THE POTENTIAL FOR A CALIFORNIA OAK WILT EPIDEMIC

by David N. Appel

Abstract. The relative disease susceptibilities of 14 *Quercus* species from Texas and California were tested in three inoculation studies with different isolates of the oak wilt pathogen, *Ceratocystis fagacearum*. Ten of the oaks were evergreen or semi-evergreen live oaks while the remaining four were deciduous species. The species represented 3 different *Quercus* sub-genera. All species were susceptible to the pathogen, but there was significant variability in disease response. In the first study, there was variability among different selections of live oak from Texas, and there were distinct differences in disease response among the California oaks in the other two experiments. In two of the studies, the most susceptible species was the exotic cork oak, *Q. suber*. *Q. kelloggii*, the only deciduous red oak inoculated, responded similarly to *Q. suber*, an evergreen white oak. The two evergreen red oaks, *Q. agrifolia* and *Q. wislizenii*, were the least susceptible in one of the studies while the two evergreen "intermediate" oaks, *Q. chrysolepis* and *Q. tomentella*, were the least susceptible in another. Significant differences in pathogenicity were observed between two Texas isolates of *C. fagacearum*. The implications of these results for the California oak woodlands is discussed.

The known host range of the oak wilt pathogen, *Ceratocystis fagacearum*, includes species of the genus Quercus and some related members of the family Fagaceae (5). There is, however, a wide range of susceptibility to *C. fagacearum* among species within the genus *Quercus*. The most obvious difference is in disease response between deciduous, red or black oaks (sub genus Erythrobalanus), and deciduous white oaks (sub genus Leucobalanus)(19). Red oaks are extremely susceptible to infection, often dying within weeks following initial appearance of symptoms (19). White oaks may survive infection by *C. fagacearum* indefinitely, losing portions of their crowns but eventually recovering. This contrast in host response has been consistently observed in every state reporting an outbreak of oak wilt. For example, of 365 infected red oaks examined in Missouri over a five year period, only three survived and those were infected for less than one year (13). The red oak species included black oak (*Q. velutina*), scarlet oak (*Q. coccinea*), blackjack oak (*Q. marilandica*), and northern red oak (*Q. rubra*). The mortality rate in 97 white oaks (*Q. alba* and *Q. stellata*) was lower. Only 18 of 97 white oaks died, and 54 of the diseased trees recovered during the five year period with no further symptom development (13). Similar differences in rates of disease progress have been recorded in Wisconsin for *Q. ellipsoidalis* (northern pin oak = red oak) when compared to *Q. macrocarpa* (bur oak = white oak) (19).

In recent years, observations of oak wilt in the live oak savannas and urban forests of central Texas have increased our understanding of the potential for damage by *C. fagacearum* on different *Quercus* species growing outside the known oak wilt range. The epidemic in Texas is the first record of oak wilt occurring in naturally growing, semi-evergreen live oaks (*Q. fusiformis* and *Q. virginiana*) (2,14). Live oaks are considered to be white oaks, but retain some anatomical characteristics of the red oak group. Typical red oaks in central Texas, such as Spanish oak (*Q. texana*) and blackjack oak also are affected by oak wilt. These deciduous red oaks respond the same as related species in other states, but the live oaks in Texas are atypical in their response to infection. Most live oaks die within 3 - 6 months following initial symptoms, but 10% - 20% may live indefinitely (1,4). This contrasts with the uniform, total susceptibility exhibited by red oaks. The response of post oak (*Q. stellata*) in Texas, a typical white oak, is similar to white oaks elsewhere; they rarely die of oak wilt infections.

Species differences in response to the oak wilt fungus have an important influence on an epidemic that goes beyond the rate of disease progress in individual trees. The oak wilt fungus must form

spore pads, called fungal mats, on red oaks in order for insects to acquire and transmit the pathogen over long distances to new trees (7). Fungal mats do not form on white oaks, nor have they been found on diseased live oaks in Texas. Fungal mats will form on infected Spanish oaks and blackjack oaks in Texas under proper environmental conditions, thus providing the opportunity for long distance spread by insect vectors. *Ceratocystis fagacearum*, like other vascular parasites, also is able to spread via functional root connections between diseased and healthy trees (15).

The live oaks are affected more seriously by oak wilt than any other *Quercus* species in Texas (1,14). Drought tolerance, dense crowns for shade, abundant mast for wildlife, and tolerance to urban environments make them the most valued tree species in central Texas. The live oaks, which grow in large, homogenous stands, are prolific root sprouters in the thin, shallow soils common to the central portion of the state. Root connections resulting from vegetative reproduction by sprouting and the propensity for root grafting in the thin soils provide for highly interconnected root systems and an efficient mechanism for *C. fagacearum* to spread through live oak stands. These interconnected roots are believed to be responsible for the extremely high rates of spread and large disease centers found in live oaks relative to other states, where oak wilt occurs exclusively in deciduous oaks (4). The spatial distribution of oak wilt in Texas therefore is influenced strongly by stand composition. Isolated, rapidly expanding disease centers with distinct boundaries are typical in homogenous live oak stands whereas insect spread in red oak stands results in large numbers of "satellite" centers forming irregular patches of dying trees (4).

The geographic range of oak wilt consists of 22 states in the Mid-Atlantic, Midwestern, and North Central U.S.A. (15). The expansion rates of this range are unknown, but there are unaffected states with important oak resources in the U.S. that may be vulnerable to epidemic losses by C. fagac*earum*. The oak woodlands of California, for example, have many similarities to the structure of the Central Texas oak savannahs. There are 15 endemic oak species in California. Eleven of the 15 are semi-evergreen or evergreen live oaks (20). Interest in the ecology and silviculture of these oaks is increasing with an awareness of their value as a natural resource for private and public use (12,22) In addition to representing the red and white oak subgenera, some taxonomists consider certain California oaks as an intermediate sub genus, Protobalanus, having a mixture of characteristics from each of the other groups (24). The susceptibilities of some California *Quercus* species to the oak wilt fungus have been tested in prior inoculations, but none of these previous studies attempted to measure disease response relative to other live oaks (2,10). Also, our understanding of the live oak epidemic in Texas provides a basis for predicting how an introduction of *C. fagacearum* might impact the California oak woodlands. The following report describes inoculation screenings of California oaks with the oak wilt fungus and a discussion of the ecology of the California oaks with consideration of the influence of stand structure and tree growth habits on a potential oak wilt epidemic. Reference will be made to specific forest cover types and regions in California to illustrate how oak speciation and disease susceptibility may influence a potential epidemic.

Materials and Methods

All oaks used in inoculation screenings ranged 6 mo - 3 yr old. A list of the species, common names, and the sub-generic classification of trees inoculated and discussed in this report is given in Table 1. In the preliminary inoculations (Study I), the canyon live oak from California *(Q. chrysolepis)* was compared to three selections of live oaks from Texas. One of these selections was derived from acorns collected by the author at the Robinson Ranch in Williamson Co., Texas, approximately 11 miles north of Austin; it is presumably *Q. fusiformis*. The remaining two Texas selections (TFS 522 and 160) are from urban trees included in a tree improvement program conducted by Dr. Tom Greene with the Gulf States Tree Improvement Cooperative, Texas Forest Service, College Station, TX. These trees are probably southern live oaks, *Q. virginiana*, and are progeny from urban

Table 1. Quercus species, common names, and sub-generic classification of oaks used in the inoculation screenings with *C. fagacearum*.

Species	Common name	Sub genus
Q. agrifolia Nee	coast live oak	red
Q. *chrysolepis* Liebm.	canyon live oak	intermediate
Q. *dumosa*[y]	scrub oak	white
Q. *durata*[y]	leather oak	white
Q. *engelmanii* Greene	Engelmann oak	white
Q. *fusiformis* Small	Texas live oak	white
Q. *garryana* Dougl.	Oregon white oak[z]	white
Q. *kelloggii* Newb.	California black oak[z]	red
Q. *lobata* Nee	valley oak[z]	white
Q. *suber*	cork oak	white
Q. *tomentella* Engelm.	island live oak	intermediate
Q. *virginiana* Mill.	southern live oak	white
Q. *wislizenii* A. DC.	interior live oak	red

[y] During shipping, unmarked containers of these two closely related species were intermingled; they are referred to as Q. d*umosa* in the text.
[z] Indicates a deciduous growth habit. All others are evergreen or semi-evergreen species.

trees with superior shade tree characteristics. The taxonomic status of live oaks in central Texas is uncertain and problems in identification result from similarities between the two species and probable hybridization (18). The canyon live oak seedlings inoculated in Study I were derived from acorns collected by the author from a mature tree growing approximately 10 mi. west of Riverside, CA.

In addition to the two Quercus spp. from Texas and *Q. chrysolepis*, nine California *Quercus* spp. and a Mediterranean introduction (*Q. suber*) were inoculated in Studies II and III (Table 1). These trees were obtained as liners or in 1 gal. containers from Calaveras Nursery (Valley Springs, CA, 95252). During shipping, two of the closely related white oaks, *Q. durata* and *Q. dumosa* , were intermingled and lack of individual labelling made it impossible to distinguish the two. Since some taxonomists have equated the two and they are known to freely hybridize (24), they were included in the screenings and will subsequently be referred to as *Q. dumosa*. Trees were inoculated with a conidial suspension of *C. fagacearum* isolate TR278 (Study I), BAN932 (Study II and III), or FW1777 (Studies I - III) at 1 - 5 x 10^6 conidia/ml. Two of these isolates TR278 and BAN932, were mating type A while FW1777 is mating type B. Disease response is more reliable when the fungus is recently isolated from a tree, necessitating the use of a different A isolate in Study II. The conidia were introduced within 1 cm of the soil line into a fresh wound made on the young trees with a sterile syringe. Controls were treated in a similar manner with a drop of sterile, distilled water or 0.2% saline solution. Disease progress was measured as numbers of symptomatic trees and the severity of symptom development. Symptoms appeared as scorching and necrosis of foliage accompanied by defoliation. Rating scales of 0 - 3 (Study II), or 0 - 4 (Study I and III) were used where; 0 = no visible symptoms, 1 and 2 = < 0.5 of the tree with wilt symptoms (mild to moderate), 2 and 3 = > 0.5 of the tree with wilt symptoms (moderate to severe) and 4 = dead. Observations also were made on the occurrence of sprouting at the base of defoliated seedlings. Isolations were periodically done to confirm the association of *C. fagacearum* with the appearance of symptoms.

The trees in Study I were inoculated on June 31, 1989. Those in Study II were treated on May 8, 1990, and Study III on Oct. 5, 1990. In all the studies there were 10 trees/species/fungal isolate. Disease ratings were analyzed utilizing Analysis

of Variance and Duncan's Multiple Range Test (21).

Results

In Study I, at 7 weeks following inoculation, the live oak selection from the Robinson Ranch (*Q. fusiformis*) had a significantly higher disease rating (2.7) than the canyon live oaks from California or the two other Texas selections (*Q. virginiana*) (Table 2). This difference in symptom ratings at 7 weeks also was evident in the numbers of diseased trees for each group; none of the Robinson Ranch trees was symptomless, while at the other extreme 6 of TFS 160 were. The Robinson Ranch selection continued to be the most symptomatic group 11 weeks after inoculation with all of the trees rated as "dead" (Table 2). There were no differences among the groups in responses to the two isolates BAN 932 and FW1777. Each isolate was equally pathogenic in Study I. None of the Canyon live oaks had sprouted 7 weeks after inoculation, while 7 of the 20 Robinson Ranch selections, 5 of the 20 TFS 522, and 10 of the 20 TFS 160 seedlings had sprouted. After 11 weeks, most of the diseased seedlings in the Texas live oak selections had sprouted, while only 4 of the 20 Canyon live oaks sprouted.

There also were significant differences in responses of the various California species to inoculation in Study II, although all of them were susceptible (Table 3). *Quercus suber* had the highest disease rating (1.3) and largest number of diseased trees at 10 weeks following inoculation (n = 20), whereas *Quercus wizlesnii* was the least susceptible (disease rating = 0.9, 14 symptomatic trees). There was little change between week 6 and week 10 following inoculation; no observations were recorded on the sprouting behavior of the diseased trees in Study II. There were pathogenicity differences in Study II between the two isolates (Table 5). The isolate FW1777 induced a higher disease rating (1.7) than that of BAN932 (1.3).

In the final set of inoculations, Study III, *Q. suber* again was among the most susceptible of the species (Table 4). Symptom development on *Q. durata* was as severe as that of *Q. suber*. The least susceptible species in Study III were *Q. tomentella* and *Q. chrysolepis*. One of the species, *Q. tomentella* exhibited no sprouting. In contrast, 40% of the *Q. suber* and *Q. garryanna* seedlings were sprouting at the end of the experiment. All of the other species had 3 - 5 of the diseased seedlings with basal sprouts. As in Study II, isolate

Table 2. Mean disease ratings for 4 live oak selections at 7 and 11 weeks following inoculation with Ceratocystis fagacearum (Study I).

	Seven weeks		Eleven weeks	
Selections[x]	No. diseased trees	Rating[y]	No. diseased trees	Rating
Robinson Ranch *Q. fusiformis*	20	2.7a	20	3.0a[z]
Canyon Live Oak *Q. chrysolepis*	15	1.6b	17	2.2b
TFS 522 *Q. virginiana*	16	1.5b	19	2.1b
TFS 160 *Q. virginiana*	14	1.1b	16	1.9b

[x] See text for further explanation of sources of selections; there were 20 trees inoculated for each selection.
[y] The disease rating system consisted of; 3 = dead, 2 = >0.5 of seedling with wilt symptoms, 1 = <0.5 of seedling with wilt, and 0 = healthy, no symptoms.
[z] Means with the same letter are not significantly different at alpha = 0.05.

Table 3. Mean disease ratings for 7 oak species at 10 weeks following inoculation with Ceratocystis fagacearum(Study II).

Quercus sp.[y]	No. diseased trees	Rating[z]
Q. suber	20	1.3a
Q. chrysolepis	18	1.1ab
Q. kelloggii	13	1.1ab
Q. lobata	16	1.0ab
Q. virginiana	17	1.0ab
Q. agrifolia	15	0.9b
Q. wislizenii	14	0.9b

[y] See text for further description of species; there were 30 trees inoculated (10 controls) for each species.
[z] Means with the same letter are not significantly different at alpha = 0.05.

FW1777 was more virulent than BAN932 (Table 5).

Ceratocystis fagacearum was isolated consistently from randomly selected, symptomatic trees in all three studies. In each set of inoculations, control trees treated with distilled water or saline occasionally developed scorch or some other non-distinct symptom, but from none was *C. fagacearum* isolated. Symptoms on control trees were attributed to powdery mildew or abiotic stress. Growth of the containerized California live oaks in Texas was poor beyond the first season and many died or appeared extremely stressed during the hottest months.

Table 4. Mean disease ratings for 7 oak species at 10 weeks following inoculation with Ceratocystis fagacearum (Study III).

Quercus sp.[x]	No. diseased trees	Rating[y]
Q. suber	20	2.5a[z]
Q. durata	26	2.1a
Q. garryana	16	1.4b
Q. virginiana	11	1.4b
Q. engelmannii	13	1.4b
Q. tomentella	18	0.8c
Q. chrysolepis	10	0.5c

[x] See text for further description of species; there were 30 trees inoculated (10 controls) for each species.
[y] The disease rating system consisted of; 3 = dead, 2 = >0.5 of seedling with wilt symptoms, 1 = <0.5 of seedling with wilt, and 0 = healthy, no symptoms.
[z] Means with the same letter are not significantly different at alpha = 0.05.

Table 5. Mean disease ratings in inoculated oaks for two isolates of C. fagacearum at 10 weeks after treatment.

Isolate	Disease rating[z] Study I	Study II
FW177	1.7a	2.3a
BAN932	1.3b	1.6b
Control	0.2c	0.3c

[z] See text for explanation of rating systems used in Studies I and II. Means with same letters not significantly different at alpha = 0.05.

Discussion

Inoculation of containerized trees has been used on numerous occasions to test for host susceptibility to the oak wilt fungus. Hoffman (10) and Bretz (5) used young trees to demonstrate susceptibility of four California species that also were used in the present study, including *Q. agrifolia*, *Q. chrysolepis*, *Q. lobata*, and *Q. wislizeni*. Those species were studied to identify potential host resistance and clarify origins of the pathogen. Although they represent species from each of three sub-genera, no specific information on the relative resistance of the species was reported. Fenn et al. (6) in Wisconsin proposed that seedling inoculations with *C. fagacearum* reflected relative resistance between red and white oaks by observing rates of disease progress exhibited by each group. At 6 weeks following inoculation, only 54% of white oak seedlings were symptomatic whereas all red oak seedlings had symptoms after only 3 weeks (6). In addition to symptom development, the ability of the inoculated trees to survive, as indicated by sprouting, may be an important parameter to consider when screening young trees for resistance to a pathogen. In the inoculated live oaks, many of the most severely diseased seedlings with top dieback were the first to produce healthy, disease-free sprouts around the root collar. The long-term survival of these trees was not determined, but the ability to produce sprouts may play an important role in the survival of mature

trees infected with *C. fagacearum* under natural conditions.

In each of the three inoculation studies, there were significant differences in responses of the various *Quercus* species to the oak wilt pathogen. These species represented different growth habits, i.e. deciduous vs. semi-evergreen or evergreen live oaks, as well as three different sub-genera. The live oaks in particular exhibited a wide variety of responses to the pathogen. In Studies II and III, *Q. suber* had the highest disease rating. *Q. suber* is an evergreen white oak introduced into California from Mediterranean regions as an ornamental shade tree, and contrary to results would be expected to exhibit relatively greater resistance than the other species. The only deciduous red oak, *Q. kelloggii*, responded as expected with only a slightly lower disease rating than *Q. suber*; the difference was too small to be statistically significant. In Study III, *Q. dumosa*, another evergreen white oak, also had a disease response that was significantly greater than the others. In Study II, the two evergreen red oaks showed the least response to inoculation (Table 3). In general, the results of seedling inoculations with live oaks were not as expected in comparison to previous inoculations of deciduous *Quercus* spp. (6).

Sub-generic classification of live oaks has presented complex taxonomic difficulties when strict adherence to criteria for separating the red and white oaks is used. These criteria include season of acorn maturity, the inner surface smoothness of acorn shells, presence or absence of leaf tips, style and stigma characteristics, and positions of abortive ovules. Further, red oaks are known to have rounded summerwood vessels with thick walls (23). The summerwood vessels of the white oaks are characterized as having thin, angular walls (23). However, there are many exceptions to this anatomical distinction in the white oaks, most of which are evergreen live oaks. Live oaks, although classified with white oaks, have wood of the red oak type (23). Many live oaks also have semi-ring-porous wood and other anatomical peculiarities which distinguish them from either the red oaks or white oaks. This variability in xylem anatomy may explain the unusual responses observed in the *C. fagacearum* inoculations. Taxonomic classification of live oaks in Leucobalanus, therefore, cannot be relied upon to indicate that they are resistant to *C. fagacearum*. The impact of oak wilt on *Q. suber* in urban environments may be particularly severe due to the widespread use of that species as a shade and ornamental tree. Detailed study of the anatomical features of live oak, accompanied by responses to infection by *C. fagacearum*, also may contribute to our understanding of resistance and susceptibility to the pathogen.

The isolates chosen for inoculation were selected on the basis of opposite mating types. The differences in virulence exhibited in studies II and III were unexpected, and reinforce the need to use more than one pathogen isolate when screening trees for resistance. The reasons for the difference in virulence between these two particular isolates are unknown. One is from a diseased live oak in Fort Worth (FW1777), and the other came from several hundred miles to the south in Bandera, TX (BAN932). Similar inoculum levels were used for each, and trees periodically were inoculated with both isolates during routine laboratory practices to maintain pathogenicity. These results indicated that comprehensive inoculation experiments on live oak seedlings may be useful for studying variability in virulence among larger populations of the oak wilt fungus.

None of the California *Quercus* spp. tested in this project exhibited any unusual immunity or resistance to the oak wilt pathogen. It is likely that an introduction of *C. fagacearum* into certain California woodlands would lead to significant losses, especially in areas where deciduous red oaks are intermixed with live oaks; examples of such stand compositions are common (9,16). Presumably, fungal mats would develop on red oaks in California, although this characteristic could not be determined because mat formation did not occur on the small diameter seedlings used in the inoculations. In the foothill woodlands surrounding the Central Valley, upland sites are common where the deciduous red oak, *Q. kelloggii*, forms a significant component of total stand composition. In the Coast Ranges, it is intermingled with *Q. agrifolia*, coast live oak, and in the Sierra Nevada - Cascades, with *Q. wizlesnii*, interior live

oak (8). *Quercus kelloggii* is the most widely distributed of prominent California oaks (20), and could be expected to be found frequently in association with other species. For example, in the South Sierra Hardwood Range, *Q. kelloggii* coexists with *Q. chrysolepis* on moist sites (22). In these locations, where there is a potential for fungal mat formation on California black oak, the susceptible live oaks may be particularly vulnerable to an epidemic. In Texas, mat formation only occasionally forms on the sparsely distributed red oak *Q. texana*, but is sufficient to stimulate destructive epidemics in the widespread live oak, *Q. fusiformis* (3).

Another important consideration is the potential for fungal mat formation on interior live oak and coast live oak, both of which are classified as red oaks. If the fungus has the ability to produce inoculum on these species, then the potential for epidemic increases of oak wilt would be much greater. Alternatively, none of the California live oaks is noted to be a prolific root sprouter, as are *Q. fusiformis* and *Q. virginiana* in Texas (17). The lack of clonal reproduction by root sprouting would remove what is considered to be one of the most destructive means of transmission in the Texas oak wilt epidemic, common root systems. Root grafting is also undoubtedly important in *C. fagacearum* transmission in Texas, and could be expected to play a role in dense live oak stands in California.

The means of introduction of *C. fagacearum* would probably be by interstate movement of firewood from infected stands (11). Red oak logs may actually support formation of mats when diseased trees are cut and transported elsewhere (7), or contaminated insect vectors may be harbored on any diseased oak logs from a region with a high incidence of the disease. Westward expansion of the pathogen through natural vectors such as sap-feeding nitidulid beetles from Texas, the nearest state with oak wilt, is unlikely in the near future, although diseased live oaks are continually being found in the westernmost counties of the Texas panhandle near the New Mexico border (*personal communication*, Dr. Jerral Johnson, Texas Agricultural Extension Service, College Station, TX). Once introduced, the existing populations of known vectors in California would probably maintain a developing epidemic (11). The possibility also exists that new, more efficient vectors will be encountered as the pathogen expands westward. There are no known vectors that would acquire and transmit the pathogen in diseased nursery stock. However, reasonable caution should be maintained in the movement of any plant materials, including firewood, from areas with oak wilt into states where the disease does not occur.

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Résumé. La susceptibilité à la maladie de 14 espèces du genre Quercus du Texas et de la Californie était mise à l'essai au moyen de trois tentatives d'innoculation de différentes souches du champignon pathogène de la brûlure du chêne, Ceratocystis fagacearum. Dix des espèces de chêne étaient semper virens ou semi-semper virens tandis que les quatre autres étaient décidues. Toutes les espèces étaient sensibles au pathogène, mais il y avait aussi une variabilité significative quant à la réponse à la maladie. Sur deux des expériences, les espèces les plus susceptibles étaient les chênes-liège exotiques, Q. suber et Q. kelloggii; la seule espèce décidue du groupe des chênes rouges réagissait de façon similaire au Q. suber, une espèce semper virens du groupe des chênes blancs. Les deux espèces semper virens du groupe des chênes rouges, Q. agrifolia et Q. wislizenii, étaient celles les moins sensibles dans l'une des expériences alors que deux espèces semi-semper virens, Q. chrysolepis et Q. tomentella, étaient les moins sensibles dans une autre expérience. Des variations significatives de virulence étaient observées parmi deux souches texanes de C. fagacearum. Les implications de ces résultats sur les forêts de chênes de la Californie sont discutées.

Zusammenfassung. Die relative Krankheitsanfälligkeit von 14 Quercus-Arten aus Texas und Kalifornien wurde in drei Inokulationsversuchen mit verschiedenen Isolaten des Eichenwelkeerregers, *Ceratocystus fagacearum*, getestet. Zehn der Eichen waren immergrüne oder halb-immergrüne lebende Eichen und die anderen vier sommergrüne Arten. Alle Arten waren anfällig für den Erreger, aber es zeigte sich eine signifikante Variabilität im Krankheitsverlauf. In zweien der Versuche war die exotische Korkeiche, *Q. suber*, die Art mit der größten Anfälligkeit. *Q. kelloggii*, die einzige inokulierte sommergrüne Roteiche reagierte ähnlich wie *Q. suber*, eine immergrüne Weißeiche. Die zwei immergrünen Roteichen, *Q. agrifolia* und *Q. wislizenii*, waren am wenigsten anfällig in einer der Studien, während die zwei immergrüne "dazwischen liegenden" Eichen, *Q. chrysolepsis* und *Q. tomentella* sich als am wenigsten anfällig in einer anderen Studie erwiesen. Signifikante Unterschiede in der Virulenz wurden beobachtet zwischen zwei texanischen Isolaten von *C. fagacearum*. Die Schlußfolgerungen dieser Ergebnisse für die kalifornischen Eichenwälder wurden dargestellt.