies. Open grassland was composed of *Bromus mollis*, *Erodium botrys*, *Trifolium hirtum*, *Taeniatherum asperum*, *Vulpia megalura* (sic), and *Lolium multiflorum*, while the denser woodlands were *Cynosurus echinatus*, *Lolium multiflorum*, *Bromus mollis*, *Geranium molle*, *Trifolium hirtum*, *Bromus madritensis*, and *Stipa pulchra*.

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In ungrazed woodlands and savannas in the central coast, Callaway and others (1991) found that some blue oaks facilitated understory productivity and some suppressed it. Composition in open grassland was mostly *Avena fatua* with some *Bromus mollis*, *Stipa pulchra*, and *Erodium botrys*. The understory was mainly *Bromus diandrus*, *Bromus mollis*, *Avena fatua*, and *Hordeum leporinum*. Savanna trees that facilitated understory productivity had relatively more *Hordeum leporinum* cover while the suppressive trees had relatively more *Stipa pulchra* understory cover. Holland (1980) described ungrazed open grassland and understory of blue oak canopies in the San Joaquin Valley and Central Coast. *Erodium botrys*, *Bromus mollis*, *Avena fatua*, and *Bromus diandrus* characterized open grassland. Species under trees dead for more than 25 years were *Bromus diandrus*, *Avena fatua*, *Erodium botrys*, and *Hordeum leporinum* while the live tree understory was primarily *Bromus diandrus*, *Avena fatua*, and *Bromus mollis*.

In their survey of the grazed understory of blue oaks at about 50 percent canopy along a rainfall gradient from 40 to 90 cm/yr, McClaran and Bartolome (1989) found that differences in composition of the understory and adjacent open grassland were consistent over wide areas. *Bromus mollis*, *Erodium cicutarium*, *Avena barbata*, and *Lupinus bicolor* dominated the grassland while *Festuca megalura* and *Bromus diandrus* were the most common understory species.

Live oaks appear to have comparable effects on understory composition in north and south coastal areas. Maranon and Bartolome (1993) report that light-requiring species *Lolium multiflorum*, *Bromus mollis*, and *Hypochoeris glabra* occurred primarily in open grassland, while shade-tolerant species in an adjacent coast live oak understory were *Montia perfoliata* and *Stellaria media*. *Bromus diandrus* did well in both habitats. *Avena fatua* dominated full-sun unclipped plots while *Bromus diandrus*, *Bromus mollis*, and *Lolium multiflorum* did better with clipping. In Southern California, Parker and Muller (1982) described an ungrazed grassland dominated by *Avena fatua*, and a live oak understory dominated by *Pholistoma auritum* and *Bromus diandrus*.

According to the work cited above, three widespread grass species, *Bromus mollis*, *B. diandrus*, and *Lolium multiflorum*, are generally common in both open and canopy. *Avena barbata* was reported common only in open, while *A. fatua* was reported common in southern grasslands and canopy. *Erodium botrys* and *Taeniatherum asperum* were common only in grassland. Striking and consistent differences in understory composition between open grassland and tree canopy understory are found throughout the State's oak woodlands and savannas.

Herbage Productivity

Tree canopy effects on understory composition and productivity depend upon rainfall, tree cover, and persistence of oak leaves on the tree. The basic pattern of biomass accumulation in California grasslands may be described as rapid fall growth following germination, slow winter growth, rapid spring growth, and summer seed set (Jackson and others 1990) (fig. 1). The basic pattern is altered by presence of an oak overstory.

In higher rainfall areas, the canopy suppresses understory biomass throughout the growing season. The degree of suppression depends on canopy density and is greater with evergreen species than deciduous species on similar sites (Pitt and Heady 1978). Sites comparing areas with trees to areas with trees cut and removed furnish most of the information about canopy effects in the northern part of the state.

Jansen (1987) studied canopy effects for 7 years on sites with 25, 50, and 75 percent tree cover and examined the effects of subsequent clear-cutting on seasonal production and composition at the Sierra Foothill Range Field Station

(SFRFS) near Marysville in the eastern Sacramento Valley. He found that clear-cut areas always produced more total herbage than treed areas or even grassland, although there was considerable yearly variation. Grassland produced more than the treed areas but differences were not apparent until spring.

Results from another site at Sierra Foothill Range Field Station produced long-term data on understory productivity. Kay and Leonard (1980) reported more grass under killed blue oaks than in a dense woodland. Forage productivity averaged 66 percent more if the tree roots were killed, 45 percent if only the tops were killed. In a later report (Kay 1987), productivity measurements during 21 years after tree removal showed mostly increased herbage productivity for the first 15 years (3 of 15 years were lower). Natural grasslands produced 26 percent more forage than treed areas. Increased production disappeared after the 15th year on the cleared sites. They removed accumulated mulch each year, at first by grazing, then later by mowing. On yet another SFRFS site, Jackson and others (1990) did not find differences in herbage productivity between canopy and open. Similar amounts of herbaceous biomass were present in two areas; soil moisture potential also differed little between canopy and open in their study.

Murphy (1980) reported 20 years of data from the Hopland Field Station in Mendocino County. Forage yield averaged 2,200 kg/ha in open grassland, 1,300 kg/ha under a mostly blue oak canopy. Similar reports from Hopland were reported by Bartolome and McClaran (1992) who found few within-year effects of seasonal grazing, but many between-year effects. They found less seasonal and total productivity in oak understory and more variation among years in fall-winter productivity compared to open grassland. Understory productivity averaged 50 percent of open grassland in fall/winter and 33 percent of open in spring.

Kay (1987) discussed the effect of canopy cover on year-to-year variability in forage yield. He found the improved forage yield on cleared sites was greatest in dry years, and he observed a greater yearly variation under the canopy than in open grassland. Jansen (1987) did not find a significant canopy effect on year-to-year variability.

Farther south, in regions with less precipitation such as the San Joaquin Valley, the canopy effect becomes neutral or enhances understory productivity. In contrast to the information from northern California, which is derived from experimental removal of canopy, most of the information about the south is derived from comparisons of intact canopy and adjacent open grassland. The effect appears to be highly variable by season and year for a given site.

Several important studies were conducted at the San Joaquin Experimental Range in the San Joaquin Valley north of Fresno. In a 2-year study, Frost and

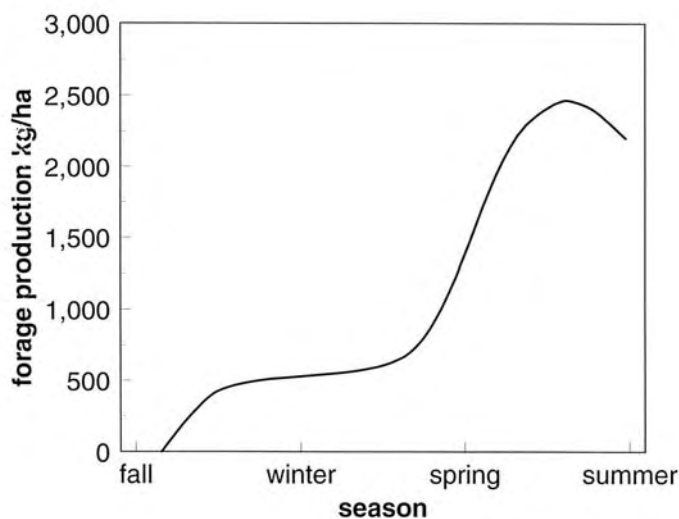


Figure 1—Typical pattern of seasonal forage growth on California's hardwood rangelands.

McDougald (1989) reported that early-season production increased in some years under the canopy. Compared to open grassland, the peak herbage under blue oak canopy was about 1,000 kg/ha greater and peak herbage under interior live oak was 700 and 1,000 kg/ha greater in the 2 years. Under foothill pine, forage was 500 kg/ha greater the first year, then not different in the second. Both years of this study had below-average precipitation. Frost and others (1991) also reported more productivity under blue oaks in late winter and at the spring peak. Frost and Edinger (1991) found more herbage production under scattered blue oak (6 percent tree canopy cover), less under foothill pine and interior live oak (12 percent tree canopy cover).

Bartolome and others (1994) removed blue oaks in San Luis Obispo County and produced a moderate increase in herb cover from 24.3 percent to 32.6 percent but no increase in herbage production. This result differs from other studies based on comparison of canopy and open, suggesting that tree-occupied sites may not have the same productive potential as nearby open grassland. McClaran and Bartolome (1989) reported that understory peak forage productivity was not enhanced in comparison to open grassland by 50 percent local canopy cover of blue oak in areas with less than 50 cm annual precipitation.

In the driest savannas with sparse canopy cover, individual trees may enhance productivity in comparison to adjacent grassland (Callaway and others 1991). Holland (1980) documented forage under blue oaks to be double that of open grassland in an ungrazed area. Once trees die, the level of productivity gradually declines to grassland levels. Duncan and Clawson (1980) note that Duncan has found more forage under blue oak in winter and spring.

Denser stands of trees, especially evergreen, consistently suppress understory forage productivity in the northern part of California. When trees are removed, productivity increases, often dramatically for a few years. In sparser stands and in the central part of the State, the tree canopy has a neutral or positive effect on forage productivity.

Forage Quality

Understory forage consistently is significantly higher in important nutrients than adjacent open grassland. Frost and others (1991) reported more protein and lower acid-detergent fiber and lignin in canopy compared to open. Blue oaks generally improve both the amount and quality of forage in the area of the San Joaquin Experimental Range. Holland and Norton (1980) found that herbs under blue oak had significantly more nitrogen, protein, phosphorus, potassium, and biomass than adjacent grassland. Kay (1987) observed significantly more nitrogen in tree understory forage and also more phosphorus, phosphate, and sulfate than in open grassland.

Kay and Leonard (1980) found that understory botanical composition shifted to more desirable forage species after tree killing, mainly because of an increase in *Bromus mollis*. This claim was repeated by Menke (1989). In contrast, Bartolome and McClaran (1992), Murphy and Crampton (1964), and Pitt and Heady (1978) observed negligible differences in forage quality due to species composition and suggested that overall quality of understory and open grassland is similar. Jansen (1987) claims that there are more undesirable plants in open than understory.

Reports of differences in composition of forage species in relation to forage quality are inconsistent: the differences in chemical composition are not. However, forage quality varies so much seasonally within sites that small differences in composition and quality between understory and open are usually unimportant as management considerations. An exception could be early-season enhancement of forage growth under canopy in the San Joaquin Valley. Frost

and others (1990) suggested that moving cattle to areas with scattered blue oaks helps deal with drought because of better early-season forage under trees.

Grazing in the Understory

Very few studies have investigated grazing effects on oak understories. This contrasts dramatically with the many studies of grazing in open grassland.

Hatch and others (1992) found that recovery of native species from grazing has been highly erratic over a 25-year period in exclosures at the Hopland Field Station. In an ungrazed grassland, perennials increased from 1.8 plants/m² in 1958 to 2.6/m² in 1991 after a decline to 1.1/m² in 1979. In adjacent ungrazed woodland, perennials increased dramatically from 0.3/m² in 1958 to 2/m² in 1991. Change in the understory was mainly a steady increase in *Elymus glaucus*. The successional pathways differed strikingly in woodland and grassland.

Most observers have commented subjectively on the differences in grazing pressure in open grassland and the oak understory. For example, Duncan and Clawson (1980) reported that cattle prefer forage under blue oak canopy. But on the basis of utilization data, Bartolome and McClaran (1992) found no important seasonal or overall differences in utilization between canopy and open at Hopland. They also found few within-year effects of seasonal grazing by sheep on composition or productivity, but many between-year effects, which were apparently closely tied to weather patterns and the level of residual dry matter.

Management of Understory Forage

Table 1 summarizes the effects of oak canopies on understory forage productivity. The amount and quality of forage differs according to oak species and canopy cover. Given equal canopy density, live oaks suppress understory forage more than deciduous oaks. Figure 2 generalizes the effect of 50 percent blue oak canopy on understory productivity, illustrating differences due to rainfall and/or geographic location. In the drier zone of the blue oak woodland with less than 50 cm annual precipitation, understory productivity is similar to or greater than open grassland.

Clearing of oaks was frequently recommended for range improvement and where stands are dense, especially with live oaks dominant, understory forage production can be considerably enhanced. In drier areas, especially those with deciduous canopies, less than 50 cm annual precipitation, and canopy cover less than 50 percent, the understory will not reliably respond to tree removal with increased productivity. There is considerable evidence that scattered trees consistently enhance forage productivity (table 1).

Forage quality under oak canopies is related to chemical composition of herbage and species composition. The oak understory is consistently higher in nitrogen and other minerals than adjacent grassland which should lead to better nutrient quality. However, when species composition is included, unpalatable species may be present. Although seasonal preference for understory forage has been frequently noted, it appears likely that species composition includes desirable and undesirable species in both open grassland and oak understory. Understory forage quality should not be a major consideration in forage management.

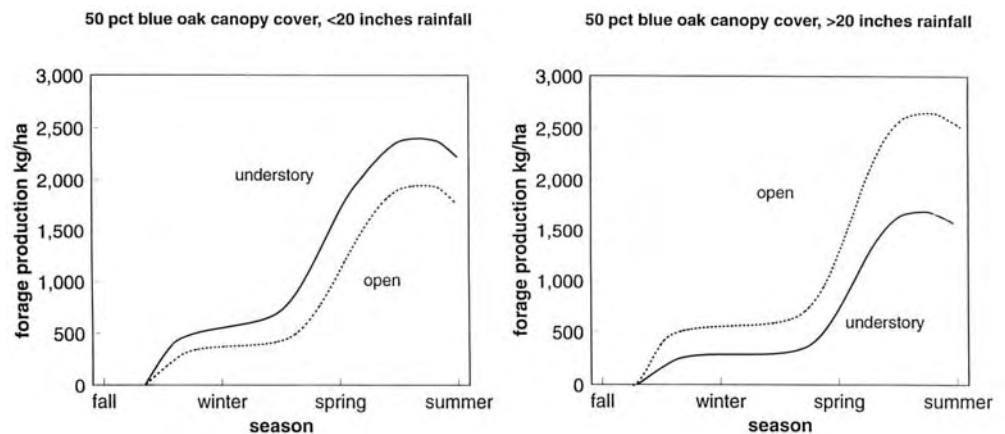
The effects of grazing on understory forage are very little studied, as are the successional relationships among understory species. This lack of information contrasts strikingly with the abundant information about open grasslands. Management of the understory forage has been assumed to fit the model for a scheme based on residual dry matter successfully applied to grasslands, but

Table 1—Effect of oak canopy on hardwood rangeland forage production summarized from the literature

Species group	Canopy cover	Winter forage	Spring forage production
Live oaks	Scattered (cover <10 pct)	-/+	-/+
	Sparse (cover 10-25 pct)	-/+	-/+
	Moderate (cover 25-60 pct)	-	-
	Dense (cover >60 pct)	-	-
Deciduous oaks	Scattered (cover <10 pct)	+	+
	Sparse (cover 10-25 pct)	+	+
	Moderate (cover 25-60 pct)	-/+	-/+
	Dense (cover > 60 pct)	-	-

¹A "+" indicates that forage production is enhanced by oak canopy and a "-" indicates that forage production is inhibited by oak canopy.

Figure 2—Effect of 50 percent blue oak canopy cover on seasonal forage production compared with open annual grassland in two rainfall zones (adapted from data of McClaran and Bartolome 1989).



there is little good research to back up this assumption. Because of the highly variable nature of the canopy effect, many more site-specific studies are needed to fully examine management options.

The mechanisms for canopy influence on the understory have been frequently investigated but rarely successfully. The expression of canopy dominance has been variously ascribed to shade (Maranon and Bartolome 1994), allelopathy (Parker and Muller 1982), water relations (Callaway and others 1991), and nutrient dynamics (Jackson and others 1990) in different combinations of sites, species, and circumstances. It appears that the generalizations about overstory-understory patterns do not have a simple suite of causal explanations. Likewise, management recommendations need to be developed conservatively, with overstory removal for forage enhancement limited to dense stands exceeding 50 percent canopy and with more than 20 inches of mean annual precipitation.

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