Nutrient distribution in *Quercus gambelii* stands in central Utah

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NUTRIENT DISTRIBUTION IN QUERCUS GAMBELII STANDS IN CENTRAL UTAH

A. R. Tiedemann1 and W. P. Clary2

ABSTRACT.—Gambel oak (Quercus gambelii Nutt.) is increasingly recognized as a valuable fuelwood throughout Arizona, Colorado, New Mexico, and Utah. Knowledge of the distribution of nutrients among biotic and abiotic components is an important step in developing prescriptions for managing these stands for sustainable productivity.

Eight Q. gambelii stands were sampled for concentrations (%) and accumulations (kg ha⁻¹) of total nitrogen (N), phosphorus (P), sulfur (S), calcium (Ca), magnesium (Mg), potassium (K), and sodium (Na) among aboveground and belowground biomass components and the upper 30 cm of soil. Highest concentrations of N, P, and S occurred in oak leaves, understory leaves, and the forest floor layer. Generally, highest concentrations of Ca, Mg, K, and Na occurred in the soil.

The greatest proportion of the total capital of individual nutrients was contained in the soil (82%–99%). Aboveground components of live biomass, standing and down-dead, and forest floor contained 10%, 14%, and 8%, respectively, of total capitals of N, P, and S. The forest floor had the largest accumulation (63%) of total nutrients (N, P, S, Ca, Mg, K, and Na) of live and dead aboveground components. Nutrient accumulation in live biomass was heavily weighted to the belowground component. The dense system of roots, rhizomes, and lignotubers comprising 56% of total biomass contained 62% of the total accumulation of nutrients in live biomass.

Low levels of total P in the soil and accumulation of 14% of the ecosystem total of P in aboveground biomass components suggest the need for a better understanding of the role of P in productivity of these stands in development of prescriptions for management of residues after harvest.

Key words: nutrient cycling, soil nutrients, nitrogen, phosphorus, sulfur, cations, Quercus gambelii, Utah.

Gambel oak (Quercus gambelii Nutt.) is found as a small shrub or large tree on about 3.8 million ha in Colorado, Arizona, New Mexico, and Utah. It is a clonal species that sprouts readily after harvest or other disturbance from a dense belowground system of lignotubers and rhizomes (Tiedemann et al. 1987). The lignotubers are similar to those found on Eucalyptus (Carrodus and Blake 1970). Rhizomes (belowground stems) are also common in oaks (Muller 1951).

With increasing demands for fuelwood throughout its range, Q. gambelii is coming under close scrutiny for its initial value as a fuelwood source and for continued fuelwood production potential (Wagstaff 1984, Clary and Tiedemann 1992). The density of the wood, its superior heat-yielding qualities compared with softwoods (Barger and Ffolliott 1972), and its sprouting nature (Tiedemann et al. 1987) make this species ideal for fuelwood management.

In the development of management strategies for sustainable productivity of Q. gambelii, an important step is to determine the manner in which nutrients are distributed among the abiotic and biotic components of the system. This information will help develop management guidelines so that harvest activities do not deplete nutrients to the extent that future site productivity may be jeopardized.

Our objectives were to determine the concentrations and total amounts of major plant nutrients—nitrogen (N), phosphorus (P), sulfur (S), calcium (Ca), potassium (K), magnesium (Mg), and sodium (Na)—in live and dead Q. gambelii biomass components and in soil, understory, and forest floor of a representative portion of the Q. gambelii ecosystem in central Utah; and to relate findings to similar studies in other hardwood stands. This study was a companion to a study of biomass distribution (Clary and Tiedemann 1986).

STUDY AREAS AND METHODS

Eight Q. gambelii stands (plots) were selected near Ephraim in central Utah. The stands were on slopes with gradients from 5% to 40%. Soils

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are Typic Calcixerolls formed on alluvium and colluvium derived from limestone, sandstone, and shale (Swenson et al. 1981). Soils are cobbly loams in the surface 50 cm and very stony clay loams in the substratum to depths of 150 cm. Elevations of the 8 stands range from 2089 to 2480 m. Average annual precipitation ranges from 36 to 51 cm, and the annual frost-free period is 90 to 110 d (Swenson et al. 1981).

Plot sizes varied in approximately inverse proportion to tree stem density (Clary and Tiedemann 1986). We attempted to obtain a sample of the range of stand densities and stem heights. A 3 × 3-m plot was used for the densest stand (34,444 stems/ha), a 10 × 10-m plot for the least dense stand (5000 stems/ha). Mean ages of stems ranged from 37 to 109 yr (Clary and Tiedemann 1986).

At each plot, all live stems were counted and numbered, and 5 were selected at random for measurement of height, diameter, biomass, and nutrient concentration. Sample stems were cut about 4 cm above the ground, partitioned into 60-cm sections, and weighed in the field. Live and dead branches and leaves were removed. A 10-cm portion of each bole section was placed in a plastic bag, sealed, and returned to the laboratory for determination of moisture content and nutrient concentrations. Live branches, dead branches, and leaves from each tree were bagged, returned to the laboratory, and oven-dried at 70°C to constant weight. Standing dead trees were counted on each plot, and 5 were randomly selected to be cut and weighed in the field. A section was taken from each including any attached branches for determination of moisture and nutrient concentrations.

Understory biomass—including Q. gambelii <1 m, other shrubs, herbaceous plants, forest floor, and down and dead oak—was sampled on three 1-m² subplots randomly located within each plot, except plot 8, where only 1 subplot was sampled. Plot 8 was sampled at a different time from plots 1–7, with the main objective of excavation to determine characteristics of the underground system (Tiedemann et al. 1987). We inadvertently collected only 1 subplot for determination of understory biomass, forest floor, down and dead oak, and soil. On all subplots, forest floor was collected to mineral soil. No separation into litter (L), fermentation (F), and humus (H) layers was made. Hence, the forest floor includes plant detritus accumulated above mineral soil including down and dead oak <0.5 cm. All samples were oven-dried at 70°C and weighed to determine mass per unit area (kg ha⁻¹) of the forest floor. Weight of down and dead oak >0.5 cm was assigned to the category of down and dead oak trees. A small sample of each component from each 1-m² plot was used for nutrient analysis. Forest floor samples contained some soil as a result of wind deposition and the fact that sampling results in collection of a small amount of soil from the forest floor/soil interface. Therefore, weights of forest floor samples were adjusted for content of soil by determining weight loss on combustion of small samples in a muffle furnace at 900°C. Combustion of organic materials results in a small amount of mineral ash residue of 5 g per 100 g of forest floor (Tiedemann 1987b). We adjusted forest floor weights by this amount.

Soil volume weight (bulk density) was determined by collecting a 15- to 20-cm-diameter sample to a depth of 30 cm at each of the subplots after vegetation was harvested and the forest floor sampled. This was the maximum depth feasible to collect without using mechanized digging apparatus because of the increased rocks, cobbles, roots, and rhizomes at greater depths. The soil hole was lined with plastic and the volume determined by measuring the quantity of water to the nearest 10 mL required to fill the hole. Soil was oven-dried at 70°C, weighed, and retained for nutrient analysis. This method of bulk density determination compares favorably with the paraffin clod technique (Howard and Singer 1981).

One plot (plot 8) was hydraulically excavated to a depth of 1 m by use of a hydraulic pump capable of supplying 114 L/min (Tiedemann et al. 1987). All roots, rhizomes, and lignotubers were removed and transported to the laboratory for drying, dissecting, weighing, and nutrient analysis. Weight of roots at depths >1 m was estimated from taper-weight relationships established for the first 1 m of vertical roots. A composite sample of the roots (<1.0 cm, 1.0–2.5 cm, and >2.5 cm) and rhizomes was taken for nutrient analysis. The proportion of each component in the sample was weighted on the basis of its proportion of total weight.
Each 10-cm bole portion was separated into 8 equal radial segments. One of these from each portion was further separated into heartwood, sapwood, and bark. Samples from each radial segment were then composited for each tree prior to analysis. All vegetation samples were ground to 0.25-mm fineness in preparation for analysis of nutrient concentration. Soil samples were sieved through a 2-mm mesh screen and ground to 0.125-mm fineness prior to analysis.

All samples were analyzed for total N by Kjeldahl digestion followed by titrimetric determination of distilled ammonium (Bremner 1965); for total P by sulfuric acid–selenium digestion (Parkinson and Allen 1975) followed by molybdenum blue determination of P (Olsen and Dean 1965); for total S by the procedure of Tiedemann and Anderson (1971); and for total cations Ca, Mg, Na, and K by atomic absorption spectroscopy (Jones and Isaac 1969) on the sulfuric acid–selenium digest used for total P.

Mass per unit area (kg ha\(^{-1}\)) of individual plot values for each individual biomass component of trees (leaves, live branches, standing dead, etc.) from the study of Clary and Tiedemann (1986) were used to convert concentrations of individual nutrients to mass per unit area (kg ha\(^{-1}\)). In the biomass determination (Clary and Tiedemann 1986), stems were not partitioned into bark, heartwood, and sapwood. We determined the percentage by weight of these 3 components for each bole and converted weights to kg ha\(^{-1}\) for each plot using values from Clary and Tiedemann (1986). These values were then multiplied by concentrations of individual nutrients for determination of mass per unit area (kg ha\(^{-1}\)) content of nutrients. Mass per unit area (kg ha\(^{-1}\)) values for understory vegetation, down-dead oak, and the forest floor were multiplied by concentration values for individual nutrients to determine mass per unit area of each nutrient. Bulk density of the upper 30 cm of soil (minus particles >2 mm) was used to develop mass per unit area (kg ha\(^{-1}\)) values for soil so we could convert nutrient concentration values to mass of individual nutrients per hectare. Mass per unit area values of Quercus roots, rhizomes, and lignotubers in the upper 1 m of the excavated plot plus the extrapolation of larger (>2.5 cm) vertical roots to their extinction point was used to convert concentration values of nutrients to a kg ha\(^{-1}\) basis. Extrapolation was based on application of taper-weight relationships for each root.

For purposes of data presentation, nutrient contents (kg ha\(^{-1}\)) of individual aboveground biomass components were grouped into three categories: (1) aboveground live overstory and understory vegetation; (2) standing and downdead that includes standing dead trees, dead branches on live trees, down and dead trees, and dead branches on the ground >0.5 cm; and (3) the forest floor that includes all plant detritus above mineral soil except for Quercus branches >0.5 cm.

Analysis of variance in a randomized complete block design with the 8 individual plots as blocks was used to determine differences in concentration among aboveground biomass components for each nutrient constituent (Steel and Torrie 1960). Biomass component was the main effect term in the analysis. Values for the 5 individual trees and for the 3 forest floor and understory subplots in each of the 8 plots (blocks) were pooled, and the means were used in the analysis of variance. Statistical comparison with underground biomass components was not possible because this was determined on only 1 plot. Where the F-test was significant, differences among individual biomass components were determined using the LSD test (Carmer and Swanson 1971). Significant differences are expressed at \(P < 0.01\). No statistical tests were applied to kg ha\(^{-1}\) nutrient content data because individual components were summed to provide more inclusive groupings. For example, live aboveground biomass includes oak leaves, live branches, heartwood, sapwood, bark, and understory leaves and stems.

**RESULTS AND DISCUSSION**

**Nutrient Concentrations**

There were no significant differences in concentrations of nutrients in biomass (\(P < 0.01\)) among plots (blocks) for any nutrient constituent except Ca. Differences among biomass components were highly significant for every nutrient constituent.

Nitrogen concentrations in the forest floor and in Quercus leaves were significantly higher than in any other component (Table 1). Understory leaves were significantly lower in N concentration than the forest floor or Quercus...
leaves. We did not observe increases in N concentration of the forest floor that usually accompany decomposition, mineralization, and leaching of other constituents from the fallen overstory leaves (Bocock 1963, Gosz et al. 1973). In a litter bag study, Klemmedson (1992) measured a 60% increase in N concentration in *Quercus* gambelii leaves in the litter layer over a 750-d time span. Differences between our observations and those of Klemmedson were probably because we report comparisons between *Quercus* leaves and the entire forest floor, whereas his comparisons were for the litter layer only. Lowest concentrations of N were observed in the heartwood. Standing dead and down-dead trees were both higher in N concentrations than were heartwood and sapwood of living stems. This probably resulted from selective decomposition and loss of other elements causing an increase in the concentration of N in standing dead and down-dead trees.

Concentration of N in the upper 30 cm of soil (0.42) was greater than would be expected for this site. According to Jenny (1941), the normal range of soil N for semiarid sites is 0.10%–0.25% for the surface 10 cm. The high content of N in these soils can probably be attributed to 2 principal factors: (1) the high clay content is conducive to retention of high levels of organic N (Klemmedson and Jenny 1966, Millar et al. 1966); and (2) the extraordinary accumulation of forest floor (37,348 kg ha⁻¹) at this site (Clary and Tiedemann 1986) provides a continuous supply of N to the soil through decomposition and leaching.

Leaves of understory plants (0.27%), *Quercus* leaves (0.21%), and forest floor (0.12%) had highest concentrations of P. Differences among these 3 components were significant. Reduced concentration of P in the forest floor compared to *Quercus* leaves corresponded to observations of Klemmedson (1992). Concentration of P in *Q. gambelii* leaves at the surface of the forest floor began to decrease shortly after deposit and declined steadily for 500 d to about 60% of original concentration. Concentration then leveled off for the remaining 250 d of the experiment. Our lowest levels of P occurred in the heartwood (0.003%). Although there were some significant differences among other biomass components, the actual differences were slight and probably of little biological significance. Total P in soil (0.02%) was substantially below normal levels, which are 0.09%–0.13% for soils of the United States (Parker et al. 1946).

Concentrations of S were greatest in forest floor (0.12%) and understory leaves (0.11%), and there was no significant difference between these 2 components. However, S concentration in both was significantly higher than in *Quercus* leaves. Lowest S concentrations in aboveground components were in the sapwood and heartwood. Our comparisons of N and S

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Leaves</th>
<th>Live branches</th>
<th>Heartwood</th>
<th>Sapwood</th>
<th>Bark</th>
<th>Dead branches</th>
<th>Standing dead trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>1.57</td>
<td>0.56</td>
<td>0.15</td>
<td>0.27</td>
<td>0.62</td>
<td>0.55</td>
<td>0.35</td>
</tr>
<tr>
<td>LSD 0.01</td>
<td>0.08</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>0.21</td>
<td>0.03</td>
<td>0.003</td>
<td>0.02</td>
<td>0.02</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>LSD 0.01</td>
<td>0.024</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S</td>
<td>0.08</td>
<td>0.03</td>
<td>0.03</td>
<td>0.02</td>
<td>0.04</td>
<td>0.04</td>
<td>0.04</td>
</tr>
<tr>
<td>LSD 0.01</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ca</td>
<td>0.91</td>
<td>0.90</td>
<td>0.17</td>
<td>0.17</td>
<td>1.55</td>
<td>0.98</td>
<td>1.00</td>
</tr>
<tr>
<td>LSD 0.01</td>
<td>0.30</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mg</td>
<td>0.35</td>
<td>0.16</td>
<td>0.02</td>
<td>0.04</td>
<td>0.20</td>
<td>0.14</td>
<td>0.08</td>
</tr>
<tr>
<td>LSD 0.01</td>
<td>0.29</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K</td>
<td>0.68</td>
<td>0.36</td>
<td>0.33</td>
<td>0.15</td>
<td>0.32</td>
<td>0.26</td>
<td>0.21</td>
</tr>
<tr>
<td>LSD 0.01</td>
<td>0.18</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Na</td>
<td>0.04</td>
<td>0.01</td>
<td>0.01</td>
<td>0.002</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>LSD 0.01</td>
<td>0.007</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Comparisons among aboveground biomass components only.*
levels in the forest floor with *Quercus* leaves presented an anomaly. We would expect S comparisons between forest floor and *Quercus* leaves to be similar to those for N, because S is a companion to N in several amino acids (Allaway and Thompson 1966, Coleman 1966). Klemmedson's (1992) observations bear this out because both N and S concentrations in *Quercus* leaves increased about 60% over a 750-d period after deposition at the surface of the forest floor. However, when we compared *Quercus* leaves and the entire forest floor, it appeared that N and S responded differently over the long periods required for development of the forest floor. Nitrogen concentration tended to remain constant and S concentration increased over time. Mineralization of S in deeper layers of the forest floor may proceed more slowly than mineralization of N, thereby resulting in an increase in S concentration. Products of decomposition for N may also be more mobile than those for S.

Total S concentration in soil (0.01%) was in the middle of the range reported for U.S. soils, 0.01–0.06 (Burns 1968). The ratio of N:S of 10:1 in soil indicates that the S level is great enough that N will be efficiently utilized for the formation of plant proteins (Black 1968, Burns 1968).

Concentrations of the 4 measured cations, Ca, Mg, K, and Na, were generally higher in the soil than in any plant component. Exceptions were higher concentrations of Ca in the forest floor and in the bark of *Quercus* trees and K in understory leaves.

Calcium concentrations in the forest floor layer were more than 2.5 times greater than *Quercus* leaves. The content of Ca in bark was nearly 10 times greater than heartwood or sapwood. *Quercus* leaves, live branches, dead branches, standing dead trees, and down-dead trees were all comparable in Ca concentration.

Magnesium concentrations in biomass components were highest in the forest floor layer—approximately 3 times greater than in *Quercus* and understory leaves. In contrast to Ca patterns, Mg concentrations in live branches and standing dead and down-dead trees were significantly lower than in *Quercus* leaves.

Understory leaves were significantly higher in K concentration (1.14%) than were *Quercus* leaves (0.68%) or understory stems (0.64%). Potassium concentrations were about equal for live branches, heartwood, and bark, and about half the concentration found in *Quercus* leaves. Concentration of K in forest floor was substantially lower than in *Quercus* leaves and may reflect the ease with which K is leached from the forest floor relative to the other cations (Attwill 1968).

Highest concentrations of Na occurred in *Quercus* leaves and in the forest floor. Differences among other biomass components were
Comparisons of cation levels in *Quercus* leaves with levels in the forest floor were variable between our study and results of the litter bag study of Klemmedson (1992). We showed significantly greater Ca and Mg in the forest floor than in *Quercus* leaves. Klemmedson (1992) found similar increases in Ca in *Quercus* leaves over 750 d. However, Mg concentration in his study declined to about 80% of the level in fresh leaves over the 750-d study. Differences in K concentration that we found between *Quercus* leaves and the forest floor were not nearly as great as the decline in K concentration over time in the litter layer measured by Klemmedson (1992). Potassium concentration in *Quercus* leaves declined about 70% in 500 d and then stabilized to the end of the 750-d study. Differences between Klemmedson’s observations and ours were probably a result of the fact that he studied changes in nutrient concentration in the litter layer and our comparisons were with the entire forest floor.

There is little information on the concentrations of nutrients in biomass components in western hardwood stands. There are 2 apparent reasons for this. Compared with the eastern United States, the area occupied by stands of hardwood species in the West is minor. Therefore, until recently, western hardwoods have not been viewed as an economically important resource; rather, they were considered weed species because they were assumed to compete with marketable coniferous trees or with understory forage-producing species. With emerging demands for fuelwood and new markets for unique woods for furniture, there is increased awareness of the value of western hardwoods and, especially, *Q. gambelii* (Wagstaff 1984, Clary and Tiedemann 1992).

Nutrient concentrations of leaves agreed closely with those reported by Klemmedson (1992) for *Q. gambelii* in northern Arizona. Bartos and Johnston (1978) determined the concentrations and proportions of individual nutrients in the various components of 3 clones of *Populus tremuloides* Michx. (quaking aspen) trees in Utah and Wyoming but did not consider the forest floor, understory, and down-dead components of the nutrient pool. Concentrations of N in the various tree components of *Q. gambelii* and *P. tremuloides* were comparable except for higher concentrations of N (2.5%) in leaves of *P. tremuloides*; concentrations of P, K, and Ca were similar for all tree components. Sodium concentrations were generally greater in *Q. gambelii* than in *P. tremuloides*. Concentrations of N, P, and S in live aboveground biomass of *Q. gambelii* were comparable to those reported for *Q. robur* in Russia (Rodin and Bazilevich 1967) and in Belgium (Duvigneaud and Denaeyer-De Smet 1970). Concentrations of N in forest floor and dead branches also were comparable to values for southern and eastern U.S. *Quercus* stands (Lang and Forman 1978). Concentrations of cations in our study did not agree as well with those presented in the literature as for N, P, and S. For example, *Q. gambelii* forest floor concentrations of K and Mg were 3 and 8 times greater than those reported for *Q. robur*. Calcium concentrations in *Q. gambelii* were substantially greater than those observed in other studies in forest floor, live branches, dead branches, standing dead trees, and down-dead trees.

**Distribution of Nutrient Capital Among Components**

Comparisons of nutrient distribution between above- and belowground components must be considered from the perspective that our soil sampling was restricted to the upper 30 cm because of rock and the massive underground structures of *Q. gambelii*. The actual zone of rooting and nutrient acquisition was undoubtedly much greater than the area we sampled. Therefore, our estimates of the proportions of nutrients in aboveground components were likely to be higher than if the entire rooting zone had been sampled. Also, the kg ha⁻¹ estimates were for areas of the actual clone sampled. Clones of *Q. gambelii* do not occupy the entire area of the sites on which they occur. Most studies take into account the high- and low-density areas of tree occupancy in determining nutrient distribution. Therefore, in making projections to an areal basis, the actual area occupied by *Q. gambelii* clones must be considered.

The greatest proportion of total nutrient capital sampled was contained in the soil (Table 2). Of the total capitals of individual nutrients, 82%–99% were contained in the soil. Aboveground accumulations of individual nutrients in live biomass, standing and down-
Table 2. Distribution of nutrients among biomass, forest floor, standing plus down-dead, and soil components of Q. gambelii stands.

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Livea above-ground biomass</th>
<th>Standing plus dowe-dead</th>
<th>Forestb floor</th>
<th>Total above-ground</th>
<th>Livec below-ground biomass</th>
<th>Totald live biomass</th>
<th>Soile capital</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen (kg ha⁻¹)</td>
<td>245</td>
<td>140</td>
<td>654</td>
<td>1039</td>
<td>270</td>
<td>515</td>
<td>9500</td>
</tr>
<tr>
<td>% of total aboveground</td>
<td>24</td>
<td>13</td>
<td>63</td>
<td>10</td>
<td>2</td>
<td>2</td>
<td>88</td>
</tr>
<tr>
<td>% of total capital</td>
<td>10</td>
<td>2</td>
<td>88</td>
<td>9</td>
<td>2</td>
<td>82</td>
<td>90</td>
</tr>
<tr>
<td>Phosphorus (kg ha⁻¹)</td>
<td>19</td>
<td>4</td>
<td>48</td>
<td>71</td>
<td>19</td>
<td>38</td>
<td>410</td>
</tr>
<tr>
<td>% of total aboveground</td>
<td>19</td>
<td>4</td>
<td>68</td>
<td>14</td>
<td>4</td>
<td>82</td>
<td>90</td>
</tr>
<tr>
<td>% of total capital</td>
<td>14</td>
<td>4</td>
<td>82</td>
<td>9</td>
<td>2</td>
<td>90</td>
<td>90</td>
</tr>
<tr>
<td>Sulfur (kg ha⁻¹)</td>
<td>19</td>
<td>13</td>
<td>46</td>
<td>78</td>
<td>22</td>
<td>41</td>
<td>946</td>
</tr>
<tr>
<td>% of total aboveground</td>
<td>19</td>
<td>13</td>
<td>59</td>
<td>8</td>
<td>2</td>
<td>90</td>
<td>90</td>
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<tr>
<td>% of total capital</td>
<td>24</td>
<td>17</td>
<td>99</td>
<td>9</td>
<td>2</td>
<td>90</td>
<td>90</td>
</tr>
<tr>
<td>Calcium (kg ha⁻¹)</td>
<td>334</td>
<td>303</td>
<td>1167</td>
<td>1804</td>
<td>924</td>
<td>1258</td>
<td>28844</td>
</tr>
<tr>
<td>% of total aboveground</td>
<td>18</td>
<td>17</td>
<td>65</td>
<td>6</td>
<td>3</td>
<td>91</td>
<td>91</td>
</tr>
<tr>
<td>% of total capital</td>
<td>62</td>
<td>35</td>
<td>80</td>
<td>1</td>
<td>&lt;1</td>
<td>99</td>
<td>99</td>
</tr>
<tr>
<td>Magnesium (kg ha⁻¹)</td>
<td>62</td>
<td>35</td>
<td>381</td>
<td>478</td>
<td>63</td>
<td>125</td>
<td>42485</td>
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<tr>
<td>% of total aboveground</td>
<td>13</td>
<td>7</td>
<td>80</td>
<td>1</td>
<td>&lt;1</td>
<td>99</td>
<td>99</td>
</tr>
<tr>
<td>% of total capital</td>
<td>42</td>
<td>35</td>
<td>80</td>
<td>1</td>
<td>&lt;1</td>
<td>99</td>
<td>99</td>
</tr>
<tr>
<td>Potassium (kg ha⁻¹)</td>
<td>201</td>
<td>72</td>
<td>144</td>
<td>417</td>
<td>116</td>
<td>317</td>
<td>20268</td>
</tr>
<tr>
<td>% of total aboveground</td>
<td>48</td>
<td>18</td>
<td>34</td>
<td>2</td>
<td>&lt;1</td>
<td>98</td>
<td>98</td>
</tr>
<tr>
<td>% of total capital</td>
<td>22</td>
<td>13</td>
<td>65</td>
<td>2</td>
<td>&lt;1</td>
<td>98</td>
<td>98</td>
</tr>
<tr>
<td>Sodium (kg ha⁻¹)</td>
<td>7</td>
<td>4</td>
<td>20</td>
<td>31</td>
<td>7</td>
<td>14</td>
<td>1765</td>
</tr>
<tr>
<td>% of total aboveground</td>
<td>22</td>
<td>13</td>
<td>65</td>
<td>2</td>
<td>&lt;1</td>
<td>98</td>
<td>98</td>
</tr>
<tr>
<td>% of total capital</td>
<td>7</td>
<td>4</td>
<td>20</td>
<td>3</td>
<td>&lt;1</td>
<td>98</td>
<td>98</td>
</tr>
<tr>
<td>Total (kg ha⁻¹)</td>
<td>887</td>
<td>571</td>
<td>2460</td>
<td>3918</td>
<td>1421</td>
<td>2308</td>
<td>24588</td>
</tr>
<tr>
<td>% of total aboveground</td>
<td>23</td>
<td>14</td>
<td>63</td>
<td>2</td>
<td>&lt;1</td>
<td>98</td>
<td>98</td>
</tr>
<tr>
<td>% of total in living biomass</td>
<td>38</td>
<td>14</td>
<td>63</td>
<td>2</td>
<td>&lt;1</td>
<td>98</td>
<td>98</td>
</tr>
</tbody>
</table>

aIncludes living aboveground overstory and understory vegetation.  
bIncludes all forest floor layers above mineral soil.  
cIncludes roots, rhizomes, and lignotubers in the upper 200 cm of soil.  
dStanding crop plus below-ground biomass.  
eUpper 30 cm of soil.  
fStanding crop plus standing and down-dead plus forest floor plus below-ground biomass plus soil.

dead, and forest floor ranged from 31 kg ha⁻¹ for Na to 1804 kg ha⁻¹ for Ca. Proportions of total capitals of N, P, and S in aboveground components were highest with 10%, 14%, and 8%, respectively. The proportion of N (the most widely reported nutrient) in aboveground components (10%) was comparable to that described for other semiarid and temperate forest and woodland ecosystems (Klemmedson 1975, Brown 1977, Tiedemann 1987a).

The forest floor was the most important aboveground reservoir of nutrients with 63% of the total accumulation above ground. Accumulations of individual nutrients in the forest floor ranged from 20 to 1167 kg ha⁻¹ and contributed 34%–80% of the aboveground capitals.
Total nutrient content of the forest floor in our Q. gambelii clones (2460 kg ha⁻¹) substantially exceeded the range described by Lang and Forman (1978) in their summary for U.S. Quercus forests (206 kg ha⁻¹ [Yount 1975] to 1462 kg ha⁻¹ [Gosz et al. 1976]). Greater accumulation of Ca in the forest floor layer (1167 kg ha⁻¹) compared with that reported by other observers (98-400 kg ha⁻¹; Lang and Forman 1978) accounted for much of the difference in total accumulation of nutrient elements in Q. gambelii compared with other Quercus stands. Also, forest floor biomass accumulation in our Q. gambelii stands (37,348 kg ha⁻¹; Clary and Tiedemann 1986) was near the upper limit (46,800 kg ha⁻¹) of that presented for U.S. Quercus forests (Lang and Forman 1978).

The massive belowground system of lignotubers, rhizomes, and roots comprised 56% of the total biomass of Q. gambelii (Clary and Tiedemann 1986) and contained <1% to 4% of the total of the capitals of individual nutrients. However, relative to the total nutrient accumulation in live biomass, the live belowground component was an important storage area containing 37%-74% of the individual nutrient accumulations. The proportion of total nutrients in belowground biomass (61%) substantially exceeded the range for deciduous forests worldwide (30%-40%) summarized by Rodin and Bazilevich (1967). This finding supported the conclusions of Chattaway (1958), Robbins et al. (1966), and Blake and Carrodus (1970) that storage of nutrients is an important function of belowground components such as lignotubers.

Total content of nutrients in the entire organic component (total live and dead aboveground and belowground biomass) of our Q. gambelii stands (5339 kg ha⁻¹) was in the middle of the range for deciduous forests worldwide (2000-7500 kg ha⁻¹) summarized by Rodin and Bazilevich (1967). Similarly, total nutrient content of live biomass (2308 kg ha⁻¹) was comparable to values for oak forests in Russia (2600-3400 kg ha⁻¹; Rodin and Bazilevich 1967).

Worldwide, leaves usually constitute 8%-10% of the store of mineral elements in plant biomass (Rodin and Bazilevich 1967). Mineral element accumulation in Q. gambelii leaves and understory leaves (245 kg ha⁻¹, not shown in Table 2) comprised 11% of the total mineral content of live biomass and was within the relatively constant, narrow range of 200-300 kg ha⁻¹ normally found in leaves reported by Rodin and Bazilevich (1967).

**Conclusions**

Gambel oak appears to be unique from other deciduous forests in the accumulation of nutrients in the forest floor and in belowground biomass components. Both were major areas of nutrient accumulation. The leaves, in contrast, were a minor storage area.

Accumulation of nutrients in aboveground living and dead components expressed as a proportion of total site nutrients was similar to that reported for other semiarid and temperate forest habitats. The quantity of N, the most commonly measured nutrient stored in the forest floor, also agreed well with this literature. It should be noted that had we been able to sample a larger proportion of the total rooting zone, the proportion of the total nutrient capital aboveground would likely have been smaller.

Low levels of P in the upper 30 cm of soil suggest that this element may limit productivity of Q. gambelii. Because of potential limitations in the soil, accumulation of 14% (71 kg ha⁻¹) of the total ecosystem P in aboveground living and dead components, we suggest caution in the way the forest floor and residues are managed. Fuelwood harvest followed by removal of residues by broadcast burning could cause large losses of P, depending on degree of consumption of organic matter and fire temperatures (Covington and DeBano 1988, DeBano 1988). This loss may reach 60% (of 71 kg ha⁻¹) if fuels are totally consumed (Raison et al. 1985). However, such losses need to be weighed against changes in P availability that result from burning. In his summary of plant- and litter-contained nutrients, DeBano (1988) indicated that fire-induced increases in P availability decline and reach pre-fire levels within 1 yr. DeBano and Klopatek (1988) showed that inorganic P is released by prescribed burning but is quickly immobilized and may not be readily available for plant growth.

Although there are also substantial accumulations of N and S in aboveground biomass and these are sensitive to losses from volatilization (Knight 1966, Tiedemann 1987b), they are not limiting in the soil and quantities are likely sufficient to replenish losses.
Fertilizer amendment with P may warrant consideration as a means of improving *Quercus gambelii* productivity after harvest. This decision, however, should be based on soil tests to determine the availability of P.

**LITERATURE CITED**


KNIGHT, H. 1966. Loss of nitrogen from the forest floor by burning. Forestry Chronicle (June): 149-152.


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