

Gambel oak root carbohydrate response to spring, summer, and fall prescribed burning

MICHAEL G. HARRINGTON

Abstract

Control of Gambel oak (*Quercus gambelii* Nutt.) for increased forage production and conifer regeneration is difficult because of its vigorous sprouting ability. Nonstructural root carbohydrate concentrations, generally a good indicator of sprouting potential, were measured in understory Gambel oak in a dense ponderosa pine (*Pinus ponderosa* Laws.) stand following prescribed fire. Carbohydrates in roots of 1- to 2-year-old sprouts after a single fire treatment were similar to those in unburned, mature oaks. Two prescribed burns, 2 years apart during the summer carbohydrate depression, caused these root reserves to remain low into fall dormancy and probably contributed to an observed oak reduction. This summer carbohydrate depression, also observed in open-grown Gambel oak, can be recognized by rapid stem growth and new leaf production.

Key Words: *Quercus gambelii*, sprouting potential, *Pinus ponderosa*

Gambel oak grows on about 3.8 million ha in the West as a prominent shrub in several vegetation zones (Harper et al. 1985). It ranges primarily from the higher pinyon-juniper (*Pinus-Juniperus*) woodlands into the ponderosa pine zone, and occupies much of the treeless grassland in Utah, Colorado, Arizona, and New Mexico between elevations of 1,800 and 2,700 m.

Gambel oak is a deep-rooted, highly competitive sprouter known for its suppression of herbaceous species in open rangelands (Jefferies 1965, Marquiss 1973) and suspected of restricting forage production and conifer regeneration in forests as well (DeVelice et al. 1986). Since forested areas of the Southwest have important multiple-use range values as well as timber values, oak management is desired here in addition to open rangelands. Gambel oak control has been largely unsuccessful because of a massive system of underground buds (Tiedemann et al. 1987) and lack of proper timing of control practices (Engle et al. 1983).

Most effective control of sprouting hardwoods generally follows top-killing during the growing season (Hough 1968, Berg and Plumb 1972). Root carbohydrates, which are the energy source for resprouting, are utilized in the spring for leaf development and later for flowering or additional plant growth. If a plant is top-killed shortly after new leaf development, additional carbohydrates are required for resprouting (Cook 1966). This depleted energy source theoretically leads to a reduction in both sprouting and general growth (Garrison 1972). Under frequent and intense defoliation, reduction in the total carbohydrate concentration will normally follow, causing restricted plant development and even death. Using this strategy, repeated prescribed burning during low carbohydrate periods has effectively controlled understory hardwoods in the Southeast (Hodgkins 1958, Grano 1970) and in the Lake States (Buckman 1964).

Because the sprouting potential of shrubs such as Gambel oak depends primarily on root energy reserves, knowledge of seasonal carbohydrate variation is important in timing of control application. Objectives of this study were: 1) to examine seasonal changes in total nonstructural carbohydrate (TNC) concentrations in roots of Gambel oak in a ponderosa pine understory, 2) to compare

seasonal TNC variations between Gambel oak as a ponderosa pine understory species and as a dominant overstory range species, and 3) to examine TNC changes in Gambel oak after single and repeated prescribed burns applied in different seasons.

Study Site and Methods

The study area is on the San Juan National Forest in southwestern Colorado, 40 km northeast of Durango, at an elevation of 2,300 m. Aspect is south with less than 5% slope and precipitation at the study site averages 44 cm annually, with dry periods in the late spring and heavy midsummer thundershowers. Soil is generally a clay loam with about 30% clay and classified as a fine, mixed Mollic Eutroboralf. Overstory is an uneven-aged ponderosa pine stand averaging 740 trees/ha and 28 m²/ha basal area. Gambel oak forms a dense understory, mostly less than 1.5 m tall.

Four, 3-ha units were established, one for each of the burn treatments (spring, summer, or fall burns, or unburned controls). Homogeneous plant and site conditions existed between units before burning. Season of burning was related more directly to oak growth stages than to specific calendar dates. The spring unit was burned shortly after leaf-out in mid-June, when oak leaves were 1/2 to 3/4 full size. Summer burns took place in mid-August, a few weeks after the start of the rainy season, when stem elongation and new leaf development became obvious. Fall burning was conducted in late October or early November when oaks had become dormant and most leaves had fallen.

The fall unit was burned first (1977), and the spring and summer units were burned the following year (1978). Gambel oak roots were sampled and analyzed for TNC concentration beginning the year after the spring and summer burns (1979). Roots and rhizomes, which were not differentiated, were collected from 5 plants which represented the general oak condition throughout each of the 3 burn and 1 control treatment. Sampled plants were sprouts in burned units and mature oaks in the controls. Roots were collected at intervals of approximately 2 weeks from mid-May, before oaks had broken dormancy, until leaf fall in mid-October. At each collection period, a sample of branches, buds, and leaves were taken so oak phenology could be related to carbohydrate concentration.

The fall unit was burned again in October, 1979, and the spring and summer units were reburned in June and August 1980, respectively, when oak phenology was the same as in the 1978 burns. Oak root sampling was resumed for all treatments just before the 1980 spring burn. Samples for this period were collected monthly until mid-October. The burning and sampling schedule is shown in Table 1.

During the initial burns, fire intensities and fuel consumption were very similar for all 3 seasons. In the repeat burns, fire intensities and fuel consumption were greatest on the spring plot, and lowest on the fall plot. Even though the fire missed some oaks, all oaks sampled for TNC concentrations had been top-killed by the fire treatments.

On each sample date, the selected oak plants were excavated to a depth of 30 cm. Only roots smaller than 1 cm in diameter were

Author is with the USDA, Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory, P.O. Box 8089, Missoula, Montana 59807.
Manuscript accepted 28 February 1989.

Table 1. Schedule of burning treatments and root sampling for TNC analyses.

Treatment	Year			
	1977	1978	1979	1980
Spring		Burn(June)	Sample(May-Oct.)	Sample(June-Oct.) Burn(June)
Summer		Burn(Aug.)	Sample(May-Oct.)	Sample(June-Oct.) Burn(Aug.)
Fall	Burn(Oct.)		Sample(May-Oct.) Burn(Oct.)	Sample(June-Oct.)
Control			Sample(May-Oct.)	Sample(June-Oct.)

collected, cut into 5 to 7 cm sections, placed into plastic bags, and set on ice. As soon as possible, the roots were dried in a forced-air oven at 50° C for a minimum of 48 hours. Samples were then ground in preparation for laboratory analysis.

Concentrations of TNC were determined using procedures described by Trlica et al. (1977). Total nonstructural carbohydrates include reducing and nonreducing sugars, starch, dextrans, and fructosens, which are a readily available source of energy. Hemicellulose and cellulose are not included. Values reported are milligrams of nonstructural carbohydrates per gram of dry material.

T-tests were used to determine if carbohydrates differed between burned and unburned oaks at each sample date following the first burn. In addition, seasonal TNC averages of treatments were compared using a t-test based on a seasonal variance for the mean of each treatment. This seasonal variance was computed by summing variances of the means at each sample date and dividing by number of sample dates. Independence of observations at different sample dates were assumed. An analysis of variance was conducted to determine if differences, after 2 burns, existed among the 4 burn treatments and among the 5 sample dates. Because interaction was present between date and burn treatment, a one factor analysis of variance, followed by Duncan's multiple range test, was used to compare carbohydrate differences between treatments at each sample date. Seasonal TNC averages of treatments were compared by estimating a separate seasonal variance for each burn treatment mean and pooling such information as in a one factor analysis of variance. A 5% level of significance was used unless otherwise specified.

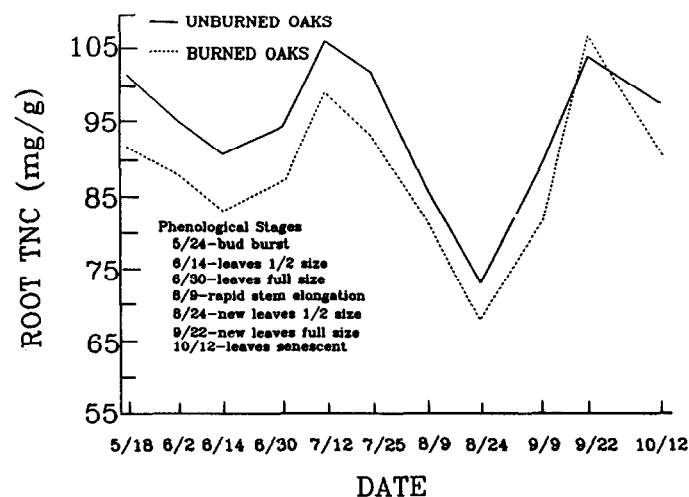


Fig. 1. Seasonal TNC cycles in burned and unburned Gambel oak. Phenological stages are included.

Phenological Stages
 5/24—bud burst
 6/14—leaves 1/2 size
 6/30—leaves full size
 8/9—rapid stem elongation
 8/24—new leaves 1/2 size
 9/22—new leaves full size
 10/12—leaves senescent

Results and Discussion

TNC Response to a Single Burn

During the first sampling season, root TNC concentrations of oak sprouts from the 3 burning season treatments were very similar and, therefore, were combined and contrasted to those of control treatment mature oaks. Figure 1 shows a lower, but insignificantly different, carbohydrate level in the burned oaks throughout the growing season. In addition, seasonal TNC average \pm SE of 88.3 ± 7.5 mg/g in the oaks in the burn plots was not significantly lower than the 94.5 ± 6.8 mg/g of the unburned oaks. Small sample size probably contributed to lack of significance. Gambel oak presumably has abundant energy reserves to draw on because of its massive underground biomass, much of which serves as storage organs (Tiedemann et al. 1987). Therefore, a single top-killing treatment was insufficient to cause marked reductions in TNC. Engle and Bonham (1980) reported no TNC reduction after single or repeated herbicide application on Gambel oak.

Comparison of TNC Levels in Other Gambel Oak Sites

Seasonal trends in Gambel oak root TNC have been reported in 2 other situations—in untreated, mature oak plants (Marquiss 1969) and in 2-year old sprouts resulting from a roller chopping treatment (Engle 1978). Both of these studies were conducted in oak-dominated communities, about 32 km southeast of the current

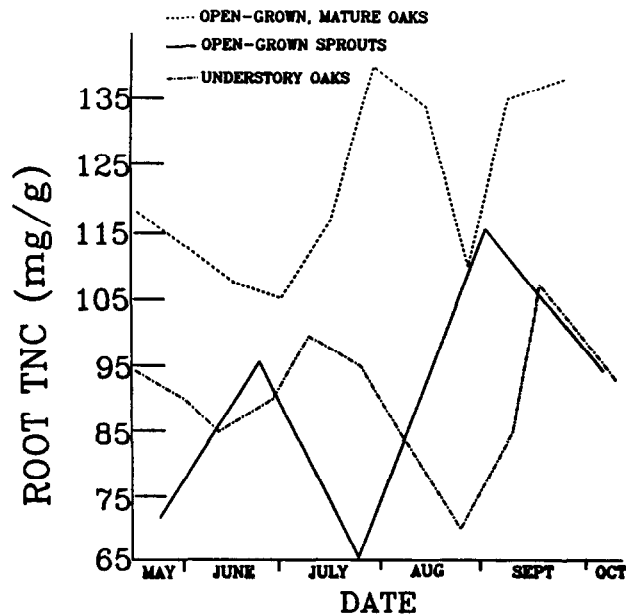


Fig. 2. Comparison of root TNC cycles of Gambel oak in 3 growth stages; open-grown mature oaks (Marquiss 1969), open-grown sprouts (Engle 1978), and understory mature oaks and sprouts (current study).

study site at approximately the same elevation. A major difference between these study sites and the present study site is that the latter is dominated by ponderosa pine with oak as a somewhat suppressed understory. Figure 2 compares Gambel oak TNC fluctuations from the 3 sites. Because TNC trends of burned (sprouts) and unburned (mature plants) were similar in the current study, those data were combined for each sample date.

Absolute TNC values from the 3 studies differed; Marquiss' (1969) values were consistently highest, and Engle's (1978) data had both higher and lower points than those from the current study, but the data were quite similar (Fig. 2). Because oaks sampled in the current study were shaded by pine overstory and were presumably photosynthesizing suboptimally, less carbohydrate production and storage could be expected compared to open-grown oaks (Kramer and Kozlowski 1979). Other possible reasons for absolute TNC differences between studies could be dissimilar sites, climates, clone ages, and growth rates. These factors were shown to be influential in clonal TNC differences in *Populus tremuloides* (Schier and Johnston 1971) and *Quercus havardii* (Bóo and Pettit 1975).

Perhaps more important than absolute TNC values are comparisons of the timing of depletion and accumulation cycles, which generally indicate periods of low and high sprouting potential, respectively (Berg and Plumb 1972). Oak root carbohydrates measured in the 3 studies had similar trends, especially those of Marquiss (1969) and the current study. However, low points and subsequent peaks sometimes appeared at different times of the growing season. This could be partially explained by Engle's (1978) infrequent sampling and also by differences in climate from year-to-year which affects plant phenology and resulting TNC trends. For example, Sweeney (1975) reported that late snowmelt delayed Gambel oak leaf-out. This, in turn, will delay the first depletion and accumulation cycle. Also, the second cycle is apparently associated with the rainy season, which varies yearly.

Because root carbohydrate storage cycles are not necessarily related to specific dates, storage trends are better compared using oak phenology. In all 3 studies, early TNC depletion was observed or assumed in May during bud break and leaf expansion (Fig. 2). Marquiss (1969) reported that this depression occurred in mature, open-grown oaks until full-leaf size. However, 2-year-old, open-grown sprouts (Engle 1978), as well as both sprouts and mature oaks in an understory, showed TNC accumulation before full-leaf stage. This implies that carbohydrate storage exceeds export in roots and rhizomes before leaves are fully mature. In all 3 studies, midsummer reduction apparently was the result of a rapid regrowth period. Rapid stem elongation and appearance of new leaves were reported by Engle (1978) and observed in the current study. In both cases, root carbohydrates had been declining for about 1 month before observed stem elongation. In the current study, new leaves were about 1/2 full size at the August 24 TNC minimum. Photosynthesis and translocation from both old and new leaves evidently led to carbohydrate gain in late summer. All leaves were full size by the early fall peak in both Engle's (1978) and the current studies. Root carbohydrates declined by the last sample date as oak leaves were falling indicating either unobserved growth, perhaps in the roots, or translocation to stems and buds. Marquiss (1969) did not report detailed oak phenology and probably missed the last TNC reduction by terminating root collection early in fall.

These root carbohydrate/phenological comparisons imply that treatments for oak control should be applied at specific growth stages, depending on age and position in the stand. Generally, reduced vigor and, therefore, best control of sprouting species may be expected from repeated mechanical or fire treatments applied when carbohydrate reserves are lowest (Berg and Plumb 1972). For

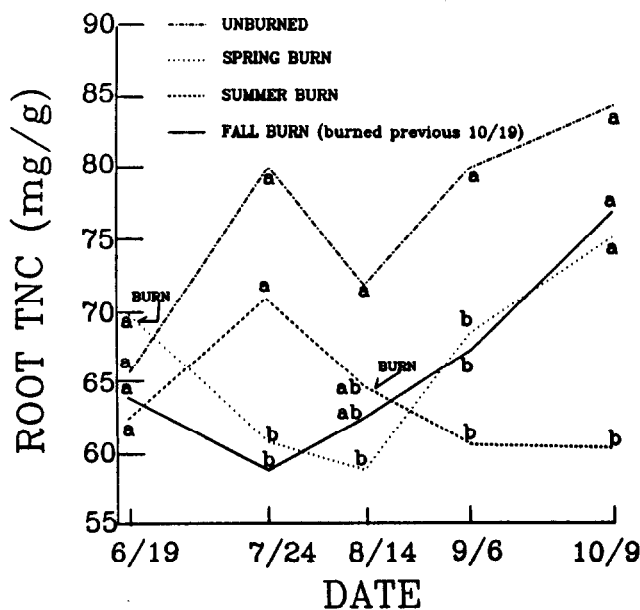


Fig. 3. Comparison of root TNC cycles of Gambel oak burned twice in spring, summer, fall, or unburned. For each date, different letters indicate significant differences ($P < 0.05$).

mature oaks, open-grown oak sprouts, and understory oaks, this period appears when leaves are approximately 1/2 full size. In all 3 situations, midsummer TNC low point would be approximated by 1/2 full size of new summer leaves. It should be noted that because vigorous sprouting follows initial mechanical or fire treatments (Marquiss 1971, Harrington 1985), maintenance programs are required and should be repeated at expected TNC low points.

TNC Response to Two Burns

Two years after initial fire treatments, oaks were burned again during the 3 respective seasons. Unburned oaks had a significantly higher mean carbohydrate concentration (76.1 ± 6.2 mg/g) over the entire growing season than summer-burned oaks (63.8 ± 5.0 mg/g) but not spring- or fall-burned oaks (66.7 ± 5.0 and 66.1 ± 4.5 mg/g, respectively).

Figure 3 shows varying root carbohydrate storage trends. The treatment by date interaction, ($P = 0.08$), indicated that TNC trends varied in different treatments depending on date. Accumulation/depletion cycles similar to those previously illustrated in Figures 1 and 2 are denoted by the control trace (Fig. 3). Because sampling began late (mid-June) and was infrequent, initial TNC reduction had passed and exact dates of peaks and low points may have been missed. The fall unit was burned the previous October, and TNC depletion continued until late July, as supplemental reserves were used for growth of new sprouts from underground buds. Spring burning occurred immediately after the first sample date resulting in a 2-month period of root carbohydrate utilization as resprouting occurred. Following depletion, root TNC accumulation in fall- and spring-treated oaks for the last 2 to 3 months as carbohydrates were produced in excess of growth requirements and approached levels of the controls (Fig. 3). Berg and Plumb (1972) also reported that early and dormant season defoliation allowed for greater regrowth and TNC accumulation than active season defoliation.

Oak root carbohydrate cycles in the summer unit were comparable to those in the controls until the burn following the mid-August sample. As resprouting commenced, carbohydrates decreased and remained low because plants failed to grow photosynthetic maturity before dormancy. Because restoration of spent energy

reserves was not apparent, summer-burned oaks entered dormancy with TNC levels significantly below those of other treatments (Fig. 3). With additional utilization of carbohydrates for respiration during winter and for spring leaf-out, a 9-month depletion could be expected before any accumulation could occur. Reduced oak growth may be expected from this sequence and was observed as oak density, canopy cover, and frequency declined (Harrington 1985).

These treatment TNC differences were primarily reflecting direct fire effects influences. Changes in the ponderosa pine overstory was an indirect fire effect that could have influenced oak response by promoting rapid oak growth and TNC utilization. During the study period, the summer-burned plot lost 18% of its original stand density compared to 11% and 13% for fall- and spring-burned plots, respectively. However, most mortality occurred in small, suppressed trees as indicated by near equal basal area changes. Therefore, overstory differences should have had little influence on oak TNC differences.

Conclusion

Engle and Bonham (1980) reported that top-killing Gambel oak in 2 successive years with herbicides failed to reduce root carbohydrate levels and sprouting potential. They speculated that treatment application made at the proper phenological stage may have produced TNC reductions. Engle et al. (1983) emphasized the need for maintenance control methods based on ecological characteristics of Gambel oak. In this case study, repeated top-killing with prescribed fire during midsummer TNC depression appears to be successfully following this recommendation, as indicated by significant oak reductions (Harrington 1985).

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