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Effects of Nitrogen Enrichment, Wildfire, and Harvesting on Forest-Soil Carbon and Nitrogen

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ABSTRACT

Northern forest soils represent large reservoirs of C and N that may be altered by ecosystem perturbations. Soils at three paired watershed in Maine were investigated as case studies of experimentally elevated N deposition, wildfire, and whole-tree harvesting. Eight years of experimental $(NH_4)_2SO_4$ additions at the Bear Brook Watershed in Maine significantly reduced forest-floor C/N ratios from 30.6 to 23.4. Forest-floor C and N pools were lower in the treated watershed (38 Mg C ha^{-1}, 1612 kg N ha^{-1}) compared with the reference (75 Mg C ha^{-1}, 2372 kg N ha^{-1}). Fifty years after wildfire at Acadia National Park, the burned watershed with hardwood regeneration had significantly lower forest-floor C and N concentrations (208 g C kg^{-1} soil, 9.9 g N kg^{-1} soil) than the reference watershed dominated by a softwoods (437 g C kg^{-1} soil, 12.8 g N kg^{-1} soil). Forest-floor C and N pools were lower in the burned watershed (27 Mg C ha^{-1}, 1323 kg N ha^{-1}) compared with the reference (71 Mg C ha^{-1}, 2088 kg N ha^{-1}). At the Weymouth Point, the harvested watershed regenerated to spruce-fir, the dominant stand type that existed before the harvest, and it had significantly lower forest-floor C concentrations and pools (406 g C kg^{-1} soil, 24 Mg C ha^{-1}) than the reference (442 g C kg^{-1} soil, 39 Mg C ha^{-1}) after 17 yr. All perturbations studied were associated with lower forest-floor C pools.

On a global scale, soil organic matter (SOM) contains approximately twice as much C as the atmosphere, and comprises 2/3 of the terrestrial C pool (Post et al., 1990). North American soils are estimated to represent ≈22% of the world's terrestrial C pool (Bruce et al., 1999). Significant changes in the C storage of these soils may alter the global C cycle. Carbon stored in SOM represents the net balance between litter inputs and heterotrophic respiration in terrestrial ecosystems. The factors that control organic matter levels in soils include climate, topography, parent material, biological activity, vegetation, and time (Jenny, 1941). Terrestrial C balances may also be influenced by perturbations, such as N deposition, fire, and harvesting.

Elevated emissions of nitrogen oxides and ammonia are primarily because of combustion of fossil fuels, manufacture and use of fertilizers, livestock waste, and burning of biomass (Galloway et al., 1995). Subsequent increases in N deposition have been concentrated in mid-latitude regions where fertilizer use and industrial emissions are the highest (Peterson and Mellilo, 1985; NADP/NTN, 1998). Increased N deposition has been estimated to increase global terrestrial C uptake at a rate of 0.1 to 2.3 Pg yr^{-1} (Peterson and Mellilo, 1985; Schindler and Bayley, 1993; Townsend et al., 1996; Holland, 1997), assuming that terrestrial productivity is limited by N (Townsend et al., 1996). Nadelhoffer et al. (1999b) demonstrated that soils are the dominant sink for N deposition in Maine and other northern temperate forests. Although soils were shown to assimilate nearly 15 times more N deposition than wood, soils sequestered slightly less C due to lower soil C/N ratios. However, soil acidification associated with N deposition may reduce decomposition rates (Martikainen et al., 1989; Nohrstedt et al., 1989; Prescott, 1995), thereby increasing the soil C reservoir. Clearly, the effect of N deposition on the soil C reservoir remains complex and subject to debate.

The potential for a warmer climate with altered precipitation patterns and lightning frequency, in response to or exacerbated by increased greenhouse gas emissions, may change wildfire frequency. Flannigan and Van Wagner (1991) predicted a 50% increase in fire frequency in the boreal and subboreal forests in Canada if the concentration of atmospheric CO_2 doubled. Increased fire occurrence may act as a positive feedback to climate change by reducing terrestrial C and N reservoirs and increasing atmospheric CO_2 and NO_x concentrations. Wildfire could be an important factor in determining the long-term sequestration of C and N in forest soils. Despite the current low fire frequency in Maine forests, the long-term effects of wildfire on soil C and N pools must be better understood, given future climatic uncertainties.

As the demand for forest products increases, there is also a concomitant concern about the potential effects of forest harvesting on soil C storage. In a review of the literature, Johnson (1992) found no change in average soil C content with forest harvesting, although individual sites showed net losses or gains depending on residue management. However, Fan et al. (1998) attributed modeled terrestrial uptake of C in North American forests to the regrowth of abandoned farmland and previously logged forests. In Maine, ≈90% of the land area is forested, of which 43% is owned by large industrial forest companies who provide 25% of the nation's paper (Seymour and Lemin, 1989; Gadzik et al., 1998). Thus forest harvesting and forest policy in Maine has the potential to significantly influence soil C storage.

The objective of this study was to evaluate soil C and N pools at three forested watersheds in Maine that

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Abbreviations: ANP, Acadia National Park; BBWM, Bear Brook Watershed in Maine; BRN-REF, reference watershed for the wildfire; BRN-TRT, burned watershed; GLM, general linear model; MWD, moderately well drained; NIT-REF, reference watershed for the $(NH_4)_2SO_4$ treatment; NIT-TRT, $(NH_4)_2SO_4$–treated watershed; SOM, soil organic matter; VPD, very poorly drained; WPW, Weymouth Point Watershed; WTH-REF, reference watershed for whole-tree harvesting; WTH-TRT, whole-tree harvested watershed.

represented perturbations due to experimental N enrichment, wildfire, and whole-tree harvesting.

MATERIALS AND METHODS

Site Descriptions

Three-paired forested watershed sites in Maine were used to evaluate soil C and N pools and the potential influence of forest ecosystem perturbation. The perturbations studied were experimentally elevated N deposition at the Bear Brook Watershed in Maine (BBWM), wildfire at Acadia National Park (ANP), and whole-tree harvesting at the Weymouth Point Watershed (WPW). In addition, BBWM provided an opportunity to contrast forest vegetation types, while WPW provided an opportunity to contrast soil drainage class.

The BBWM is located in eastern Maine (44°52′N, 44°52′W), 50 km from the Gulf of Maine, on the upper 265 to 475 m of the southeast slope of Lead Mountain. The average slope from the top of the watershed to the weirs is 31%. The West Bear watershed has been treated bimonthly with ammonium sulfate [$(NH_4)_2SO_4$] since November 1989 as part of a whole-watershed manipulation experiment designed to investigate the effects of atmospheric deposition of N and S. Granular $(NH_4)_2SO_4$ has been aerially applied at ≈28.8 kg S ha^{-1} yr^{-1} and 25.2 kg N ha^{-1} yr^{-1}. The treated watershed, West Bear (NIT-TRT, 10.2 ha), is adjacent to the reference watershed, East Bear (NIT–REF, 10.7 ha). The upper reaches of the watersheds are predominately pure red spruce (*Picea rubens* Sarg.) stands, and the lower ≈60% of the watersheds are mixed northern hardwood stands, dominated by American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh), and red maple (*Acer rubrum* L.). Hardwood stands are 40 to 50 yr old, reflecting previous harvesting practices, while softwood stands on the upper slope are 80 to 100 yr old. Soils are predominantly Typic and Lithic Haplorthods formed from dense basal till. Additional site characteristics and biogeochemical data on soils and soil solutions from this study site may be found in Fernandez et al. (1999), Kahl et al. (1999), and Norton et al. (1999b).

During the dry season of 1947, wildfires consumed thousands of hectares throughout northern New England. Approximately 6956 ha burned on Mount Desert Island, located on the coast of eastern Maine (44°23′N, 69°15′W), which included >4000 ha of ANP. The Canon Brook watershed (BRN-TRT) is located on the eastern slope of Cadillac Mountain at a 152- to 457-m elevation in an area of ANP that burned in 1947. The southern tributary of the Canon Brook stream is located in the BRN-TRT watershed. Pioneer species such as paper birch (*Betula papyrifera* Marsh) and striped maple (*Acer pennsylvanicum* L.) currently dominate the BRN-TRT watershed. Prior to European settlement in the late 1700s, fires burned infrequently (approximately every 500 yr) in coastal Maine forests (Patterson et al., 1983). However, large fires occurred on Cadillac Mountain in 1889 and in 1896 or 1889 (Moore and Taylor, 1927). The Hadlock Brook watershed (BRN-REF) lies on the southeastern slope of Sargent Mountain at an elevation of 152 to 396 m, and is used as a reference watershed. Hadlock Brook drains an area that escaped the 1947 fire and red spruce is the dominant canopy species. Both watersheds have similar soils, predominantly coarse-loamy, mixed, frigid, Aquic Haplorthods. The watersheds are ≈4.5 km apart and sampling sites had slopes of 20 to 30%.

The WPW is located on commercial spruce-fir forest land in northern Maine (49°57′N, 69°19′W) at an elevation of 287 to 315 m. In 1981, a whole-tree harvest was conducted, removing ≈90% of the 232 Mg ha^{-1} of available biomass from a 48-ha watershed (WTH-TRT) (Smith et al., 1986). An adjacent watershed (73 ha) was not harvested and served as the reference watershed (WTH-REF). Vegetation on WTH-REF consists of a two-aged red spruce and balsam fir [*Abies balsamea* (L.) Mill.] forest that developed from the 1913 to 1919 spruce budworm [*Choristneura fumiferana* (Clem.)] epidemic. Regeneration on the WTH-TRT watershed is predominantly red spruce and balsam fir, which were ≈2 to 3 m in height at the time of sampling. Soils in the WPW are coarse-loamy, mixed, frigid Aquic Haplorthods and Aeric Haplaquepts of the Chesuncook catena formed from dense basal till. Drainage class differs significantly across the gently sloping landscape because of classic pit and mound topography, ranging from moderately well drained (MWD), which accounts for 25% of the total WPW area, to very poorly drained (VPD), which accounts for 34% of the total WPW area.

Soil Sampling

Soil sampling depth increments included the forest floor, the upper 5 cm of the B horizon, and the 5- to 25-cm increment of the B horizon. A horizons were not present. The E horizon was thin, discontinuous, and typically low in C or N content in the soils at our sites. The chemical characterization of E horizons also often reflects admixtures of overlying O or underlying B horizon material incorporated during sampling. For these reasons, E horizons were sampled, but chemical analyses were not conducted on these samples. Forest floors were quantitatively sampled at each site with a 0.71 by 0.71 m frame (Fernandez et al., 1993). Mineral soil was also quantitatively sampled at BBWM, but grab samples were collected at ANP and WPW.

Sampling at BBWM focused on capturing potential contrasts between NIT-TRT and NIT-REF watersheds within two dominant forest types after 8 yr of N additions. The contrast of forest stand types at BBWM also allowed potential differences between hardwood and softwood forest types to be evaluated. Within each watershed, three soil pits were excavated in hardwood stands and three in softwood stands within the Tunbridge (coarse-loamy, isotic, frigid Typic Haplorthods) soil series. Soil samples were collected June through August of 1998, and watershed and forest types were equally represented during each sampling month.

Sampling at ANP was intended to capture potential differences in BRN-TRT and BRN-REF watersheds 50 yr after a wildfire. Soil sampling at ANP was limited to two stands to minimize destructive sampling within the national park as per our sampling permit. One stand was selected in each of the BRN-TRT and BRN-REF watersheds at similar elevations (≈275 m). A transect was established in each stand with 12 equidistant sampling points spaced at 4-m intervals. At each sampling point, a 15 by 15 cm soil sample was excavated from the Dixfield (coarse-loamy, isotic, frigid Aquic Haplothods) soil series. Three adjacent sampling points were bulked and homogenized in the field to create four samples per transect. Sampling at BRN-TRT was conducted in September 1998 prior to leaf fall, and BRN-REF was sampled in October 1998.

Sampling at WPW focused on capturing potential contrasts between WTH-TRT and WTH-REF watersheds within two soil drainage classes 17 yr after the harvest. Sixteen study plots (10 by 10 m) were selected from the 27 plots described in the experimental design of Briggs et al. (1999). The selected study plots were stratified by two soil drainage classes, MWD and VPD. For this study, soil pits were excavated adjacent to the four existing plots in each of MWD and VPD soil drainage classes in each watershed. Samples were collected in June and

July of 1998, and watersheds and drainage classes were equally represented during each sampling month.

Mineral soils from all sites were sieved (6 mm) and homogenized in the field, and subsamples were taken to the laboratory for analysis. However, WPW-VPD soils were too wet to sieve in the field and were sieved (2 mm) in the laboratory after they were air dried. Forest-floor samples were collected in their entirety and taken to the laboratory for analysis.

Laboratory Analysis

Soils were air dried, then sieved through either 2-mm (mineral) or 6-mm (organic) mesh sieves to isolate the respective fine earth and coarse fractions. Coarse fragments were removed from the coarse organic samples (>6 mm). Percent air-dry moisture was measured for fine earth soils and coarse organic soils (>6 mm) (Robarge and Fernandez, 1986). Fine earth soils were measured for pH using 0.01 M $CaCl_2$ (Hendershot et al., 1993), and SOM by loss-on-ignition at 450°C for 12 h. Total C and N were measured using a LECO CN 2000 (St. Joseph, MI) analyzer employing the Dumas method of combustion at 1350°C in a pure O_2 environment. Coarse organic soils were ground and homogenized prior to C and N analysis.

Computations

Quantitative soil sampling allowed for direct computation of soil mass per unit area (Fernandez et al., 1993) for the O horizon at all sites and for all sampling increments at BBWM. To calculate C, N, and SOM concentrations for the entire forest floor, fine (<6 mm) and coarse (>6 mm) O horizon data were mass weighted. The concentration of SOM in the coarse fraction of the forest floor was assumed to be 100%.

Statistical Analysis

All analyses were carried out using the Statistical Analysis System (SAS Institute, 1988) with an alpha level of 0.05. Because the data did not meet the assumptions of normality and equality of variance, a rank transformation was used (Conover, 1971; Zar, 1984). A general linear model (GLM) was applied to the ranked data for each site to analyze the differences among main effects (watersheds, forest types, and drainage class) and interactions. Layout for the statistical analyses are shown in Table 1.

Table 1. Layout for the statistical analyses for the Bear Brook Watershed in Maine (BBWM), Acadia National Park (ANP), and the Weymouth Point Watershed (WPW), including degrees of freedom (df) and formulas for F calculations.

Site	Source	df	F_{calc}
BBWM	Total	11	
	Model	3	MS_{Model}/MS_{Error}
	Watershed (W)	1	MS_W/MS_{Error}
	Forest type (F)	1	MS_F/MS_{Error}
	Watershed × forest type (WF)	1	MS_{WSF}/MS_{Error}
	Error	8	
ANP	Total	7	
	Model	1	MS_{Model}/MS_{Error}
	Watershed (W)	1	MS_W/MS_{Error}
	Error	6	
WPW	Total	15	
	Model	3	MS_{Model}/MS_{Error}
	Watershed (W)	1	MS_W/MS_{Error}
	Drainage class (D)	1	MS_D/MS_{Error}
	Waterhsed × drainage (WD)	1	MS_{WD}/MS_{Error}
	Error	12	

RESULTS AND DISCUSSION

Three paired-watershed research sites used in this research offered an opportunity to study the effects of N enrichment, wildfire, and whole-tree harvesting on forest soil C and N pools. Paired watershed studies offer a unique opportunity to investigate treatment effects at the whole-ecosystem level. These watershed pairs were selected because they had topographic and vegetative characteristics that suggested they were similar prior to their respective disturbance. No soil data prior to disturbance at these sites, however, were available. At BBWM, stream monitoring prior to treatments provided additional evidence of watershed comparability since the integrated responses evident in stream chemistries were highly comparable in the pretreatment calibration years (Norton et al., 1999b). Because soil C and N data specifically were not available for these watersheds prior to treatments, differences between treated and reference watersheds, or the lack thereof, may reflect a combination of treatment effects and antecedent conditions.

Nitrogen Enrichment

After 8 yr of experimental whole-watershed $(NH_4)_2SO_4$ additions at BBWM, N concentrations were significantly higher in the upper 5 cm of the B horizon of NIT-TRT than NIT-REF (Table 2). Soil C/N ratios in the upper 5 cm of the B horizon of NIT-TRT reflected higher N concentrations and were significantly lower than NIT-REF. Because of numerically lower C and significantly higher N concentrations in the forest floor of NIT-TRT, forest-floor C/N ratios in NIT-TRT were also significantly lower than NIT-REF. After 3 yr of treatment at BBWM, Wang and Fernandez (1999) found significantly lower forest-floor C concentrations in mixedwood stands of NIT-TRT compared with NIT-REF, although no significant differences were detected in softwood and hardwood stands. We used power analyses (Zar, 1984) with our data to determine that future studies of similar design would require 106 and 536 samples per watershed for forest-floor C and N concentrations, respectively, to detect significant differences (power = 0.80) between NIT-TRT and NIT-REF watersheds.

Nadelhoffer et al. (1999a) showed that soils were the dominant sink for N at BBWM, using ^{15}N tracer studies in the second and third year of the experiment. The NIT-TRT watershed retained 96% of the ambient N deposition prior to treatment and ≈82% of the cumulative N additions from 1989 to 1997 (Kahl et al., 1999). Nitrogen enrichment in the NIT-TRT watershed produced higher foliar N concentrations (White et al., 1999), higher soil solution NO_3^- concentrations (Fernandez et al., 1999), and higher stream N export (Kahl et al., 1993, 1999; Norton et al., 1999a). Higher concentrations of N in surface soil horizons of NIT-TRT than NIT-REF are consistent with anticipated increases in N because of surface applications of the $(NH_4)_2SO_4$ treatment and litter inputs with higher N concentrations.

Nitrogen pools in the upper 5 cm of the B horizon were significantly greater (22%) in NIT-TRT than NIT-

Table 2. Means (and coefficients of variation) for soil organic matter (SOM), C, and N concentrations and pools, C/N ratios, and pH for the Bear Brook Watershed in Maine (BBWM), Acadia National Park (ANP), and the Weymouth Point Watershed (WPW) soils. Means are presented by depth for the $(NH_4)_2SO_4$-treated (NIT-TRT) and reference (NIT-REF) BBWM watersheds, the burned (BRN-TRT) and reference (BRN-REF) ANP watersheds, and the whole-tree harvested (WTH-TRT) and reference (WTH-REF) WPW watersheds.

Watershed	Depth	n	SOM	C	N	C/N	pH	Horizon thickness	Soil mass	SOM	C	N
			g kg^{-1}				$CaCl_2$	cm	Mg ha^{-1}			kg ha^{-1}
						BBWM						
NIT-TRT	Forest floor	6	498 (41.2)	335 (31.3)	14.2 (24.9)	23.4 (14.7)*	3.3 (8.5)	6.3 (71.1)	112 (63.6)*	74 (70.5)*	38 (69.2)*	1612 (64.9)*
	B, 0–5 cm	6	168 (14.1)	79 (14.2)	3.8 (7.5)*	20.6 (9.5)*	3.9 (2.2)	4.9 (2.0)	149 (14.3)	25 (12.1)	12 (8.4)	568 (7.9)*
	B, 5–25 cm	6	123 (23.8)	51 (18.7)	2.4 (20.6)	21.7 (6.6)	4.2 (4.0)	19.5 (6.1)	806 (19.9)	96 (18.4)	40 (20.8)	1881 (23.9)
NIT-REF	Forest floor	6	635 (13.0)	398 (9.0)	13.2 (9.35)	30.6 (17.4)	2.9 (4.4)	9.3 (40.9)	182 (50.4)	135 (50.8)	75 (56.9)	2372 (50.5)
	B, 0–5 cm	6	152 (29.6)	75 (28.9)	2.9 (23.4)	25.3 (11.0)	3.7 (5.5)	5.0 (0.9)	165 (34.1)	24 (31.2)	12 (31.2)	466 (28.4)
	B, 5–25 cm	6	113 (52.0)	50 (47.1)	2.1 (47.0)	23.9 (8.5)	4.2 (4.4)	19.6 (3.8)	977 (27.0)	99 (29.0)	44 (24.9)	1857 (24.9)
						ANP						
BRN-TRT	Forest floor	4	434 (15.0)	208 (12.7)*	9.9 (12.3)*	21.1 (9.2)*	4.0 (8.9)*	7.0 (3.4)	136 (29.1)	62 (12.2)*	27 (15.3)*	1323 (22.6)*
	B, 0–5 cm	4	165 (35.9)	73 (28.0)*	3.9 (29.5)*	19.0 (5.2)*	4.5 (7.7)*	5.0	–	–	–	–
	B, 5–25 cm	4	142 (26.0)	58 (23.4)	3.0 (19.8)	19.4 (5.0)	4.6 (5.0)*	19.0 (7.0)	–	–	–	–
BRN-REF	Forest floor	4	657 (29.0)	437 (5.53)	12.8 (1.76)	34.1 (6.6)	2.8 (2.9)	14.8 (15.5)	163 (14.5)	138 (15.7)	71 (16.3)	2088 (16.3)
	B, 0–5 cm	4	92 (52.3)	41 (50.1)	1.7 (51.0)	24.2 (2.8)	3.6 (3.5)	5.0	–	–	–	–
	B, 5–25 cm	4	127 (30.6)	55 (29.7)	2.4 (31.3)	22.8 (29.7)	4.0 (2.0)	16.0 (24.2)	–	–	–	–
						WPW						
WTH-TRT	Forest floor	8	698 (7.7)	406 (9.4)*	11.8 (18.8)	35.2 (14.9)	3.5 (0.1)	8.6 (21.8)	59 (37.0)*	46 (37.4)*	24 (38.6)*	679 (39.0)
	B, 0–5 cm	8	116 (47.1)	53 (45.8)	2.4 (53.4)	22.6 (8.3)	3.9 (10.7)	5.0	–	–	–	–
	B, 5–25 cm	8	73 (93.0)	32 (86.9)	1.6 (82.5)	19.3 (16.3)	4.2 (8.0)	20.0	–	–	–	–
WTH-REF	Forest floor	8	720 (18.0)	442 (4.2)	12.0 (14.7)	37.7 (16.1)	3.0 (8.4)	11.3 (42.2)	89 (37.0)	73 (39.6)	39 (35.1)	1088 (45.52)
	B, 0–5 cm	8	189 (104.0)	96 (113.5)	4.4 (122.9)	22.8 (12.9)	3.6 (6.3)	5.0	–	–	–	–
	B, 5–25 cm	8	66 (59.1)	34 (66.0)	1.4 (57.9)	24.2 (13.9)	4.0 (6.1)	20.0	–	–	–	–

* Significant at the 0.05 probability level.

REF, reflecting higher N concentrations in NIT-TRT (Table 2). However, forest-floor SOM, C, and N pools were significantly lower in NIT-TRT than NIT-REF. These differences were driven by a significantly lower forest-floor mass in NIT-TRT than NIT-REF. It is possible that N enrichment in NIT-TRT may have increased forest-floor decomposition rates compared with NIT-REF, reducing NIT-TRT forest-floor mass (Gill and Lavender, 1983; Hunt, 1988; Fenn, 1991; McNulty et al., 1991; Conn and Day, 1996; Downs et al., 1996). Higher C turnover in the NIT-TRT forest floor leading to N-pool depletion could have contributed to some illuvial accumulation of N in the underlying 5 cm of mineral soil. Because C and SOM concentrations were not statistically different between watersheds by depth, it is also probable that these forest-floor differences may simply reflect antecedent conditions.

Forest Type Effects

We also evaluated the potential effects of stand composition on soil C and N at BBWM. The distribution of C and N concentrations and pools in hardwood and softwood stands by depth are shown in Table 3. Significantly lower forest-floor C and N pools were found in soils supporting hardwoods compared with softwoods

Table 3. Hardwood and softwood mean soil C and N concentrations and pools, and C/N ratios at the Bear Brook Watershed in Maine (BBWM). Means are presented by depth for the $(NH_4)_2SO_4$-treated watershed (NIT-TRT, n = 3) and the reference watersheds (NIT-REF, n = 3), and collectively for both BBWM watersheds (n = 6).

Forest type	Watershed	Depth	C	N	C/N	Soil mass	C	N
			g kg^{-1}			Mg ha^{-1}		kg ha^{-1}
Hardwood	NIT-TRT	Forest floor	301	12.9	23.0	53	16	675
		B, 0–5 cm	77	3.8	20.2	157	12	588
		B, 5–25 cm	45	2.0	22.4	771	34	1527
	NIT-REF	Forest floor	373	13.4	27.8	101	38	1360
		B, 0–5 cm	59	2.4	24.2	197	12	478
		B, 5–25 cm	33	1.5	23.2	1168	38	1663
	Both	Forest floor	337	13.1	25.4	77*	27*	1018*
		B, 0–5 cm	68*	3.1*	22.2	177	12	533
		B, 5–25 cm	39*	1.7*	22.8	970	36*	1595*
Softwood	NIT-TRT	Forest floor	369	15.5	23.8	171	61	2549
		B, 0–5 cm	82	3.9	21.0	142	11	548
		B, 5–25 cm	56	2.7	20.9	840	47	2236
	NIT-REF	Forest floor	422	12.9	33.3	263	111	3383
		0–5 cm	90	3.4	26.3	134	12	453
		5–25 cm	66	2.7	24.7	785	50	2052
	Both	Forest floor	395	14.2	28.6	217	86	2966
		0–5 cm	86	3.7	23.7	138	12	501
		5–25 cm	61	2.7	22.8	812	48	2144

* Significant at the 0.05 probability level.

when comparing the main effects in the data ($n = 6$). Forest-floor C and N concentrations were not significantly different between softwood and hardwood stands. Power analyses suggest that future studies would require 14 and 86 samples per forest type to detect significant differences (power = 0.80) in forest-floor C and N concentrations, respectively, between these forest types based on these data. Lower forest-floor C and N pools in hardwood stands compared with softwood stands were driven by significantly lower forest-floor masses. Carbon and N concentrations in the upper 5 cm of the B horizon were significantly lower in hardwood soils compared with softwood soils, although C and N pools were not different between forest types. Carbon and N pools in the 5- to 25-cm increment of the B horizon were significantly lower in hardwood stands than in softwood stands. Unlike the forest floor, differences in the 5- to 25-cm increment were a consequence of significantly lower C and N concentrations in hardwood stands than softwood stands. Significant interactions among watersheds and forest types were not found; however, Table 3 shows trends in soil C and N data consistent with the main effect response of reduced C and N pools and narrower C/N in hardwood soils at all depth increments compared with softwoods. This is also consistent with evidence of higher rates of N mineralization and C turnover in NIT-TRT soils compared with NIT-REF soils as shown by Wang and Fernandez (1999).

Litter quality is a key factor governing decomposition rates (Meentemeyer, 1978; Stump and Binkley, 1992); therefore, litter-quality differences between forest types may account for lower forest-floor masses and C and N concentrations and pools in the 5- to 25-cm increment in hardwood stands than softwood stands. White et al. (1999) reported significantly higher foliar N concentrations in all species studied in NIT-TRT compared with NIT-REF watersheds, but the increase in N concentration was much greater for hardwoods compared with red spruce, with the greatest difference (+33%) for sugar maple. Past harvesting in the ≈50-yr-old hardwood stands may have also exacerbated differences between hardwood and softwood soils, particularly in the forest floor and uppermost mineral soils (0–5 cm). Nevertheless, these findings highlight the importance of considering forest type when quantifying forest-soil C and N pools, even though forest type differences often reflect a combination of ecological and management factors.

Wildfire

Fifty years after the wildfire in ANP, C and N concentrations and C/N ratios in the forest floor of BRN-TRT were significantly lower than BRN-REF (Table 2). Consequently, C, N, and SOM pools in the forest floor of BRN-TRT were significantly lower than BRN-REF. Forest-floor C and N pools in BRN-TRT were 52 and 23% lower than forest-floor C and N pools in BRN-REF, respectively. Because this wildfire occurred during a particularly dry period and because wildfires generally have a low frequency in coastal Maine forests (Moore and Taylor, 1927; Patterson et al., 1983), the wildfire in this study was an intense burn. Thus fire may have directly reduced forest-floor C and N concentrations and pools in BRN-TRT in gaseous or particulate forms via volatilization or ash convection (Boerner, 1982; Raison et al., 1985). Fire may have also induced additional C and N losses by increasing soil erodibility (Díaz-Fierros et al., 1987; McNabb and Swanson, 1990; Andreu et al., 1996) and decomposition rates (Schoch and Binkley, 1986; Fernández et al., 1997).

Despite the plausible reduction in forest-floor C and N at the time of the fire, the concomitant change from a softwood to hardwood forest in BRN-TRT probably contributed to lower forest-floor C and N concentrations and pools in BRN-TRT 50 yr after the wildfire.

At BBWM, forest-floor C and N pools were similarly lower in hardwood stands than softwood stands; however, this was a result of lower forest-floor masses in hardwood stands. At ANP, lower forest-floor C and N pools in BRN-TRT reflected lower C and N concentrations rather than lower forest-floor masses. The interplay between changes in forest-floor mass and composition with different forest types deserves further study. Nevertheless, it is probable that the change in forest type and thus litter quality increased forest-floor decomposition rates at BRN-TRT compared with BRN-REF. Furthermore, antecedent conditions may have also contributed to lower C and N pools in BRN-TRT. Given the variability in the ANP data, future studies at this site would require 22 samples per watershed to detect significant differences (power = 0.80) between forest-floor masses in these watersheds.

In contrast to the forest floor, the upper 5 cm of the B horizon in BRN-TRT had higher C and N concentrations and lower C/N ratios than BRN-REF (Table 2). Elevated C and N concentrations in the upper mineral soil may be a direct result of the fire. Charcoal and partially burned organic matter may have been incorporated into the mineral soil, increasing mineral soil C and N concentrations (Johnson, 1992). In addition, an increased presence of N-fixing species after the wildfire may have increased mineral soil C and N concentrations (Johnson, 1992). Downward movement of finely divided particulate matter can also contribute to C and N enrichment in the upper mineral soil after fires (Dyrness and Norum, 1983). However, the shift from softwood to hardwood forest types probably contributed to higher C and N concentrations and lower C/N ratios in the upper 5 cm of the B horizon in BRN-TRT 50 yr after the wildfire. Thus presumably faster rates of decomposition in the hardwood forests of BRN-TRT compared with BRN-REF may have redistributed C and N from the forest floor to the upper 5 cm of the B horizon in BRN-TRT soils. Contrary to our results at ANP, C and N concentrations were significantly lower in the upper 5 cm of B horizon soils in hardwood stands compared with softwood soils at BBWM (Table 3). Therefore, differences at ANP may reflect additional influences of the 1947 wildfire beyond contrasting vegetation and litter quality between watersheds, including differences in antecedent conditions prior to the fire. It is probable that all of these factors played a role in the results.

Whole-Tree Harvest

Seventeen years after the whole-tree harvest at WPW, forest-floor C concentrations were significantly lower in WTH-TRT than WTH-REF (Table 2). The WTH-TRT forest-floor mass and forest-floor C and N pools were significantly lower than WTH-REF. Forest-floor C and N pools in WTH-TRT were ≈36% and 38% of the forest-floor C and N pools, respectively, in WTH-REF. Because conifer forest types were present at WTH-TRT before and after the harvest, differences are not attributed to forest-type effects. However, whole-tree harvests commonly result in increased rates of decomposition because of increased soil temperature and moisture (Ovington, 1968; Witkamp, 1971; Marks and Bormann, 1972; Edwards and Ross-Todd, 1983; Mroz et al., 1985), and in initial decreases in leaf and wood litter inputs because of overstory removal. Thus accelerated decomposition rates and reductions in litter production probably resulted in lower forest-floor C concentrations and masses in WTH-TRT. Lower biological nutrient demands and increased decomposition rates in the WTH-TRT watershed may also explain increases in stream water N concentrations immediately following the whole-tree harvest in 1981 to 1984 (Hornbeck et al., 1990).

In northern hardwood forests, Covington (1981) found that the mass of SOM in the forest floor decreased by more than 50% (a decrease of 30.7 Mg ha^{-1}) in the 15 yr following a whole-tree harvest. During the next 50 yr in that study, SOM content in the forest floor increased by 28.0 Mg ha^{-1} and by Year 64 was within 5% of an equilibrium value of 56.0 Mg ha^{-1}. Aber et al. (1978) used a modeling approach that predicted declines in forest-floor organic matter for 15 to 30 yr after harvesting, and estimated that 60 to 80 yr may be required for SOM levels to recover. Thus at 17 yr after harvest, WPW may have shifted from the degradation phase to the aggradation phase for SOM.

Drainage Class Effects

Contrasting soil drainage classes (MWD and VPD) at WPW allowed us to evaluate the potential effects of soil drainage class on C and N pools at this site. One might expect that anaerobic conditions in WPW-VPD soils would increase soil C and N by reducing heterotrophic oxidation of SOM compared with more aerobic conditions in WPW-MWD soils. However, C and N concentrations and pools were not different between drainage classes. In addition, significant interactions between watershed and drainage class were not found. Given the variability in these data, power analyses indicated that future studies at this site would require 93 and 42 forest-floor samples, 85 and 128 upper B horizon (0–5 cm) samples, and 49 and 74 lower B horizon (5–25 cm) samples per drainage class to detect significant differences (power = 0.80) between C and N concentrations, respectively, in these highly variable WPW-VPD and WPW-MWD soils.

CONCLUSIONS

Experimentally elevated N deposition at BBWM, wildfire and subsequent regeneration at ANP, and whole-tree harvest and subsequent regeneration at WPW were all associated with significantly lower forest-floor C pools. Lower forest-floor C pools were consistent with lower C concentrations in the burned and harvested watersheds, although lower forest-floor masses also contributed to differences in the whole-tree harvested watershed. Lower forest-floor C pools at the $(NH_4)_2SO_4$–treated watershed at BBWM were almost totally explained by lower forest-floor masses. It is probable that each perturbation increased forest-floor decomposition rates, thereby reducing forest-floor masses and/or C concentrations. Antecedent soil differences in these watersheds prior to treatment were not measured and may have also contributed to apparent treatment effects. Lower C and N pools in the forest floor of hardwood stands compared with softwood stands at BBWM are consistent with lower C and N pools in the hardwood forests of the burned watershed compared with the softwood forests of the reference watershed at ANP. Higher C and N concentrations in the upper 5 cm of the underlying B horizon soils of the burned watershed could be evidence of C and N redistribution from the forest floor to the upper mineral soil. Forest type was associated with significant differences in soil C and N, but the lack of antecedent soil measurements, as well as management practice and land use history, limits our ability to define cause and effect. The data do suggest that shifts in species composition that might result from forest disturbance could be at least as important in determining soil C and N content as the level of removal or additions of C and N from the disturbance itself. These three paired-watershed case studies in Maine indicated that the perturbations represented (i.e., N deposition, wildfire, and whole-tree harvesting) have long-term impacts on soil C and N, particularly C pools in the forest floor.

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REFERENCES

Aber, J.D., D.B. Botkin, and J.M. Melillo. 1978. Predicting the effects of different harvesting regimes on forest floor dynamics in northern hardwoods. Can. J. For. Res. 8:306–315.

Andreu, V., J.L. Rubio, J. Forteza, and R. Cerni. 1996. Postfire effects on soil properties and nutrient losses. Int. J. Wildland Fire 6:53–56.

Boerner, R.E.J. 1982. Fire and nutrient cycling in temperate ecosystems. Bioscience 32:187–192.

Born, B. 2000. Litter decomposition and organic matter turnover in northern forest soils. For. Ecol. Manage. 133:13–22.

Briggs, R.D., R.C. Lemin, Jr., and J.W. Hornbeck. 1999. Impacts of precommercial thinning and fertilization on a spruce-fir ecosystem: Final report. CFRU Res. Bull. 12, Univ. Maine, Orono, ME.

Bruce, J.P., M. Frome, E. Haites, H. Janzen, R. Lal, and K. Paustain. 1999. Carbon sequestration in soils. J. Soil Water Conserv. 54:382–389.

Conn, C.E., and F.P. Day. 1996. Response of root and cotton strip decay to nitrogen amendment along a barrier island dune chronosequence. Can. J. Bot. 74:276–284.

Conover, W.J. 1971. Practical nonparametric statistics. John Wiley & Sons, New York.

Covington, W.W. 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. Ecology 62:41–48.

Díaz-Fierros, F., E. BeNito Ruenda, and R. Pèrez Moreira. 1987. Evaluation of the U.S.L.E. for the prediction of erosion in burnt forest areas in Galicia (N.W. Spain). Catena 14:189–199.

Downs, M.R., K.J. Nadelhoffer, J.M. Mellilo, and J.D. Aber. 1996. Immobilization of a ^{15}N-labeled nitrate addition by decomposing forest litter. Oecologia 105:141–150.

Dyrness, C.T., and R.A. Norum. 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. Can. J. For. Res. 13:879–893.

Edwards, N.T., and B.M. Ross-Todd. 1983. Soil carbon dynamics in a mixed deciduous forest following clear cutting with and without residue removal. Soil Sci. Soc. Am. J. 47:1014–1021.

Fan, S., M. Gloor, J. Mahlman, S. Pacala, J. Sarmiento, T. Takahashi, and P. Tans. 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. Science 282:442–446.

Fenn, M. 1991. Increased site fertility and litter decomposition rate in high-pollution sites in San Bernardino Mountains. For. Sci. 37: 1163–1181.

Fernández, I., A. Cabaneiro, and T. Carballas. 1997. Organic matter changes immediately after a wildfire in an Atlantic forest soil and comparison with laboratory soil heating. Soil Biol. Biochem. 29:1–11.

Fernandez, I.J., L. Rustad, M. David, K. Nadelhoffer, and M. Mitchell. 1999. Mineral soil and solution responses to experimental N and S enrichment at the Bear Brook Watershed in Maine (BBWM). Environ. Monitor. Assess. 55:165–185.

Fernandez, I.J., L.E. Rustad, and G.B. Lawrence. 1993. Estimating total soil mass, nutrient content, and trace metals in soils under a low elevation spruce-fir forest. Can. J. For. Res. 73:317–328.

Flannigan, M.D., and C.E. Van Wagner. 1991. Climate change and wildfire in Canada. Can. J. For. Res. 21:66–72.

Gadzik, C.J., J.H. Blanck, and L.E. Caldwell. 1998. Timber supply outlook for Maine: 1995–2045. Maine Dep. Conserv., Maine For. Serv., Augusta, ME.

Galloway, J.N., W.H. Schlesinger, H. Levy II, A. Michaels, and J.L. Schnoor. 1995. Nitrogen fixation: Anthropogenic enhancement-environmental response. Global Biogeochem. Cycles 9:235–252.

Gill, R.S., and D.P. Lavender. 1983. Litter decomposition in coastal hemlock (*Tsuga heterophylla*) stands: Impact of nitrogen fertilizers on decay rates. Can. J. For. Res. 13:116–121.

Hendershot, W.H., L. Lalande, and M. Duquette. 1993. Soil reaction and exchangeable acidity. p. 141–145. *In* M.R. Carter (ed.) Soil sampling and methods of analysis. Lewis Publishers, Boca Raton, FL.

Holland, E.A. 1997. Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems. J. Geophys. Res. 102:15849–15866.

Hornbeck, J.W., C.T. Smith, Q.W. Martin, L.M. Tritton, and R.S. Pierce. 1990. Effects of intensive harvesting on nutrient capital of three forest types in New England. For. Ecol. Manage. 30:55–64.

Hunt, H.W., E.R. Ingham, D.C. Coleman, E.T. Elliot, and C.P.P. Reid. 1988. Nitrogen limitation of production and decomposition in prairies, mountain meadow, and pine forest. Ecology 69:1009–1016.

Jenny, H. 1941. Factors of soil formation. McGraw-Hill, New York.

Johnson, D.W. 1992. Effects of forest management on soil carbon storage. Water Air Soil Pollut. 64:83–120.

Kahl, J.S., S.A. Norton, I.J. Fernandez, K.J. Nadelhoffer, C.T. Driscoll, and J.D. Aber. 1993. Experimental inducement of nitrogen saturation at the watershed scale. Environ. Sci. Technol. 23:565–568.

Kahl, J., S. Norton, I. Fernandez, L. Rustad, and M. Handley. 1999. Nitrogen and sulfur input-output budgets in the experimental and reference watersheds, Bear Brook Watershed in Maine (BBWM). Environ. Monitor. Assess. 55:113–131.

Marks, P.L., and F.H. Bormann. 1972. Revegetation following forest cutting: Mechanisms for return to steady-state nutrient cycling. Science 176:914–915.

Martikainen, P.J., T. Aarnio, V.-M. Taavitsainen, L. Päivinen, and K. Salonen. 1989. Mineralization of carbon and nitrogen in soil samples taken from three fertilized pine stands: Long-term effects. Plant Soil 114:99–106.

McNabb, D.H., and F.J. Swanson 1990. Effects of fire on soil erosion. p. 159–176. *In* J.D. Walstad et al. (ed.) Natural and prescribed fire in Pacific Northwest forests. Oregon State Univ. Press, Corvallis, OR.

McNulty, S.G., J.D. Aber, and R.D. Boone. 1991. Spatial changes in forest floor and foliar chemistry of spruce-fir forests across New England. Biogeochemistry 14:13–29.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59:465–472.

Moore, B., and N. Taylor. 1927. Vegetation on Mount Desert Island Maine, and its environment. Brooklyn Bot. Garden Mem. Vol. 3. Brooklyn Bot. Garden, Brooklyn, NY.

Mroz, G.D., M.F. Jurgensen, and D.J. Frederick. 1985. Soil nutrient changes following whole tree harvesting on three northern hardwood sites. Soil Sci. Soc. Am. J. 49:1552–1557.

Nadelhoffer, K., M. Downs, B. Fry, A. Magill, and J. Aber. 1999a. Controls on N retention and exports in a forested watershed. Environ. Monitor Assess. 55:187–210.

Nadelhoffer, K.J., B.A. Emmett, P. Gundersen, O.J. Kjønaas, C.J. Koopmans, P. Schleppi, A. Tietema, and R.F. Wright. 1999b. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature 398:145–148.

National Atmospheric Deposition Program/National Trends Network. 1998. National atmospheric deposition 1997 wet deposition. Illinois State Water Survey, Champaign, IL.

Nohrstedt, H.-Ö., K. Arnebrant, E. Bååth, and B. Söderström.1989. Changes in carbon content, respiration rate, ATP content, and microbial biomass in nitrogen-fertilized pine forest soils in Sweden. Can. J. For. Res. 19:323–328.

Norton, S.A., J. Kahl, I. Fernandez, T. Haines, L. Rustad, S. Nodvin, J. Scofield, T. Stickland, H. Erickson, P. Wigington, Jr., and J. Lee. 1999a. The Bear Brook Watershed in Maine (BBWM), USA. Environ. Monitor Assess. 55:7–51.

Norton, S.A., J.S. Kahl, and I.J. Fernandez. 1999b. Altered soil-soil water interactions inferred from stream water chemistry at an artificially acidified watershed at Bear Brook Watershed, Maine (USA). Environ. Monitor Assess. 55:97–111.

Ovington, J.D. 1968. Some factors affecting nutrient distribution within ecosystems. p. 95–105. *In* F.E. Eckardt (ed.) Functioning of terrestrial ecosystems at the primary production level. UNESCO, Liege, Belgium.

Patterson, W.A. III, K.E. Sunders, and L.J. Horton. 1983. Fire regimes of the coastal Maine forest of Acadia National Park. Rep. OSS 83-3. U.S. Dep. Interior, National Park Serv., North Atlantic Region, Office of Sci. Progr., Boston, MA.

Peterson, B.J., and J.M. Melillo. 1985. The potential storage of carbon caused by the eutrophication of the biosphere. Tellus 37B:117–127.

Post, W.M., T.-H. Peng, W.R. Emmanuel, A.W. King, V.H. Dale, and D.L. DeAngelis. 1990. The global carbon cycle. Am. Sci. 78:310–326.

Prescott, C.E. 1995. Does nitrogen availability control rates of litter decomposition in forests? Plant Soil 169:83–88.

Raison, R.J., P.K. Khanna, and P.V. Woods. 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. Can. J. For. Res. 15:132–140.

Robarge, W.D., and I.J. Fernandez. 1986. Quality assurance methods manual for laboratory analytical techniques. USEPA. Corvallis Environ. Res. Lab, Corvallis, OR.

SAS Institute. 1988. SAS/STAT User's Guide, 6.03 ed. Cary, NC.

Schindler, D.W., and S.E. Bayley. 1993. The biosphere as an increasing sink for atmospheric carbon: Estimates from increased nitrogen deposition. Glob. Biogeochem. Cycles 7:717–733.

Schoch, P., and D. Binkley. 1986. Prescribed burning increased nitrogen availability in a mature loblolly pine stand. For. Ecol. Manage. 14:13–22.

Seymour, R.S., and R.C. Lemin. 1989. Timber supply projections for Maine, 1980–2080. Misc. rep. 337. Univ. Maine Agric. Exper. Station, Orono, ME.

Smith, C.T., M.L. McCormack, Jr., J.W. Hornbeck, and C.W. Martin. 1986. Nutrient and biomass removals from red spruce-balsam fir whole-tree harvest. Can. J. For. Res. 16:381–388.

Stump, L.M., and D. Binkley. 1992. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. Can. J. For. Res. 23:1402–1407.

Townsend, A.R., B.H. Braswell, E.A. Holland, and J.E. Penner. 1996. Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen. Ecol. Applic. 6:806–814.

Wang, Z., and I.J. Fernandez. 1999. Soil type and forest vegetation influences on forest floor Nitrogen dynamics at the Bear Brook Watershed in Maine (BBWM). Environ. Monitor. Assess. 55:221–234.

White, G., I. Fernandez, and G. Wiersma. 1999. Impacts of ammonium sulfate treatment on the foliar chemistry of forest trees at the Bear Brook Watershed in Maine (BBWM). Environ. Monitor. Assess. 55:235–250.

Witkamp, M. 1971. Soils as components of ecosystems. Annu. Rev. Ecol. Sys. 2:85–110.

Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.

Soil and Weathered Bedrock: Components of a Jeffrey Pine Plantation Substrate

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ABSTRACT

Virtually all of the commercial forests in the southern Sierra Nevada are on granitic terrain, where bedrock may be weathered to depths >15 m while soils are <1 m thick. Because plant-available water is depleted in these thin soils by midsummer, study objectives were to characterize the edaphic role of the weathered bedrock relative to the soil. The site was a 30-yr-old Jeffrey pine (*Pinus jeffreyi Grev.* & Balf.) plantation growing on relatively thin soils (75 cm in depth) overlying weathered granitic bedrock. The average depth to hard bedrock was 350 cm. A trench was excavated and physical and chemical properties of the soil and bedrock were evaluated. Cation-exchange capacities (CEC) were lower in the weathered bedrock (Cr1 horizon = 4.6 cmol kg^{-1}) than in the soil (A horizon = 13.4 cmol kg^{-1}), but pH values were similar (4.6–5.5). Organic C content was negligible in the weathered bedrock matrix (<0.1%), but was higher within joint fractures (3.7%), where roots were concentrated, than within the soil A horizon (2.7%). Carbon/N ratios were much lower in the soil A horizon (19.6) than in the bedrock fractures (62.0). Saturated hydraulic conductivities (K_{sat}) of the soil and the weathered bedrock were similar and high (8–11 cm h^{-1}). Mean root length density (RLD) was greater within the joint fractures than within the soil, but on a whole rock basis bedrock RLD was much lower (<0.08 cm cm^{-3}). Total plant-available water storage capacity of 48.8 cm was calculated for the 350 cm thickness of regolith, with 14.7 cm (30%) contributed by soil and 34.1 cm (70%) by weathered bedrock. Weathered bedrock underlying soils is critical to the survival of forest ecosystems, particularly with regard to water supply, and should not be neglected in ecosystem site evaluations and models.

GRANITIC ROCK CONSTITUTES 20% of California's land area, and underlies >65% of the Sierra Nevada range (Donley et al., 1979; Norris and Webb, 1976). Most of California's forests grow on upland sites where soils are generally thin and are underlain by thick zones of weathered bedrock. The prevalent granitic bedrock is commonly weathered to depths of several to many meters (Wahrhaftig, 1965), whereas overlying soils are often <1 m thick (Fig. 1a). In early to midsummer, the water status of these thin soils indicates that little or no plant-available moisture remains (Anderson et al., 1995; Sternberg et al., 1996).

Weathering processes generate substantial porosity, giving the weathered granitic bedrock soil-like water-holding characteristics (Jones and Graham, 1993; Graham et al., 1997). The ability of a substrate to transmit and hold water is a factor critical to plant survival in Mediterranean climates. The rate of water movement at saturation through the weathered bedrock is similar to that through coarse-textured soils, with K_{sat} on the order of 1 to 5 cm h^{-1} (Johnson-Maynard et al., 1994; Graham et al., 1997). Available water capacities of 0.124 (Jones and Graham, 1993) and 0.15 m^3 m^{-3} (Anderson et al., 1995; Sternberg et al., 1996) have been reported for weathered granitic bedrock.

Weathered bedrock can act as a rooting medium for shrubs and trees (Hellmers et al., 1955), providing plant-available water during the summer dry season (Arkley, 1981; Anderson et al., 1995; Sternberg et al., 1996). Pine species have root systems that are deep and widespread and can exploit water held in bedrock by growing into and following joint fractures. Conifer roots have been observed growing in joint fractures of weathered bedrock to depths >25 m (Stone and Kalisz, 1990). Roots form thick mats and develop severely flattened cortexes within the joint fractures, allowing for greater surface area contact between the roots and fracture wall (Zwieniecki and Newton, 1995).

It is clear from the literature, as well as observations of roadcuts, that both soil and weathered bedrock are components of the substrate supporting forests in the mountains of California. The relative contributions of these two components with regard to supporting plant growth have not been specifically investigated. In this

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Abbreviations: AWC, available water capacity; CEC, cation-exchange capacity; ECEC, effective cation-exchange capacity; FC, Field capacity; Ksat, saturated hydraulic conductivity; PWP, permanent wilting point; RLD, root length density.