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Polyphenols as regulators of plant–litter–soil interactions in northern California's pygmy forest: A positive feedback?

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Abstract. The convergent evolution of polyphenol-rich plant communities has occurred on highly acidic and infertile soils throughout the world. The pygmy forest in coastal northern California is an example of an ecosystem on an extremely infertile soil that has exceptionally high concentrations of polyphenols. Many 'negative feedbacks' have been identified whereby plants degrade fertile soils through production of polyphenol-rich litter, sequestering soil nutrients into unavailable form and creating unfavorable conditions for seed germination, root growth, and nutrient uptake. But in the context of plant–litter–soil interactions in ecosystems adapted to soils that are inherently acidic and infertile (such as the pygmy forest), there are also many 'positive feedbacks' that result from polyphenol production. By inhibiting decomposition, polyphenols regulate the formation of a mor-humus litter layer, conserving nutrients and creating a more favorable medium for root growth. Polyphenols shift the dominant pathway of nitrogen cycling from mineral to organic forms to minimize potential N losses from the ecosystem and maximize litter-N recovery by mycorrhizal symbionts. Polyphenol complexation of Al, Mn and Fe reduce potential Al toxicity and P fixation in soil. Polyphenols regulate organic matter dynamics, leading to the accumulation of organic matter with cation exchange capacity to minimize leaching of nutrient cations. Humic substances derived from polyphenolic precursors coat rhizosphere soil surfaces, improving physical and chemical conditions for root growth and nutrient cycling. Although their long-accepted adaptive value for antiherbivore defense is now in doubt, polyphenol alteration of soil conditions and regulation of nutrient cycling illustrate how fitness can be influenced by the 'extended' phenotype in plant–litter–soil interactions.

Introduction

The idea that plant communities alter environmental conditions to enhance their fitness was proposed long ago (Clements 1916). This view was later discredited as being inconsistent with the paradigm that natural selection can only operate on competing individuals (Gleason 1926). Subsequent studies of plant–litter–soil interactions have overemphasized competition (such as allelopathy) when interpreting the fitness-related impacts of plant-derived organic compounds in the soil environment. Neighboring plants can be of benefit to each other in various ways (Callaway 1995; Hunter & Aarssen 1988), and terms such as 'bootstrapping' or 'positive feedbacks' have been used to describe such favorable conditions during plant succession (Chapin 1993; Perry et al. 1989). Foremost among these feedbacks is the input of organic matter, which profoundly influences soil as a medium for plant growth and nutrient cycling (Van Breemen 1993). Organic matter inputs include the litter of leaves, stems, bark, flowers, fruits and roots, and also dissolved and suspended organic compounds in throughfall, stemflow or exuded by roots.

Many genetically-determined aspects of plant interactions with their environment are not directly reflected in the physical phenotype. For example, the allelopathic effects of toxic metabolites contained in leaf litter may alter soil conditions to the disadvantage of competing vegetation. Overlapping zones of influence between adjacent plants select against individuals that cannot tolerate their neighbor's litter. This plant–litter–soil interaction may influence reproductive success, but the decomposing leaf litter is not generally considered to be part of the plant's phenotype. The potential capacity for plants to improve their fitness by influencing the soil environment could be interpreted as the result of natural selection operating on the plant's 'extended' phenotype (Dawkins 1982; Jones et al. 1994). Individual plants have been reported to control nutrient cycling and humus dynamics in the soil (Boettcher & Kalisz 1990; Hobbie 1992; Raulund-Rasmussen & Vejre 1995), and especially where inherent soil conditions are unfavorable for growth, natural selection could favor individuals that alter the soil environment to their advantage.

The importance of edaphic conditions is sometimes shown by abrupt boundaries between highly contrasting plant communities along soil gradients (Goldberg 1982; Westman 1975a). Traits that are frequently observed in plant species adapted to acidic, infertile soils include slow growth-rates, long life spans, and evergreen, sclerophyllous leaves with high nutrient resorption prior to senescence and high foliar concentration of polyphenols (Chapin et al. 1993a; Coley et al. 1985). Intraspecific variation of polyphenol concentration along soil acidity/fertility gradients further suggests that edaphic factors are involved in natural selection for polyphenol-rich plants (Northup et al. 1995a).

Polyphenols such as condensed tannins were once considered to be waste products and were classified as 'secondary' metabolites because they served no obvious purpose in primary metabolism. The hypothesis that they are selectively produced because they are chemical defenses against other organisms revolutionized the field of chemical ecology (Fraenkel 1959). This theory gained such widespread acceptance among ecologists that the words 'polyphenol' or 'tannin' have become nearly synonymous with presumed-adaptive-value terms such as 'digestibility-reducing compounds' or 'immobile defenses'. These attempts to account for differential production of polyphenols among different genera of plants, or within species in contrasting environments, assumed a defensive-chemistry function. For example, the occurrence of exceptionally high concentrations of polyphenols in the vegetation of highly-leached and infertile soils has been interpreted as the result of greater selective pressure for defense where limited soil nutrient availability creates greater 'cost' for replacing foliage lost to herbivory (Janzen 1974; McKey et al. 1978).

However, recently the adaptive value of polyphenols as chemical defenses has become a topic of debate, and many ecological studies show no significant correlation between foliar concentrations of polyphenols and degree of herbivory (Coley 1983; Faeth 1985; Hartley & Lawton 1987; Laine & Henttonen 1987). In fact, beneficial effects of polyphenols on herbivores, such as protection from predators and disease, have been reported (Hunter & Schultz 1993; Taper & Case 1987). Studies of herbivore digestion have shown that the 'digestibility-reducing' function of polyphenols can be circumvented physiologically (Bernays et al. 1990; Martin et al. 1987), or behaviorally (Johnson et al. 1993). For example, salivary tannin-binding proteins permit mammalian herbivores to feed on polyphenol-rich plants (Mehansho et al. 1987; Juntheikki et al. 1996). Researchers who published that high polyphenol concentration in rainforests on acid white sands resulted in reduced herbivory later reported contradictory evidence (Oates et al. 1990). Comparison of four adjacent rainforests on contrasting soils showed that levels of herbivory are not lowest in the exceptionally polyphenol-rich community associated with an acid white sand (Proctor et al. 1983). The idea that herbivores have co-evolved tolerance mechanisms has been proposed because ecological studies have failed to demonstrate that polyphenol production significantly influences herbivory (Tempel 1981). Intraspecific comparison of trees on contrasting soils further confirms that levels of herbivory are not affected by higher concentrations of phenolics in *Quercus coccifera* and *Cistus monospeliensis* (Glyphis & Puttick 1989) or *Fagus sylvatica* (Balsberg Pahlson 1989). These intraspecific comparisons are particularly significant because they minimize variation in other confounding forage quality factors that affect the palatability of foliage to herbivores.

Polyphenols comprise up to 60% plant dry weight (Cates & Rhodes 1977). This large 'investment' of photosynthate presumably imparts some benefit to the producer. The convergent evolution of polyphenol-rich plant communities on highly acidic and infertile soils throughout the world suggests that there is an important feedback with soil conditions. The increasing evidence that polyphenols may not significantly influence herbivory contradicts widelyheld assumptions and reopens debate over how this feedback might have been selected for.

The importance of organisms as a factor in soil development is well established (Jenny 1941). Recently there has been a renewal of interest in the feedbacks through which plants can create favorable or unfavorable soil conditions (Van Breemen 1993). For example, development of a mull-type humus during maturation of spruce forests can be altered by the presence of *Vaccinium myrtillus*, which instead creates a mor-type humus (Bernier et al. 1993). Whereas ecological studies have focused on the possible role of polyphenols as chemical defenses, soil scientists long ago recognized their importance in pedogenic processes (Bloomfield 1957; Coulson et al. 1960; Davies 1971). The impact of polyphenol-rich vegetation on soil conditions, such as the accumulation of a mor-type litter layer, is generally considered to decrease productivity (Kuiters 1990). As a result, the high polyphenol concentration in vegetation associated with inherently infertile soils is believed to contribute to 'negative' feedbacks that further diminish soil fertility (Chapin 1993; Muller et al. 1987). There is no disagreement that polyphenols in plant litter can profoundly alter soil properties and nutrient cycling dynamics, but very little has been published regarding the possible benefits to the plants (Bernays et al. 1990; Van Breemen 1993). In the context of dynamics that are unique to strongly acidic and inherently infertile soils, there are many ways that the adaptive value for producing polyphenols can be construed as resulting from their interaction with the soil (Northup et al. 1995a). For example, formation of protein-tannin complexes by polyphenols in decomposing litter impedes mineralization, thereby minimizing N losses to leaching or denitrification and maintaining litter-N in a form for which the plant's mycorrhizal fungi have a competitive acquisition advantage (Northup et al. 1995b).

We hypothesize that polyphenols contribute to the 'extended' phenotype of plants that are adapted to acidic, infertile soils and that they influence fitness through changes in soil properties. Polyphenols play a dominant role in controlling many aspects of plant–litter–soil interactions, such as the regulation of nutrient cycling and organic matter dynamics, amelioration of chemical and physical infertility factors, and alteration of soil properties. In the following discussion, we compare plant–litter–soil interactions in contrasting ecosystems along an extreme edaphic gradient in the Ecological Staircase on the coast of northern California to elucidate the adaptations that permit vegetation to survive, compete, and sustain productivity on acidic, infertile soils. We examine mechanisms through which polyphenols contribute to the 'extended' plant phenotype in this edaphic climax ecosystem, and we also identify similar interactions in more-common ecosystems adapted to acidic, infertile soils.

Table 1. Locations, soil age, and classifications for five study sites on the Ecological Staircase.

Terrace	Distance inland (km)	Elevation (m)	Estimated soil age[†] (years)	Soil classification
T1	0.5	22	100,000	Ustic Humitropept
T2	1.5	61	200,000	Typic Albaquult
T3	3.0	90	>240,000	Typic Tropaquod
T4	4.0	130	330,000	Typic Albaquult
T5	5.0	160	>400,000	Typic Albaquult

[†] Estimated soil ages from Merritts et al. 1991

Study sites

The ecological staircase

The 'Ecological Staircase' is a sequence of coastal terraces near Mendocino, in northern California, that comprise an extreme edaphic gradient supporting distinct plant communities. Continuous geologic uplift of the coastline for the last 500,000 years, in combination with periodic changes in sea level, has exposed a staircase-like series of wavecut coastal terraces (Fox 1976; Merritts et al. 1991). Along this narrow section of coastline a unique combination of geomorphologic conditions has preserved the soils of the ancient terraces. Study sites were selected on the five terraces in the Jug Handle Reserve (Table 1). The lowest, most recently exposed, terrace has a highly fertile soil that supports productive prairie or mixed-conifer forests. The soil on the second terrace is much older and of moderate fertility, supporting tall forest of *Pinus muricata* D. Dons (Bishop pine). Pygmy forests of dwarf *Pinus muricata*, *Pinus contorta* var. *bolanderi*, and *Cupressus pygmaea* occur in areas of extremely infertile soil on the three oldest (>240,000 y) terraces. Taller pines and cypress typically occur at the margins of pygmy forest sites, and a very tall mixed-conifer *Sequoia sempervirens* and *Pseudotsuga menziesii* forest occurs wherever erosion or deposition has created fresh parent material. Transitions between the contrasting soil-vegetation associations are often abrupt (<10 m).

The pygmy conifer forest only occurs in the ancient coastal terrace soils that are extremely acidic and infertile (McMillan 1956). Two species of conifers, *Cupressus pygmaea* (Mendocino cypress) and *Pinus contorta* ssp. *bolanderi* (Bolander pine), are edaphic ecotypes that are endemic to the pygmy forest. While cypress and pines comprise the majority of pygmy forest biomass, ericaceous shrubs comprise the majority of the dozen or so vascular plant species present (Westman 1975b). *Pinus muricata* is not endemic and occurs only as a rare member in extreme (<2 m high) pygmy forests, although it is very common in 'transitional' (<5 m high) pygmy forests, typically comprising about a third of the trees. *P. muricata* usually occurs in tall and nearly-pure stands on terraces with more fertile soil.

Only a short distance from the pygmy forest, fertile young soils formed on eroding terrace edges support some of the world's largest trees in mixed-conifer forest of *Sequoia sempervirens* (redwood) and *Pseudotsuga menziesii* (Douglas fir). Proximity of contrasting ecosystems on the Ecological Staircase permits dispersal of seeds between different soil-vegetation associations. Severely stunted and visibly malnourished redwoods sometimes establish at the margins of the pygmy forest, but never reproduce. Large pines and cypress occasionally occur at the margin of the coastal prairie where they grow into large (>30 m) specimens; however, seedlings rarely established in the surrounding grassland.

A soil chronosequence

Soils are dynamic systems having properties derived from the combined effect of climate and organisms, modified by topography, acting on geologic parent materials over periods of time (Jenny 1941). On the terraces of the Ecological Staircase, the most important distinguishing soil-forming factor is age. Soils were all formed from similar geologic parent material; graywacke-sandstone-derived beach deposits overlying level, wavecut-platforms of graywacke sandstone bedrock. Mean annual temperature is 12.5 °C, mean annual precipitation is 983 mm, and because of their close proximity to each other, macroclimate shows little variation between terraces on the Ecological Staircase. All five terraces are within 5 km of each other, indicating that the same set of organisms has the opportunity to establish throughout. All terraces include central areas where level topography results in negligible soil erosion or deposition of material for new soil formation. These unique topographic conditions have permitted continuous development of undisturbed soils for exceptionally long periods of time. Protected in the Jug Handle Reserve, the Ecological Staircase has minimal human impact. Differences in soil properties are due primarily to differences in age, with minimal variation in other factors of soil formation. This Ecological Staircase is, in fact, one of the world's best examples of a soil chronosequence (Jenny et al. 1969).

Soils vary dramatically along the Ecological Staircase (Table 1). The lowest and youngest terrace in the sequence (T1) has highly fertile, near-neutral pH soils with primary minerals able to supply exchangeable cations through weathering. Soils on the second terrace (T2) have been weathered and leached for approximately 100,000 more years, are more acidic and much less fertile than the soil of T1. On higher terraces (T3, T4, and T5), older soils have been intensively weathered, making them extremely acidic and infertile. Soils at study sites on the three oldest terraces are nearly identical in spite of enormous age differences between them, suggesting that they have reached a steady-state.

Weathering and leaching over extremely long periods of time have left soils of the pygmy forest virtually devoid of nutrients and strongly acidified. The small remaining pool of nutrients is contained exclusively in the biomass and soil organic matter (Westman 1975b). pH($CaCl_2$) is as low as 3.1 in the mineral soil or as low as 2.2 in the mor-litter layer (Table 2), and aluminum toxicity, phosphorus fixation, nutrient cation deficiency, and very low cation exchange capacity, which become more severe with decreasing pH, all contribute to extreme edaphic stress in the pygmy forest. Nitrogen availability is also extremely limited (McMillan 1956), and there is high potential for nitrate leaching through the acid quartz sand or denitrification in the periodically flooded soils. The vast majority of fine roots occur in the upper 5 cm of the mineral soil and in the mor-litter layer, because of these poor soil conditions.

State factors in ecosystem selection

Directly analogous to Jenny's (1941) 'state factors' of soil formation, environmental factors also interact to influence properties and dynamics of whole ecosystems (Major 1951; Van Cleve et al. 1991). Environmental conditions on the Ecological Staircase provide a unique opportunity to elucidate the role of state factors in plant succession and evolution. An extreme edaphic gradient exists across sites that otherwise have the same conditions of macroclimate, topography and potential biota. Among the state factors on the Ecological Staircase study sites, only soil properties vary significantly, creating an 'edaphosequence' of ecosystems. In this unique environment, identification of plant traits that are adaptations specifically to contrasting soil conditions is not confounded by variability in climate, topography, potential vegetation gene pool, or selective pressure from herbivores and pathogens.

The unique combination of state factors on the Ecological Staircase has created islands of extreme edaphic conditions and sharp boundaries between contrasting soil-vegetation associations that have remained stable for a long time. This long-term stability has permitted evolution of distinct subspecies, some of which may have occupied ancient pygmy forests and other edaphic ecotypes that probably colonized these infertile sites more recently (Aitken & Libby 1994). The combination of relatively stable edaphic and climatic conditions in the pygmy forest is illustrated by the presence of four endemic taxa, three of which comprise the majority of the biomass in this final sere of succession.

Table 2. Selected soil characterization data (mean of three soil cores) for the five study sites along the soil chronosequence.

Terrace	Horizon	Depth	pH(H_2O)	pH($CaCl_2$)	N	C	Avail. P	Exch-Ca	Exch-Mg	Exch-Al	<2-mm Roots
		cm			g/kg		mg/kg		cmol$_c$/kg		kg/m^3
T1	Oi/Oa	8–0	5.01	3.90	10.0	431	314	4.0	2.1	2.5	<0.01
	A1	0–20	5.96	4.97	2.2	36.1	32	3.7	1.3	0.8	0.30
	A2	20–40	6.18	5.14	1.6	28.6	28	4.0	1.1	0.3	0.26
	A3	40–58	6.33	5.31	1.1	22.8	23	3.7	1.3	0.2	0.11
	AB	58–75	6.36	5.40	0.7	12.7	21	3.3	1.7	0.1	0.10
	Bw	75–85	6.25	5.35	0.8	12.8	20	2.8	1.5	<0.1	0.11
T2	Oi/Oa	10–0	4.11	2.84	8.7	362	284	3.2	1.3	4.2	1.00
	A	0–13	5.18	4.15	1.5	33.1	22	1.9	1.0	3.6	0.69
	E	13–35	5.27	4.31	1.1	26.0	11	1.3	0.8	2.8	0.88
	Btg1	35–53	5.35	4.39	0.8	14.8	7	0.8	0.6	2.0	0.51
	Btg2	53–70	5.29	4.27	0.6	9.3	5	0.5	0.6	2.5	0.76
	Btg3	70–90	5.08	4.20	0.5	5.3	1	0.4	0.6	2.9	0.03
T3	Oi/Oa	4–0	3.89	2.16	5.8	378	128	1.3	0.7	4.2	3.86
	A	0–3	3.95	3.07	1.8	70.5	6	1.8	0.9	1.4	2.09
	E1	3–10	4.19	3.04	0.8	29.0	4	0.3	0.4	0.8	2.14
	E2	10–28	4.63	3.58	0.7	4.3	1	0.1	0.1	0.2	0.67
	Bh	28–43	4.73	3.96	1.0	21.4	5	0.1	0.1	6.8	0.12
	Hardpan										

Table 2. Continued.

Terrace	Horizon	Depth	pH(H_2O)	pH($CaCl_2$)	N	C	Avail. P	Exch-Ca	Exch-Mg	Exch-Al	<2-mm Roots
		cm			g/kg		mg/kg		$cmol_c$/kg		kg/m^3
T4	Oi/Oa	4–0	3.93	2.21	6.1	363	123	1.4	0.9	4.2	4.52
	A	0–3	4.04	3.13	2.4	114.7	10	4.7	1.3	0.7	2.87
	E1	3–12	4.09	3.12	0.7	20.6	3	1.4	0.5	0.5	1.53
	E2	12–25	4.42	3.38	0.3	5.7	2	0.2	0.1	0.6	0.82
	Btg1	25–48	4.92	3.98	0.6	9.0	2	0.1	0.1	5.0	0.26
	Btg2	48–60	5.14	4.21	0.5	7.5	1	0.2	0.2	5.1	0.01
	Clay pan										
T5	Oi/Oa	4–0	4.05	2.39	6.5	419	118	2.6	1.4	3.8	2.63
	A	0–4	4.14	3.27	2.3	101.1	10	2.8	1.3	1.4	0.81
	E1	4–10	4.47	3.43	0.4	11.3	5	0.3	0.1	1.1	0.81
	E2	10–18	4.85	4.02	0.4	8.6	4	0.2	0.1	1.6	0.83
	Btg1	18–27	5.02	4.09	0.5	10.0	3	0.2	0.2	2.9	0.26
	Btg2	27–53	5.08	4.14	0.5	4.6	<1	0.2	0.3	3.5	0.16
	Clay pan										

Relatively few plant species have been able to establish in the pygmy forest and they are all presumed to possess traits that are adaptations to highly acidic and infertile soil conditions. Identification of such traits should provide clues to some of these adaptations. A few species such as *P. muricata* grow elsewhere along the edaphic gradient and exhibit distinct traits in the contrasting soil conditions. These differences in soil-related traits might result from phenotypic plasticity within a genotype or from the selection of genetically distinct ecotypes. The ability to vary these traits in contrasting soil conditions could enable a plant species to colonize less fertile sites, or remain established where soil conditions are becoming infertile. Therefore, intraspecific variation along the Ecological Staircase 'edaphosequence' should reveal how adaptations to infertile soil conditions may have evolved.

Methods

Soil samples collected from the five study sites of the Ecological Staircase were air-dried, gently crushed, and passed through a 2-mm sieve. Potentiometric measurement of pH (1:1, soil:0.01 *M* $CaCl_2$) was performed after a 15-min equilibration. Organic carbon and Kjeldahl nitrogen were determined by dry combustion (Leco furnace) and a modified Kjeldahl digest (Parkinson & Allen 1975), respectively. An index of P availability was determined using the Bray #2 extraction (Olsen & Sommers 1982). Exchangeable cations were measured following displacement with 1 *M* NH_4OAc (pH = 7) and exchangeable Al by displacement with 1 *M* KCl (Soil Survey Staff 1984). Fine roots were collected from soil cores by wet-sieving and hand-sorting. Roots were dried at 65 °C and the mass recorded as a function of soil horizon.

Primarily current-year sun foliage was collected from mature specimens *Pinus muricata*, *Cupressus pygmaea*, and *Pinus contorta* ssp. *bolanderi* on the five coastal terraces of the Ecological Staircase at the end of the growing season, approximately halfway up the canopy to minimize variability due to light intensity (Mole et al. 1988). Mature leaves of *Arctostaphylos nummularia*, *Myrica californica*, *Arctostaphylos columbiana*, *Vaccinium ovatum*, *Rhododendron macrophyll*um, and *Gaultheria shallon* were collected from pygmy forest sites on the three highest terraces. Decomposing litter (Oa horizon) was collected from under monospecies clusters of *P. muricata* in three contrasting environments along this edaphic gradient.

Samples of foliage and litter were dried for 24 h at 65 °C before grinding to pass a 20-mesh screen. After grinding, samples were extracted for 24 h in 50% aqueous methanol. Extracts were passed through Whatman 41 filter paper for spectrophotometric analysis. Total phenolics were measured by the Prussian Blue method (Price & Butler 1977) using Fisher tannic acid (CAS reg. 1401-55-4) as the standard. Condensed tannins were measured by the acidified vanillin assay (Broadhurst & Jones 1978) using catechin (CAS reg. 88191-48-4) as the standard. Additional analyses on *P. muricata* litter samples included organic carbon by Leco furnace combustion, nitrogen by a modified Kjeldahl digest (Parkinson & Allen 1975) followed by conductimetric assay (Carlson 1978), and lignin by the acid detergent method (Goering & Van Soest 1970). Extracts obtained from *P. muricata* litter during a three-week aerobic incubation (Cassman & Munns 1980) were measured for mineral nitrogen ($NH_4^+ + NO_3^-$) conductimetrically (Carlson 1978) and for dissolved organic N following persulfate oxidation (Yu et al. 1994).

Statistical analyses were performed using SYSTAT for Windows, Version 5 (SYSTAT Inc., Evanston, IL). ANOVAs were performed using concentration of total phenolics or condensed tannin as the dependent variable and site or nitrogen release rate as the independent variable. Regressions were performed using concentrations of total phenolics, condensed tannins, C/N ratio, or lignin concentration as the dependent variable and ratios of mineral nitrogen ($NH_4^+ + NO_3^-$):dissolved organic nitrogen release rates as the independent variable.

Polyphenols and plant–litter–soil interactions

Polyphenol production in contrasting ecosystems

The convergent evolution of polyphenol-rich plant communities such as pine forests and heathlands has occurred on highly infertile soils throughout the world (Chapin et al. 1993a). Exceptionally high concentrations of polyphenols are found in equatorial rain forests on extremely infertile acid white sands (Janzen 1974; McKey et al. 1978). Foliar concentrations of total phenolics and condensed tannins are very high in all major species of the pygmy forest (Figure 1); with its strongly acidified quartz sand and overlying humus layer, the soil is comparable to the tropical acid white sands, and the plant species are also slow-growing, evergreen, sclerophyllous, forming dense root mats in the leaf litter layer with high foliar concentrations of polyphenols.

Intraspecific variation of polyphenol concentration on contrasting soils has been reported in many species, including *Fagus sylvatica* (Nicolai 1988), *Cornus florida* and *Acer rubrum* (Muller et al. 1987), and *Quercus coccifera* and *Cistus monospeliensis* (Glyphis & Puttick 1989). Intraspecific variation of polyphenol concentration also occurs on the edaphic gradient of the Ecological Staircase (Figure 2). All major species of the pygmy forest are polyphenol-rich, and those species that also grow elsewhere on the gradient have the highest concentrations of polyphenols when growing on the least

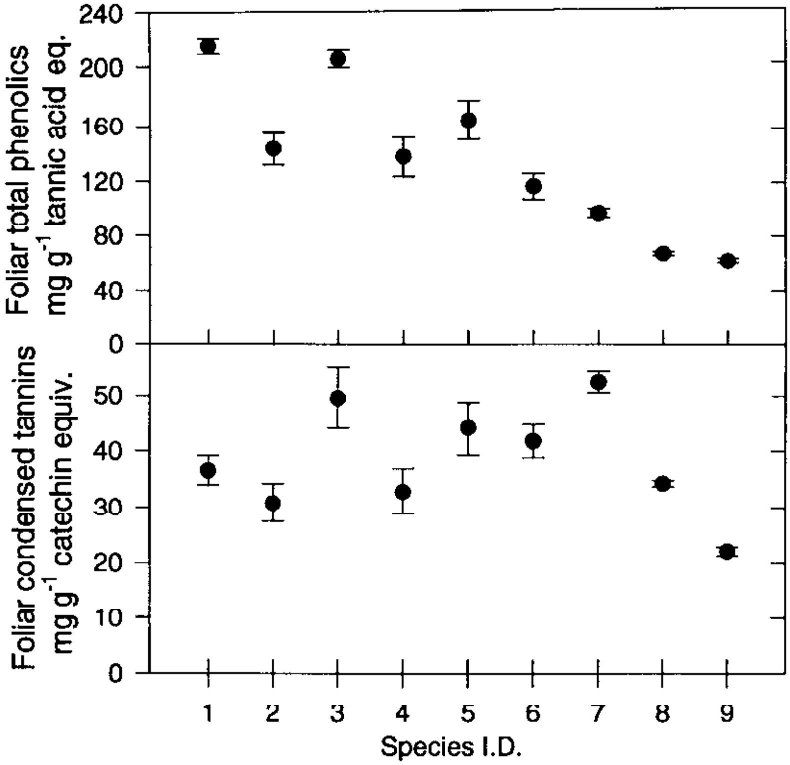

Figure 1. Foliar concentrations (mean ± SEM) of total phenolics in nine vascular plant species of the pygmy forest. Plant species are 1 = *Arctostaphylos nummularia*; 2 = *Myrica californica*; 3 = *Arctostaphylos columbiana*; 4 = *Vaccinium ovatum*; 5 = *Rhododendron macrophyllum*; 6 = *Gaultheria shallon*; 7 = *Cupressus pygmaea*; 8 = *Pinus muricata*; 9 = *Pinus contorta* var. *bolanderi*.

fertile sites. Unlike most other studies of intraspecific variation, these data were collected from sites within a few kilometers of each other. Relatively uniform conditions of macroclimate and potential attack from herbivores and pathogens rule out most factors other than soil conditions as contributing to these results. Natural selection seems to favor plant communities and species that produce higher concentrations of polyphenols under infertile soil conditions.

The 'carbon-nutrient balance' theory suggests that on infertile soils plant production is limited by mineral nutrient availability (Bryant et al. 1983). 'Surplus' photosynthate therefore accumulates and is allocated to polyphenol production rather than growth. This may explain the occurrence of higher polyphenol concentration in less fertile sites, regardless of what the adaptive value for polyphenol production might be. However, fertilization experi-

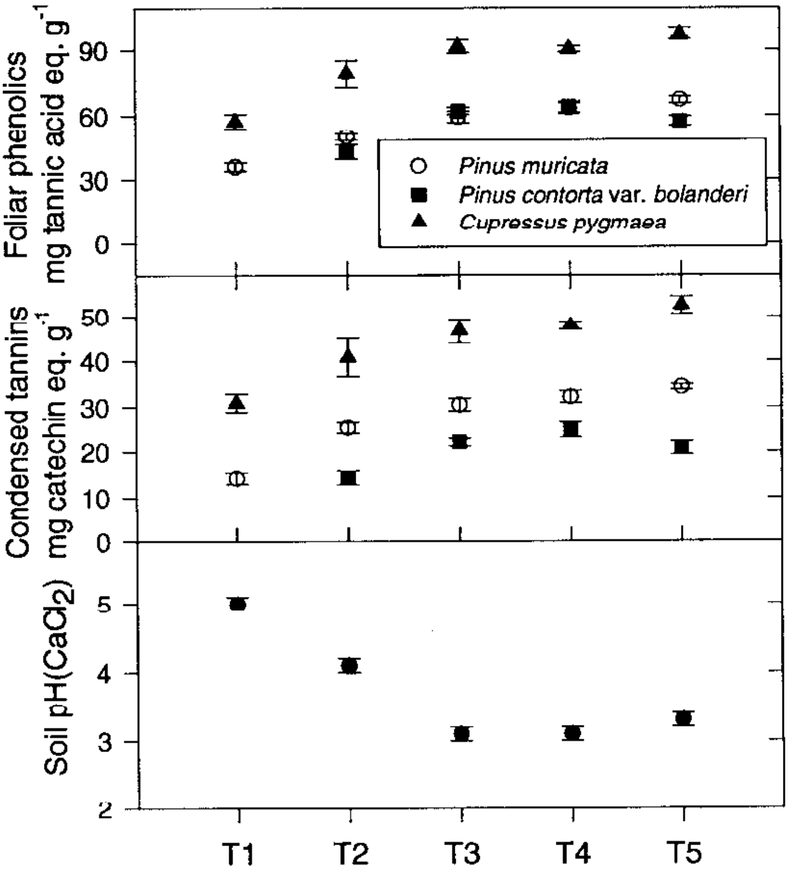

Figure 2. Foliar concentrations of condensed tannins and total phenolics in three conifer species on the Ecological Staircase. Current-year sun foliage was collected from mature *Pinus muricata*, *Pinus contorta* var *bolanderi*, and *Cupressus pygmaea* on five coastal terraces.

ments often do not support the theory (Iason & Hester 1993; Kyto et al. 1996). Furthermore, plants adapted to infertile soils allocate a larger proportion of their photosynthate to roots, root turnover is high, and high rates of carbohydrate exudation feed symbiotic mycorrhizal fungi (Vogt et al. 1982), thus some of the 'surplus' photosynthate that results from low soil nutrient availability can be allocated below-ground to improve nutrient acquisition, rather than be used for the accumulation of foliar polyphenols.

Plant-detritivore interactions

Although it has been difficult to demonstrate reduced herbivory resulting from higher polyphenol concentration, the impact on detritivore activity is irrefutable. High polyphenol concentration significantly reduces the palatability of leaf litter to earthworms (Satchell & Low 1967; Hendriksen 1990). The initial mechanical breakdown of litter by detritivores facilitates subsequent decomposition and mineralization by soil microbes. Suppressed detritivore activity due to polyphenol-rich litterfall results in distinct stratification of the soil profile and contributes to the accumulation of mor-type humus on the soil surface (Anderson 1973). Litter layer accumulation is a feedback to polyphenol production, which is a feedback to soil conditions. One illustration of these feedbacks is in the gradients of humus mat thickness which have been reported in transition zones between contrasting soil types (Jordan & Hererra 1981).

In the California pygmy forest, polyphenol-rich litter accumulates despite very low rates of litter production (Table 2). The litter remains structurally intact and individual plant parts remain identifiable years after they have fallen to the ground. The distinction between polyphenol impact on detritivores as opposed to herbivores reflects the nutritional difference between green versus senescent foliage. Before abscission, plants resorb much of the mobilizable proteins, carbohydrates, and other nutrients from foliage. Among plants that do not fix N in ecosystems adapted to infertile soils, a higher proportion of foliar N is removed during senescence (Schlesinger et al. 1989). Much of the small amount of protein that remains in polyphenol-rich litterfall is contained in recalcitrant protein-tannin complexes and/or physically occluded by lignin in the cell walls.

Polyphenol production may enable plants to influence the physical fate of their litter. Even if mechanical breakdown of litterfall is accomplished in the absence of detritivores, high polyphenol concentrations make further degradation by microbial decomposers difficult. Deactivation of extracellular enzymes by complexation with phenolics has been shown for proteases (Ladd & Butler 1969), ureases (Mishra et al. 1980), phosphatases (Malcolm & Vaughan 1979), and cellulases (Sinsabaugh & Linkins 1987), and polyphenols generally inhibit microbial decomposition (Schimel et al. 1996). Subsequent effects include accumulation of a litter layer and an increased mean-residence-time for soil organic carbon. The capacity of polyphenols to suppress detritivores and impede decomposition is widely recognized, but has rarely been given consideration as an adaptive value for their production (Bernays et al. 1990).

Control of nitrogen release from decomposing litter

The importance of polyphenols as inhibitors of organic matter decay and N mineralization has long been recognized (Handley 1961). Studies of litter quality factors influencing N mineralization have generally focused on the carbon/nitrogen ratio, but this ratio is often a poor predictor (Muller et al. 1988; Carlyle et al. 1990). Lignin concentration or lignin/N ratios have been shown in some studies to be better in predicting N release (Aber et al. 1990; Berg & McClaugherty 1987). Some studies have shown that when polyphenol assay is included in statistical analysis, N release rates from decaying leaf litter are more strongly correlated with polyphenol concentration, or polyphenol/N ratios, than they are with C/N ratios, lignin concentration, or lignin/N ratios (Fox et al. 1990; Oglesby & Fownes 1992; Palm & Sanchez 1991). Variation of N mineralization rates from *Pinus radiata* litter on contrasting soils has been attributed to differences in polyphenol concentration (Lamb 1975), and in some *P. radiata* plantations on acidic, infertile soils, rates of N mineralization are far lower than those of N uptake by the trees (Dyck et al. 1987).

On the Ecological Staircase in California, *P. muricata* Oa horizon litter collected from three contrasting edaphic conditions shows intraspecific variation in N mineralization rates during aerobic incubation, and these are significantly (negatively) correlated to concentrations of phenolics (Figure 3). Rates of mineral N release are lowest in the pygmy forest, and site means vary more than five-fold along the edaphic gradient (Figure 4). Whereas mineralization rates and the proprotion of N released in mineral versus organic forms are negatively correlated with concentrations of condensed tannins or total phenolics, there is no correlation with lignin (Figure 5). Polyphenol and lignin concentrations are often autocorrelated because polyphenol-rich species also tend to be lignin-rich (Barry & Manley 1986; Rittner & Reed 1992). Unlike polyphenol concentration, intraspecific comparison on contrasting sites shows that lignin is not any higher on strongly acidic, nutrient-poor soils (Berg 1986; Muller et al. 1987; Northup et al. 1995b). Lignin has often been negatively correlated to N release when comparing litter of different species, but this relationship is not significant when intraspecific comparisons are made (Stump & Binkley 1993). 'Lignin' is often operationally-defined according to solubility in strong acid, and the availability of improved chemical analyses shows that this fraction often contains as much polyphenols as true lignin (Leary et al. 1986; Love et al. 1994; Preston 1996). Identification of lignin as the single most important litter quality factor controlling N mineralization (comparing different species) may be an artifact of its covariance with polyphenol concentration or the inability to segregate polyphenols from lignin in lignin assays.

Polyphenols minimize release of N (as ammonium) from litter (e.g. Northup et al. 1995b) and consequently minimize the availability of substrate for nitrate production. Nitrification proceeds rapidly in fertile soils and nitrate is the dominant N species taken up by vegetation in these ecosystems (e.g.

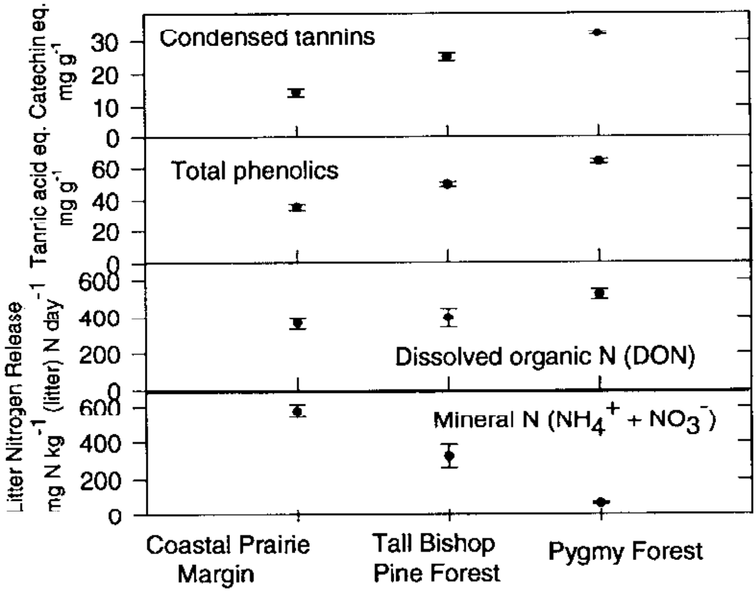

Figure 3. Release rates of mineral-N (NH_4^+ and NO_3^-) and dissolved organic nitrogen (DON) from decomposing *P. muricata* litter. N release from Oa horizon samples collected from under monospecies clusters in three contrasting soils was measured during a three-week aerobic incubation.

Chapin 1995). Forests on strongly acidic soils show little conversion of ammonium to nitrate, and no correlation between net mineralization and net nitrification (Aber et al. 1985). Although low soil pH *per se* was once believed to account for this inhibition of nitrification, strains of nitrifying bacteria that can sustain activity at very low pH have been isolated from acidic forest soils (Hankinson & Schmidt 1988). Soil nitrification rates have been found to be controlled more by the presence or absence of particular tree species than by soil pH (Ellis & Pennington 1989), and nitrification is often negligible in the litter layer, even where it occurs vigorously in the underlying mineral soil (Olson & Reiners 1983). Low pH probably does contribute to the occurrence of very low rates of nitrification in coniferous forest floors, but water potential, nutrient status, temperature, and especially the allelopathic influence of polyphenols, are also important controlling factors (Killham 1990).

Polyphenols (as purified tannins or polyphenol-rich litter extracts) have been shown to inhibit nitrification in incubation studies (Baldwin et al. 1983; Basaraba 1964; Lodhi & Killingbeck 1980; Rice & Pancholy 1973; Thibault et al. 1982). Intraspecific variation in nitrification potential under *Pseudotsuga menziesii* litter on contrasting sites parallels differences in astringent polyphenols (White et al. 1988). The suppression of nitrification by pine

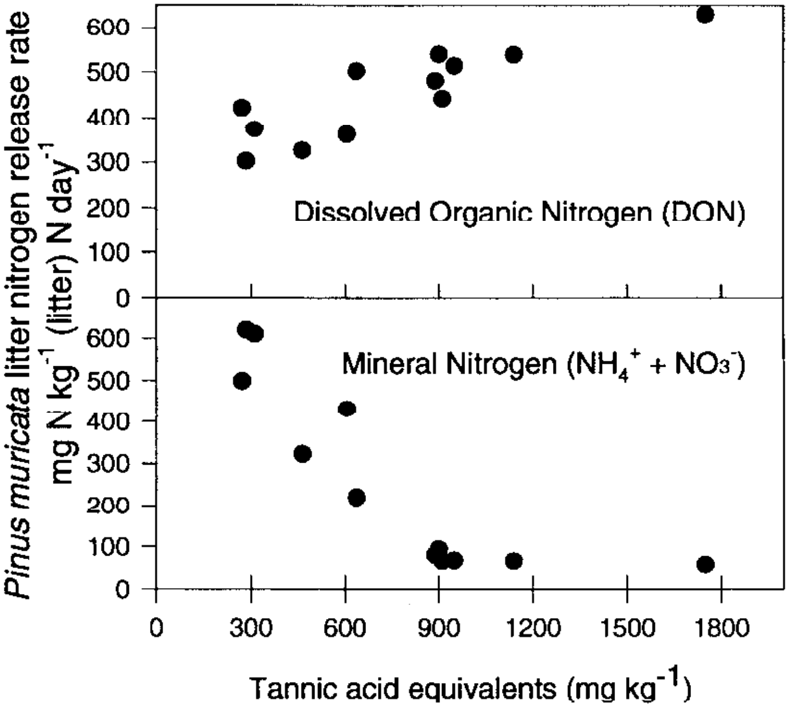

Figure 4. Nitrogen mineralization versus litter quality in *P. muricata.* Mineral-N (NH_4^+ + NO_3^-) released from Oa litter during aerobic incubation.

litter is also highly correlated with the presence of monoterpenes, indicating that polyphenols may not be the only allelopathic agents involved (White 1991). Polyphenolic constituents in litter can immobilize nitrite into organic compounds (Azhar et al. 1986), which may also contribute to the observed low concentrations of nitrate in mor-humus ecosystems.

Nitrate is much more mobile than ammonium in soil, highly subject to leaching and also capable of gaseous loss due to denitrification under low-oxygen conditions. In highly leached and periodically-flooded ecosystems such as the pygmy forest, nitrate loss is potentially high. Polyphenols in litter slow the release of ammonium and inhibit nitrate production by other mechanisms as well. One consequence of minimizing the formation of nitrate is to act as a N conservation mechanism in N-limited ecosystems (Jordan et al. 1979).

Studies of nutrient cycling in forest ecosystems have generally assumed that ammonium and nitrate are the only significant mobile forms of N in soil. Therefore, mineralization is believed to be the major 'bottleneck' regulating release and bioavailability of N from litter (Attiwill & Adams 1993; Chapin

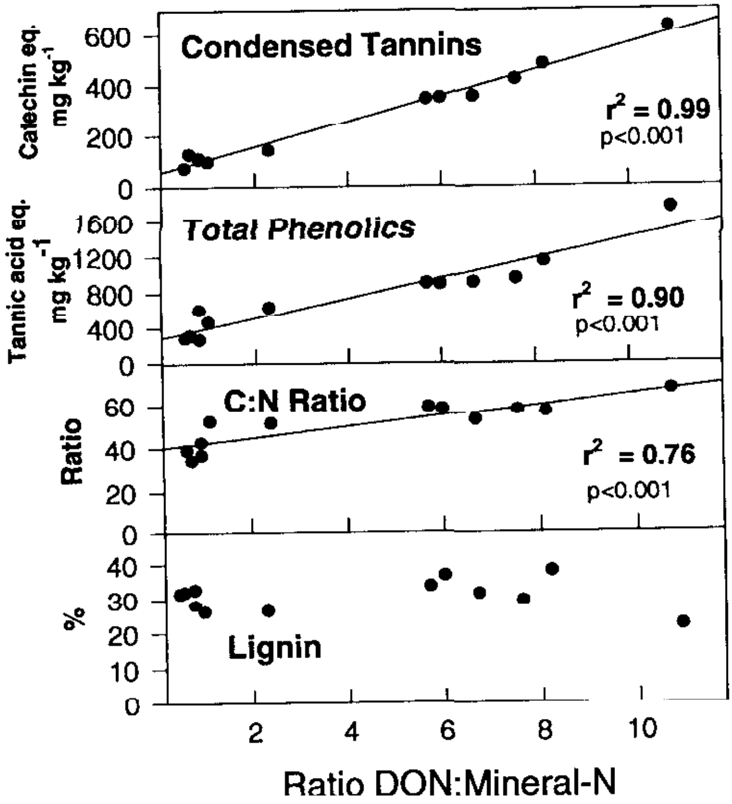

Figure 5. ***Pinus muricata*** litter quality versus proportion of N released in dissolved organic forms relative to mineral-N ($NH_4^+ + NO_3^-$) during a three-week aerobic incubation.

1995), but dissolved organic nitrogen (DON) has been found to be the dominant form of N leached from the forest floor in paper birch (Van Cleve & White 1980), lodgepole pine (Fahey & Yavitt 1988), deciduous forest ecosystems (Qualls et al. 1991), and on the Ecological Staircase in California (Figure 4).

Rates of mineral N release from *P. muricata* litter on the least fertile soils of the Ecological Staircase are extremely low, but DON release rates are actually higher than on the more fertile sites (Figure 4). In low fertility sites (pygmy forest), rates of DON release are about an order of magnitude higher than rates of mineralization (Figure 4). Measurement of mineral-N alone would give very misleading estimates of N fluxes from pygmy forest litterfall because DON is the dominant vehicle of N mobilization from decomposing organic matter.

Polyphenols and pathways of nitrogen cycling

The word 'tannin' (synonymous with polyphenols) derives its name from the capacity to tan leather by forming strong complexes that retard microbial decomposition. Acting as polydentate ligands, polyphenols occlude reactive sites on the proteins with which they form complexes, impeding enzymatic attack by decomposing organisms (Haslam 1988). Protein-tannin complexes are generally only slightly soluble, but more soluble forms also occur (Hagerman & Robbins 1987). Mycorrhizal fungi are among the soil organisms capable of utilizing N from soluble (DON) or insoluble protein-tannin complexes. Ectomycorrhizal fungi associated with coniferous forests utilize N from insoluble protein-tannin complexes (Griffiths & Caldwell 1992). Similarly, ericoid mycorrhiza have been shown to produce extracellular enzymes that release N from these insoluble complexes, and this ability partially explains why ericaceous plants are so successful in N-deficient ecosystems (Leake & Read 1989). Particularly in forests on highly infertile soils, up to 80% of the net primary productivity is allocated below-ground, with much of it being supplied to mycorrhizal fungi (Vogt et al. 1982).

We do not have quantitative evidence for mycorrhizal uptake of N from organic matter on the Ecological Staircase, but this is a logical explanation for the capacity of the pygmy forest to survive despite extremely low concentrations of mineral-N. Contributing evidence, however, is that one of the common mycorrhizal fungi (*Amanita muscaria*) directly utilizes N from organic matter (Abuzinadah & Read 1989). Mycorrhizal *Pinus contorta* Doulg. ex Loud., closely related to *P. contorta* ssp. *bolanderi* of the pygmy forest, has also been shown to take up N transferred from organic matter by fungi (Finlay et al. 1992). Polyphenol-rich ericaceous plants comprise the majority of species in the pygmy forest on the Ecological Staircase, and ericoid mycorrhizae are known to be able to use N from protein-tannin complexes. In the absence of some capacity to recover N from polyphenol complexes in litter, production of exceptionally high concentrations of polyphenols in the foliage of all major pygmy forest species would appear to be maladaptive. There may be advantages for the plants to complex any N that cannot be resorbed from senescent foliage into a minimally-mobile form until their mycorrhizal symbionts are able to take it back up. However, one exception to the dependence on mycorrhizal fungi for use of organic N in the pygmy forest might be the endemic *Carex californica*. A related species of non-mycorrhizal sedge in tundra ecosystems has been shown to directly utilize organic forms of N (Chapin et al. 1993b).

The vast majority of N leaching from *Pinus contorta* litter occurs as DON that accumulates in the mineral soil rooting zone (Fahey & Yavitt 1988) by physical sorption to soil organic matter, or by precipitation of sparingly soluble protein-tannin complexes from solution. Preserved against leaching loss, DON immobilized in this manner is unavailable to the majority of soil organisms. One impact of polyphenols in mor-humus ecosystems may be to shift the dominant pathway of N cycling to minimize mineral-N fluxes and favor direct uptake of organic-N through mycorrhizal symbionts. Organic forms of N could eventually be transferred to plants via mycorrhizae without ever being converted to mineral form (Chapin 1995). This 'short-circuiting' of the N cycle may have the effect of giving the plants, and their associated mycorrhizal fungi, a competitive advantage for recovering N that cannot be resorbed from senescent foliage (Northup et al. 1995b). Through the production of polyphenols, plants control whether litterfall N is released in a highly mobile form that is available to a wide range of soil organisms, or alternatively, released in a slightly mobile form that is available only to those few soil organisms endowed with appropriate enzyme systems and supplied with adequate energy.

Polyphenols may enable plants to exert spatial and temporal control over nitrogen cycling dynamics. For example, exceptionally high polyphenol concentration in tropical rain forests on acid white sands can result in the accumulation of litter layers more than 150 cm thick, despite temperature and moisture conditions favorable for rapid decomposition (Proctor et al. 1983). Organic surfaces in the litter layer have much greater capacity than the underlying quartz sand to immobilize soluble organic compounds through physical sorption (e.g. Jardine et al. 1989). Spatial control of nitrogen dynamics through polyphenol production may include shifting the dominant zone of N release upward to an alternative medium where N loss is minimized and where litter-N is more likely to remain in a form which is utilizable by mycorrhizal fungi. By delaying the mineralization of N from organic forms, polyphenols may synchronize N availability with plant uptake capacity (Horner et al. 1987). In colder climates this could decrease N loss during snowmelt, when low temperature limits uptake (Kuiters 1990).

Allelopathic suppression of competing vegetation

In addition to their presumed role as antiherbivore defenses, polyphenols may play an *offensive* role in chemical ecology by allelopathically suppressing competing vegetation through toxic effects on seed germination and root growth (Kuiters 1990). Although there is evidence that the physical impact of litter layer accumulation can impede understory seedling establishment (Facelli & Pickett 1991), toxic effects of polyphenols may occur only at concentration higher than those in nature. Another mechanism of allelopathy, however, may be to limit nutrient availability to competing organisms. During plant succession, slow-growing and polyphenol-rich species can eventually tie-up the available nutrients into recalcitrant soil organic matter, impeding faster-growing species (Van Cleve et al. 1991). For example, within forest communities, polyphenol-rich species such as *Vaccinium myrtillus* can create microsites of mor-type humus where low nutrient availability impedes other understory species (Bernier et al. 1993; Gallet & Lebreton 1995). At boundaries between contrasting soil-vegetation associations, the mor-humus community can extend beyond the soil boundary where inherent low mineral nutrient availability puts the faster growing plants at a disadvantage (Goldberg 1982).

One adaptive value for polyphenol production on fertile sites may be to create conditions unfavorable to faster-growing competitors. This kind of 'negative' feedback would suggest a niche for polyphenol producers as invaders of fertile soils during plant succession. Exceptionally polyphenol-rich species, however, are most competitive where soils are already highly infertile. In environments where faster-growing plants could not possibly grow, there are presumably fewer competitive advantages for expending energy to allelopathy. Polyphenols reduce nutrient availability in fertile soils through litter accumulation, formation of recalcitrant organic complexes, and impeded mineralization/nitrification. In the highly infertile soils where polyphenol-rich species dominate, these same mechanisms could function to maximize recovery of nutrients from litter and minimize nutrient losses from the ecosystem. Root distribution in the pygmy forest suggests that the litter layer is the preferred medium, where about half the fine roots occur (Table 2). Soils in the pygmy forest are so extremely infertile that, through development of a mor-humus, polyphenol producers substantially *improve* conditions for root growth and nutrient cycling.

Amelioration of acid soil infertility factors

Aluminum toxicity can be a major constraint to crop productivity on highly leached acid soils such as Oxisols, Ultisols, and Spodosols (Fageria et al. 1988; Roy et al. 1988). Some of the soils and mor-litter layers on the Ecological Staircase are extremely acidic, with pH($CaCl_2$) as low as 2.2 (Table 2), and this is presumed to result in a Al toxicity (Westman 1975a). Aluminum toxicity in some crop species can occur at concentrations less than 0.4 micromolar, but no toxicity is seen in forests with soil solution Al concentrations higher by orders of magnitude (Adams & Moore 1983). The lack of apparent toxicity in forest soils is presumed to result from the vast majority of dissolved Al being complexed by organic acids (Adams & Moore 1983). Although chelated Al is soluble in the rhizosphere, roots are able to prevent its uptake into the symplasm (Taylor 1988). Chelating organic acids added to acidic soil reduce the toxicity of Al to tomatoes, corn, and other crops (Bartlett & Riego 1972).

Aluminum complexation by organic acids in a mor-humus extract prevents toxicity to *Allium* roots (Berggren & Fiskesjo 1987). Similarly, humic acids formed from polyphenols, added to acidic sand culture, prevented Al toxicity in maize (Tan & Binger 1986).

Among the specific organic acids added to an acidic subsoil, the greatest degree of detoxification was with those that form 5- and 6-bond chelate rings with aluminum (Hue et al. 1986). Such 5- and 6-bond rings are what make phenolic acids in conifer forest floors strong complexing agents for Al, Fe, and Mn (McColl et al. 1990). Polyphenols are strong complexing agents for Al (Powell & Rate 1987), and in particular the ortho-phenolic group (Sikora & McBride 1990), which is ubiquitous among polyphenols.

Phosphorus availability can be a major constraint to productivity, particularly in acidic soils. Phosphorus 'fixation' in acidic soils can limit P availability via precipitation with soluble Al, Fe, and Mn or specific sorption to reactive surfaces. In the pygmy forest, highly weathered Al and Fe oxide clays under conditions of low pH provide anion exchange and ligand exchange sites to sorb phosphate from solution. There are at least two different mechanisms through which polyphenols can act to enhance phosphorus availability under such conditions. Organic anions can compete with phosphate for sorption sites on mineral surfaces to prevent fixation of soluble phosphate (Kafkafi et al. 1988). The ortho-phenolic group is such a strong competitor for these sites that phenolic acids have been shown to desorb previously fixed phosphate (Davis 1982). Complexation of soluble Al by added organic acids can reduce its reactivity toward phosphate, presumably accounting for the increased P availability with addition of humic acids in acid sand culture experiments where there was no involvement of anion exchange sites on clay minerals (Tan & Binger 1986). The capacity of polyphenols to lower Al, Fe, and Mn activities in solution minimizes precipitation of phosphate. Addition of chelating organic acids to soils previously fertilized with phosphate, can increase concentrations of extractable P by as much as 1000% (Comerford & Skinner 1989), perhaps resulting from the combined effect of desorption from anion exchange sites, complexation of 'active' forms of Al and Fe, and dissolution of phosphate minerals by metal-chelating agents.

The capacity of polyphenols to complex Fe and solubilize P is one reason suggested for natural selection of high polyphenol concentration in *Eucalyptus* growing on Spodosols (Hingston 1962). Soluble organics leached from surface layers of sawdust or mulch dramatically increase the solubility and bioavailability of P in the underlying soil (Anderegg & Naylor 1988; Moss et al. 1989; Wade & Sanchez 1983). The pygmy forest produces polyphenol-rich litter, which is a source of chelating agents and organic anions that can compete with phosphate for sorption sites, lower Al, Mn, and Fe activities and solubilize previously 'fixed' phosphate.

The cation exchange capacity (CEC) of soils largely prevents leaching of nutrient cations due to its adsorptive property. In highly fertile (non-acid) soils, a large proportion of the CEC arises from negative charges on layer silicate clay minerals. In contrast, the vast majority of CEC in highly-leached, acidic soils arises from organic matter of the litter layer (Kalisz & Stone 1980). The acidified quartz sand soil of the pygmy forest is an extreme case in which the soil minerals have virtually no CEC, and positively-charged anion exchange sites on the highly-weathered Al and Fe oxide clays can actually accelerate leaching loss through cation repulsion.

Polyphenols provide much of the CEC of soil organic matter, either in the humus layer (Kalisz & Stone 1980), or as a dominant component of the recalcitrant organic fraction that eventually becomes stable soil humus, often the largest source of CEC in the mineral soil (Schnitzer et al. 1984). In the extreme case of the pygmy forest, CEC in the rooting zone arises exclusively from the organic matter produced by the plants. In spite of the absence of primary minerals to replace nutrient cations and physical conditions favorable for nutrient leaching losses, the pygmy forest creates sufficient CEC to retain the small remaining pool of nutrient cations and support sustained productivity over geologic time.

Most phenolic substances in decomposing leaf litter eventually leach into the mineral soil where they are adsorbed on to organic matter, contributing to humus formation (Shindo & Kuwatsuka 1976). Oxidative polymerization of phenolics is the main process through which soil humic substances are formed (Schnitzer et al. 1984; Varadachari & Ghosh 1984). Oxidative coupling of phenolics can be catalyzed inorganically by Mn(IV) (Lehman & Cheng 1987; Pohlman & McColl 1989; Shindo & Huang 1984), or by extracellular enzymes (Katase & Bollag 1991). Phenolic acids can strongly adsorb to oxide clay surfaces via anion exchange (Davis 1982). These electrostatically-bound organic acids can then act as 'anchors' for subsequent sorption of hydrophobic organic solutes (Jardine et al. 1989). Hydrophobic organics can bind to adsorbed humic materials, at low pH, facilitating the accumulation of humus coatings on mineral surfaces (Schnitzer 1991). Humic acids formed by oxidative coupling of phenolics are very stable, with mean residence times estimated from 500–2000 years (Schnitzer 1991). The accumulation of soil humus profoundly influences the chemical properties of the mineral soil. For example, occupation of adsorption sites by organic matter causes topsoils of Oxisols and Andisols to fix much less phosphorus than subsoils of similar texture and mineralogy (Haynes 1984).

Root growth in the subsoil of the pygmy forest is confined exclusively to humus-lined channels (Westman 1975b). Insulated from the influence of the clay minerals, the humus-lined environment may be conducive to growth of roots and associated mycorrhizae. If the organic coating creates a physical barrier impeding Al release into solution and blocking anion sorption sites, it would thus mitigate precipitation or sorption of phosphate and minimize cation repulsion. Humic substances provide CEC and an organic substrate for adsorption of dissolved organic matter, and the vegetation itself provides the polyphenols that are the substrate for humus formation. So, as part of its 'extended' phenotype, polyphenol-rich vegetation of the pygmy forest appears to create a humus-lined rhizosphere that may enable roots to grow where they otherwise could not.

Implications for management of highly infertile soils

The clearing of polyphenol-rich ecosystems on infertile soils for agriculture is often followed by rapid loss of productivity. Low fertility soils are slower to recover from disturbance and are more vulnerable to damage from anthropogenic influences. Practical applications may be improved from knowledge of the ways that polyphenol production enables natural ecosystems to survive and sustain productivity on inherently infertile soils. Nutrient cycling dynamics and potential infertility problems of mor-humus ecosystems are substantially different than their more fertile counterparts. Nitrogen cycling may not even follow that same pathway in these contrasting ecosystems, yet the same land management practices are often used. Traditional agroforestry systems have been able to sustain productivity for centuries on the same soils that quickly lose fertility when cleared for tillage. Such agroecosystems often mimic the dynamics of a polyphenol-rich forest, with the maintenance of a continuous litter layer. For example, agronomic application of these principles include use of surface mulch for crop production in Amazon basin soils, which maintains cooler soil temperatures, retains soil moisture, and impedes invasion by weeds (Wade & Sanchez 1983). Similarly, growth of *Picea abies* seedlings in greenhouse experiments was dramatically improved by placing mor litter on the soil surface (Hallsby 1994), and pine growth on mine spoils was improved five-fold by the enhanced water-holding capacity, CEC, and phosphorus solubility that results from surface applied (polyphenol-rich) organic matter (Moss et al. 1989). The capacity of the litter layer to temporarily hold water during intense rain events can minimize runoff and surface erosion while maximizing infiltration. The importance of the forest floor in the hydrologic cycle is evident in deforested areas of the subtropics where inadequate soil infiltration and water holding capacity causes flooding in the rainy season and inadequate aquifer recharge subsequently causes unusually low flow of rivers during the dry season. Although most of the beneficial impacts described result from the impact of litter layers on soil physical (rather than chemical) properties, polyphenols are largely responsible for litter accumulation. Management practices for sustained productivity or reclamation on soils of mor-humus ecosystems should ideally include maintenance or restoration of a polyphenol-rich litter layer on the soil surface.

Summary and conclusions

There are many potential feedbacks between polyphenol production and soil conditions that are worthy of further research. Like other plant species that are adapted to strongly acidic and highly infertile soils, plants in the pygmy forest produce high foliar concentrations of polyphenols, and those species that also grow outside the pygmy forest show the highest polyphenol concentrations on the least fertile soils. Although the adaptive value of polyphenols as antiherbivore defenses is no longer universally accepted, there is clearly a feedback between soil conditions and polyphenol production. Polyphenols have multiple effects on plant–litter–soil interactions, including the suppression of detritivore activity, formation of mor-type humus, retardation of N mineralization, and the sequestration of nutrients into a very-slowly-available pool of organic matter. In the context of degrading the productivity of otherwise fertile soils, these interactions can all be construed as 'negative' feedbacks. A very different conclusion arises from an analysis of their impact in soils that are already highly infertile.

Higher polyphenol concentrations in pine trees of less fertile sites of the Ecological Staircase cause litterfall-N to be released primarily in dissolved organic forms rather than NH_4^+ or NO_3^-. Sparingly-soluble protein-tannin complexes formed by polyphenols in decomposing litter accumulate in the rooting zone. There is evidence that these protein-tannin complexes can be utilized as a N source by very few soil organisms, other than the mycorrhizal fungi associated with the roots of the polyphenol producer. This would provide a feedback to soil conditions that involves an adaptation to N limitation, enabling the plant to maximize N recovery by minimizing potential leaching or denitrification, and by maintaining litter N in a form that the plant's associated mycorrhizal fungi can utilize.

In addition to their impact on N cycling, production of polyphenol-rich litter on acidic, infertile soils could enable plants to ameliorate Al toxicity, enhance the bioavailability of P, minimize leaching loss of nutrient cations, and create more favorable conditions for root growth. In such environments natural selection favors plants with 'extended' phenotypes that alter soil properties and dynamics through formation of mor-type humus. The convergent evolution of polyphenol-rich plant communities on such soils throughout the world, is therefore construed to be a *positive* feedback to soil conditions through which plants improve the properties of the soil as a medium for root growth and nutrient cycling.

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