# DIFFERENCE IN SEEDLING GROWTH MORPHOLOGY AS A FACTOR IN THE DISTRIBUTION OF THREE OAKS IN CENTRAL CALIFORNIA

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ABSTRACT

Seedling growth morphology and initial elongation of roots of *Quercus douglasii, Q. lobata,* and *Q. agrifolia* were compared in artificial and field environments. *Quercus douglasii* had established longer main roots by spring than the other two species. This was attributed to its early germination and high rate of root elongation. *Quercus douglasii* has the smallest leaf area/root weight ratio among the three species, which enables it to occupy xeric sites. Restriction of *Q. agrifolia* to mesic sites is related to its relatively slow germination, low rate of root elongation, and larger leaf area/root weight ratio.

Vegetation in California, which has developed under summer drought, has been related to depth of water table and the rate of drying of surface soils after winter rains (Cannon 1914a,b, Cooper 1922, 1926, Helmers et al. 1955, Griffin 1967, Krause and Kummerow 1977, Ng and Miller 1980, Arkeley 1981, Kummerow and Mangan 1981). Oaks dominate many of the California plant communities that cover the area from coastal regions up to the middle elevation of the mountainous regions. Griffin (1971, 1973, 1976) discussed the distribution and regeneration of California oaks in relation to moisture availability of habitats. The amount of available water in soils and the growth characteristics of individual species, such as a germination time, root growth rate of seedlings, material distribution within a seedling, etc., apparently have important effects on success or failure of seedling establishment. Information on such autecological aspects is necessary for better understanding the difference in distribution of species.

*Quercus agrifolia* Née, *Q. douglasii* H. & A., and *Q. lobata* Née dominate the local foothill woodland, although they are generally segregated along gradients of moisture availability (Griffin 1973). *Quercus agrifolia,* which is the only evergreen species of the three, occupies mesic sites, such as canyon bottoms or north-facing slopes, and *Q. douglasii* occupies xeric sites, such as south-facing slopes adjacent to chaparral vegetation. *Quercus lobata* occurs on alluvial

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terraces and natural levees along rivers and also on ridge tops (Griffin 1977).

The aim of this study is to clarify the relationship between seedling growth characteristics and the habitats of the three oaks. We examined seedling growth morphology, the effects of temperature on initial root growth, and the rate of root elongation of these oaks, together with germination and root growth under the field conditions.

## Materials and Methods

Mature acorns were collected from 10 trees of each species in the Central Coast ranges of California during October and November, 1981 and 1982. Acorns of *Q. agrifolia* were collected in the Berkeley Hills, 190 to 300 m above sea level, and in Carmel Valley (100 to 300 m). Those of *Q. douglasii* were collected in Mt. Diablo State Park, near Walnut Creek (800 to 1000 m) and at the Hastings Reservation (550 to 600 m); those of *Q. lobata* were collected near Pine Grove (760 m) and at the Hastings Reservation (550 to 600 m). Acorns were sealed in plastic bags and stored at temperatures between 2.5° and 5°C until used in the experiments, except for an outdoor experiment when they were planted immediately following collection. The storage period was two to three months.

*Seedling growth morphology.* For each species, 70 acorns (seven from each of the 10 seed source trees) previously germinated on moist vermiculite were planted in tar paper tubes (6 × 90 cm) filled with U. C. mix (25% top soil, 25% organic matter, and 50% sand) in late December to early January. The tar paper tubes were placed in a lath house and protected from precipitation by a transparent (polyethylene) roof. The tubes were watered when the soil surface appeared to be dry. The epicotyl length of each seedling was measured every four days. Forty of the seedlings of each species were harvested one by one when their epicotyls grew over 2 cm tall. Leaves had not appeared yet at this stage. The 30 remaining seedlings of each species were transferred to a warm greenhouse to accelerate shoot growth. These seedlings were harvested one by one when the last leaf from the initial bud on each seedling had fully expanded. Main root length, shoot length, and leaf area of each seedling were measured. Seedlings were then divided into leaves, stems, and roots and dried at 80°C.

*Effects of temperature on root growth.* Seedlings were grown in two temperature-controlled greenhouses: 1) high temperature, 20°C day (12 hr) and 15°C night (12 hr); 2) low temperature, 10°C day (18 hr) and 5°C night (6 hr). Forty germinated acorns of each species, four from each of the ten seed source trees, were planted into tar paper tubes and grown until epicotyls were 2 cm tall. The seedlings were then harvested and the main root length and root weight were measured.

*Root elongation rate.* The relationship between acorn size and the rate of root elongation was tested by using only *Q. agrifolia* and *Q. lobata.* From each of the 10 seed source trees, a relatively large, a relatively small, and a medium-sized acorn were selected, totaling 30 acorns for each species. The fresh weight of each acorn was recorded prior to germinating on moist vermiculite. Once germinated, each acorn was transferred to one of five root observation boxes (30 × 30 × 120 cm) filled with U. C. mix. The front side of each box was made of glass set at an oblique angle so the roots of each seedling could be observed as they grew in contact with the glass. The glass was covered to screen the developing roots from light. The length of each main root was measured every three days, from January to June, until each main root touched the bottom of the box. Dry weight of cotyledons inside acorns at the beginning of the experiment was estimated from a correlation between acorn fresh weight and dry weight of cotyledons. The correlation was established by measurement on 50 extra acorns of each species, five from each of the 10 seed source trees. The amount of storage material in cotyledons utilized during seedling development was obtained by subtracting the weight of the shrivelled cotyledons at the end of the experiment from the estimated weight of cotyledons at the beginning.

*Germination and root growth under outdoor conditions.* The experiment was conducted in the shade of an oak woodland canopy at the University of California Botanical Garden in Berkeley. Twenty to 30 acorns of each of the 10 seed source trees of *Q. douglasii, Q. lobata* and *Q. agrifolia* were sown on the soil surface soon after collection and covered with oak litter. Acorns were observed once a week and germination was recorded separately for each of the seed source trees. Germinated acorns were transplanted in tar paper tubes (6 × 90 cm) buried vertically in the ground. Seedlings were harvested on 3 March 1982, and the length of main roots was measured.

## RESULTS

*Seedling growth morphology.* During the first period of seedling development, until the epicotyl was 2 cm tall, significantly more root growth was exhibited by *Q. douglasii* than by *Q. agrifolia* or *Q. lobata* (Table 1). Main root length of *Q. douglasii* averaged 36% greater than that of both *Q. agrifolia* and *Q. lobata.* In fully developed seedlings, the length of main roots of *Q. douglasii* and *Q. lobata* were not significantly different from each other, but both were significantly longer than that of *Q. agrifolia.* Corresponding to the

TABLE 1. SEEDLING MORPHOLOGY OF *Quercus agrifolia, Q. lobata,* AND *Q. douglasii.* For each characteristic, values attached by a same superscript are not significantly different from each other ($p < 0.05$, Student's t-test). *$D^2 \times L$ = (diameter)$^2$ × length of acorns and is correlated with cotyledon dry weight ($r > 0.8$). **Number of days between germination and sampling.

| Characterstics | Species | | |
|---|---|---|---|
| | *Q. agrifolia* | *Q. douglasii* | *Q. lobata* |
| Seedlings with 2 cm epicotyls | | | |
| Length of main roots (cm) | 34.6[a] | 49.0 | 37.3[a] |
| Root weight (g) | 0.139 | 0.404[a] | 0.301[a] |
| $D^2 \times L$ of acorns* ($cm^3$) | 5.51 | 8.11 | 10.51 |
| Number of days** | 42[a] | 55 | 40[a] |
| Seedlings with fully expanded leaves | | | |
| Main root length (cm) | 69.8 | 86.1[a] | 86.2[a] |
| Main root diameter at base (cm) | 0.306[a] | 0.320[a] | 0.399 |
| Root weight (g) | 0.306 | 0.667 | 1.070 |
| Leaf number | 5.6[a] | 6.1[a] | 6.2[a] |
| Leaf area ($cm^2$) | 45.1 | 24.9 | 66.8 |
| Leaf weight (g) | 0.279[a] | 0.159 | 0.326[a] |
| Stem length (cm) | 7.0[a] | 5.1 | 8.2[a] |
| Stem weight (g) | 0.116 | 0.084 | 0.191 |
| Leaf area/root weight ($cm^2$/g) | 145.0 | 41.3 | 67.2 |
| Total seedling weight (g) | 0.701 | 0.910 | 1.580 |
| $D^2 \times L$ of acorns* ($cm^3$) | 4.29 | 7.53 | 13.02 |
| Number of days** | 64[a] | 78 | 66[a] |

increase in the acorn size, total seedling weight and root weight increased in the order of *Q. agrifolia, Q. douglasii,* and *Q. lobata. Quercus douglasii,* however, showed the smallest values in leaf area, leaf weight, stem length, and stem weight. Leaf area/root weight ratio was smallest in *Q. douglasii* and largest in *Q. agrifolia.*

*Effects of temperature on root growth.* Low temperature increased significantly the length and weight of roots of the three species built in the first period of seedling development (Table 2). At both temperatures, *Q. douglasii* exhibited greatest and *Q. agrifolia* least root length. Roots of *Q. lobata,* however, were heavier than those of *Q. douglasii* in the low temperature greenhouse ($p < 0.05$).

*Root elongation rate.* The correlation coefficient (r) between estimated dry weight of the cotyledons and the root elongation rate was 0.64 ($p < 0.005$) for *Q. agrifolia* and 0.11, not significant, for *Q. lobata* (Fig. 1). The amount of storage material utilized during seedling development in *Q. agrifolia* also showed a good correlation ($r = 0.65$, $p < 0.005$) with root elongation rate, but this was not true in *Q. lobata* ($r = 0.12$, not significant). Elongation rates also were estimated from the data of seedling morphology mentioned

TABLE 2. ROOT LENGTH AND WEIGHT OF OAK SEEDLINGS WITH 2 CM EPICOTYLES GROWN IN HIGH (20°–15°C) AND LOW (10°–5°C) TEMPERATURE GREENHOUSES. Intraspecific differences between values of the temperature treatments are significant for all species ($p < 0.05$, Student's t-test). Interspecific differences between values of any two species under the same temperature treatment are significant ($p < 0.05$) except for marked (a) pairs. *Number of days between germination and sampling.

| *Quercus* species | No. of days* | | Root length (cm) | | Root weight (g) | |
|---|---|---|---|---|---|---|
| | High | Low | High | Low | High | Low |
| *Q. agrifolia* | 17[a] | 61 | 25.4 | 31.4 | 0.069 | 0.129 |
| *Q. douglasii* | 21 | 71[a] | 39.8 | 53.9 | 0.182[a] | 0.396 |
| *Q. lobata* | 18[a] | 79[a] | 32.7 | 42.1 | 0.215[a] | 0.651 |

above. Main root length of the seedlings harvested with 2 cm epicotyls was divided by the number of days between germination and harvesting. The rate of growth for *Q. agrifolia* was 0.78 cm/day; for *Q. douglasii*, 0.86 cm/day; and for *Q. lobata*, 0.93 cm/day (significantly different from one another, $p < 0.05$).

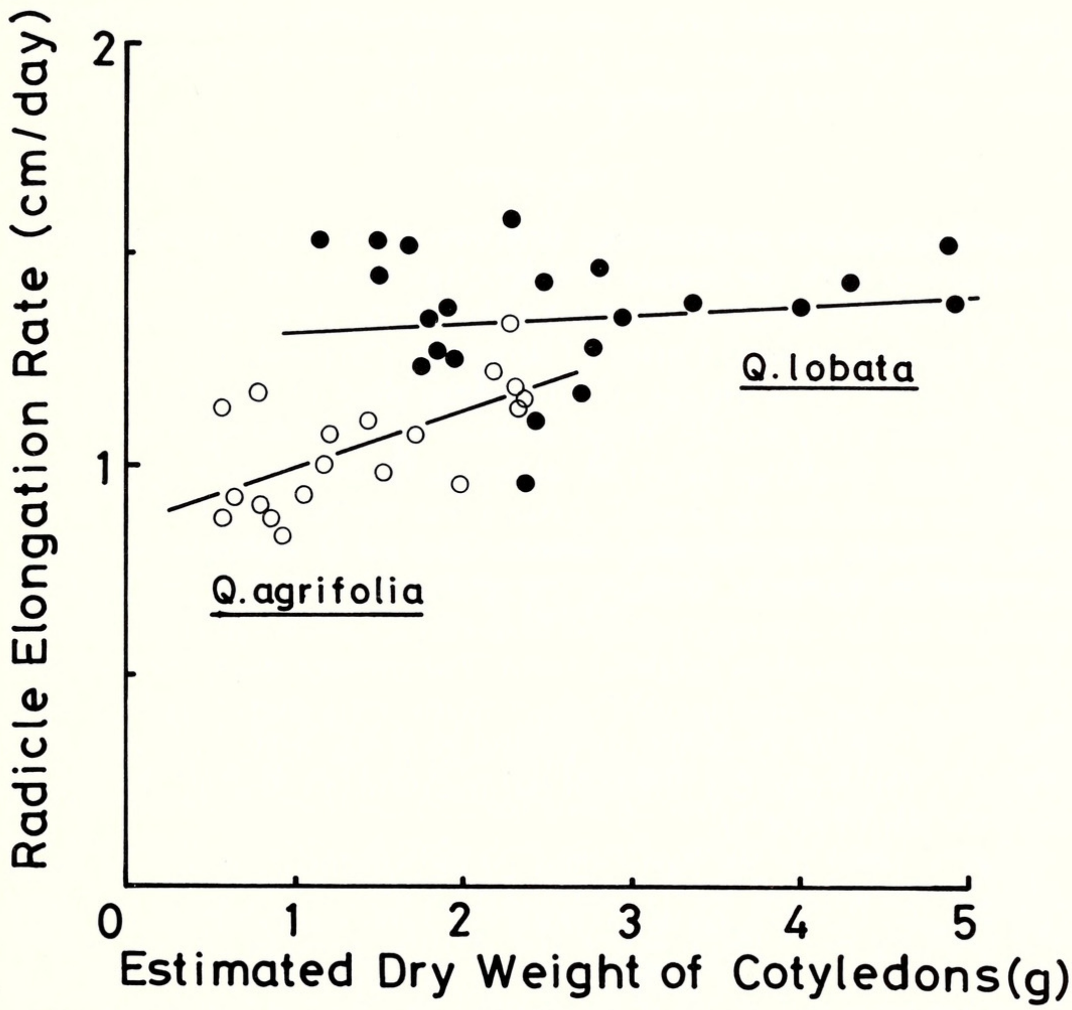


FIG. 1. Correlation between elongation rates of main roots and estimated dry weight of cotyledons of *Q. agrifolia* (○) and *Q. lobata* (●).

TABLE 3. MEAN MAXIMUM AND MINIMUM AIR TEMPERATURES AND THE AMOUNT OF PRECIPITATION RECORDED IN THE UNIVERSITY OF CALIFORNIA BOTANICAL GARDEN IN BERKELEY.

| 1981–1982 | Oct | Nov | Dec | Jan | Feb | Mar |
|---|---|---|---|---|---|---|
| Mean maximum (°C) | 21.2 | 18.3 | 15.6 | 12.8 | 17.7 | 15.6 |
| Mean minimum (°C) | 7.3 | 8.1 | 6.0 | 2.0 | 5.2 | 5.1 |
| Precipitation (cm) | 9.3 | 20.3 | 12.1 | 28.3 | 13.8 | 26.1 |

*Germination and root growth under outdoor conditions.* Weather records during the observation period are shown in Table 3. Soil temperatures recorded weekly for the experimental site were 5.1°C lower (average maximum), and 4.2°C higher (average minimum) than the air temperatures.

*Quercus douglasii* germinated from late October to early November, promptly after planting, although germination of *Q. agrifolia* did not occur until mid-November to mid-December. Acorns of *Q. lobata* showed a large tree to tree variation for germination time (Fig. 2); these results were consistent with those of Griffin (1971). By March, *Q. douglasii* and *Q. lobata* had produced significantly longer main roots than had *Q. agrifolia* (Fig. 3).

## DISCUSSION

Seedling growth morphology demonstrated in the present study is consistent with the results of field observation by Griffin (1971). He investigated seedling establishment of the three species at Hastings Reservation near Carmel, California. On grass-covered south-facing slopes, all seedlings of all species died in the first growing season after a dry winter. When grasses were removed, most of the *Q. douglasii* seedlings survived, although *Q. lobata* and *Q. agrifolia* seedlings were less successful. After a wet winter, most of *Q. douglasii,* a smaller number of *Q. lobata,* and no *Q. agrifolia* seedlings survived the summer drought. He demonstrated that less precipitation in addition to competition with annual grasses greatly reduced the successful seedling establishment. The present study showed that *Q. douglasii* had significantly longer main roots than either *Q. agrifolia* or *Q. lobata* when shoots started growing, with 2 cm epicotyls (Table 1). Grown under different temperature conditions, the results were similar (Table 2).

Deep rooting in the early stage of development seems to be of primary importance for *Q. douglasii* to survive in xeric habitats. The seedling roots grow below the rooting zone of annual grasses before soil moisture is depleted by evapotranspiration. In the field condition, earlier germination of *Q. douglasii* than *Q. agrifolia* (Fig. 2) assured the production of longer roots by spring of the former

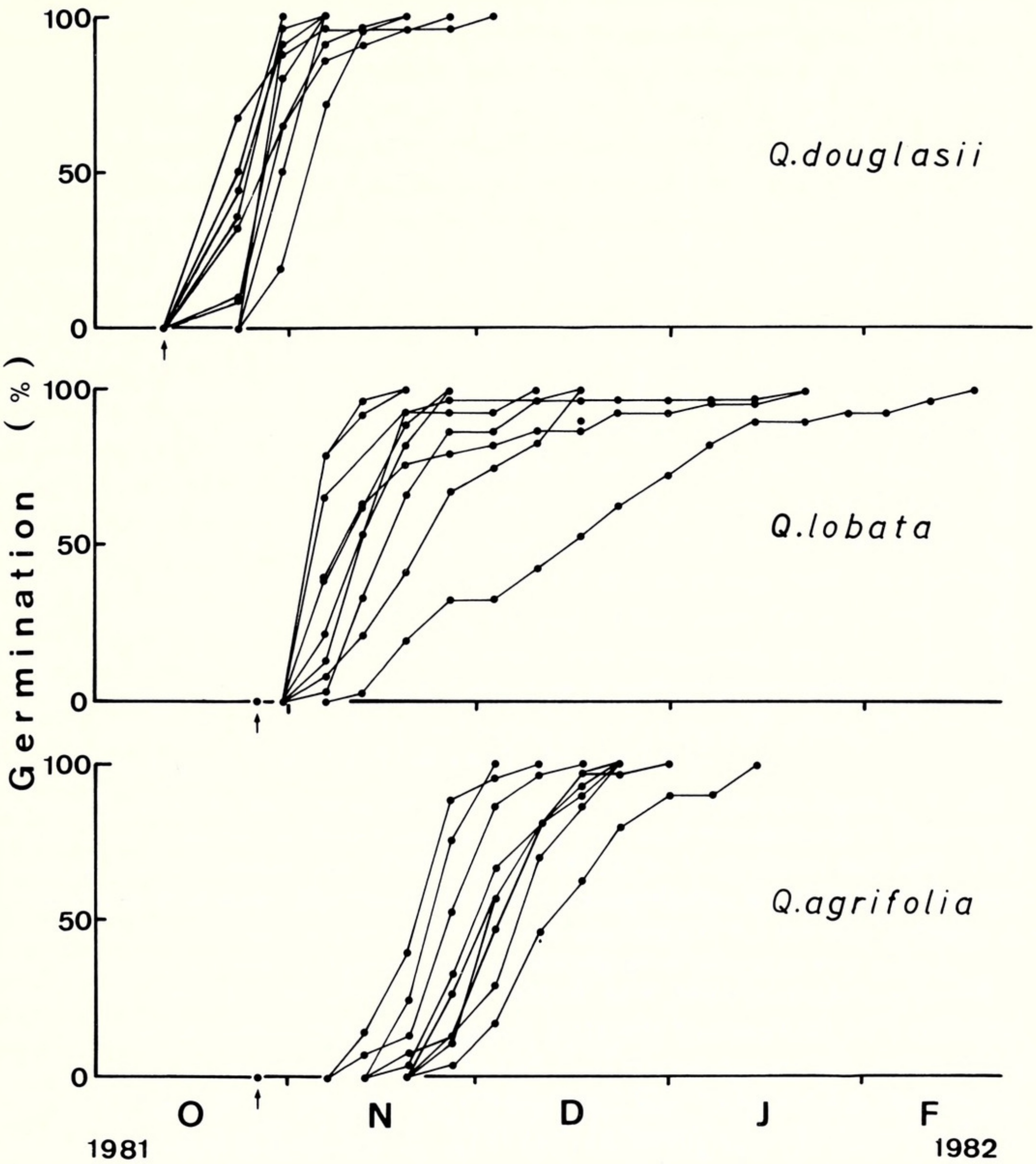


FIG. 2. Germination of oaks under outdoor conditions. Each line shows a time course of germination recorded on thirty acorns collected from each of ten seed source trees. Arrows indicate the time of acorn planting.

(Fig. 3). The long roots of *Q. douglasii* might be attributed in part to their greater growth at low temperature during winter. In fact, low temperature itself suppressed root growth in length and weight, but the start of shoot growth was greatly delayed under low temperature. As a result, longer and heavier roots had been produced, when compared at the same developmental stage of epicotyls (Table 2). *Quercus agrifolia* also developed longer and heavier roots in the low temperature greenhouse than it did in the high temperature one (Table 2). The delay in germination, however, may reduce the benefits from cold soils under field conditions.

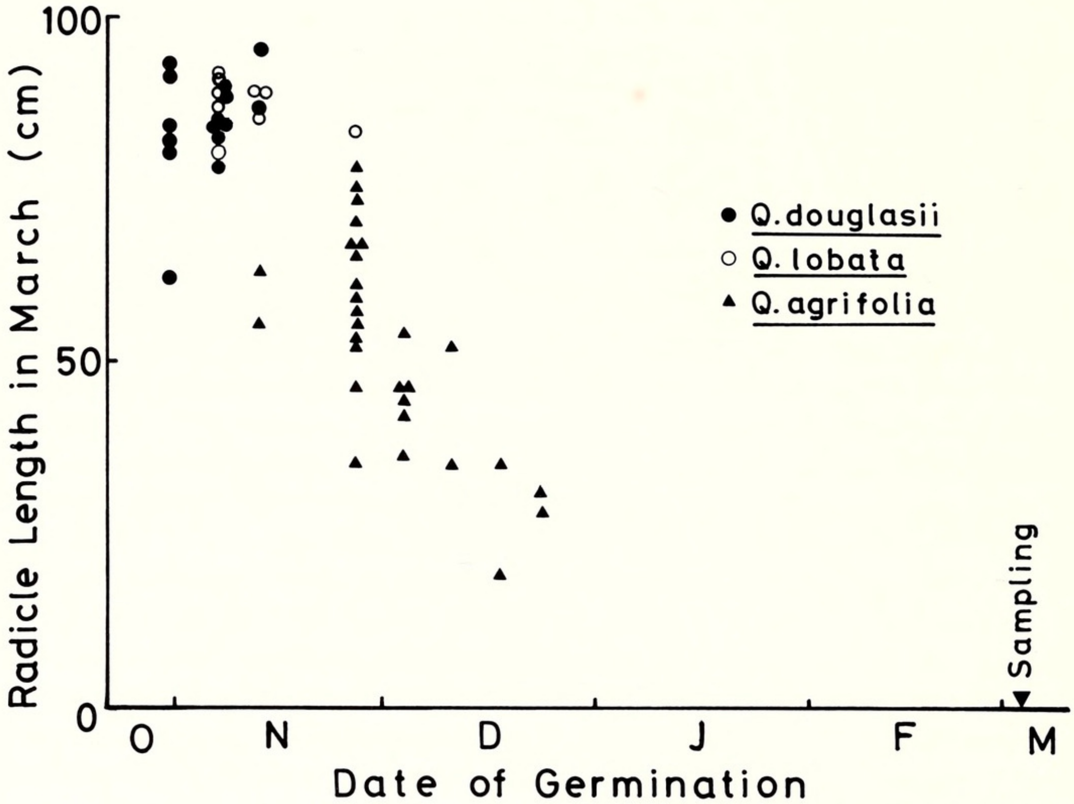


FIG. 3. Length of main roots in March of outdoor-grown oak seedlings. Seedlings germinated at the indicated date were grown outdoors until the sampling on 3 March 1982. The root length of *Q. douglasii* and *Q. lobata* was underestimated, because most of the roots had grown through the bottom of tubes, 90 cm tall, when sampled.

Root elongation rate was found to be different among the three species. The increase of the root elongation rate corresponded to the increase of the mean acorn size. Small elongation rate of *Q. agrifolia* might be responsible for its short root length in spring (Fig. 3), together with its late germination (Fig. 2). Intraspecifically, the root elongation rate of small-seeded *Q. agrifolia* correlated positively with its estimated dry weight of cotyledons; however, that of large-seeded *Q. lobata* did not (Fig. 1). Whalley et al. (1966) also showed that the rate of seedling height growth correlated with the seed size in species with small seeds, but not in a species with large seeds. There seems to be a saturation point in root elongation rate, which would be accelerated by the increase of the seed weight.

Balance between water absorption by roots and transpiration from leaves determines water economy of plants. Small leaf area/root weight ratio, therefore, can be regarded as a morphological adaptation developed by xerophytes and large leaf area/root weight ratio for that by mesophytes. Long radicles and a small leaf area/root weight ratio of fully developed *Q. douglasii* seedlings help explain its distribution in the most xeric environment. In contrast, short roots and the largest leaf area/root weight ratio of *Q. agrifolia* seedlings might restrict its distribution in the mesic sites. Cooper (1926) found that *Q. lobata* grew on alluvial terraces with deeper water tables than those supporting *Q. agrifolia.* Longer roots and smaller leaf area/root weight ratio of *Q. lobata* than *Q. agrifolia* at the seedling stage might be important for survival in such an environment. *Quercus lobata,* however, had a larger leaf area/root weight ratio than did *Q. douglasii.* This characteristic might prevent *Q. lobata* from establishment in the xeric habitat occupied by *Q. douglasii.*

Griffin (1971) observed a high percentage of *Q. douglasii* with desiccated stems at the end of the first growing season. Many of these plants resprouted the following spring. *Quercus douglasii* allocated only 27% of its dry weight to leaves and stems, which was smaller than either *Q. lobata,* 33%, or *Q. agrifolia,* 56% (Table 1). By maintaining a larger percentage of material below ground, *Q. douglasii* minimizes the desiccation of the material and can utilize it for resprouting the following spring. This may be a further adaptation of *Q. douglasii* to its xeric environment. In contrast, *Q. agrifolia* apparently does not occur in similar desiccating environments because of the large percentage of material allocated to its evergreen leaves.

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