Bryophytes and Soil Acidification Effects on Trees: The Case of Sudden Oak Death©

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Pathologists investigating the recent death of many oak trees in northern California have concluded that the problem is due to a new plant disease, dubbed sudden oak death (SOD), caused by the fungal pathogen *Phytophthora ramorum*. While not disputing that *P. ramorum* is involved in the final demise of many oaks, there are a growing number of experts who do not agree that this pathogen is the fundamental cause of the decline. They point out that most of the dying oaks in SOD-affected forests show no expression of *P. ramorum*. Instead, they suggest that acidic conditions create mineral imbalances and deficiencies in soils that weaken the trees, raising their susceptibility to secondary pests and pathogens. Here I present evidence that, due to fire suppression, there has been progressive acidification of oak forests, leading to greater incidence of disease. This helps us understand both why the SOD phenomenon is occurring now and what can be done to solve the problem.

The etiology of SOD in California coincides closely with the symptoms of decline seen in aging forest ecosystems elsewhere. Dieback starts with the upper and outer branches in the crown, showing a pattern of wilting and browning of leaves along with dying small branches and progressively spreading to the lower parts of the crown over several years. The decline affects many kinds of oaks, as well as bays, buckeyes, and pines, hitting mainly the larger trees in mixed-oak savannas and forests, most of which have been under strict fire control for more than 50 years. Areas near the coast and those experiencing frequent seasonal fog are especially hard hit by SOD. Affected trees tend to occur in mature forests (>100 years old) and are usually found in association with a heavy cover of mosses and lichens. Moss mats have been shown in both laboratory and field studies to be associated with the mortality of underlying fine roots and mycorrhizae, which leads to water and nutrient stress and reduced radial growth in nearby trees. Mosses and lichens are also observed to degrade the tree's protective bark layer, allowing for pests/pathogens to more easily infest/infect the tree.

Data on pH from 28,577 soil samples taken from a wide range of landscaped and agricultural soils in California indicate that only 10.2% of the soils are acidic (pH < 6.0). Data on samples taken from disease site soils (mostly with SOD) indicates that 79.2% of these soils are acidic (median pH = 5.7; n = 136). Soils from the disease sites were also found to be consistently low in Ca and very high in soluble Al and Fe. Spatial analysis reveals a strong coastal gradient in soil pH with the lowest pH values found near the coast. Strong coastal gradients are also apparent in soil Ca, which is lowest near the coast, and in soil Al, which is highest near the coast.

These results lend further support to the theory that systemic acidification is adversely affecting the health of the trees and soils, predisposing trees to infection by the SOD pathogen. It is recommended, thus, that the scope of SOD research be expanded to include studies of acidification by mosses and lichens in the context of forest and soil ecology.

INTRODUCTION

Sudden Oak Death (SOD), defined by the California Oak Mortality Task Force (COMTF) scientists as the decline and death of trees caused by the fungal pathogen *Phytophthora ramorum*, is widespread across the coastal forests of northern California. The pathogen has now been found in numerous species of California plants and in certain nursery plants around the U.S.A. While the current research is focused on the genetics, transmission, and epidemiology of the *P. ramorum* pathogen, information on the ecology related to SOD is sorely lacking. From an ecosystem perspective the partial or complete death of a tree indicates not only a dysfunction or disease affecting that organism, it signifies, as well, a change or shift in the composition and metabolism of the whole forest ecosystem (Klinger, 1991). In the case of SOD, such an approach seems especially pertinent given the fact that most of the trees dying in SOD-affected forests show no visible expression of the *P. ramorum* pathogen. The presence of secondary pests like Ambrosia beetles in SOD-affected forests raises the possibility that *P. ramorum*, too, may be secondary, that there are other agents acting to weaken the trees and increase their susceptibility to fungal attack. Clearly, any credible information that implicates factors other than *P. ramorum* in SOD must be carefully investigated. This paper describes the theory of systemic acidification and investigates the regional patterns of soils and precipitation chemistry from California as related to the role of bryophytes and systemic acidification in the decline of oaks in California.

FOREST DECLINE AND SYSTEMIC ACIDIFICATION

In studies of ecosystem change, ecologists have frequently reported how maturing landscapes progress through a series of characteristic communities, stages of development much like those of individual organisms. Successional (i.e., developmental) studies of forested landscapes have shown that as forests mature and age the vegetation takes on more evergreen forms, mosses and lichens increase in abundance, and surface soils become more acidic. This process of systemic acidification is due, in part, to the buildup of biomass (mainly plant organic matter), which, upon microbial decomposition, releases organic acids that acidify and leach mineral nutrients from the soils. Older forests that escape burning or otherwise go undisturbed for several generations will eventually show symptoms of decline such as top dieback, reduced rates of radial growth, and fine-root mortality (Huettl and Mueller-Dombois, 1993).

In the early 1970s scientists in the U.S.A. and Europe started to pay attention to observations of rapid dieback in certain forests that previously appeared healthy. As these forests were often within a few hundred kilometers of highly industrialized regions, air pollution and acid rain were implicated as probable culprits. But upon completion of the major research programs, forest scientists concluded that acid rain and air pollution were not the primary causes of forest decline. The reasons for this are obvious. Forest decline with symptomology identical to that found in polluted regions occurs extensively in unpolluted areas such as Alaska (Klinger, 1988), Hawaii (Mueller-Dombois, 1987), New Zealand (Wardle and Allen, 1983), and the southern Andes (Veblen and Lorenz, 1987). This pattern suggests the involvement of natural processes in tree death, which are somehow exacerbated by pollution.

Many scientists now see forest decline as a global phenomenon that has been occurring sporadically for thousands of years (Mueller-Dombois, 1987, 1988). "Decline" and "dieback" are terms used synonymously to describe forests where the majority of trees show reduced vigor or are standing dead. In some forests the obvious causal mechanisms of fire, wind, or flooding can explain the death of trees. However, in many areas forest dieback cannot be explained by these or other mechanisms. Insects, fungal pathogens, mistletoe, or other forest pests are often, but not always, present in declining forests. Forest decline tends to occur in moist-to-wet sites, though not always, and there is growing evidence that tree death can be drought-induced. In some areas tree death occurs in groups, but more often mortality is scattered throughout an affected forest in a seemingly random pattern. Forest decline affects mainly mature or old-growth forests and tends to affect canopy trees more severely than subcanopy trees. Yet, growing within heavily damaged forests are some canopy trees, which are barely, if at all, affected. Seedling and sapling growth in damaged areas appears to be inhibited in many but not all situations.

With regards to the etiology of global forest decline, scientists note that affected trees tend to exhibit dieback beginning at the top or outermost branches and progressing downward or inward (Mueller-Dombois, 1987). Decreased diameter growth is commonly associated with forest decline, as are symptoms of nutrient deficiencies and water stress (Ash, 1988; Hinrichsen, 1987; Schütt and Cowling, 1985). In studies where belowground plant tissue has been examined, mortality of very fine (feeder) roots and mycorrhizae has also been documented (Hinrichsen, 1987; Jane and Green, 1987; Klein, 1984; Schütt and Cowling, 1985). Of particular importance is the observation that feeder root and mycorrhizae mortality occurs prior to the onset of aboveground dieback symptoms (Klein, 1984; Manion, 1981). The decline is often, though not always, accompanied by attacks of pathogenic fungi and/or insects. Surface soils in declining forests are typically found to be acidic (Klinger, 1990), depleted in base cations (Huntington, 2000), and enriched in soluble Fe and Al (Klinger, 1996).

THE ROLE OF BRYOPHYTES

Field studies focusing on the role of mosses in forest decline have reported a significant relationship between the presence of ground-dwelling mosses and the mortality of fine (feeder) roots and mycorrhizae in the soils beneath declining forests of southeast Alaska, New York, Colorado, and Venezuela (Cornish, 1999; Klinger, 1990; Smith and Klinger, 1985). Together these studies have documented highly significant decreases in the radial growth of trees and highly significant increases in the acidity of soils with an increase in moss cover (Fig. 1). Fine root mortality is reported elsewhere to be closely tied to soil acidification, especially where calcium levels are low (Matzner et al., 1986; Schaberg et al., 2001).

Soluble Al concentrations are reported to be high in the organic soil horizons and in the soil water beneath declining trees (Joslin et al., 1988). The fine roots of declining trees are found to contain significantly more Al than those of healthy trees (McLaughlin et al., 1987). Controlled laboratory experiments show a significant inverse correlation between soil Al and the live root biomass in oaks (Joslin and Wolfe, 1989). Strong acidification and high concentrations of soluble Al in soil water are reported to inhibit the growth of endomycorrhizal fungi (Ouimet et al., 1995). Acidic soil conditions are reported in declining oak forests in the eastern U.S.A. (Demchik and Sharpe, 2000) and in Europe (Thomas et al., 2002).

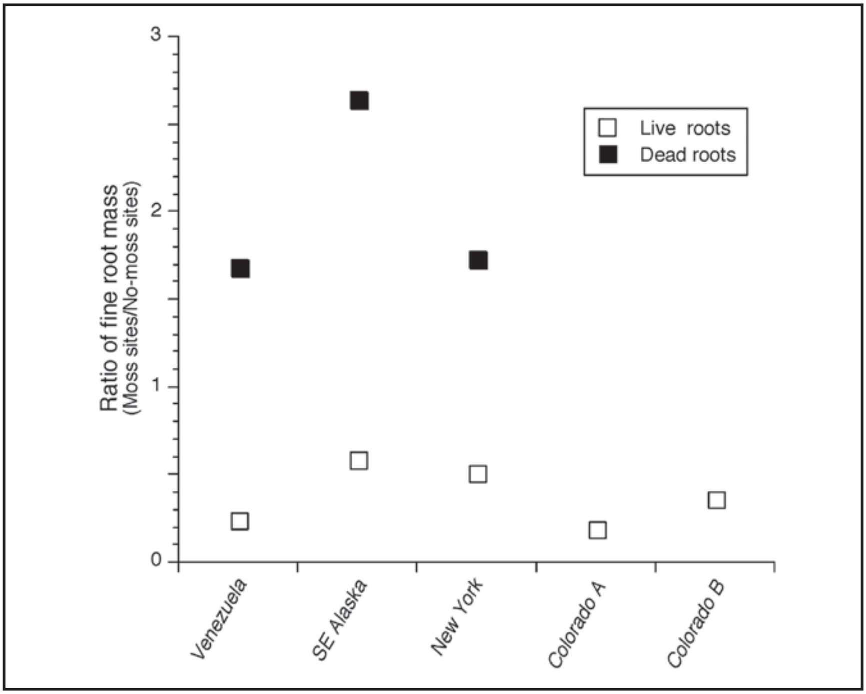

Figure 1. Ratios of fine root mass, compiled from Cornish (1999), Klinger (1990), Smith and Klinger (1985), and Klinger (unpublished data). Expected ratio if mosses have no effect on roots is around "1."

In all, the evidence indicates that acids from precipitation and those released by humus, mosses, and lichens leach the surface soils of base cations and mobilize heavy metals (especially Al) to toxic levels, thus killing the fine roots and mycorrhizal fungi, interfering with the Ca and Mg uptake and transport, and slowing the cambial growth of trees (Alva et al., 2002; Cornish, 1999; Klinger, 1988; Shortle and Smith, 1988).

With the heavy Ca requirements of trees for maintaining healthy wood and bark (see Fig. 2), Ca and related mineral deficiencies rank high on the list of concerns of many scientists studying forest decline.

The acids produced by mosses and lichens are notorious for their ability to accelerate the weathering of substrates, including bark and rock. This raises the distinct possibility that the thick buildup of mosses and lichens on the trunks and branches of SOD-infected trees is degrading the protective bark layer and creating points of entry for *P. ramorum* and other pathogens into the stem. This buildup of mosses and lichens does not tend to occur in oaks managed with prescribed fires.

THE ROLE OF FUNGAL PATHOGENS

While *P. ramorum* ranges across the coastal forests of Northern California, its expression follows a general pattern whereby cankers occur mainly at the base of the older canopy trees in mixed-oak forests in moist valleys and on hillsides, especially where fog is frequent. The incidence of SOD is highest near the coast and declines

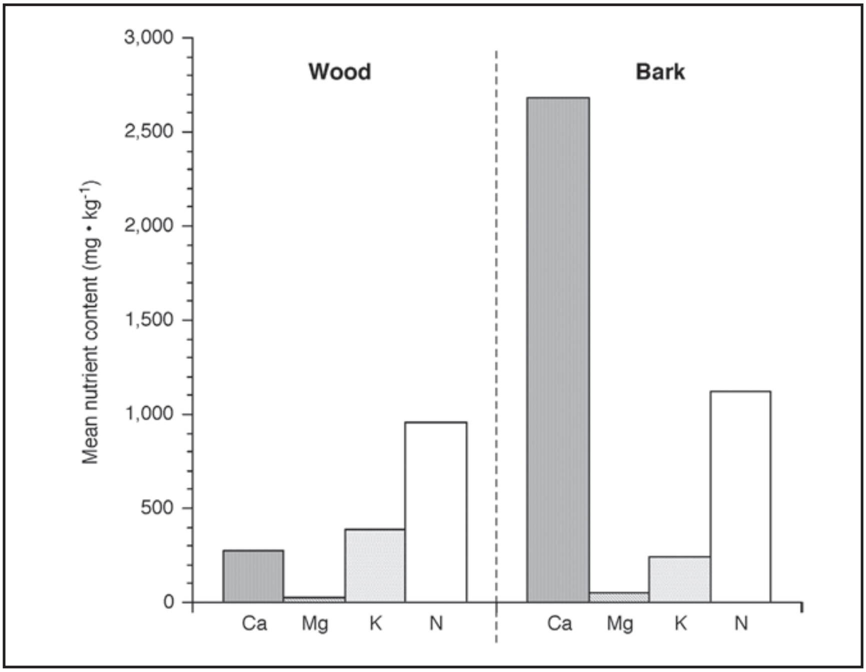

Figure 2. Summary of tissue assay for nine English Oaks (*Quercus robur*) (compiled from Bosman et al. 2001).

significantly with increasing distance from the coast (Murphy and Rizzo, 2005). Affected trees tend to occur in forests greater than 100 years old and with a heavy cover of mosses. The entire region has been under strict fire control for more than 50 years. A coastal to inland gradient of increasing precipitation pH, which has been observed elsewhere along the north Pacific coast (Klinger and Erickson, 1997), is also apparent here in northern California (McColl, 1980). The decline patterns and environment of this region are comparable to those of other forests around the world affected by decline (Huettl and Mueller-Dombois, 1993).

Both *Phytophthora* and *Pythium* pathogens have been observed to play a role in the decline of trees in Europe (Nechwatal and Oswald, 2001). These and other fungal pathogens attack the roots and cambium of certain trees and clearly contribute to the demise of these trees. Fungal pathogens are commonly associated with acidic environments and could well be opportunists preying upon trees weakened by mineral and water deficiencies. The addition of alkaline-rich minerals is well known to have a mitigating effect on the pathogenicity of *Phytophthora* species (Jung et al., 2000; Shea and Broadbent, 1983). Researchers have recently confirmed the fire-disease relationship for SOD, finding that the incidence of *P. ramorum* is extremely rare within the perimeter of any area burned since 1950 (Moritz and Odion, 2005).

Michael Coffey, Curator of the World *Phytophthora* Collection at the University of California, Riverside, believes that the concept of new *Phytophthora* species could be misleading since likely many, if not all, have been in place for decades, some perhaps for thousands of years. He suggests that the recent ability to use molecular

Table 1. Summary statistics of the chemical constituents in soil samples from sites of unhealthy trees in California.

Variable	Mean	Median	Std Dev	Units	N
Al	24.3	5.3	41.7	(ppm)	70
B	0.6	0.4	0.4	(ppm)	119
Ca	1389.0	1201.5	758.7	(ppm)	136
CEC	14.4	12.4	6.6	(meq/100g)	120
Cu	1.6	1.2	1.7	(ppm)	123
Fe	75.4	68.5	78.6	(ppm)	123
K	207.1	180.6	125.0	(ppm)	124
Mg	451.9	363.6	321.9	(ppm)	124
Mn	14.8	11.5	12.9	(ppm)	123
Na	56.3	34.7	86.3	(ppm)	124
NO_3-N	11.0	5.7	21.2	(ppm)	120
Org. Matter	4.8	4.2	3.4	(%)	120
P	28.4	13.5	34.0	(ppm)	132
pH	5.8	5.7	0.6		136
SO_4-S	21.6	7.0	66.8	(ppm)	117
Sol. Salts	0.6	0.4	0.9	(mmhos/cm)	117
Zn	6.5	2.7	9.4	(ppm)	123

methods to rapidly and accurately identify microbes such as *Phytophthora* has created the illusion that these pathogens are recently introduced and on the increase. In the case of SOD the extremely close similarity with a root pathogen *P. lateralis*, which has been recorded in the Pacific region forests since 1920, suggests the possibility that *P. ramorum* has been in the region for many decades. <http:www.geocities.com/m_d_coffey/sodoff2.html>

SOIL REMINERALIZATION

Not surprisingly, success in treating forest decline has been widely achieved using methods such as liming and burning, which ameliorate soil acidity and cryptogam cover. Burning and liming produce similar results as they both reduce the sources of acidity and raise the base cation concentration in the surface soils (Schreffler and W.E. Sharpe, 2003).

The traditional practice of applying limewash to the trunks of trees (i.e., whitewashing) has long been known to improve tree health. Limewashing is still a common practice in many traditional forest cultures around the world (e.g., in Mexico, China, and India). The large volume of studies on lime treatments of declining forests together indicate that the addition of lime-rich minerals clearly improves the health of trees (Wilmot et al., 1996), improves root and mycorrhizae growth (Coughlan, 2000), improves soil fertility (Hindar et al., 1996), reduces levels of toxic metals in soils (Alva et al., 1993), and reduces moss cover (Hallbacken and Zhang, 1998). In short, the application of lime-rich minerals appears to revitalize declining forest ecosystems.

OBSERVATIONS IN CALIFORNIA

Over the past few years soil samples and observations at sites with diseased trees (mainly SOD-infected oaks) provide some evidence that systemic acidification is occurring in California. Between February 2000 and December 2004, 136 surface soil samples were collected near unhealthy trees from a range of locations in California.

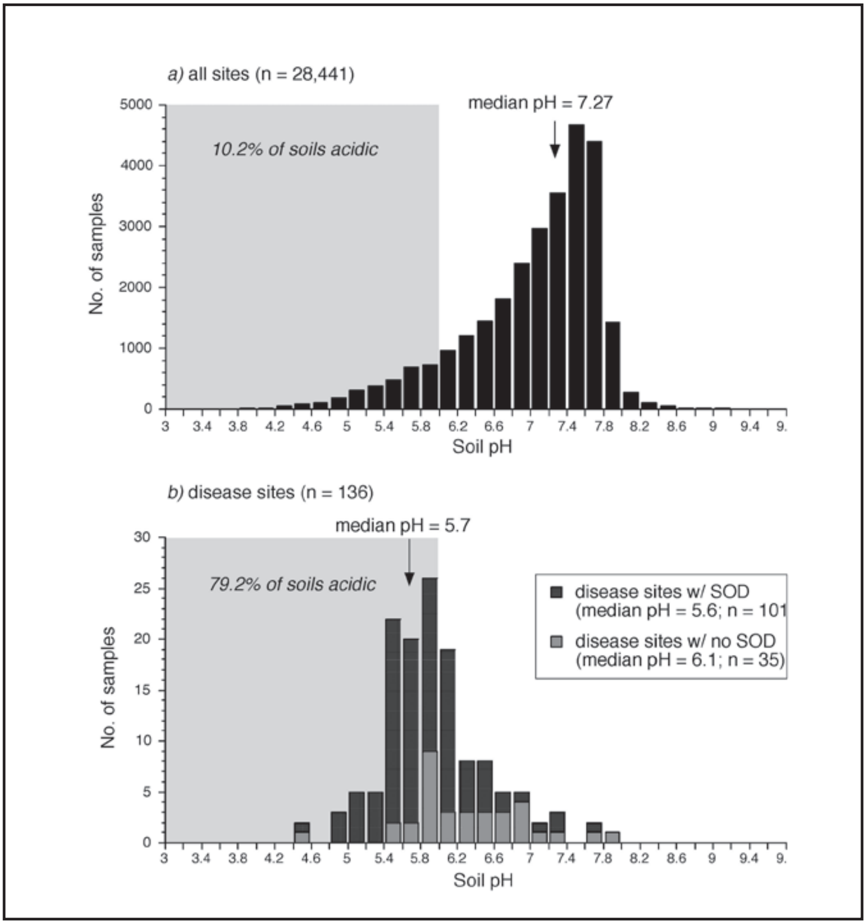

Figure 3. Frequency distributions of soil pH data from a) non-diseased sites (R. Miller, unpublished data) and b) diseased sites (this study) in landscaped and agricultural areas of California. SOD = sudden oak death.

Chemical analyses were performed on each soil sample by A & L Western Agricultural Laboratories (Modesto, California) (Klinger and Zingaro, 2005).

Table 1 lists the mean, median, standard deviation, and sample size for 17 soil chemistry variables. These results suggest that soils near SOD-affected trees are low in pH (median = 5.8) and Ca (median = 1201.5 ppm) and high in soluble Al (24.3 ppm) and Fe (75.4 ppm). Also, of the soils analyzed for lime content, nearly all (116 out of 120) were found to be low in excess lime.

Figure 3 shows the frequency distributions of soil pH, comparing the above data with a larger data set of soil pH from landscaped and cultivated soils in California. This figure indicates that soil pH is significantly lower in disease sites (median pH = 5.7) compared to the broader suite of other sites in California (median pH = 7.27).

Soil pH values as a function of nearest distance to the coast is plotted in Figure 4. For comparison, precipitation pH values from northern California are also

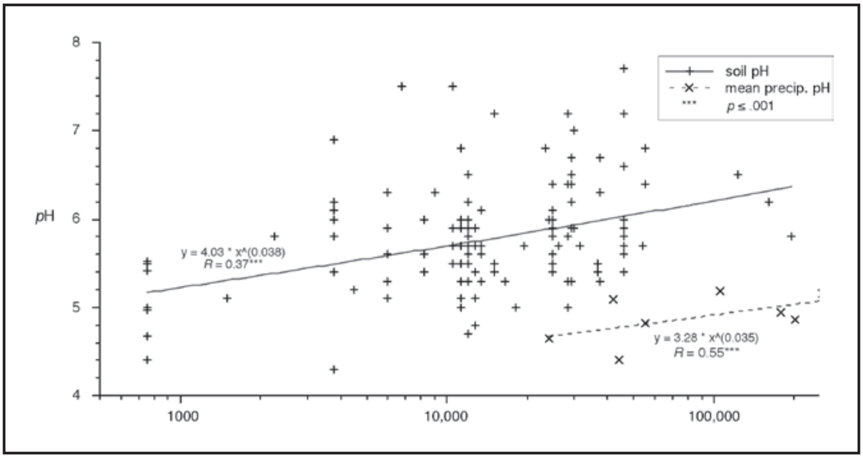

Figure 4. pH of soils (this study) and mean pH of precipitation (McColl 1980) as a log function of nearest distance to the coast in the sudden oak death-affected region of California. Best-fit lines of the data are power law functions (see equations). *R* is the regression coefficient; probability (*p*) ≤ .001 (***).

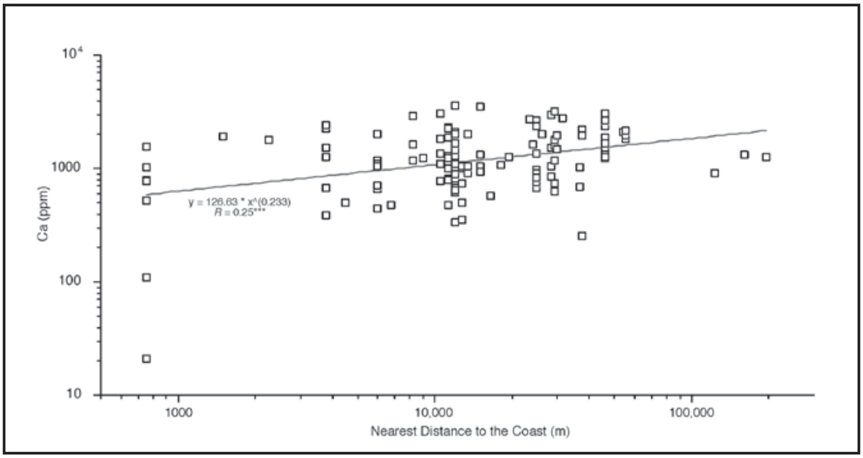

Figure 5. Calcium content of soils in this study as a log-log function of nearest distance to the coast in the sudden oak death-affected regions of California. Best-fit line of the data is a power law function (see equation). *R* is the regression coefficient; probability (*p*) ≤ .001 (***).

shown. These values were obtained from the NADP California region data sets <http://nadp.sws.uiuc.edu/> and from McColl (1980). The soil data reveal a strong coastal pH gradient, with the lowest pH levels found nearest the coast. Strong coastal gradients are also apparent in Ca (Fig. 5), which is lowest near the coast, and in Al (Fig. 6), which is highest near the coast.

As an interesting aside, these and other variables in this data set exhibit gradients that are best fit by power law functions (best fit equations are given in the figures). Power law functions are commonly used to describe systems that are frac-

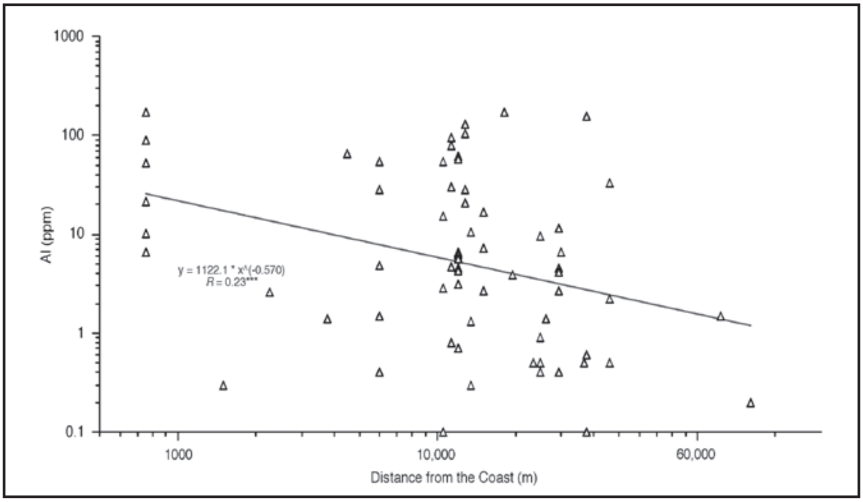

Figure 6. Aluminum content of soils in this study as a log-log function of nearest distance to the coast in the sudden oak death-affected region of California. Best-fit line of the data is a power law function (see equation). R is the regression coefficient; probability (p) $\leq .001$ (***).

tal, or self-similar, and are indicative of criticality in complex systems (Bak, 1996). The implication here is that the ecological and atmospheric systems in this region are behaving according to the principles of systems theory, which is the conceptual basis for systemic acidification in forest ecosystems (Klinger, 2004).

Finally, observations of declining trees in California (including many SOD-infected oaks) before and after being treated with mineral nutrient amendments to the soil and bark are showing vigorous new growth (see <http://www.suddenoaklife.org/>). These findings are only a few years along, but the consistency and quickness in the response of the trees to the lime-rich minerals is strongly indicative of a systemic acidification problem in these forests. Furthermore, recent findings suggest that the Native Americans in California knew about the role of acidification in tree decline and the importance of mineral amendments in sustaining older trees. Besides managing the forests with fires (Anderson, 2005), evidence indicates that they crushed seashells, bones, and other mineral-rich materials and then spread them to amend the soils around oaks and other important trees (Klinger, 2006).

CONCLUSIONS

The geographic and temporal patterns in soils and rainfall chemistry reported here for the SOD-affected regions of California are consistent with those that would be expected if the decline is associated with systemic acidification. These findings are similar to those found in southeast Alaska where forest decline has been incorrectly attributed to a fungal pathogen (Klinger, 1988).

Given these results and considering, as well, other evidence that systemic acidification is associated with forest decline in California, I conclude that an expanded definition of and approach to SOD is warranted.

Acknowledgements. The author would like to thank all those who have helped in the development of this work, and to acknowledge M. Coffey, Q.-J. Li, M. Cornish, L. Herrli, R. Zingaro, and R. Miller for sharing their related findings.

LITERATURE CITED

Alva, A.K., J.H. Graham, and **D.P.H. Tucker.** 1993. Role of calcium in amelioration of copper phytotoxicity for citrus. Soil Sci. 155:211-218.

Alva, A.K., B. Huang, S. Paramasivam, and **K.S. Sajwan.** 2002. Evaluation of root growth limiting factors in spodic horizons of spodosols. J. Plant Nutr. 25:2001–2014.

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

Ash, J. 1988. *Nothofagus* (Fagaceae) forest on Mt. Giluwe, New Guinea. New Zealand J. Bot. 26:245-258.

Bak, P. 1996. How nature works. Springer-Verlag, New York, New York.

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

Cornish, M. 1999. Forest decline as a successional process: the role of bryophytes in a montane ecosystem in the Colorado Rocky Mountains. M.Sc. Dissertation, The University of Oxford, Oxford.

Coughlan, A.P., Y. Dalpe, L. Lapointe, and **Y. Piche.** 2000. Soil pH-induced changes in root colonization, diversity, and reproduction of symbiotic arbuscular mycorrhizal fungi from healthy and declining sugar maple forests. Can. J. For. Res. 30:1543–1554.

Demchik, M.C. and **W.E. Sharpe.** 2000. The effect of soil nutrition, soil acidity and drought on northern red oak (*Quercus rubra* L.) growth and nutrition on Pennsylvania sites with high and low red oak mortality. For. Ecol. Mgt. 136:199–207.

Hallbacken, L. and **L.Q. Zhang.** 1998. Effects of experimental acidification, nitrogen addition and liming on ground vegetation in a mature stand of Norway spruce (Picea abies (L.) Karst.) in SE Sweden. For. Ecol. Mgt. 108:201–213.

Hindar, A., F. Kroglund, E. Lydersen, A. Skiple and **R. Hogberget.** 1996. Liming of wetlands in the acidified Lake Roynelandsvatn catchment in southern Norway: effects on stream water chemistry. Can. J. Fisheries Aquatic Sci. 53:985–993.

Hinrichsen, D. 1987. The forest decline enigma. BioSci. 37:542–546.

Huettl, R.F. and **D. Mueller-Dombois** (eds.) 1993. Forest Decline in the Atlantic and Pacific Regions. Springer-Verlag, Berlin.

Huntington, T.G. 2000. The potential for calcium depletion in forest ecosystems of southeastern United States: Review and analysis. Global Biogeochem. Cycles 14:623–638.

Jane, G.T. and **T.G.A. Green.** 1987. Etiology of forest dieback areas within the Katmai Range, North Island, New Zealand. New Zealand. J. Bot. 24:513–527.

Joslin, J.D., J. M. Kelly, M.W. Wolfe, and **L.E. Rustad.** 1988. Elemental patterns in roots and foliage of mature spruce across a gradient of soil aluminum. Water, Air Soil Poll. 40:375–390.

Joslin, J.D. and **M.H. Wolfe.** 1989. Aluminum effects on northern red oak seedling growth in six forest soil horizons. Soil Sci. Soc. Amer. J. 53:274–281.

Jung, T., H. Blaschke, and **W. Oswald.** 2000. Involvement of soilborne Phytophthora species in Central European oak decline and the effect of site factors on the disease. Plant Pathol. 49:706–718.

Klein, R.M. 1984. Effect of acidity and metal ions on water movement through red spruce, p. 303–322. In: D.D. Adams and W.P. Page (eds.) Acid deposition. Plenum Press, New York, New York.

Klinger, L.F. 1988. Successional change in vegetation and soils of southeast Alaska. Doctoral dissertation, Department of Geography, University of Colorado, Boulder, Colorado.

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

Klinger, L.F. 1991. Peatland formation and ice ages: a possible Gaian mechanism related to community succession, p. 246–255. In: S.H. Schneider and P.J. Boston (eds.) Scientists on Gaia, The MIT Press, Cambridge, Massachusetts.

Klinger, L.F. 1996. Coupling of soils and vegetation in peatland succession. Arctic Alpine Res. 28:380–387.

Klinger, L.F. and **D.J. Erickson III.** 1997. Geophysiological coupling of marine and terrestrial ecosystems. J. Geophys. Res.-Atmos. 102:25,359–25,370.

Klinger, L.F. 2004. Gaia and complexity, p.187–200. In S.H. Schneider, J.R. Miller, E. Crist, and P.J. Boston (eds.), Scientists Debate Gaia: The Next Century. The MIT Press, Cambridge, MA.

Klinger, L., and **R. Zingaro.** 2005. Etiology and evidence of systemic acidification in SOD-affected forests of California. Sudden Oak Death Science Symposium II, 18–21 Jan. 2005, Monterey, California.

Klinger, L.F. 2006. Ecological evidence of large-scale silviculture by California Indians. In: Wahinkpe Topa (Four Arrows) (ed.), Unlearning the language of conquest. Univ. Texas Press, Austin, TX (in press).

Manion, P.D. 1981. Tree disease concepts. Prentice Hall, Inglewood Cliffs, New Jersey.

Matzner, E., D. Murach, and **H. Fortmann.** 1986. Soil acidity and its relationship to root growth in declining forest stands in Germany. Water Air Soil Poll. 31:273–282.

McColl, J.G. 1980. A survey of acid precipitation in Northern California. Final Rept. Agric. Exper. Station, Univ. California, Berkeley, California.

McLaughlin, D.L., S.N. Linzon, D.E. Dimma, and **W.D. McIlveen.** 1987. Sugar maple decline in Ontario, p. 101–116. In: T.C. Hutchinson & K.M. Meema (eds.), Effects of atmospheric pollutants on forests. Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin.

Moritz, M.A. and **D.C. Odion.** 2005. Examining the strength and possible causes of the relationship between fire history and sudden oak death. Oecolgia DOI 10.1007/s00442–005–0028–1.

Mueller-Dombois, D. 1987. Natural dieback in forests. BioSci. 37:575–583.

Mueller-Dombois, D. 1988. Forest decline and dieback — A global ecological problem. TREE 3:310–312.

Murphy, S. and **D. Rizzo.** 2005. Incidence of *Phytophthora ramorum, P. nemorosa,* and *P. pseudosyringae* in three coastal California forest communities. Sudden Oak Death Science Symposium II, 18–21 Jan. 2005, Monterey, California.

Nechwatal, J. and **W. Oswald.** 2001. Comparative studies on the fine root status of healthy and declining spruce and beech trees in the Bavarian Alps and occurrence of *Phytophthora* and *Pythium* species. For. Pathol. 31:257–273.

Ouimet, R., C. Camire, and **V. Furlan.** 1995. Endomycorrhizal status of sugar maple in relation to tree decline and foliar, fine-roots, and soil chemistry in the Beauce region, Quebec. Can. J. Bot.73:1168–1175.

Schütt, P. and **E. Cowling.** 1985. Waldsterben, a general decline of forests in central Europe: Symptoms, development, and possible causes. Plant Dis. 69:548–558.

Schaberg, P.G., D.H. DeHayes, and **G.J. Hawley.** 2001. Anthropogenic calcium depletion: A unique threat to forest ecosystem health? Ecosystem Health 7:214–228.

Schreffler, A.M. and **W.E. Sharpe.** 2003. Effects of lime, fertilizer, and herbicide on forest soil and soil solution chemistry, hardwood regeneration, and hardwood growth following shelterwood harvest. For. Ecol. Mgt. 177:471–484.

Shea, S.R. and **G.C.P. Broadbent.** 1983. Developments in cultural and biological control of *Phytophthora* diseases, p.335–350. In: Erwin, Bartnicki-Garcia, and Tsao (eds.), *Phytophthora*: Its biology, taxonomy, ecology and pathology. APS Press, Saint Paul, Minnesota.

Shortle, W.C. and **K.T. Smith.** 1988. Aluminum-induced calcium deficiency syndrome in declining red spruce. Science 240:1017–10118.

Smith, J.M.B. and **L.F. Klinger.** 1985. Aboveground-belowground phytomass ratios in Venezuelan Paramo vegetation and their significance. Arctic Alpine Res. 17:189–198.

Thomas, F.M., R. Blank, and **G. Hartmann.** 2002. Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. For. Pathol. 32:277.

Wardle, J.A. and **R.B. Allen.** 1983. Dieback in New Zealand *Nothofagus* forests. Pac. Sci. 37:397–404.

Wilmot, T.R., D.S. Ellsworth, and **M.T. Tyree.** 1996. Base cation fertilization and liming effects on nutrition and growth of Vermont sugar maple stands. For. Ecol. and Mgt. 84:123–134.