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A holistic approach to mitigating pathogenic effects on trees

Lee F. Klinger M.A, Ph.D. Independent Scientist, Big Sur, CA lee@suddenoaklife.org

Summary

The conventional 'disease model' approach to tree health focuses on identifying and controlling a specific pathogen (or pest) implicated as the causal agent of tree decline. Alternatively there are more holistic approaches in tree health that address a broader suite of processes occurring at the ecosystem level which may be predisposing the trees to infection by disease. Here I describe a holistic methodology that takes into account not only the proximal agents involved in tree decline, but also the age and structure of the forest, the abundance of cryptogams, the fire history, the acidity of the precipitation, the fertility of the soil, and the historical land care practices. This methodology is being implemented in the oak forests of coastal California which are experiencing high levels of mortality attributed, by most scientists, to the pathogen *Phytophthora ramorum* (aka sudden oak death). Evidence reported here of 1) acid rain, 2) acidifying effects of mosses and lichens, 3) the presence of acidic and nutrient deficient soils, and 4) a much lowered incidence of disease in recently burned areas, points to the likelihood that fire suppression has radically altered the structure and successional status of the forests, leading to enhanced competition and systemic acidification. Case study results of sick and diseased coast live oaks receiving holistic care, aimed not at treating P. ramorum but at reducing the environmental acidity, fertilizing the soils, and otherwise mimicking the effects of fire, show noticeable improvement in the health of the oaks after one year (78%, n=152), with further improvement in years two (84%, n=134) and three+ (81%, n=80). While the results do not indicate that the incidence of P. ramorum has changed significantly in the population of treated oaks, there is evidence that the sick, non-diseased trees are better able to resist infection.

Models of Tree Health

When trees fall ill a typical response is to go examine the trees, identify the causal agent(s), such as a stem canker, bark beetle, root collar fungus, etc., and apply a procedure or chemical treatment which hinders the progression of the disease or pest. This 'disease model' approach focuses on understanding the biology, physiology, and genetics of the individual organisms involved, in this case the causal agent, its tree host, and any carriers of the disease or pest, for the purpose of finding a treatment or cure. Most plant pathologists and entomologists are closely aligned with the disease model and are often quick to attribute the regional decline of trees to a disease epidemic or insect outbreak. Thus, under the guidance of these experts, spraying and injecting the trees with pesticides of variable toxicities has become standard practice in the tree care industry.

A small but growing number of experts are digging deeper into the reasons why trees are succumbing to diseases and pests by attempting to understand the ecology of the whole

forest as opposed to the biology of the infectious agent(s). This kind of holistic approach considers not only the health of the individual trees but also the location and abundance of surrounding plants, the nutrient inputs and outputs, and the structure and fertility of the soils. By paying attention to the health of the entire ecosystem, a holistic practitioner is attuned to a wider variety of clues and symptoms that can be useful in diagnosing problems. Holistic methods used to address these problems do not involve finding cures or treatments for specific maladies, rather, they are designed to boost the health of the trees by improving the site conditions and soil fertility. In this way the trees are better able to resist or survive infectious diseases and pests. The holistic approach in no way precludes efforts to control aggressive pathogens and pests with more conventional techniques. Wherever there are non-toxic means at hand to help control a given pest/pathogen, such as field intervention, biological agents, and/or natural mitigating compounds, holistic practitioners are wise to incorporate them into their methodology, all the while recognizing the limitations inherent in those methods that focus solely on the control of a particular organism.

From their first beginnings, trees have co-evolved with pests and pathogens. Thus, pests and pathogens are undoubtedly critical for maintaining a healthy, evolving forest ecosystem. They interact both positively and negatively with many organisms in the forest, providing food for some species, while competing with other species. Most importantly, they act to help weed out the weak and inferior trees. Trees, then, have had to develop robust defense mechanisms for coping with diseases and pests. Some trees produce chemicals that deter insects from eating their leaves. Other trees have formed symbiotic relationships with beneficial fungi that work to inhibit the spread of certain fungal pathogens. Therefore, as a holistic practitioner, I attribute most sicknesses and diseases in trees to some kind of imbalance or breakdown in the trees' ability to fight off the infectious agent. This, I believe, is linked to resource limitation in the ecosystem attributable to two fundamental problems: nutrient deficiency of the soils due to acidification, and/or enhanced competition for light, water, and nutrients due to overcrowding of neighboring plants. In the oak forests of California, both of these problems are widespread in areas where fires have long been suppressed.

Ecosystem Succession

Succession, as viewed here, is a developmental process innate in all ecosystems that is closely analogous to the maturation process of an organism (Odum 1971; Klinger 2004). Characteristic stages of development, or successional sequences, have been described for plant and animal ecosystems in all the major biomes, both terrestrial and marine. Some terrestrial successions are known to span thousands to tens of thousands of years and involve a long series of vegetation and soil transformations from grasslands to shrublands to deciduous forest to evergreen forests to swamp forests to peat swamps (Jenny 1980; Klinger 2004). As ecosystems age, the soils undergo corresponding transformations in organic matter content (low to high), pH (high to low), and base mineral content (high to low). At any time along this sequence disturbances like fires, grazing, floods, hurricanes, landslides, and volcanoes may occur and significantly impact the ecosystem. Disturbances tend to arrest, or even set back to an earlier stage, the process of succession. It is well-known that the health and maintenance of early successional savanna and forest

ecosystems requires some kind of regular disturbance regime, typically fire.

Vegetation and soil successions involving oak forests usually begin with grasslands that are comprised mainly of herbaceous monocots (grasses) and dicots (forbs) growing in entisol, inceptisol, or mollisol soil types with neutral to alkaline surface horizons¹. The youthful grasslands exhibit high rates, per unit biomass, of productivity and nutrient cycling and, consequently, can support a large amount of animal life. In the absence of disturbance, grasslands are typically replaced in one to several decades by shrublands. Early successional shrublands are dominated by deciduous shrubs and small trees, and/or woody vines. Left undisturbed shrublands are soon replaced by oak woodlands and forests dominated by one or more species of oaks, along with other early successional species such as aspens, buckeyes, chestnuts, or hickories. Once formed, oak-dominated forests will thrive for often 50 to 100 years. They tend to grow in inceptisol and alfisol soil types with slightly to moderately acidic surface horizons. If a fire occurs the oaks, for reasons discussed below, tend to survive and reproduce, thus rejuvenating the oak forests and re-alkalinizing the surface soils. However, if fire or some other disturbance does not occur, the oaks are replaced by other, more shade-tolerant and acid-tolerant species such as maple, pines, and firs. Eventually, the oaks will disappear and a later successional conifer forest will ensue. Conifer forests typically grow in spodosols and other soil types that show highly acidic and leached surface horizons. Many conifer species, too, require periodic fires to spur regeneration, though not as often as that required for oak regeneration.

Oaks are widely considered to be fire-adapted species. The thick bark of a mature oak tree acts to insulate the trunk from the heat and damage of wild fires. Fire-damaged twigs and branches of oaks will often respond with a dense flush of new leaves within a year. Oaks have thus evolved to benefit from fire in several ways: 1) fire removes other tree competitors, those that are less fit or adapted to survive the effects of burning, 2) fire removes many of the brushy understory plants that are also competitors and in some cases aid in the transmission of diseases and pests, 3) fire frees up nutrient cations, which then re-alkalinize the soils and are more readily available to the surviving oaks, 4) fire removes dead and dying plants that may be harboring diseases and pests, and 5) the heat and pollutants (smoke) from the fire suppress or kill many of the mosses and lichens growing on the branches, trunks, and ground. While commonly overlooked, mosses and lichens may have a significant negative impact on the health of oaks and other tree species.

Mosses and Lichens

Cryptogams such as mosses and lichens are generally considered to be benign organisms in forests. This may well be true where the cover of cryptogams is low. However, as ecosystems age mosses and lichens become more abundant, and together can eventually equal or even exceed the green biomass of all other plants in the forest combined (Klinger et al. 2002). Where their abundances are high there is evidence that mosses and lichens are contributing heavily to the acidification of the soils and to the mortality of the fine roots of trees (Klinger 1990). For instance, *Usnea* lichens collected from the

¹ Soil types follow the USDA Soil Survey taxonomy

branches of several Oregon oaks (*Quercus garryana*) in southern Oregon were soaked in distilled water² for 20 minutes. The pH of the water was then measured³ and found to be very acidic (mean pH [\pm s.d.] = 3.40 \pm 0.06). Thus, any precipitation and throughfall that comes into contact with these lichens has a high likelihood of being acidified. These waters then fall to the forest floor and acidify surface soils as well as leach away nutrient (base) cations. Mosses are also known to acidify surrounding waters and their effects are most pronounced in the surface soils (Klinger 1990), which is where the majority of tree roots occur. A heavy cover of mosses is also linked to fine root mortality of trees (Klinger 2005). With regards to fire, mosses and lichens are found to be noticeably less abundant in oak forests and woodlands that have recently burned or are regularly burned.

Acid Rain

Countless studies have examined the relationship of forest decline to elevated levels of acidity in the precipitation and soils. Scientists investigating the decline of forests in the eastern U.S. and in Europe in the 1970s and 80s concluded that while acid rain was not the sole cause of forest decline, it contributed significantly to acidification and loss of fertility in soils, especially in areas with poorly buffered substrates. As noted above central and northern California forests are currently experiencing heavy oak mortality, with the highest rates found near the Pacific coast. Some scientists have suggested that acid rain cannot be a factor in the oak decline because coastal areas are not subject to much air pollution, the presumed source of acid rain (Treasurefield 2004). However, studies in Alaska (Klinger & Erickson 1997) and Washington (Vong 1990) show that precipitation collected in rural areas near the Pacific coast is often found to be acidic, with reported pH values ranging from 3.5 to 5.0. For the past two years I have been monitoring the pH of rainfall events in Big Sur, CA⁴. During the 2006-2007 rainy season there were 24 measurable rainfall events with a mean pH (\pm s.d.) of 4.73 \pm 0.05⁵. Similarly, during the 2007-2008 rainy season there were also 24 measurable rainfall events with a mean pH (\pm s.d.) of 4.87 \pm 0.02. These values are an order of magnitude lower than what would be expected for relatively unpolluted air, and are on the lower end of precipitation pH values reported elsewhere in more populated areas of California⁶.

Regarding the source of the acidity in the precipitation of unpolluted areas such as Big Sur, little is known. In California, studies have focused almost entirely on man-made pollution sources. In southeast Alaska, however, where pH values of unpolluted rain were found to be between 3.5 and 4.0, Klinger and Erickson (1997) surmised that the sources of the acidity were probably related to dimethyl sulfide and other gaseous emissions of oceanic phytoplankton, leading to the formation of sulfuric acid and various organic acids in the rainwater. A tendency for precipitation pH values in northern California to be lower nearer the coast (Klinger 2005) suggests that oceanic sources of acidity in this region, too, may be relatively strong. Regardless of the source, the above data indicate

² Mean pH (\pm s.d.) of distilled water = 5.81 \pm 0.02

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³ Measurements taken on July 7, 2008 with a high-precision Beckman pH meter using a standard two-point (4.00 & 7.00) calibration

⁴ 36° 14' 11.96" N; 121° 46' 46.82" W, 317m elevation

⁵ pH monitoring methods are described in Klinger & Erickson (1997)

⁶ See http://nadp.sws.uiuc.edu

that the rainfall in areas of California with severe oak decline is clearly acidic, and this may well be playing a role in compromising the health of the trees and soils.

Acid rain is closely linked to the depletion of base cations (e.g., potassium, calcium, and magnesium) in surface soils. Recent research has shown that while some of these mineral nutrients in trees are derived from the breakdown of rocks and soils, the majority arrive from the atmosphere (Kennedy et al. 2001). In unpolluted forests, dilute amounts of base cations dissolved in rainwater were shown to be the dominant source of these and other essential minerals in trees. These scientists go on to explain how acid rain, by accelerating the rate of leaching, decreases the levels of available base nutrients, including the macronutrients potassium, calcium, and magnesium, as well as a number of the essential micronutrients. They conclude that particular attention should be paid to the levels of available base-rich nutrients in the soils of declining forests that are experiencing acid rain.

The Native People

Recent works on the ethnobotany of California's tribes reveal that the native people possessed a rich ecological knowledge of the land and its inhabitants (Anderson 2005; Klinger 2006). Long before the arrival of ecologists, the people here understood the importance of fire and used it as a tool to maintain healthy oak forests and savannas. The oaks provided them fuel, shelter, tools, medicine, and most importantly acorn, a major staple in their diets (Anderson 2005). The native people are known to have tended the oaks by burning around them frequently, every one to three years in many places. They did this to control the invasion of brush, improve the fertility of the soils, and inhibit the spread of diseases and pests. Burning was used not only to manage the oaks, but also to improve the habitat for other useful plants and for game.

Coastal tribes in California are reported to have collected seaweed and spread it around the oaks to fertilize the soils. In addition, a number of large, Indian-era oaks are found to have scatterings of seashell and bone fragments in the soils around the base of the trunk. The structure, composition, and stratigraphy of these remains do not support the commonly-held belief that they are simply the discarded remains of native people living around the oaks. These shell-rich soil layers, as well as thicker accumulations called 'middens', are interpreted to have been mineral fertilizers applied to the soils of cultivated sites near the coasts (Klinger 2006), which, in California, tend to be depleted in calcium and other mineral nutrients (Klinger 2005).

The Ecology of Sudden Oak Death

Over the past decade elevated levels of oak mortality in northern and central California has been observed, and in 2000 the causal agent was identified by University of California pathologists to be *Phytophthora ramorum* (aka "sudden oak death"), a stem canker disease affecting mainly coast live oaks (*Q. agrifolia*), and tan oaks (*Lithocarpus densiflorus*). Following the 'disease model' approach, research on methods to control and/or mitigate oak decline have focused almost exclusively on understanding the biology and genetics of *P. ramorum* and its hosts⁷. The pathogen is considered invasive

⁷ See http://www.suddenoakdeath.org

and scientists have implicated the nursery industry as being the origin of the disease, via the importation of infected plants, as well as being the main vectors for the spread of the disease to different regions. Thus, the spread of sudden oak death has ignited great concern among policy makers and regulators who have made it a high priority to mitigate the spread of the disease through tightened controls on nurseries that deal in key hosts such as rhododendrons and camellias.

There is no question that this disease is finishing off large numbers of coast live oaks and tan oaks in many areas of California. However, a much larger question remains. Has acidification and other processes associated with aging of the ecosystem changed the environment enough to have weakened the oaks and/or aided the spread of the disease and its carriers, thus predisposing the oaks to infection and death by disease? As an ecologist and holistic practitioner of tree care, it is the answer to this question that guides my approach to dealing with this and other forest maladies.

Looking at the larger context of sudden oak death, we find many places in the U.S. beyond the range of the *P. ramorum* pathogen that are currently experiencing heavy mortality of oaks (e.g., Texas, Virginia, West Virginia, Pennsylvania, and New York). Systemic acidification has also been documented in most of these forests (Little 1995). In Pennsylvania, for instance, the decline in red oaks is occurring where significant decreases in exchangeable Ca and Mg concentrations and in pH (i.e. increased acidity) have been measured in the soils (Bailey et al. 2005).

Within the range of sudden oak death we find serious declines of white oaks (e.g., valley oaks, blue oaks, and Oregon oaks) that cannot be attributed to the sudden oak death pathogen. Even among the oak species that are susceptible, a significant number of the dead and dying coast live oaks (nearly 50%) have no sign of *P. ramorum* (Swiecki & Bernhardt 2005).

In my holistic view, the problem of sudden oak death is ultimately related to the profound ecological shift of the oak forests in California brought about by a fundamental change in management practices associated with white settlement of the lands. The oak forests that, for centuries, were tended by native people were suddenly abandoned. Under the assumption that the oak forests are a product of natural balances free of human influence, many land managers have taken a hands-off approach to conserving oaks, simply letting nature take its course. Meanwhile the fire regime, which provides the primary means of rejuvenating the oak forests, has been radically altered. Not only has there been a cessation of traditional burning of lands, there has also been a strict suppression of any fires that may have started naturally.

And nature has responded accordingly, showing us how ephemeral oak forests are in the overall sequence of forest succession. Throughout California the early successional oak forests are being taken over by bay laurels, coast redwoods, pines, Douglas firs, and other later successional species as the ecosystem matures. Some of these later successional trees, like bay laurel, are major vectors of sudden oak death and other oak diseases. The invasion of shrubs and trees also adds a competitive burden on the oaks for water and

nutrients. Some of the more shade-tolerant invasive species (e.g. bay laurel, coast redwood, Douglas fir) will eventually overtop the oaks and out-compete them for light. Along with the shift in species composition there is a corresponding increase in the acidity and a decrease in the mineral nutrient content of forest soils. This is largely due to the cumulative effects of acid rain and to the spread of acidifying cryptogams such as mosses and lichens. Under these conditions oak trees have become weakened and stressed, predisposing them to diseases such as sudden oak death. Thus, while diseases and pests may be the proximal cause of death of many oaks, they may not be the main players in the overall demise of oak forests.

Relevant Findings and Lingering Questions on Sudden Oak Death

In 2005, I reported on the results of a study showing evidence that sudden oak death may be related to acidic conditions and base nutrient deficiencies of the soil (Klinger 2005). Described in the paper were findings by other scientists that the incidence of sudden oak death tended to increase (highly significantly) along a transect from inland to coastal sites. My juxtaposed findings show there are corresponding (highly significant) decreases in soil pH, precipitation pH, and soil calcium along the same inland to coastal gradient. In that paper, the role of fire in systemic acidification was touched upon, but not in detail. Here I have attempted to elaborate on the links between fire suppression and oak health due to systemic acidification and to the replacement of oaks by later successional species. The link between fire frequency and sudden oak death has already been studied and documented by Moritz and Odion (2005), who found the incidence of sudden oak death to be "extremely rare" within the perimeter of any area burned since 1950. These particular findings are offered as major evidence for the central thesis of this paper, that oak decline is due to the cumulative effects of fire suppression which have weakened the oaks and predisposed them to diseases such as sudden oak death.

Despite the fact that fires significantly raise the pH of forest soils (Sugihara et al. 2006), California Oak Mortality Task Force (COMTF) scientists have dismissed any link between sudden oak death and systemic acidification, stating that the soil pH of affected sites tends to range between 5.5 and 6, which is "not particularly acidic" (Appleby 2008). However, the fact remains that the link between sudden oak death and acidification has never been fully investigated. I am aware of no published data by COMTF scientists examining patterns of soil acidity in affected vs. unaffected sites. Nor have data on precipitation pH ever been reported by COMTF scientists.

Also left unanswered are questions about the impact of cryptogams on the health and susceptibility of oaks to disease. Despite reports that mosses have been linked to soil acidification and fine root mortality (Klinger 2005), COMTF scientists have made little effort to characterize the role of mosses or lichens in sudden oak death. In addition, there are important questions that remain regarding the effects of mineral depletion on oak bark health. Noting reports that healthy oak bark has a particularly high requirement of minerals such as calcium (Bosman et al. 2001), I have proposed that the degradation of the bark in oaks affected by sudden oak death may be linked to acidification and calcium depletion (Klinger 2005). Indeed, studies have shown that of eight measured properties of oak bark, the occurrence of recent bark expansion fissures was the bark property that

correlated most strongly with the incidence of sudden oak death (Swiecki & Bernhardt 2005). The formation of these splits and fissures is assumed, by COMTF scientists, to be caused by the higher growth rates and, thus, greater vitality of affected oaks. This has led these scientists to make the unlikely conclusion that the healthier oaks (as suggested by the splits in the bark) are more susceptible to infection by sudden oak death than the less healthy oaks (Treasurefield 2004). This, they argue, is a reason why not to use mineral fertilizers to combat sudden oak death.

Results of Case Studies

There are any number of ways to help ascertain the role of fire suppression and systemic acidification in sudden oak death (Moritz & Odion 2005) and other associated diseases. For my part, I have been investigating the possible links between fire and oaks by simply implementing fire substitution methods to treat sick and diseased trees and documenting the results in case studies. Treatment protocols were tailored to suit the particular situation and needs of each ailing tree. The protocols involve a suite of methods designed to mimic the effects of fire, as well as other land care practices of native people. These include some or all of the following: 1) the removal of most shrubs and young trees from beneath the canopies of the oaks, 2) pruning of dead limbs and branches, 3) excavation of root crowns, 4) removal of mosses and lichens from the lower trunks, 5) removal of mosses growing on the ground around the oaks, 6) application of a mineral-rich spray or poultice to the trunks with degraded and split bark, 7) application of shell and volcanic ash fertilizers⁸, enriched in trace elements, to the soil surface from the trunk to the dripline of the oaks, and 8) application of compost, compost tea, and/or mulch to the soil surface from the trunk to the dripline. It should be apparent how most of the above methods achieve the effects similar to those of burning. Together these methods promote regeneration and vitality in oaks by reducing competition, removing carriers and vectors of disease, improving soil fertility, reducing soil acidity, and removing sources of acidity (e.g., cryptogams). In this way the oaks stand a better chance of resisting or surviving infection by sudden oak death and other diseases and pests.

To assess the results of these treatments, I have compiled 152 sets of photos of individual coast live oak trees with symptoms of sickness and disease that were treated using some combination of the above methods. Before treatment all of the trees showed symptoms of canopy decline and over half (80) exhibited bleeding stem cankers characteristic of sudden oak death disease. The first photo of the set is of the canopy of the tree the day of or just prior to the first treatment. The remaining photos are from the same perspective after one, two, and/or three or more years' time. As an example of a tree with a muchimproved response to treatment, Figure 1 shows the before-and-after photos for year 3 of a sick coast live oak, case number 20050430.4. More examples of the before-and-after photo sets can be viewed online⁹. Some trees received multiple treatments, others only one. Thus, each photo-documented tree constitutes a unique case study of an oak responding (or not) to the treatments. Responses to the treatments were determined by the degree of change in the canopy fullness, or leaf density observable in the photos.

⁸ e.g., AZOMITE[™] Soil Sweetener

⁹ See http://www.suddenoaklife.org

A summary of these case studies is presented in Figure 2, which shows the year-by-year assessments of canopy changes in the oaks undergoing holistic treatment. These results indicate that a large majority of the sick/diseased oaks are responding positively (improved canopy density) to the treatments after only one year (78%, n=152), with continued improvement in year two (84%, n=134). After three or more years 81% of all sick trees (n=80) showed positive responses (improved or much improved canopy density) to the treatments, and, of the trees most likely infected with *P. ramorum*, 72% showed positive responses. Case study notes indicate that only one of the initially non-bleeding oaks appeared to have contracted *P. ramorum* (i.e. began to show bleeding) after three years. Conversely, only 5 or 6 bleeding trees were seen to have stopped bleeding after three years, suggesting that the disease remained active in most of the infected trees that were treated. Positive responses have also been seen in the analysis of before-and-after photos of numerous other kinds of sick trees, including valley oaks, madrones, pines, sycamores, and buckeyes.

The positive results in using fire substitutes (e.g., brush clearing, moss removal, spreading mineral-rich ash) for the treatment of sick and diseased coast live oaks are offered as further evidence for the thesis that fire suppression predisposes oaks to infection by pathogens such as sudden oak death, and that holistic techniques designed to improve the site conditions and the soil fertility are useful for bringing sick oaks back to health and potentially lower the incidence of disease.

Conclusion

With respect to the problem of oak mortality in California, findings reported here and elsewhere lend credit to the thesis that decades of fire suppression and hands off management practices have led to overgrown and acidified conditions around the oaks, causing them to become weak and susceptible to infection by disease. In response, a holistic methodology has been developed to address oak mortality that includes a variety of techniques aimed largely at mimicking the effects of fire and improving soil fertility. Results of case studies on sick coast live oaks and other kinds of sick trees show positive responses of the trees to holistic treatments, and provide an impetus for continuing to pursue a more ecologically-based approach to tree care.

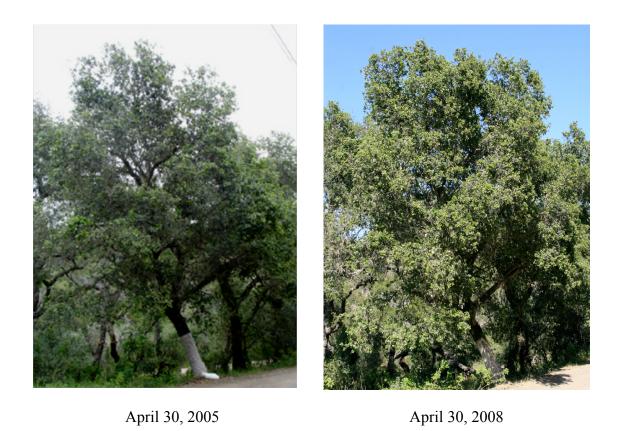


Figure 1. Before-and-after photos of a coast live oak, case number 20050430.4, showing a much improved canopy response after three years of treatments.

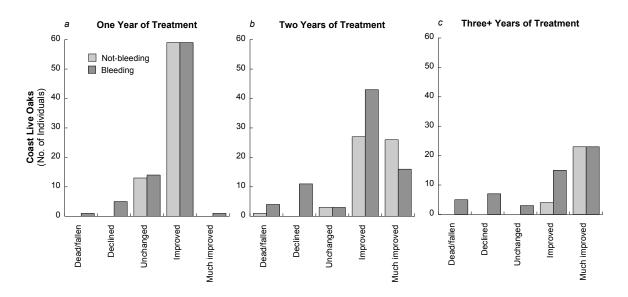


Figure 2. Frequency of the coast live oak trees occurring in each of five canopy health categories, stratified according to bleeding (symptom of P. ramorum) and non-bleeding trees, after one year (a), after two years (b), and after three+ years (c) of treatment.

References

Anderson, M.K., 2005. Tending the wild. Berkeley: Univ. of California Press.

Appleby, M., 2008. Phytophthora: a search for answers. *Horticulture Week*, 21 Aug. Available at: http://www.hortweek.com/channel/arboriculture/article/840553/Phytophthorasearch-answers/ [accessed 19 September 2008].

Bailey, S.W., Horsley, S.B., & Long, R.P., 2005. Thirty years of change in forest soils of the Allegheny Plateau, Pennsylvania. *Journal of the Soil Science Society of America*, 69, p.681-690.

Bosman, B., Remacle, J., & Carno, M., 2001. Element removal in harvested tree biomass: Scenarios for critical loads in Wallonia, South Belgium. *Water, Air, & Soil Pollution - Focus*, 1, p.153–167.

Jenny, H., 1980. The soil resource. New York: Springer-Verlag.

Kennedy, M.J., Hedin, L.O., & Derry, L.A., 2001. Unpolluted temperate forests are nutritionally decoupled from weathering sources. *Proceedings of the National Academy of Sciences*, 99, p.9639-9644.

Klinger, L.F., 1990. Global patterns in community succession. 1. Bryophytes and forest decline. *Memoirs of the Torrey Botanical Club*, 24, p.1-50.

Klinger, L.F., 2004. Gaia and complexity, In: S.H. Schneider, J.R. Miller, E. Crist, & P.J. Boston eds. *Scientists debate Gaia: the next century*. Cambridge: The MIT Press. Ch. 16.

Klinger, L.F., 2005. Bryophytes and soil acidification effects on trees: The case of sudden oak death. *Combined Proceedings International Plant Propagators' Society*, 55, p.493-503.

Klinger, L., 2006. Ecological evidence of large-scale silviculture by California Indians. In: Wahinkpe Topa (Four Arrows) ed. *Unlearning the language of conquest.* Austin: University of Texas Press. Ch. 9.

Klinger, L.F. & Erickson, D.J., 1997. Geophysiological coupling of marine and terrestrial ecosystems. *Journal of Geophysical Research* (D), 102, p.25,359-25,370.

Klinger, L.F., Li, Q.-J., Guenther, A.B., Greenberg, J.P., Baker, B., & Bai, J.-H., 2002. Assessment of volatile organic compound emissions from ecosystems of China. *Journal of Geophysical Research* (D), 107, p.4603-4616, doi:10.1029/2001JD001076.

Little, C.E., 1995. The dying of the trees. New York: Penguin Books.

Moritz, M.A., & Odion, D.C., 2005. Examining the strength and possible causes of the relationship between fire history and sudden oak death. *Oecologia*, doi: 10.1007/s00442-005-0028-1.

Odum, E.P., 1971. Fundamentals of ecology. 3rd ed. Philadelphia: W.B. Saunders Co.

Sugihara, N.G., Van Wagtendonk, J.W., Shaffer, K.E., Fites-Kaufman, J., & Thode, A.E., 2006. *Fire in California's ecosystems*. Berkeley: University of California Press.

Swiecki, T.J. & Bernhardt, E., 2005. *Phytophthora ramorum* canker in coast live oak and tanoak, 2000-2004: factors affecting disease risk, disease progression, and failure potential. Phytosphere Research, Vacaville, CA, prepared for Pacific Southwest Research Station, Forest Service, USDA, Berkeley, CA.

Available at: http://phytosphere.com/publications/ [accessed 11 Nov 2006].

Treasurefield, T., 2004. Root of the problem. *North Bay Bohemian*, 10 Nov., p.11-14. Available at: http://www.taratreasurefield.com/root.html [accessed 12 Dec 2005].

Vong, R.J., 1990. Mid-latitude northern hemisphere background sulfate concentration in rainwater. *Atmospheric Environment, Part A*, 24, p.1007-1018.