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A Etiology and Evidence of Systemic Acidification in SOD-Affected Forests of California

Lee F. Klinger
Independent Scientist
San Anselmo, CA

Ralph Zingaro
White Mountain Horticultural Consulting LLC
Harrisville, NH

and

Michael D. Coffey
Department of Plant Pathology
University of California
Riverside, CA 92521

Abstract

Pathologists investigating the widespread death of oak trees in the forest ecosystems of northern California concluded, in 2000, that the problem was due to a new plant disease, dubbed Sudden Oak Death (SOD), which was caused by the fungal pathogen *Phytophthora ramorum*. Since then this one organism has been the focal point of notable efforts to understand, monitor, and control SOD. While not disputing that *P. ramorum* is involved in the final demise of many oaks, there are a growing number of scientists and arborists who do not agree that this pathogen is the fundamental cause of the overall decline. These experts point out that most of the dying oaks in SOD-affected forests show no expression of *P. ramorum*. They further note that the etiology of SOD closely resembles that seen in other aging forests where the decline of the trees has been attributed to an increase in acidity and mineral deficiency of the water and soils. In these places, acidic conditions create mineral imbalances and deficiencies in trees, especially calcium, which greatly weaken the trees, raising their susceptibility to secondary pests and pathogens. Here we present evidence that suggests systemic acidification of forests can explain, quite well, the entire SOD phenomenon.

The etiology of SOD in California coincides closely with the symptoms of systemic acidification in aging forest ecosystems. Dieback starts with the upper and outer branches in the crown, showing a pattern of wilting and browning of leaves along with dead small branches and progressively spreading to the lower parts of the crown over several years. The decline affects nearly all kinds of oaks, as well as bays, buckeyes, pines, and so forth, 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 (greater than 100 years old) and are always found in association with a heavy cover of mosses and lichens. Moss mats have been shown in both laboratory and field studies to create conditions acidic enough to kill the 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. In general, the etiology of SOD in California is much like that seen elsewhere in dying oaks (e.g., Texas, Missouri, Pennsylvania, Manitoba, and Europe), except that *P. ramorum* is not found to be involved in these other declines.

Data on pH from 34,700 soil samples taken from a wide range of agricultural and forest soils in California indicate that between 10.2 and 21.5% of the soils are acidic (pH < 6.0) and 1.6 to 4.3% are strongly acidic (pH < 5.0). However, a set of samples taken from SOD-affected sites indicates that 72% of these soils are acidic and 4% are strongly acidic (median pH = 5.7; n = 136). The soils from these 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. Precipitation chemistry data from this region also reveal a coastal pH gradient much like that found in the soils. Similar coastal gradients in precipitation pH have been reported from the Olympic peninsula, from southeast Alaska, and from Scandinavia.

These results lend further support to the theory that systemic acidification is adversely affecting the health of the trees and soils in SOD-affected forests. The situation described here in California is not unlike that in other regions of the world where aging forests are experiencing decline. From this and other work (e.g., studies at Hubbard Brook), we strongly believe that the cause (and the definition) of SOD is still an open question, and that

the scope of SOD research should be expanded to include studies of acidification by cryptogams in the context of forest and soil ecology.

Introduction

Sudden Oak Death (SOD), defined by 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 over 40 species of California plants and in nursery plants around the US. While the current research is focused on the genetics, transmission, and epidemiology of the *Phytophthora ramorum* (*P. r.*) 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[1]. In the case of SOD, such an approach seems especially pertinent given that the Lead PI (Dr. Lee Klinger) and others[2] have observed that most of the trees dying in SOD-affected forests show no visible expression of the *P. r.* pathogen. The presence of secondary pests like Ambrosia beetles in SOD-affected forests raises the possibility that *P. r.*, too, may be secondary, that there are other agents acting to weaken the trees and increase susceptibility to fungal attack. Clearly, any credible information which implicates factors other than *P. r.* in SOD must be carefully investigated. This paper investigates the regional patterns in soils and precipitation chemistry data from California as related to the role of systemic acidification in SOD.

Background

In studies of ecosystem change, ecologists have frequently reported how maturing landscapes and seascapes progress through a series of characteristic communities, stages of development much like those of individual organisms[3]. 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[4]. This process of *systemic acidification* is due, in part, to the buildup of biomass (mainly plant organic matter) which, upon 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 (*e.g.*, top dieback, reduced rates of radial growth (Kreuter 1993 in Huettl & Mueller Dombois 1993), fine root mortality).

In the early 70s scientists in the US 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. Billions of dollars of US and European government funds were poured into research on the affects of acid rain and air pollution on trees. Well before the studies were complete the popular press picked up on the acid rain issue and soon had the public convinced that forest decline around the world was attributable to acid rain or air pollution. But upon completion of these major research programs, forest scientists concluded, still unbeknownst to the general public, that acid rain and air pollution are *not* the primary causes of forest decline[5]. Some reasons for this are obvious. Forest decline with symptomology identical to that found in polluted regions occurs extensively in unpolluted areas such as Alaska[6], Hawaii[7], New Zealand[8], the southern Andes[9], Borneo[10], and New Guinea[11]. This pattern alone suggests the involvement of natural processes of tree death, which may be exacerbated by high pollution levels. Most work on possible natural causes of forest decline centers on biotic damaging agents such as insects and fungal pathogens, and on the damaging effects of climate. Little work has been done on community and ecosystem processes related to forest decline, especially with respect to succession[12]. In general, hypotheses and investigations of forest decline have focused on patterns and processes occurring over a rather narrow range of spatial and temporal scales. For instance, there are virtually hundreds of studies on the short-term (≤ 1 year) effects of various pollutants on leaves and branches (and occasionally entire individuals) of trees and crops plants. Yet, few, if any studies address the predicted or observed ecosystem- or global-scale patterns of forest decline occurring presently or over the past few centuries.

"Decline" or "dieback" are terms used synonymously to describe forests where the majority of trees show reduced vigor or are standing dead[13]. 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 is a global phenomenon[14] that has been occurring sporadically for at least several hundred years in many areas[15]. Forest decline tends to occur in moist to wet sites, though not always[16], and there is growing evidence that tree death can be drought-induced[17]. In some areas tree death occurs in groups[18], but more often mortality is scattered throughout an affected forest in a seemingly random pattern[19]. Forest decline affects mainly mature or old-growth forests, and tends to affect canopy trees more severely than subcanopy trees[20]. Yet, growing within heavily-damaged forests are some canopy trees which are barely, if at all, affected[21]. Seedling and sapling growth in damaged areas may or may not be strongly inhibited[22]. Death of surrounding understory is rarely observed[23].

Affected trees tend to exhibit dieback beginning at the top or outermost branches and progressing downward or inward[24]. Decreased diameter growth is commonly associated with forest decline[25], as are symptoms of nutrient deficiencies (e.g., chlorosis) and water-stress[26]. In studies where belowground plant tissue has been examined, mortality of very fine (feeder) roots and mycorrhizae has also been documented[27]. Of particular importance is the observation that feeder root and mycorrhizae mortality occurs prior to the onset of aboveground dieback symptoms[28]. 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*29*, depleted in base cations*30*, and enriched in soluble Fe and Al*31*.

A recent set of 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, and Colorado*32*. These studies follow off of earlier findings from Venezuela 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. Other studies have found that the mortality of feeder roots and mycorrhizae occurs <u>prior to</u> the onset of aboveground symptoms*33*. Fine root mortality in areas of forest decline is closely tied to soil acidification*34*, especially where calcium levels are low*35*. Soluble aluminum concentrations are reported to be high in the organic soil horizons and in the soil water beneath declining trees*36*. The fine roots of declining trees are found to contain significantly more Al than those of healthy trees*37*. Controlled laboratory experiments show a significant inverse correlation between soil Al and the live root biomass in oaks*38*. Strong acidification and high concentrations of soluble Al in soil water are reported to inhibit the growth of endomycorrhizal fungi*39*. It is important to note that these soil conditions have been clearly documented in declining oak forests around the U.S.*40*. In summary, the evidence indicates that organic acids released by mosses and other cryptogams leach the surface soils of base cations and mobilize heavy metals (especially Al) to toxic levels*41*, thus killing the fine roots and mycorrhizal fungi, interfering with the Ca and Mg uptake and transport*42*, and slowing the cambial growth of trees*43*. Given the heavy Ca requirements of trees for maintaining healthy wood and bark, Ca deficiency ranks high on the list of concerns of forest scientists. Furthermore, the acids produced by mosses are notorious for their ability to accelerate the weathering of substrates, including bark and even rock. It is likely, therefore, that mosses growing thickly on the trunks and branches of certain trees are degrading the trees' protective bark and creating points of entry for pathogens, insects, and other pests into the stem.

Following the early phases of forest decline which occurs in the subtle presence of mosses, the later phases are clearly associated with peat-forming mosses, especially *Sphagnum*. The significant role of peat formation in forest decline has long been recognized by ecologists who have labelled the process *paludification*. The term paludification was first used by Auer to refer to the establishment and growth of peat-forming plant communities taking place both on dry lands and in bodies of water[44]. In recent years this term has been applied exclusively to the succession from dry land to bog, and the term "terrestrialization" has been applied to the process of bog formation from the infilling of a water body. Numerous physical mechanisms for paludification have been proposed including rising water tables[45], reduced thawing depth[46], and soil hardpan formation[47]. Extensive paludification in the British Isles and Scandanavia has been attributed to forest depradation by early humans[48]. Paludification has also been attributed to biological mechanisms such as the growth of peat-forming vegetation[49] and beaver activity[50].

Typically treated merely as indicators, *Sphagnum* and other peat-forming mosses appear to play much more an active role in paludification than previously believed. This can be clearly seen in the phenomena known as “wave dieback”. I first saw this phenomena in Peril Straits which separates Baranof and Chichagof Islands in southeast Alaska, where circular and elliptical rings of dieback appear within the old-growth forests. These rings may be anywhere from several meters to thousands of meters in circumference and are expanding outward. Dead trees, fallen logs, and large stumps abound within the rings, whereas in the forests outside the rings there is noticably less dieback. In the narrow zone of dieback forming the rings there is an abundance of *Sphagnum* mosses, and if one observes the very edge of the ring, the line between mostly healthy forest and dying forest, one finds a virtual *Sphagnum* wave moving along, slow but steady.

The wave-like progression of forest dieback has been seen in many places[51]. On Mt. Mitchell in North Carolina, the highest mountain in the Appalachians, the wave dieback of red spruce near the summit is associated with waves of *Polytrichum* mosses. On Whiteface Mountian in the Adirondack Mountains of upstate New York, the dieback of balsam fir occurs in elongated waves which move upslope at rates of about a half meter to a meter per year. At the margin are billowing mats of *Sphagnum* transforming the ecosystem into a mossy heathland. Here, and elsewhere, the pattern can be best understood if the site is visited during the brief period in spring when all but the deepest snows have melted. Sites around and under late-lying snowbanks are preferred habitats for mosses. These snowbanks provide a steady source of moisture and nutrients which extends well into the spring when sunshine is strong and air temperatures are warm. Mosses which begin growing immediately upon thawing, are able to take immediate advantage of this optimal environment, while vascular plants must await the thawing of subsoils and the growth of new leaves in order to take full advantage of this short-lived springtime condition. Thus, the waves of mosses demark shifting lines of deep snowbanks which form every winter and melt away every spring.

The acids produced by mosses are also notorious for their ability to accelerate the weathering of substrates, including bark and rock. This raises the question of whether the thick moss cover on the trunks and branches of SOD-infected trees is degrading the protective bark layer and creating points of entry for *P. r.* and other pathogens into the stem. Mosses clearly must be considered and studied if they are present in areas of tree decline.

Furthermore, the tests for pathogenicity of *P. r.* must include controls for mosses before any claims can be made that *P. r.* is the ultimate cause of SOD.

While the SOD pathogen 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. Affected trees tend to occur in forests greater than 100 years old and with a heavy cover of mosses[52]. The entire region has been under strict fire control for more than 50 years. Increasingly strongly acidic soils have been noted in Sonoma, Marin, Mendocino, and Lake Counties[53]. A coastal to inland gradient of increasing precipitation *p*H, as has been observed elsewhere along the north Pacific coast[54], is also apparent here in northern California[55]. The decline patterns and environment of this region are comparable to those of many other forests around the world affected by decline[56].

Role of Phytophthora

The role of Phytophthora species in forest decline has attracted much attention recently in both California and Europe. While not disputing that Phytophthora may have a significant role in accelerating the demise of some trees there are obviously tree losses that cannot be attributed to this pathogen. In fact other root-nibbling organisms such as Pythium have also been implicated in some European forest decline situations[57]. The Sudden Oak Death situation in California is different in that there is supposedly no function for Phytophthora ramorum as a root pathogen. Sudden oak death is attributable primarily to above ground symptoms, especially trunk cankers. However it is likely that there is a soil phase in the disease cycle of this pathogen since it produces abundant chlamydospores potentially capable of long-term survival and germinability. In addition, many oaks from which Phytophthora has not been isolated are in decline. The root health of oaks is deserving of much closer attention. Are 'root nibblers' such as Pythium, or indeed Phytophthora at work? What is the status and health of mycorrhizal associations in roots in these affected areas?

I believe there are likely to be other associated factors in forest decline, especially environmental degradation (impact of sulfur dioxide, nitrogen dioxide, acid rain, ozone, water quality, increased carbon dioxide levels, global warming, droughts, floods) that can reduce the resistance of the forest to pest and pathogen attack. It is also possible that some of the death we are seeing is attributable to the natural cycle of death and renewal in the forest. One specific example in a plethora of complex interactions is deserving of some attention. The prolonged absence of natural burning and the likely consequent excessive depletion of nutrients from the soil such as calcium might be expected to be a significant factor in disturbance of this natural cycle. There is a voluminous literature of the different effects of calcium, both direct on oak decline[58] and indirect on the biology and pathology of Phytophthora in naturally suppressive and calcium carbonate amended soils[59].

The concept of new Phytophthora species could be misleading since likely many, if not all, have been in place for decades[60], some perhaps for thousands of years. The recent ability to use molecular 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 fact even in the case of SOD the extremely close similarity with a root pathogen Phytophthora lateralis which has been recorded in the Pacific region forests since 1920 suggests the possibility that it has been in the region for many decades.

I favor the concept developed by Erwin Fuhrer[61] and others[62] in describing the oak decline situation in Central Europe. He describes oak decline as a 'complex of diseases'. No one set of stress factors nor one pathogen can accurately describe the situation. Fuhrer emphasizes a 'complex of diseases' with a 'combination of predisposing and inciting factors' dependent on the geographical location and conditions.

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 (by killing the cryptogams) and raise the base cation concentration in the surface soils[63]. The traditional practice of applying limewash to the trunks of trees (*i.e.*, whitewashing) has long been known to improve tree health and reduce insect pests and mosses growing on the bark. 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 that addition of lime-rich minerals clearly improves the health of trees[64], improves root and mycorrhizae growth[65], improves soil fertility[66], reduces levels of toxic metals in soils[67], and reduces moss cover[68]. In short, remineralization appears to slow or arrest the aging process in ecosystems.

Methods

Between February 2000 and December 2004 126 surface soil samples were collected near trees affected by Phytophthora canker disease and/or other symptoms of decline from variety of locations in California.

Chemical analyses were performed on each soil sample by A & L Western Agricultural Laboratories (Modesto, CA). The precipitation chemistry values used in this study were obtained from the NADP California region data sets[69] and from McColl[70].

Results and Interpretation

Table 1 lists the mean, median, standard deviation, and sample size for 17 soil chemistry variables. These results indicate 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.

Table 2 compares the soil pH statistics in three soil data sets representing both diseased and non-diseased sites in landscaped and agricultural areas of California. Figure 1 shows the frequency distributions for two of these data sets. Soil pH is significantly lower in disease sites (median pH = 5.7) compared to non-diseased sites (median pH = 7.27 & 6.84) . . .

These results are indicative of systemic acidification of the soils . . .

Soil pH values as a function of nearest distance to the coast is plotted in Figure 2. These data reveal a strong coastal pH gradient with the lowest soil pHs found nearest the coast. Strong coastal gradients are also apparent in Ca (Figure 3) and Na (Figure 4), which are lowest near the coast, and in Al (Figure 5), which is highest near the coast. Further indication of systemic acidification . . .

Precipitation pH data from northern California are plotted with the soil pH data in Figure 2. The results show that a coastal gradient also exists in precipitation pH. Coastal pH gradients similar to this one have been found in southeast Alaska and elsewhere[71]. Again these findings are to be expected with systemic acidification . . .

The low levels of Ca and Na in soils near the coast (Figures 3 & 4) are inconsistent with what would be expected from the elevated inputs of sea salt near the coast. As is shown in

Figure 6, ions Na and Cl from precipitation are significantly elevated near the coast. Thus, additional loss mechanisms for Ca and Na must be present in order to account for these gradients. The enhanced acidity near the coast brought about by greater moss cover and other sources of systemic acidification is a likely way to explain these results.

As an interesting aside, all of these variables exhibit a gradient that is best described by power functions (equations are given in the respective figures). Power functions are commonly used to describe systems that are fractal, or self-similar, and are indicative of criticality in complex dynamic systems[72]. 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[73].

Temporal trends in precipitation chemistry data were examined for Hopland, the only NADP site within the region affected by SOD. The annual mean pH of precipitation at Hopland for the period 1980 to 2003 (24 years) are plotted in Figure 7. This time series shows a significant decrease in pH, indicating that atmospheric input of acidity in the region of SOD is increasing. The sources for this acidity, however, are not clear. The usual candidates for acid precipitation, NO_3 and SO_4 from emissions, cannot explain the decline in pH over time. NO_3 levels in precipitation at Hopland show no trend[74] and the SO_4 levels in precipitation show a significant decrease over the same time period. Thus, the most likely sources of acidity here are organic acids (e.g., formic acid, acetic acid) derived from oxidation products of biogenic volatile compound emissions from forest and marine ecosystems. Why these biogenic emissions would be increasing over the past few decades may be related to increased ocean productivity stimulated by elevated oceanic inputs of organic Fe from adjacent terrestrial areas due to acidification[75].

Discussion

Conclusion

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 the *Phytophthora* pathogen[76] . . .

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

Table 1. Summary statistics of the chemical constituents in soil samples from disease sites.

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
NO3-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
SO4-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

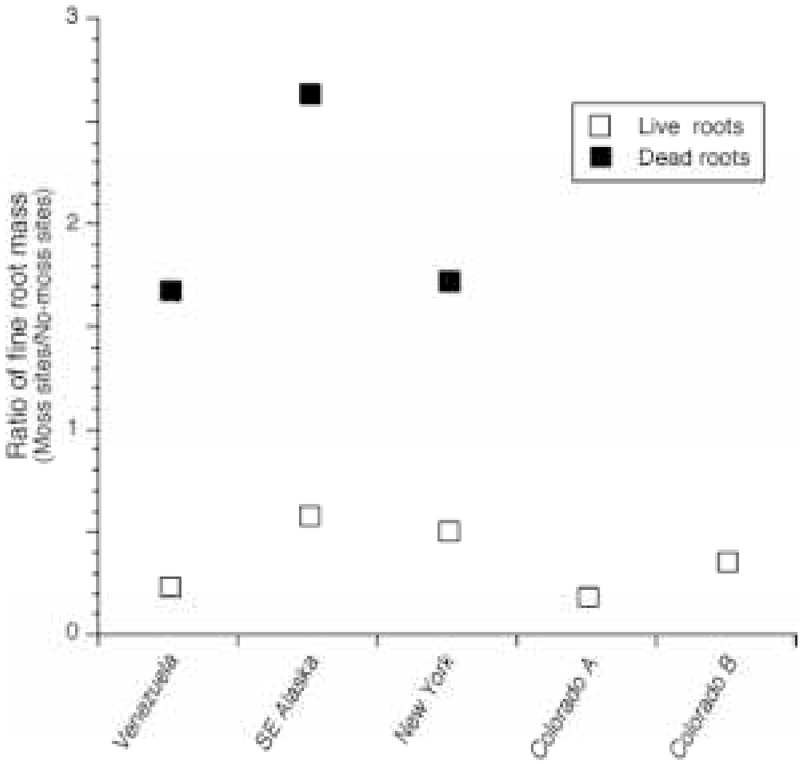

Figure x. Ratios of fine root mass.

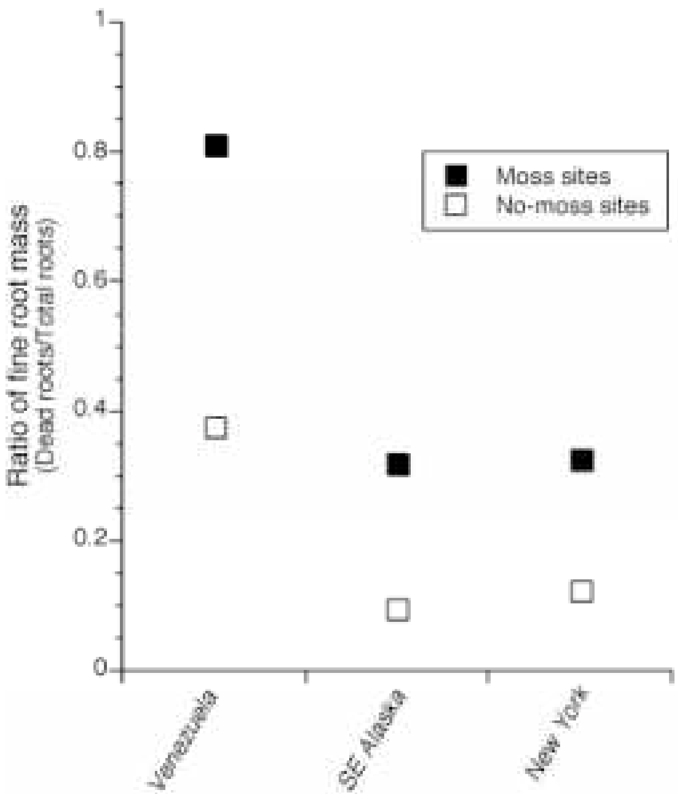

Figure x. Ratios of fine root mass.

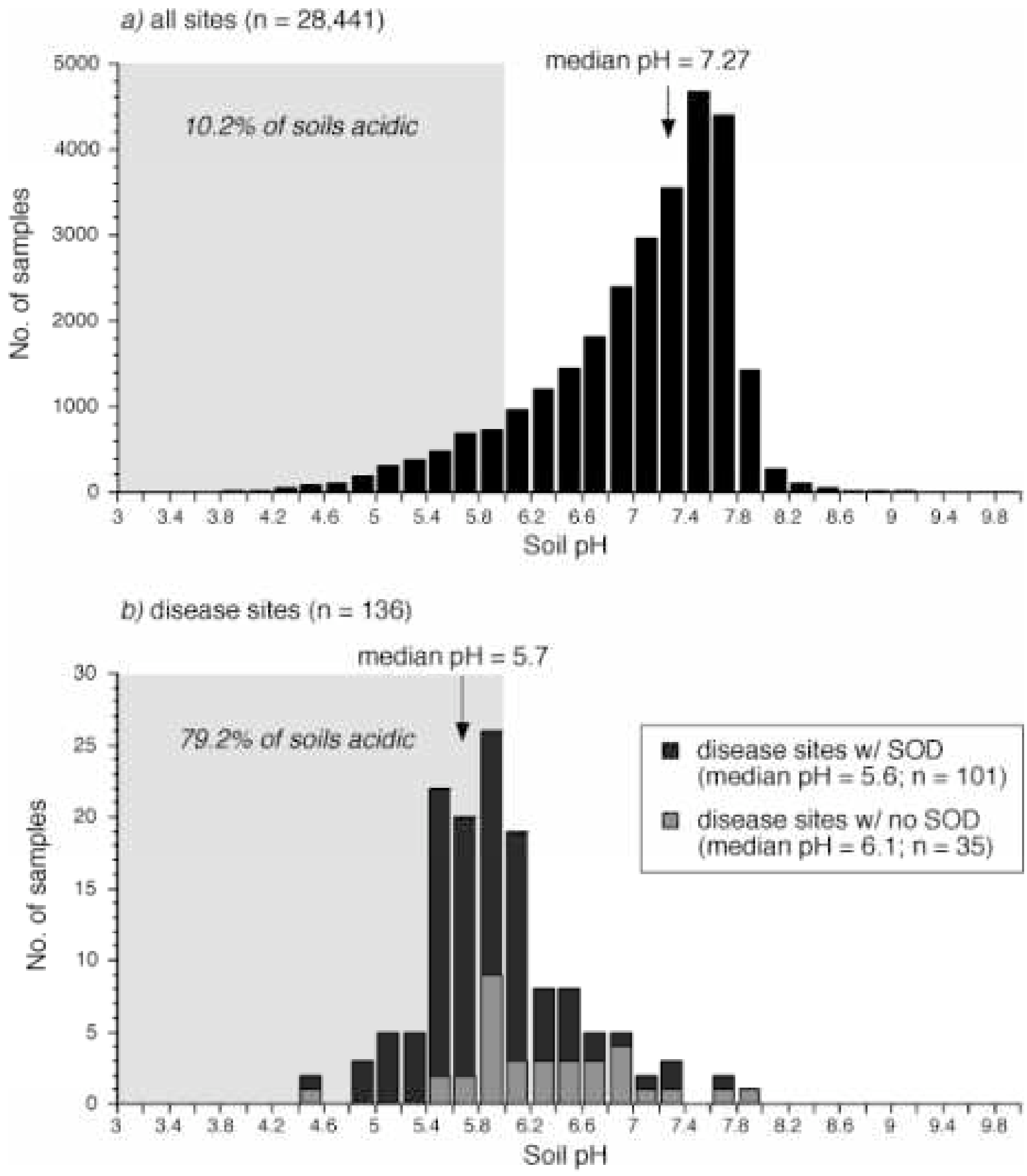

Figure 1. Frequency distributions of soil pH data from a) non-diseased sites and b) diseased sites in landscaped and agricultural areas of California.

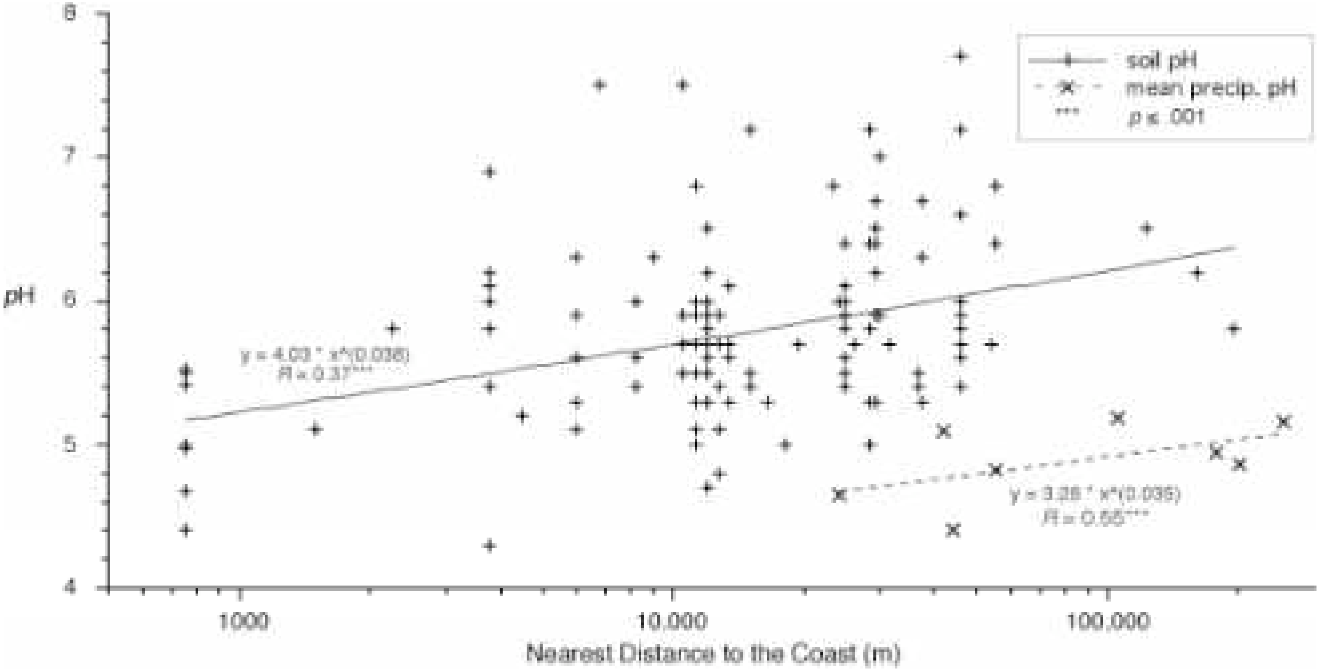

Figure 2. *p*H of soils (this study) and mean *p*H of precipitation (McColl 1980) as a log function of nearest distance to the coast in the SOD-affected region of California. Best fit lines of the data are all power law functions of a similar kind (see equations). *R* is the regression coefficient and *p* is the level of probability (*** - $p \leq .001$).

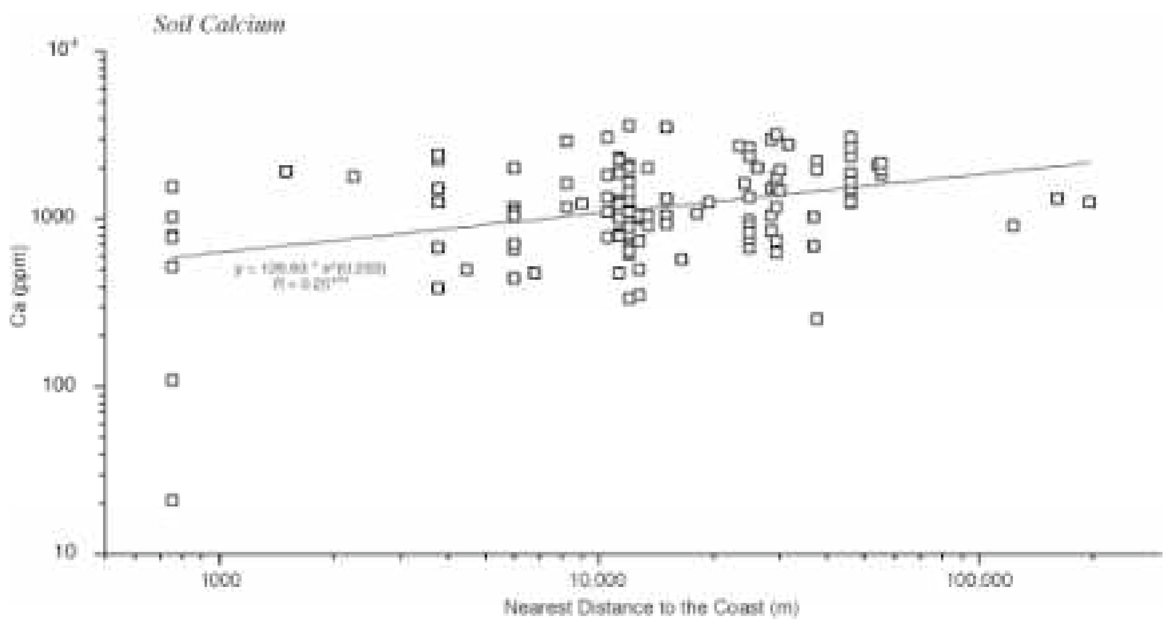

Figure 3. Ca content of soils in this study as a log-log function of nearest distance to the coast in the SOD-affected regions of California. Best fit lines of the data are power law functions (see equations). *R* is the regression coefficient (*** - $p \leq .001$).

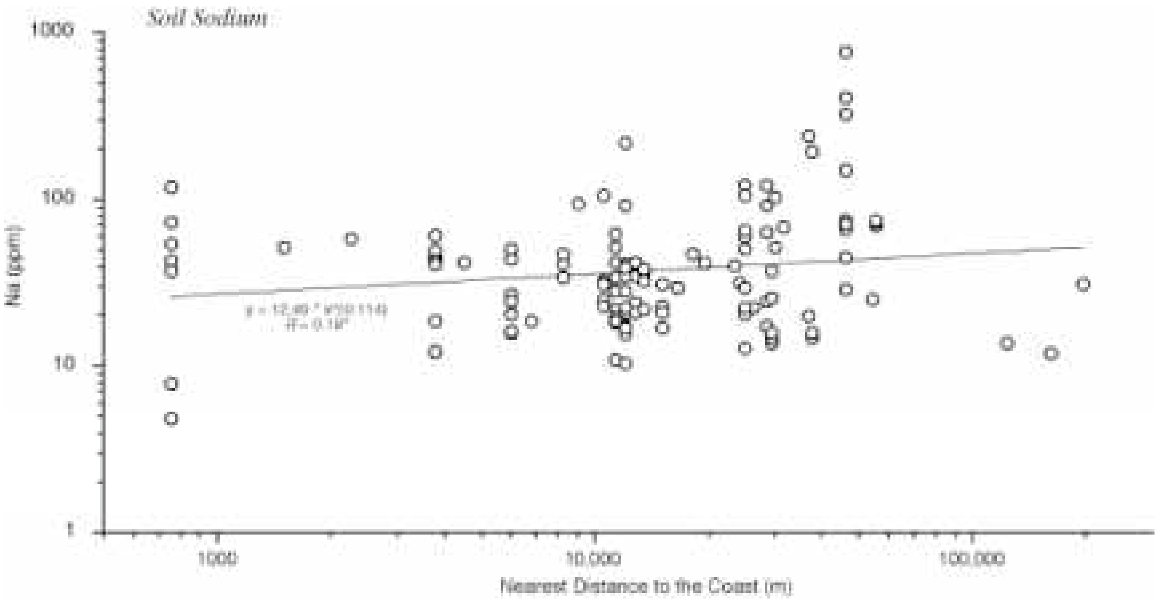

Figure 4. Na content of soils in this study as a log-log function of nearest distance to the coast in the SOD-affected region of California. Best fit lines of the data are power law functions (see equations). *R* is the regression coefficient (* - $p \leq .05$).

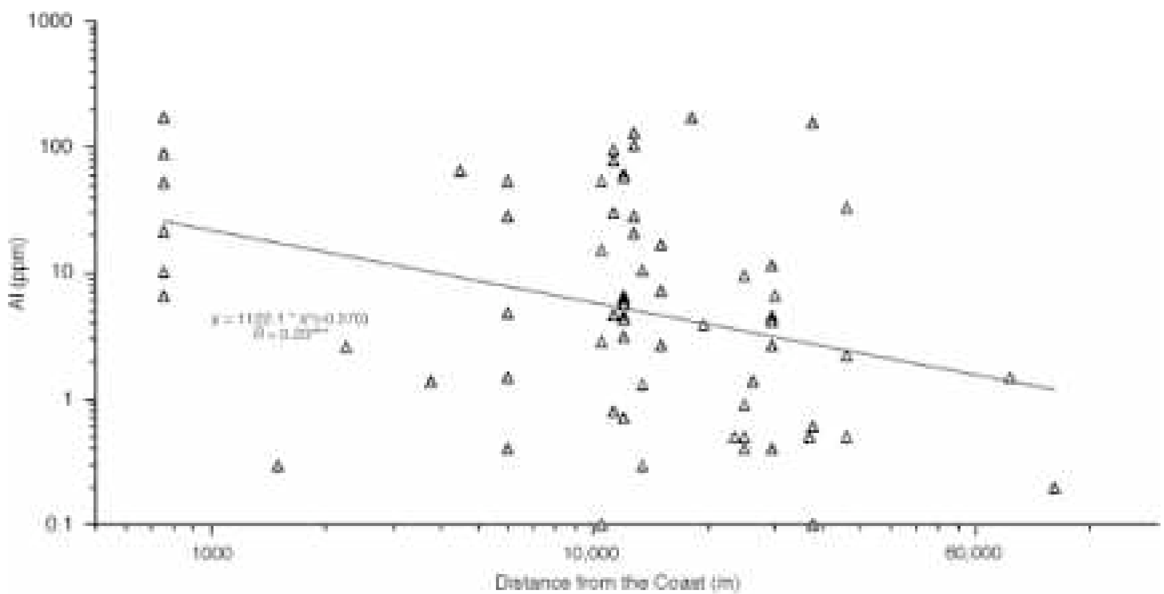

Figure 5. Al content of soils in this study as a log-log function of nearest distance to the coast in the SOD-affected region of California. Best fit lines of the data are power law functions (see equations). *R* is the regression coefficient (*** - $p \leq .001$).

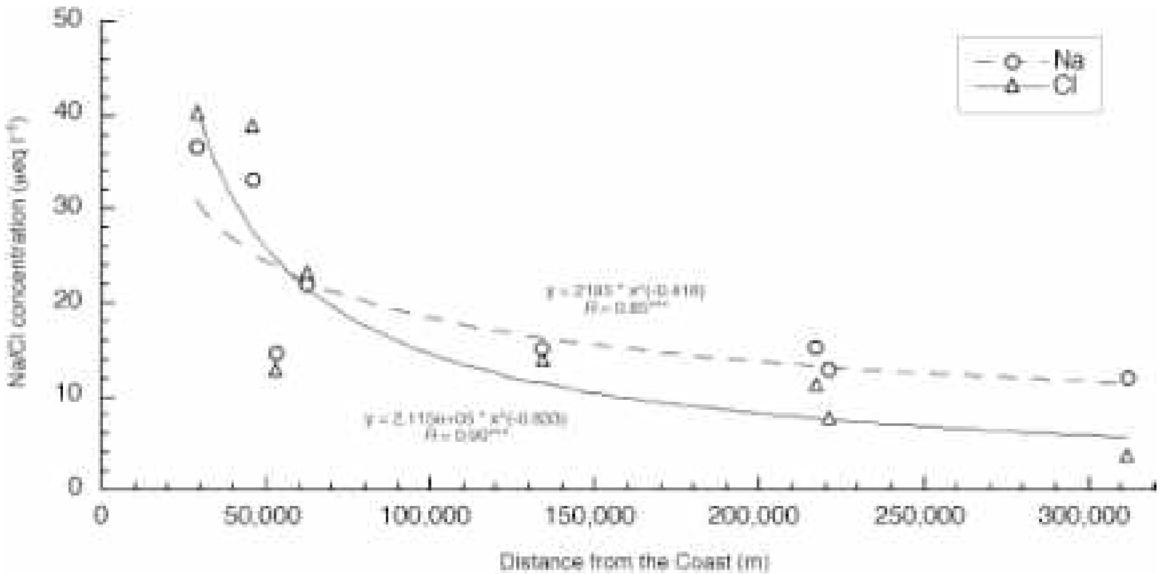

Figure 6. Na and Cl in precipitation (McColl 1980) as a function of latitudinal distance from the coast in the SOD-affected region of California. Best fit lines of the data are power law functions (see equations). *R* is the regression coefficient (*** - $p \le .001$).

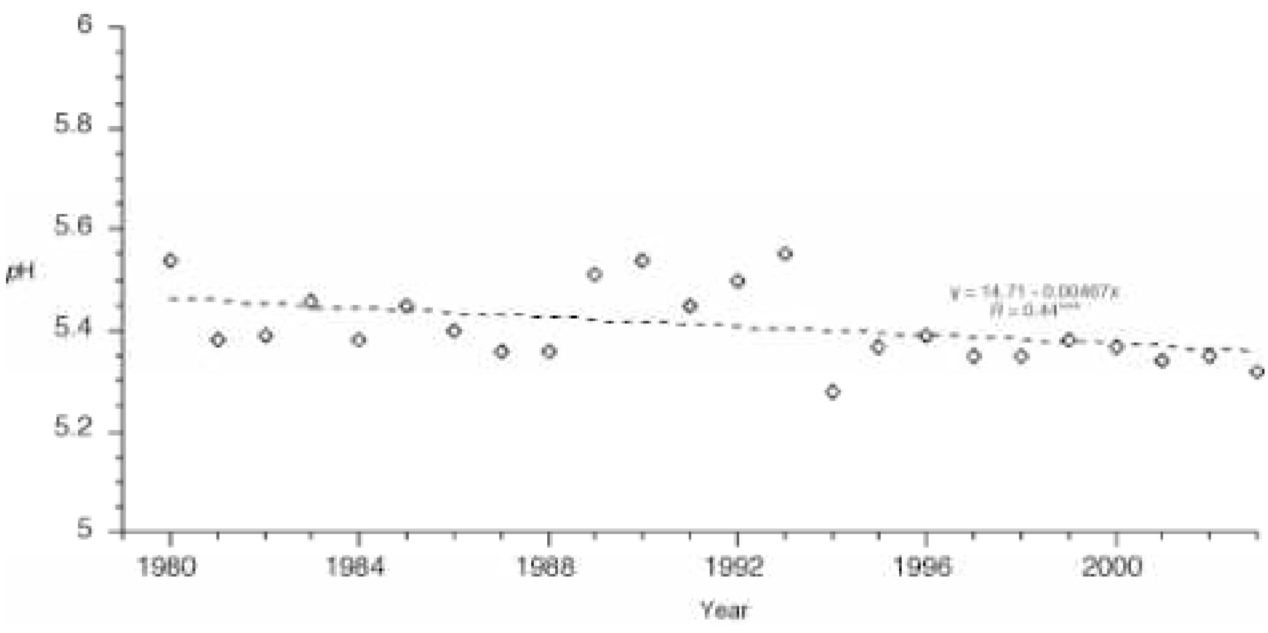

Figure 7. Time series of mean annual precipitation *p*H at Hopland, CA, a SOD-affected region of California. Linear best fit function is shown (see equation). *R* is the regression coefficient (*** - $p \le .001$).

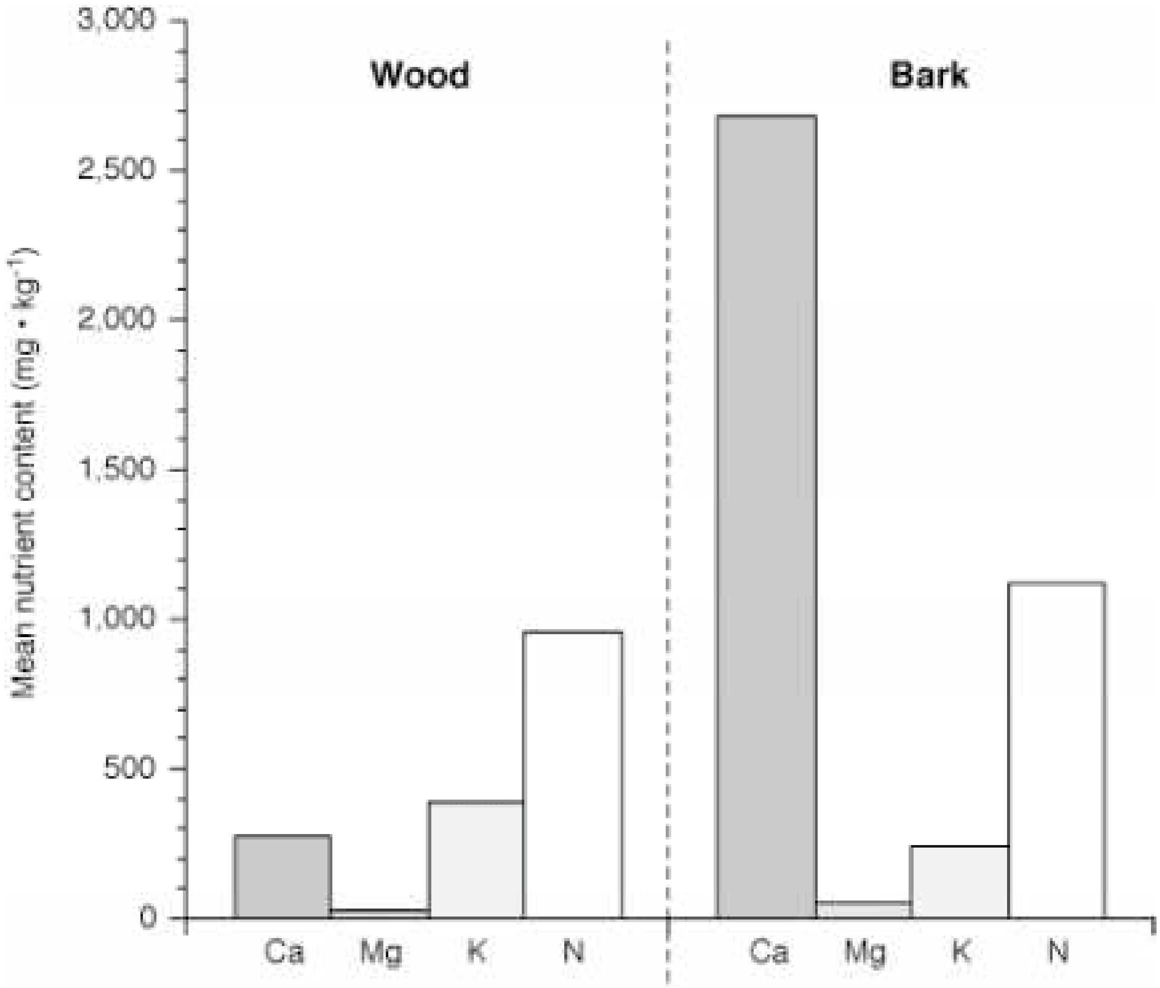

Figure 8. Summary of tissue assay for nine English Oaks (*Quercus robur*) (Bosman et al. 2001).

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[10] Anderson 1964
[11] Arentz 1983
[12] except see Mueller-Dombois 1986
[13] Mueller-Dombois 1987
[14] Mueller-Dombois 1988
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