Germination Characteristics of Engelmann Oak, and Coast Live Oak from the Santa Rosa Plateau, Riverside County, California[1]

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Abstract: Over 2,000 acorns of *Quercus agrifolia* (coast live oak) and over 500 acorns of *Q. engelmannii* (Engelmann oak) were collected in the Jim Knight pasture area of the Santa Rosa Plateau. These were used to test for temperature and moisture conditions on germination of viable acorns in the laboratory under controlled environmental conditions. At 24°C *Q. engelmannii* had almost 90 percent germination after 6 days, while *Q. agrifolia* had about 20 percent (96 percent after 20 days). At 14°C completeness and speed of germination of *Q. engelmannii* was reduced to about 80 percent after 36 days, while *Q. agrifolia* had over 90 percent at 30 days. At 4°C *Q. engelmannii* had about 60 percent germination at 72 days, while *Q. agrifolia* had over 90 percent at 72 days. At varying degrees of moisture stress from field capacity to -100 bar atmosphere (at 20°C) *Q. engelmannii* had at least 70 percent germination of viable acorns after 36 days, while *Q. agrifolia* did not germinate in a-100 bar atmosphere, reached complete germination in a -10 bar PEG-vermiculite mixture after 60 days and took 132 days for complete germination under 100 percent relative humidity conditions. Drying (20°C, 45 percent RH) acorns for up to 3 weeks with 24 percent moisture loss had no effect on *Q. engelmannii* but *Q. agrifolia* lost 42,58 and 75 percent of their initial moisture after 1, 2 and 3 weeks drying and all the seeds were dead after 2 weeks. The "self-rooting" of *Q. engelmannii is* also discussed. These germination characteristics are related to the distribution of these two oak species in the field.

The two major oak species in southern oak woodlands are Engelmann oak (*Quercus engelmannii* Greene) and coast live oak (*Q. agrifolia* Née), the former often growing in open savannas called the "Engelmann oak phase" and the latter growing in denser more widespread woodlands termed the "coast live oak phase" (Griffin 1977). Some of the factors influencing the establishment and distribution of these two species on the Santa Rosa plateau in the Santa Ana Mountains were the greater fire resistance of Engelmann oak seedlings compared to coast live oak (Snow 1980), the inhibition of seedling establishment by cattle in open areas and the concentration of coast live oak around rock outcrops (especially in cracks and the north side) due to ground squirrel transport and the apparently higher moisture requirements for germination (Snow 1973).

The only study as extensive as this one on oak germination was Korstian's (1927) study on germination and early survival in certain eastern white oaks (subgenus *Lepidobalanus*) and black or red oaks (subgenus *Erythobalanus*). Although *Q. engelmannii* is in the white oak group and *Q. agrifolia* in the black oak group, only general comparisons can be made due to the markedly different conditions under which these western "Mediterranean" climatic type oaks have developed. Also *Q. agrifolia* acorns mature in one season and have no dormancy (U.S. Forest Service, Woody-Plant Seed Manual, 1948) which are characteristics typical of white oaks rather than black oaks. In spite of these differences these two western white and black oaks show many of the same differences Korstian found in the eastern white and black oaks.

This paper focuses on the germination response to temperature and moisture conditions of these two southern oak woodland species. The temperature and moisture conditions used are assumed to cover the full range for these conditions found in the field.

METHODS

Over 2,000 acorns of *Q. agrifolia* and over 500 acorns of *Q. engelmannii* were collected from the ground under trees in the Jim Knight pasture area of the Santa Rosa plateau and air shipped to Corvallis, Oregon. After arrival the acorns were stored at 4°C and 95 ± 5 percent RH for three weeks before germination tests were begun.

For temperature germination tests wooden flats filled with wet vermiculite were maintained at 4, 14 and 24 ± 1°C in constant temperature chambers. Sixty *Q. agrifolia* and 50 *Q engelmannii* were randomly assigned to each of the temperature chambers. Acorns were planted at least 2 cm deep and maintained at field capacity with distilled water. Germination (2 mm of radicle extending beyond the pericarp) was checked one and two days after planting and then every two days for 90 days or until germination was complete. All ungerminated acorns were tested for viability by removing the pericarp and planting the seed in wet vermiculite at 20°C for up to 30 days. A germination value which varies directly and proportionally with the speed of germination, total germination or both (Czabator 1962) was calculated for each germination curve.

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In preliminary experiments, *Q. agrifolia* showed little or no germination under limited moisture conditions while *Q. engelmannii* did not appear to be affected by these conditions. In order to determine more precisely the germination-moisture response, the following moisture conditions for germination at 20 ± 1 °C were used: (I) vermiculite maintained at field capacity with distilled water; (II) 100 percent RH atmosphere; (III) vermiculite saturated with a -10 bar polyethylene glycol solution; (IV) -100 bar atmosphere. For moisture conditions I and III, the acorns were packed in vermiculite inside a vertically placed glass tube (7 cm diameter and 60 cm long) with vented rubber stoppers top and bottom. For moisture condition II an approximately 100 percent RH atmosphere was obtained by placing vermiculite saturated in distilled water over the bottom of a flat, round, clear plastic, six-liter germination chamber sealed with stopcock grease. Acorns were supported above the bottom in open glass petri dishes. For treatment III a -10 bar osmotic potential polyethylene glycol solution was added daily to the vermiculite to maintain this osmotic potential. The solution was made fresh each week and the vermiculite changed to avoid possible inhibitory effects reported for stored solutions (Greenway and others 1968). For moisture condition IV, a -100 bar atmosphere was maintained by using one liter of a saturated sodium sulfate solution (O'Brien, 1948) in a two-liter glass dish, 10 by 20 by 10 cm. Acorns were supported above the saturated salt solution in open glass petri dishes.

The use of the -10 bar polyethylene glycol osmotic solution with vermiculite may not exactly simulate the same matric potential in soil, even though identical in free energy status (Bonner and Farmer 1966). But the work of Parmar and Moore (1968) suggested that polyethylene glycol may simulate the soil rather closely in terms of the effects of water stress on total germination. Kaufmann and Ross (1970), in comparing soil and solute systems, found that for studying total germination polyethylene glycol may be satisfactory but when germination rate is important the solute system does not adequately represent the more normal soil conditions because germination in the soil system is much slower.

Thirty acorns of each species were assigned to each of the four moisture conditions. All the acorns were surface sterilized by being placed in a 2.6 percent solution of sodium hypochlorite for one minute. Germination was checked every two days for 90 days or until germination was complete, except for *Q. agrifolia* in the 100 percent RH test which continued for 132 days until germination was complete. All ungerminated acorns were tested for viability as described before.

The percent moisture on a dry weight basis of subsamples from stored and germinated acorns of the temperature and moisture tests were determined. Acorns were weighed to the nearest 0.01 g with and without the pericarp (shell), then oven dried at 95°C for 48 hours and weighed again

The relationship between germination, water uptake and moisture content was determined more specifically using 20 *Q. agrifolia* and 10 *Q. engelmannii* randomly selected acorns, half of which had their pericarps removed. All were planted together in a single vermiculite flat as described before and maintained at field capacity for 30 days. At 12, 24 and subsequently every 24 hours, each seed and acorn was weighed to the nearest 0.01 g. After germination dry weights were obtained as described before and the percent moisture determined for the various time intervals.

The effects of drying acorns for different lengths of time on their subsequent germination were also determined for a few sound, unmarred acorns selected from a single tree of each species. Fifteen *Q. agrifolia* acorns were divided into three groups of equal size and weight to be dried at 20 ± 1 ºC and 45 ±5 percent RH for one, two and three weeks. Ten *Q. engelmannii* acorns were divided into two groups of equal size and weight to be dried under the same conditions for one and three weeks. Each group was weighed as a unit every 24 hours. Following the drying period for each group, they were planted in vermiculite as described before and maintained at field capacity for 30 days to test for germination. After germination or 30 days, the dry weights were obtained as described before and the percent moisture determined for the various time intervals.

After five months under the storage conditions described before, 20 *Q. agrifolia* were tested for viability. Since this test indicated 100 percent viability, 50 acorns were randomly selected and divided into two groups to determine the percent moisture which would kill approximately 50 percent of the seeds. This was done by drying one group for three and one-half days and the other for seven days at 20 ± 1 °C and 50 ± 5 percent RH and then testing them for viability. A subsample of five acorns from each group was individually weighed and dry weights determined after each drying period.

The phenology of shoot development from mid-germination until the first leaves were expanded at 14 and 24°C was determined for both species by observations recorded for the acorns in the 14 and 24°C germination test. A 14-hour photo period at 2000 foot candles was used at each temperature.

An index of the self-rooting ability of each species was obtained. The distance to the base of the shoot from the radicle emergence point on the acorn after the leaves expanded was measured for seedlings grown at 14 and 24°C from acorns used in germination tests at these temperatures. Twenty acorns of *Q. agrifolia* and 15 of *Q. engelmannii* at each temperature were measured.

RESULTS

The results of the germination of the two species at 4, 14, and 24°C in vermiculite at field capacity are presented in figure 1. *Quercus engelmannii* had a germination value (26.8) about five times larger than *Q. agrifolia* (5.4) at 24°C. At 14°C their germination values were about the same (3.8 and 4.4 in the same order). At 4°C *Q. engelmannii* (0.9) was almost half that of *Q. agrifolia* (1.6). *Quercus engelmannii* showed a marked reduction in both speed and completeness of germination with decreasing temperatures while *Q. agrifolia* showed only a reduc-

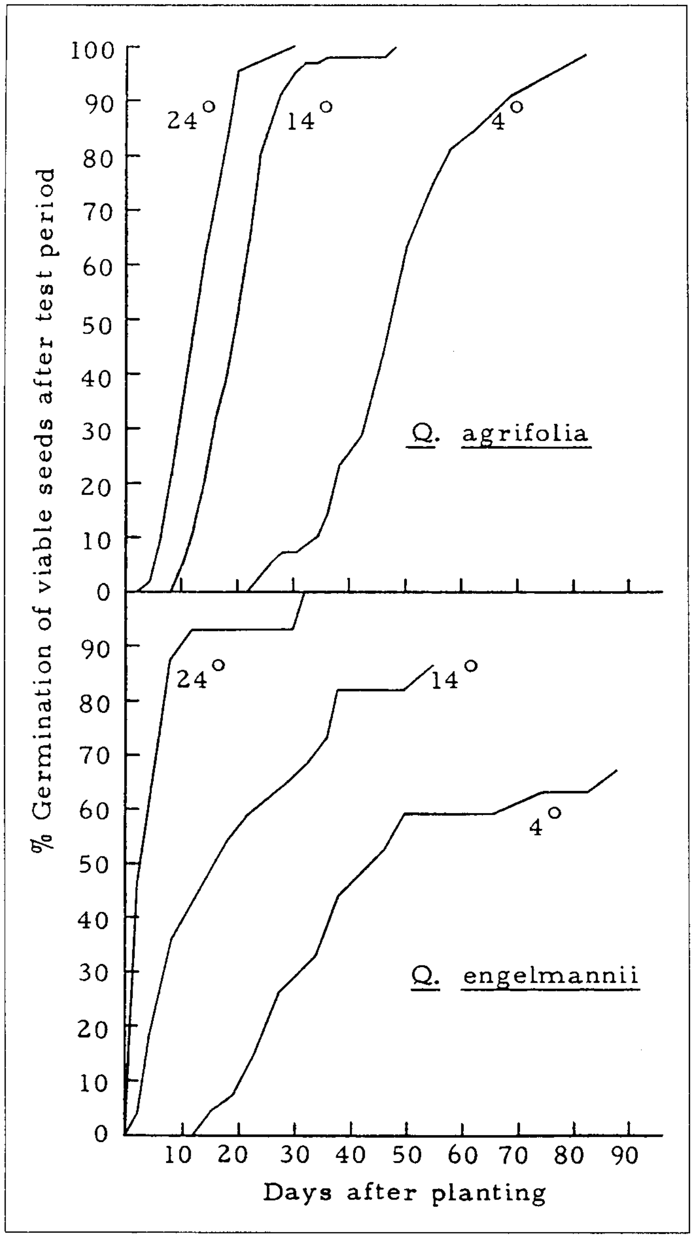

Figure 1—Germination of Q. *agrifolia* and *Q. engelmannii* at 4, 14, and 24°C. Sixty acorns of *Q. agrifolia* were planted for each temperature and 50 of *Q. engelmannii for* each temperature.

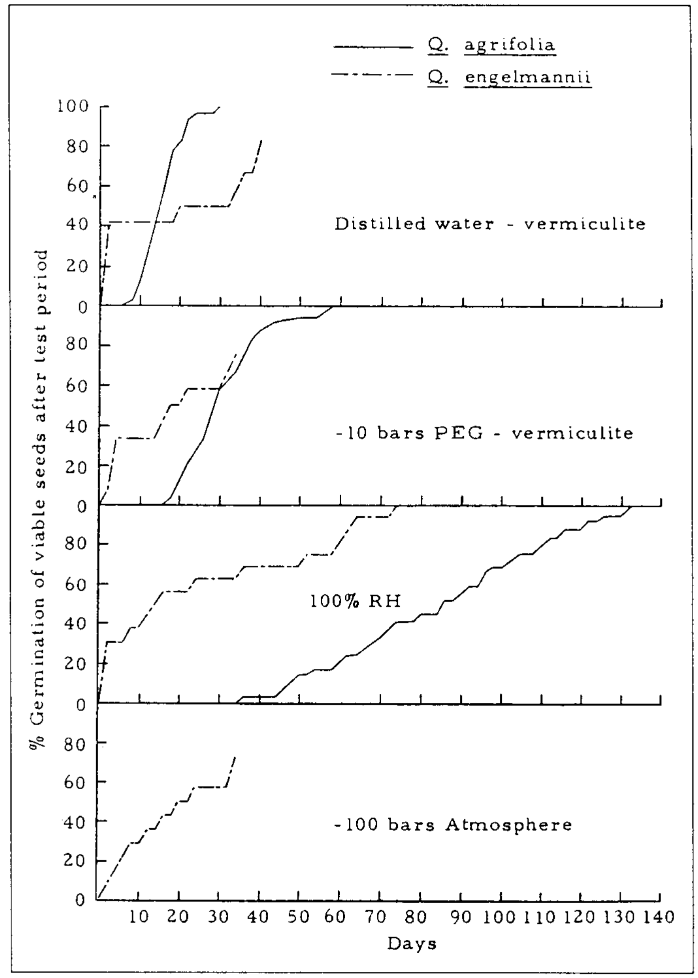

Figure 2—Germination of *Q. agrifolia* and *Q. engelmannii* under increasing degrees of moisture stress at 20°C. Thirty acorns of each species were used in each of the four moisture levels.

tion in its speed of germination.

The results of the germination of the two species under increasing degrees of moisture stress are presented in figure 2. *Quercus engelmannii* showed little influence from any of the moisture treatments with its germination values ranging between 1.9 and 2.4. After 36 days the percent germination for *Q. engelmannii* ranged between 67 and 75 percent for all four treatments. *Quercus agrifolia* showed a marked depression in germination by the increasing moisture stress. Germination values for the vermiculite at field capacity, the -10 bars polyethylene glycol (PEG) solution and vermiculite, the 100 percent RH atmosphere and the -100 bars atmosphere respectively are: 4.8, 2.5, 0.4 and 0.0. After 36 days the percent germination for *Q. agrifolia* in the same series was 100, 76, 3 and 0 percent.

The moisture content (percent of dry weight) of the seeds of the two oak species from the field and various germination conditions is summarized in table 1. The percent moisture content of *Q. engelmannii* seeds field collected and stored for nine days was 10 to 15 percent higher than *Q. agrifolia.* The range of percent moisture content for germinated seed under various conditions was very broad for *Q. engelmannii* (54-120 percent moisture) but much narrower for *Q. agrifolia* (57-78 percent moisture). Another difference between the two species indicated in the table is the ability of *Q. engelmannii* to germinate in the -100 bars atmosphere at the same moisture content as the field collected and stored seeds and lack of germination in *Q. agrifolia* under these same conditions. Apparently *Q. engelmannii* can germinate without any additional water uptake from the field and storage conditions while *Q. agrifolia* requires additional uptake for germination.

Drying for one and three weeks had no effect on subsequent germination in *Q. engelmannii.* After losing 15 percent of their initial moisture content after one week and 24 percent after three weeks of drying, all the acorns germinated from both periods.

Table 1— ***The percent moisture (dry weight) of* Q. agrifolia *and* Q. engelmannii *seeds from the field and various germination conditions.***

Condition	*Q. agrifolia*[a]		*Q. engelmannii*[b]	
	No. sampled	Pct moisture and range	No. sampled	Pct moisture and range
Field collected and stored for 9 days at 4°C and 95 pct RH	10	51(40-58)	10	61 (55-66)
Germinated at mean temperature of 14 °C	30	67(60-75)	10	79(63-120)
Germinated in wet vermiculite at 20°C	28	69(61-77)	7	77(64-118)
Germinated at 100 pct RH atmosphere at 20°C	28	65(57-71)	5	68(56-78)
Germinated in vermiculite at -10 bars and 20°C	18	68(62-78)	0	
Germinated in -100 bars atmosphere at 20°C	5[c]	51(47-57)	5	58(54-62)

[a]Acorns are 2 pct less than the values for seeds.
[b]Acoms are about 10 pct less than the values for seeds.
[c]None of these germinated.

The *Q. agrifolia* lost 42, 58 and 75 percent of their initial moisture content after the one, two and three week drying periods. After one week of drying it had 40 percent germination but after two and three weeks of drying all the seeds were dead.

Based on the above experiment and the experiment to determine the percent moisture content which would kill 50 percent of the *Q. agrifolia* seeds, it was found that a moisture content of seeds between 26 and 34 percent (for whole acorns between 25 and 31 percent) or about 30 percent less than the field and storage conditions would kill about 50 percent of the seeds. Any acorns with a moisture content of 20 percent or less were dead. This point was not determined for *Q. engelmannii* due to lack of acorns.

As expected, both species took longer to develop shoots and leaves at the cooler temperature. *Quercus engelmannii* required almost twice as much time as *Q. agrifolia.* At 24°C Q. *agrifolia* took 35 days from mid germination until the first leaves were expanded while *Q. engelmannii* took 56 days. At 14°C *Q. agrifolia* took 59 days and *Q. engelmannii* took 103 days.

An illustration of the more rapid shoot development in *Q. agrifolia* and the self-rooting mechanism of *Q. engelmannii* is seen in figure 3. The *Q. agrifolia* on the left had been growing for 13 days after germination and had a shoot more than twice as long (1.5 cm) as the *Q. engelmannii* on the right which has been growing for 16 days (its shoot is 0.7 cm). Also note that the petioles of the cotyledons of the *Q. engelmannii* have elongated downward so that the shoot base is about 2.5 cm below the radicle emergence point on the acorn. There is no downward elongation of the petioles of the cotyledons in the *Q. agrifolia* so that its shoot arises from the same point at which the radicle emerged from the acorn. The distance from the shoot base to the radicle emergence point on the acorn for Q. *engelmannii* showed no significant difference between 14 and 24°C. The mean distance for 30 acorns measured was 1.4 cm and ranged from 0.5 to 2.5 cm.

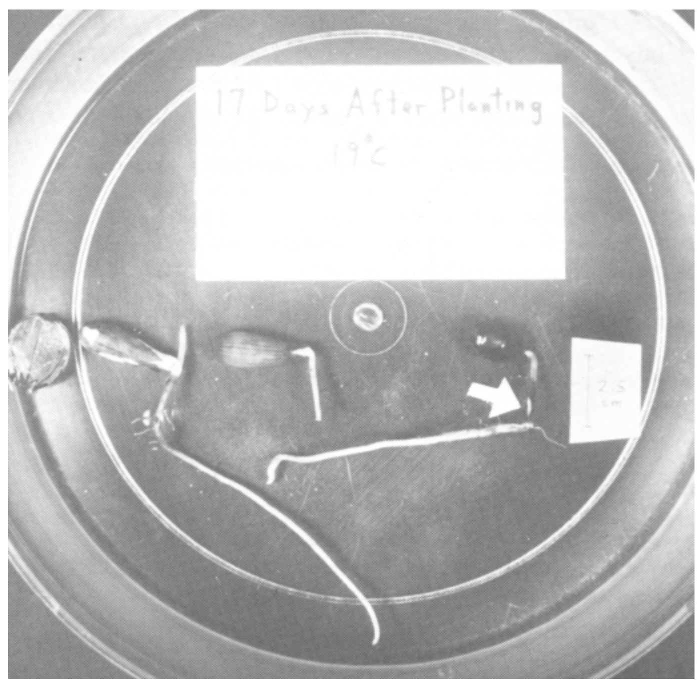

Figure 3—An illustration showing the degree of development and shoot origin in the two oak species 17 days after planting at 19°C. From left to right are the following: a *Q. agrifolia* 13 days after germination with its pericarp removed, an intact *Q. agrifolia* three days after germination, and an intact *Q. engelmannii* 16 days after germination. The arrow points to the cotyledonary node. The cotyledonary node is at the tip of the acorn in *Q. agrifolia.*

DISCUSSION

These two western white and black oaks show many of the same differences Korstian (1927) found in the eastern white and black oaks. For example, the white oaks have a higher initial moisture content than the black oaks and their acorns often germinate as soon as they are shed while the black oaks germinate later. Thirty percent of the field collected *Q. engelmannii* collected for this study had already germinated while less than 5 percent of the *Q. agrifolia* had done so and I have found *Q. engelmannii* cached in a hollow tree trunk germinating in the fall before any rains had come.

The general characteristics of the germination curves in figure 1 at 24°C for *Q. engelmannii* and *Q. agrifolia* are very similar to the warmer temperatures tested for the eastern white and black oaks (Korstian, 1927). Both *Q. engelmannii* and the eastern white oaks show very rapid initial germination rates while *Q. agrifolia* and the eastern black oaks show an initial delay in germination and sigmoid germination curves. This delay in *Q. agrifolia is* mainly due to the time required for water uptake in order to bring the seed to the moisture content required for germination.

At 4°C *Q. engelmannii* shows a marked depression in speed and completeness of germination while *Q. agrifolia* mainly shows a greater delay in the onset of germination probably mainly due to slower water uptake at this low temperature. Field temperatures may get this low, especially overnight in winter months. The eastern white and black oaks showed little or no germination at 4°C (Korstian, 1927).

Matsuda and McBride (1987) planted three species of California white oaks and three species of California black oaks, including *Q. agrifolia,* at three elevations in the Sierra Nevada and the Santa Lucia ranges. Two of the white oaks, including *Q. douglasii* germinated soon after planting at all elevations, while the black oaks germinated 1 to 3 months later. *Q. agrifolia* germinated up to 2 months later than the faster germinating white oaks.

The lack of or poor germination of *Q. agrifolia* under low moisture conditions and the insensitivity of *Q. engelmannii* to these conditions again reflects on their initial moisture content. *Q. engelmannii* requires little or no increase in moisture content and begins germination within the first day or two, whereas *Q. agrifolia* requires an increase in moisture content to effect germination by exposure to moist conditions for from one to five weeks (table 1 and figure 2). Korstian (1927) found the eastern white oaks tested had better germination in drier soil than the black oaks he tested but both had poor germination in soil a little drier than the wilting coefficient. Bonner (1968) reported little germination for stresses greater than 10 atm using a sucrose osmotic solution for the eastern black oak, *Q. palustris* Muenchh.

The eastern white oak whole acorns in Korstian's (1927) study showed more rapid and greater water uptake than the black oak acorns which also appears true for the two western species studied here (figure 4). Both species in this study showed a more rapid water uptake with the pericarps removed which was also true for four eastern black oak species studied by Bonner (1968).

Since *Q. agrifolia* has a tougher, thicker pericarp enclosing the seed much more tightly than *Q. engelmannii,* the additional water uptake by *Q. agrifolia* might be required in order to crack the pericarp and allow the radicle to grow out. The results of the relationship between water uptake, moisture content and germi-

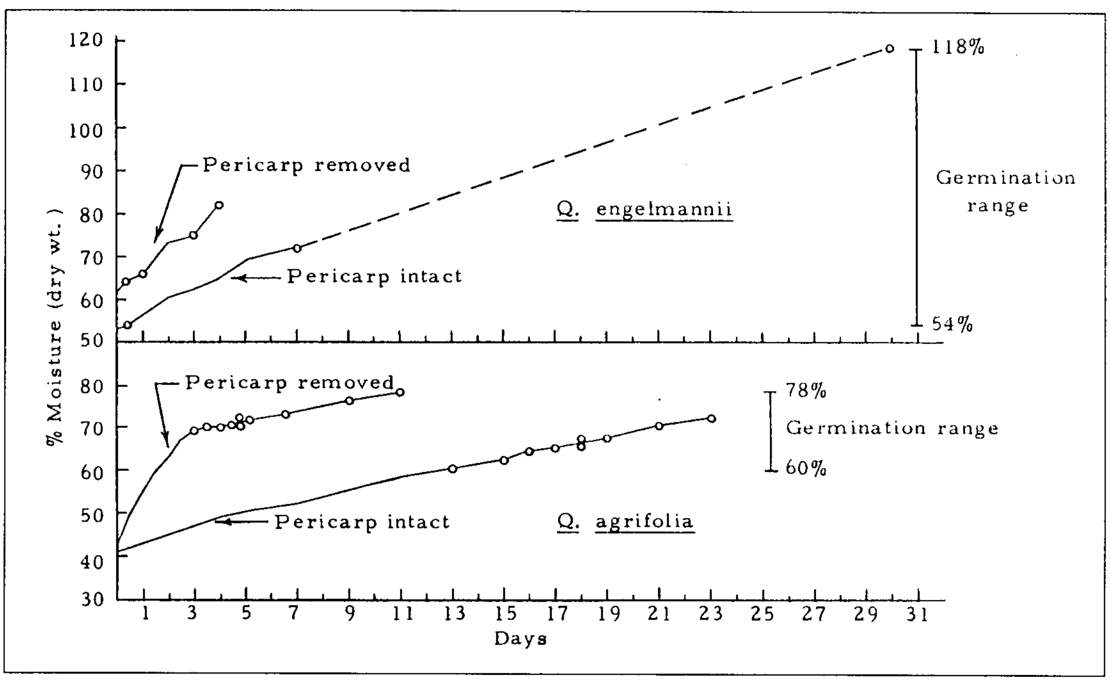

Figure 4—Water uptake and germination of *Q. agrifolia* and *Q. engelmannii* at 20°C. Circles indicate germination of individual acorns.

nation of seeds with and without the pericarp presented in figure 3 do not support that view. Even with the pericarp removed, *Q. agrifolia* seeds required a substantial increase in moisture content (from 45 percent to almost 70 percent moisture) before germination began (figure 3). Again it can be seen that *Q. engelmannii* can begin germination with little or no increase in moisture content. The typical delay in the beginning of germination in *Q. agrifolia* seen in figures 1, 2, 3 and 4 is at least in part due to the reduced rate of water uptake (figure 3) when the pericarp surrounds the seed in the typical acorn.

Krajicek (1968) found that *Q. falcata* var. *pagodaefolia* Ell. (an eastern black oak) lost moisture and viability very rapidly on air drying at room temperature. *Q. agrifolia* did not lose moisture or viability as fast as this species but it did lose moisture more rapidly than *Q. engelmannii.* Griffin (1971) air-dried in an unheated room acorns of two species of central California white oaks for 60 days with no gross effect on viability. Some of the acorns germinated during this storage.

The 50 percent loss of viability on drying for *Q. agrifolia* falls in about the same range as for the eastern black oaks in Korstian's (1927) study (moisture content between 21 and 33 percent). The eastern white oaks' 50 percent loss of viability occurred between a moisture content of 32 and 50 percent which may be similar to *Q. engelmannii* but none of them in this study got very far into this critical range.

Matsuda and McBride (1986) found that *Q. agrifolia* began to develop shoots significantly sooner after germination than the central California white oak, *Q. douglasii,* grown under the same conditions. Similar results were found in this study with much longer delays in shoot development in *Q. engelmannii* as compared to *Q. agrifolia.* This may allow *Q. engelmannii* more time for root development before moisture stresses are imposed by transpiring leaf surfaces. It would seem that this mechanism might have an adaptive advantage in establishment in more open exposed habitats where *Q. engelmannii* is normally found.

The self-rooting mechanism seen in *Q. engelmannii* in the elongation of the cotyledonary petioles carrying the radicle and plumule out of the acorn and down into the soil has also been described for the genus *Marah* (Cucurbitaceae) especially *Marah oreganus* (Torrey and Gray) Howell (Schlising 1969). Engelmann (1880) and Coker (1912) have noted this phenomenon in other oaks, especially white oaks. This pattern of germination and seedling establishment for these and a few other dicotyledonous plants occurs mainly in areas of hot and dry habitat that are generally referred to as having Mediterranean climate (Schlising 1969).

This study has shown that *Q. engelmannii* may be better adapted for establishment in more open exposed habitats than *Q. agrifolia* because it is less sensitive to moisture loss on air drying, will germinate with little or no additional water uptake, is self-rooting and has delayed shoot development. *Quercus agrifolia* may need more protected, moist habitats for initial establishment like the north side of rocks or in cracks in rock outcrops (where it is usually found on the Santa Rosa plateau) because of its greater sensitivity to moisture loss on air drying, its requirement for water uptake for from one to five weeks to effect germination (depending on temperature and moisture conditions), its lack of a self-rooting mechanism and its more rapid shoot development after germination.

REFERENCES

Bonner, F. T. 1968. Water uptake and germination of red oak acorns. Botanical Gazette 129:83-85.

Bonner, F. T.; Farmer, Jr., R. E. 1966. Germination of sweet gum in response to temperature, moisture stress and length of stratification. Forest Science 12:40-43.

Coker, W. C. 1912. The seedlings of the live oak and white oak. Journal of the Elisha Mitchell Scientific Society 28:34-41.

Czabator, F. J. 1962. Germination value: an index combining speed and completeness of pine seed germination. Forest Science 8:386-396.

Engelmann, G. 1880. The acorns and their germination. Transactions of the Academy of Science of St. Louis 4:190-192.

Greenway, H.; Hiller, R. G.; Flowers, T. 1968. Respiratory inhibition in Chlorella produced by "purified" polyethylene glycol 1540. Science 159:984-985.

Griffin, J. R. 1971. Oak regeneration in the upper Carmel Valley, California. Ecology 52:862-868.

Griffin, J. R. 1977. Oak woodland. In: Barbour, M. G. and J. Major, eds. Terrestrial vegetation of California. New York, Wiley Interscience; 338-415.

Kaufmann, M. R.; Ross, K. J. 1970. Water potential, temperature, and kinetin effects on seed germination in soil and solute systems. American Journal of Botany 57:413-419.

Korstian, C. F. 1927. Factors controlling germination and early survival in oaks. Yale University School of Forestry Bulletin 19. 115 p.

Krajicek, J. E. 1968. Acorn moisture content critical for cherrybark oak germination. North Central Forest Experiment Station, Forest Service, U.S. Department of Agriculture, Research note NC-63. 2 p.

Matsuda, K.; McBride, J. R. 1986. Difference in seedling growth morphology as a factor in the distribution of three oaks in central California. Madrono 33:207-216.

Matsuda, K.; McBride, J. R. 1987. Germination and shoot development of seven California oaks planted at different elevations. In: Plumb, T. R. and N. H. Pillsbury, Tech. Coord. Proceedings of the symposium on multiple-use management of California's hardwood resources, Nov. 12-14, 1986, San Luis Obispo, CA, Gen. Tech. Rep. PSW-100; Berkeley, CA; Pacific Southwest Forest and Range Experiment Station; 79-85.

O'Brien, F. E. M. 1948. The control of humidity by saturated salt solutions. Journal of Scientific Instrumentation 25:73-76.

Parmer, M. T.; Moore, R. P. 1968. Carbowax 6000, mannitol, and sodium chloride for stimulating drought conditions in germination studies of corn (*Zea mays* L.) of strong and weak vigor. Agronomy Journal 60:192-195.

Schlising, R. A. 1969. Seedling morphology in *Marah* (Cucurbitaceae) related to the California Mediterranean climate. American Journal of Botany 56:552-561.

Snow, G. E. 1973. Some factors controlling the establishment and distribution of *Quercus agrifolia* and *Quercus engelmannii* in certain southern California oak woodlands. Corvallis, OR, Oregon State University; Dissertation, 105 p.

Snow, G. E. 1980. The fire resistance of engelmann and coast live oak seedlings. In: Plumb, T. R., Tech. Coord. Proceedings of the symposium on the ecology management, and utilization of California oaks; June 26-28,1979, Claremont, CA. Gen. Tech. Rep. PSW-44. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 242 p.

U.S. Forest Service. 1948. Woody plant seed manual. U.S. Department of Agriculture, Misc. Publ. 654. 416 p.