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Nutrient limitation and soil development: Experimental test of a biogeochemical theory

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Abstract. Walker and Syers (1976) proposed a conceptual model that describes the pattern and regulation of soil nutrient pools and availability during long-term soil and ecosystem development. Their model implies that plant production generally should be limited by N on young soils and by P on old soils; N and P supply should more or less equilibrate on intermediate-aged soils. We tested the application of this model to nutrient limitation, using a well characterized substrate age sequence in Hawaiian montane rain forest. Earlier experiments had evaluated nutrient limitation in forests on a young (300 y) and an old (4,100,000 y) substrate on the same developmental sequence; N alone limited tree growth on the young substrate, while P alone did so on the old one. An additional fertilizer experiment based on replicated treatments with N, P, and all other nutrients combined, applied in individually and in all factorial combinations, was established in an intermediate-aged site in the Laupahoehoe Forest Reserve, Hawaii. Here, diameter increments of the dominant tree *Metrosideros polymorpha* increased slightly with N additions, and nearly doubled when N and P were added together. Additions of elements other than N and P had no significant effect on growth. These results show that N and P had equilibrated (relative to plant requirements) in the intermediate aged site. Together with the earlier experiments, these results suggest that the Walker and Syers model provides a useful starting point for explaining the nature and distribution of nutrient limitation in forest ecosystems.

Introduction

In many terrestrial ecosystems, primary production and other ecosystem processes are constrained by low rates of nutrient supply. Walker and Syers (1976) proposed a coherent explanation for patterns of soil nutrient availability during long-term soil development, one with substantial implications for the causes and distribution of nutrient limitation. They pointed out that most newly deposited primary substrates (volcanic material, dunes, glacial debris, etc.) contain most of the rock-derived nutrients that they will ever have. Upon exposure at or near the surface, weathering of the more labile minerals in primary substrates increases the biological availability of P (and Ca, Mg, K, and other rock-derived nutrients). Nitrogen is absent in most primary substrates, however, and must be obtained from the atmosphere by either biological N

fixation or atmospheric deposition. Soil fertility should be low early in soil development, with *N* in particular in short supply, and *N*-fixing organisms should have a substantial competitive advantage once they reach a site.

Over time, *N* fixation and atmospheric deposition should increase the quantity and biological availability of *N* in the system as a whole, eventually bringing it close to an equilibrium with a rock derived nutrient, generally *P* (Stevens & Walker 1970; Walker & Syers 1976; Gorham et al. 1979). Below the equilibrium *N:P* ratio, *N* fixers should retain a competitive advantage and atmospheric inputs of fixed *N* should be retained within the system; above it, any excess *N* could eventually be lost to leaching or the atmosphere. At this point in soil development, soil fertility should be relatively high, with the supply of *N* and *P* roughly in balance relative to the requirements of organisms.

As soil development proceeds further, *P* release by weathering declines as primary minerals are depleted. Most *P* should be retained on-site, because both biological and geochemical processes make *P* nearly immobile in most soils (Uehara & Gillman 1981; Cole & Heil 1981; Cole et al. 1989; Wood et al. 1984). However, each time *P* cycles through available pools, a small amount may be bound in physically or chemically protected forms, especially as soils acidify over time (Fox et al. 1991), and a little could be leached in inorganic or organic forms (cf Qualls et al. 1991). Over tens of thousands to millions of years, most *P* comes to reside in protected inorganic and recalcitrant organic forms, and the system comes to a “terminal steady state” of low soil fertility caused by low *P* availability.

Walker and Syers (1976) evaluated several soil developmental sequences in New Zealand, and demonstrated that soil *C*, *N*, and *P* pools and fractions varied as predicted by their model. More recently, a number of modifications and exceptions to Walker and Syers model have been proposed. McGill and Cole (1981) suggested that the greater importance of biochemical mineralization (by extracellular enzymes) of *P* in comparison to *N* affects *N* and *P* cycling during soil development, and Lajtha and Schlesinger (1988) showed that changes in *P* fractions during soil development are much less prominent in arid regions. More fundamentally, Dahlgren (1994) demonstrated that certain parent materials supply *N* early in soil development, and several studies have demonstrated that atmospheric deposition can be a significant source of putatively “rock-derived” elements, even *P*, in the long term (Swap et al. 1992; Hedin et al. 1994; Newman 1995).

The implications of Walker and Syers’ model for nutrient limitation to plants and ecosystems have received less attention. Nutrient limitation is defined as occurring where the rate of a process is increased by additions of a nutrient in quantities sufficient to increase its biological availability

(Chapin et al. 1986); it can only be evaluated rigorously by experimentation. A number of studies have demonstrated that plant growth is limited by *N* on young substrates (cf Leisman 1957; Lawrence et al. 1967; Marrs et al. 1983; Vitousek et al. 1993), but tests on older soils or across developmental sequences have been lacking.

Crews et al. (1995) recently described a developmental sequence of forested sites in the Hawaiian Islands that is suitable for testing implications of the Walker and Syers model. The Hawaiian Islands result from the movement of the Pacific tectonic plate over a stationary convective plume or "hot spot" in the mantle (Clague & Dalrymple 1987); the islands become progressively older from southeast to northwest. Crews et al. (1995) located six sites with substrate ages from 300 to 4,100,000 yrs; all have the same mean annual temperature and precipitation, the same soil parent material, and all are covered by similar native forest vegetation (Kitayama & Mueller-Dombois 1995). Soil nutrients along this sequence generally follow the pattern outlined by Walker and Syers (1976); *P* is present largely in primary mineral forms early, in more labile forms at 20,000 and 150,000 y old sites, and in more recalcitrant forms late, while *N* availability (estimated by several methods) increases substantially between the 300 and 20,000 y sites and remains relatively high thereafter (Crews et al. 1995; Riley & Vitousek 1995).

In this paper, we compare results of factorial fertilization experiments with *N*, *P*, and all other essential elements at 3 sites along the sequence – 300 y, 20,000 y, and 4,100,000 y. We expected that *N* but not *P* additions would stimulate tree growth in the young site, and that *P* but not *N* additions would do so in the old site. For the intermediate-aged substrate, we expected that *N* and *P* supply would have equilibrated at relatively high availability, and that tree growth would not respond to nutrient additions. Results for the young site were reported by Vitousek et al. (1993), and those for the old site by Herbert and Fownes (1995) and Herbert et al. (submitted). Here, we present results for the intermediate-aged site, and integrate results from all 3 experiments to explain patterns of *N* and *P* limitation during long-term soil and ecosystem development.

Methods

Site. In July 1993, we established a factorial fertilization experiment at the Laupahoehoe forest site (19°57′ N, 155°18′ W) of the long substrate age gradient (LSAG) described by Crews et al. (1995). Like all of the sites on the gradient, the Laupahoehoe site is near 1200 m elevation, receives $\sim$2500 mm/y in annual precipitation (Giambelluca et al. 1986), is on the constructional surface of a shield volcano, and is covered by native forest dominated by the tree *Metrosideros polymorpha*, with no evidence of human disturbance and few alien plants. However, feral pigs and alien earthworms appear relatively abundant on this site compared to others on the sequence. The Laupahoehoe site is on the northeast flank of Mauna Kea Volcano; the soil is a Typic Hydrandept developed in thick volcanic ash over in 'a'a lava flow of the Laupahoehoe formation. Soils of the LSAG are described more fully by Chadwick et al. (in preparation). The ash substrate is considered to be $\sim$20,000 y old (Crews et al. 1995), but deeper in the profile it also contains ash that is tens of thousands of years older (Chadwick, personal communication). Of all the sites on the LSAG, Laupahoehoe has the tallest trees, the greatest soil N availability and highest N concentrations in vegetation, and moderately high soil P availability and plant P concentrations (Crews et al. 1995; Kitayama & Mueller-Dombois 1995; Vitousek et al. 1995a).

Field experiment. Factorial fertilization experiments in other Hawaiian forests (Vitousek et al. 1993; Herbert & Fownes 1995; Raich et al. 1996) were based on replicated plots from 10 × 10 to 20 × 20 m in size, with each plot containing several trees. At the Laupahoehoe site, the large size and low density of the trees made this approach impractical. Instead, we selected 48 canopy trees, ranging from 60–140 cm in diameter; diameters were measured above the basal swell and/or fluted portion of the trunk, often several meters above the ground. The trees were blocked by diameter, and then randomly assigned to a treatment. Fertilizer was spread evenly over a circle 10 m in diameter centered on each tree. The treatments were N (100 $\mathrm{kg{\cdot}ha^{-1}{\cdot}y^{-1}}$ of N, half as urea and half as ammonium nitrate), P (100 $\mathrm{kg{\cdot}ha^{-1}{\cdot}y^{-1}}$ as triple superphosphate), and a complete (minus N and P fertilizer consisting of K (100 $\mathrm{kg{\cdot}ha^{-1}{\cdot}y^{-1}}$), Ca (100 $\mathrm{kg{\cdot}ha^{-1}{\cdot}y^{-1}}$), Mg (58 $\mathrm{kg{\cdot}ha^{-1}{\cdot}y^{-1}}$), S (40 $\mathrm{kg{\cdot}ha^{-1}{\cdot}y^{-1}}$), Fe (8 $\mathrm{kg{\cdot}ha^{-1}{\cdot}y^{-1}}$), and Mo (0.01 $\mathrm{kg{\cdot}ha^{-1}{\cdot}y^{-1}}$). We designated this treatment as "T"; it included potassium muriate, dolomite, gypsum, Granusol (a commercial micronutrient mixture), and supplemental *Mo*. Treatments were applied in a complete factorial combination, including all interactions; there were 8 treatments (control, N, P, T, $N+P$, $N+T$, $P+T$, and $N+P+T$), with 6 replicates/treatment.

Fertilizer was applied at the full annual rate (above) at the initiation of the experiment in July 1993; half of this quantity was applied every 6 months thereafter. We determined diameter increments of the treated trees at annual intervals, using nickel alloy steel dendrometer bands (Liming 1957). Just prior to the 2-year fertilization, we collected small branches from the canopy of each tree, using a shotgun. The youngest class of fully mature sun leaves (with a formed bud or expanding whorl of leaves above them) was selected, and leaf area was determined that day using a Delta-T leaf area meter. Leaves were then oven-dried at 70 °C, weighed to determine leaf mass per unit area (LMA), and ground for chemical analyses.

Laboratory and data analyses. Leaf tissue was digested using a persulfate procedure in a block digestor prior to *N* and *P* analyses; tissue was dry-ashed and then dissolved in hot nitric acid for cation analyses. Total *N* and *P* were determined using an Alpkem autoanalyzer, while cations were determined by atomic absorption spectrophotometry; 10% of all samples were run in duplicate. Each digestion and analytical run included NBS standard apple or pine tissue; our analyses yield 99.7±2.4 and 103.1±4.2 percent of standard values for *N* and *P* respectively. Results of the experiment were analyzed as a complete factorial ANOVA using SYSTAT; blocking by tree size did not contribute significantly (or substantially) to variation in any of the results. Where necessary, results were log-transformed prior to analysis to homogenize variances.

Results

Additions of $N + P$ caused a substantial increase in diameter growth of *Metrosideros polymorpha* at Laupahoehoe. Results for the second year post-fertilization are summarized in Table 1; similar responses were observed in the first year, but we believe that the year 2 results are more reliable in that any initial settling of the dendrometer bands should have been completed by then. Diameter growths rates under the treatments fell into 3 groups – slowest in the control and *P* (alone) treatments, fastest in the N+P and N+P+T treatments, and intermediate in the others; the two extreme groups differed significantly. In an overall ANOVA on log-transformed diameter increments, we observed a significant effect of *N* addition, with no effect of *P* or $N \times P$ interaction. However, when only *N* and *P* are considered (with +*T* combined with the corresponding $-T$ treatments), growth in the $N + P$ treatment was significantly greater than that in control, +*N*, and +*P* treatments; these last 3 did not differ significantly. Foliar analyses demonstrate that the lack of a growth response to added *P* (alone) and *T* was not due to a lack of uptake; additions of *N* or *P* increased foliar *N* or *P* concentrations significantly, and *T* additions increased foliar *Mg* and *K* concentrations (Table 1).

Responses to fertilization on this relatively fertile intermediate-aged soil were compared with results of similar experiments on younger and older sites on the LSAG, all of which used a complete factorial design with the same levels of fertilizer. Results for the second year post-fertilization at Laupahoehoe are compared with the second year response at the young Thurston site and the $2\frac{1}{2}$–$3\frac{1}{2}$ year response at the old Kokee site. We use the later interval

Table 1. Mean diameter increment (with standard error in parentheses) and leaf characteristics of *Metrosideros polymorpha* trees in the second year following fertilization at the Laupahoehoe site, Island of Hawaii. Six trees were sampled in each treatment. Sun leaves were collected for leaf mass per area (LMA) and element concentrations 2 years after the initiation of fertilization. Significant main effects and interactions from a complete factorial ANOVA are summarized at the bottom, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Treatment	Diameter Increment (mm/y)	Element Concentrations LMA (g/m^2)	*N*	*P*	*Ca* (% dry mass)	*Mg*	*K*
Control	1.6 (0.2)	148(4)	1.17(0.05)	0.090(0.003)	0.50(0.05)	0.14(0.01)	0.56(0.04)
N	2.8(0.6)	152(4)	1.34(0.05)	0.100(0.007)	0.56(0.09)	0.15(0.01)	0.36(0.07)
P	1.8(0.3)	148(5)	1.27(0.08)	0.113(0.010)	0.56(0.06)	0.14(0.02)	0.43(0.05)
T	2.7(0.6)	146(6)	1.18(0.04)	0.090(0.007)	0.50(0.06)	0.18(0.02)	0.60(0.06)
NP	4.6(0.8)	140(6)	1.33(0.02)	0.120(0.009)	0.62(0.06)	0.17(0.01)	0.41(0.03)
NT	2.8(0.4)	144(4)	1.26(0.02)	0.096(0.006)	0.47(0.06)	0.15(0.01)	0.64(0.04)
PT	2.9(0.6)	142(4)	1.25(0.02)	0.118(0.007)	0.75(0.07)	0.19(0.02)	0.68 (0.12)
NPT	3.9(0.7)	140(3)	1.30(0.06)	0.117(0.014)	0.52(0.08)	0.17(0.01)	0.54(0.06)
Significant effects	N**		N**	P***	P*, N×T*	T***	T*, N×T*

for Kokee because the forest canopy there was damaged by Hurricane Iniki 18 months into the experiment (though with little tree mortality), and tree growth stabilized a year thereafter (Herbert et al., submitted). During these intervals, we observed no significant main effects or interaction involving the *T* treatment for any plant growth-related response. Accordingly, we combine the corresponding +*T* and −*T* treatments in this comparison.

Diameter growth of *Metrosideros polymorpha* was slow at the young Thurston site (Figure 1 – note the scale on the *y*-axis). Additions of *N* increased growth significantly, with no other significant main effects or interactions. Annual litterfall and the growth and frond turnover of tree ferns also increased following *N* fertilization (Walker & Aplet 1994; Vitousek et al. 1995b). At the Laupahoehoe site, annual diameter increment was greater than that at Thurston, and growth was greatest in the *N* + *P* treatment. Concentrations of *N* and *P* in the foliage of control trees at Laupahoehoe were significantly greater than those at the other experimental sites (Vitousek et al. 1995a). Finally, diameter growth of the control trees at Kokee was intermediate between Thurston and Laupahoehoe, and *P* additions (alone) increased diameter increment significantly. Stand-level wood increment, LAI, and aboveground net primary production also were increased by *P* fertilization at Kokee (Herbert & Fownes 1995; Herbert et al., submitted). Overall, the results of the 3 experiments suggest a developmental progression from *N* limitation in the youngest site, to combined limitation by *N* and *P* in the relatively nutrient-rich intermediate-aged site, to *P* limitation in the oldest site.

Discussion

We anticipated that *N* and *P* availability would have equilibrated (relative to plant requirements) at a relatively high rate of supply in the 20,000 y old Laupahoehoe site, and that tree growth there would not respond to added nutrients. In fact, the availability of *N* and *P* had equilibrated at a ratio close to that required by the trees (Figure 1), as shown by the small or absent response to *N* or *P* alone, in contrast to the substantial response to *N* + *P* together. While *N* addition was associated with enhanced growth in the overall ANOVA, the effect of *N* alone was small compared to that of *N* + *P* (Figure 1). We did not expect that added *N* + *P* would cause a near-doubling of diameter increments in the Laupahoehoe site; clearly, nutrient supply remains limiting to tree growth even in this relatively nutrient-rich site.

In the youngest site on the developmental sequence, the Walker and Syers' model led us to predict *N* limitation, as observed (Figure 1; Vitousek et al. 1993). We also observed *N* limitation on a still younger volcanic ash site (< 30 y) where *Metrosideros polymorpha* was just colonizing (Vitousek et al. 1993).

The Walker and Syers model led Herbert and colleagues to predict *P* limitation in the oldest site on the sequence, as observed (Figure 1, Herbert & Fownes 1995; Herbert et al., submitted). The fact that *N* or *P* (or both together) limit plant growth in these sites does not mean that other resources are not limiting. Indeed, multiple resource limitation, occurring simultaneously and/or sequentially, is the rule (Bloom et al. 1985; Field et al. 1992), especially where different types of resources (e.g., light, water, depletable resources like *N* and *P*, non-depletable resources like CO_2) are considered. In our sites, an increase in CO_2 or light (the latter perhaps caused by a decrease in cloudiness) could enhance plant growth despite the presence of *N* and/or *P* limitation; such an increase could be viewed as an increase in nutrient use efficiency (Schimel et al. 1994). However, resources in the same class (i.e., depletable soil-derived nutrients) are neither acquired independently nor readily substituted for each other (Rastetter & Shaver 1992; Gleeson & Tilman 1992); the observation of limitation by *N* alone or *P* alone (among soil nutrients) does not contradict the multiple resource limitation paradigm.

Two areas of concern in our interpretation of this soil developmental sequence are: 1) the comparability of sites on the underlying age sequence; and 2) the meaning of our measure of tree response to nutrient addition. The sites on the LSAG described by Crews et al. (1995) are very similar in all of the major “state factors” described by Jenny (1980) – except of course time. However, any analysis of long term soil development must trade space for time, comparing across substrates that were established at different times – and any such analysis is inherently compromised (Fastie 1995). Crews et al. (1995) pointed out several ways in which the LSAG sequence is imperfect. For example, the older sites underwent much of their development under Pleistocene climatic conditions quite different from the present (Gavenda 1992; Hotchkiss & Juvik 1993), while the young sites escaped such variation.

Our second concern is that because of the individual-tree-based nature of the fertilizer experiment, diameter increment was the only growth response determined at the Laupahoehoe site. An increase in diameter growth does not necessarily imply an increase in overall carbon fixation at the stand level; instead it could reflect reallocation from roots to stems (Linder & Rook 1984). (Given the residence time of wood relative to other tissues, however, such a reallocation would imply increased carbon storage.) Several growth-related parameters in addition to diameter increment (height growth, litterfall, LAI, understory growth and turnover, NPP) were measured in other plot-based fertilizations in Hawaii (Vitousek et al. 1993; Walker & Aplet 1994; Herbert & Fownes 1995; Raich et al. 1996; Herbert et al., submitted); patterns of fertilizer response in all of these measures generally matched those for diameter increment. Moreover, even if increased diameter growth is due

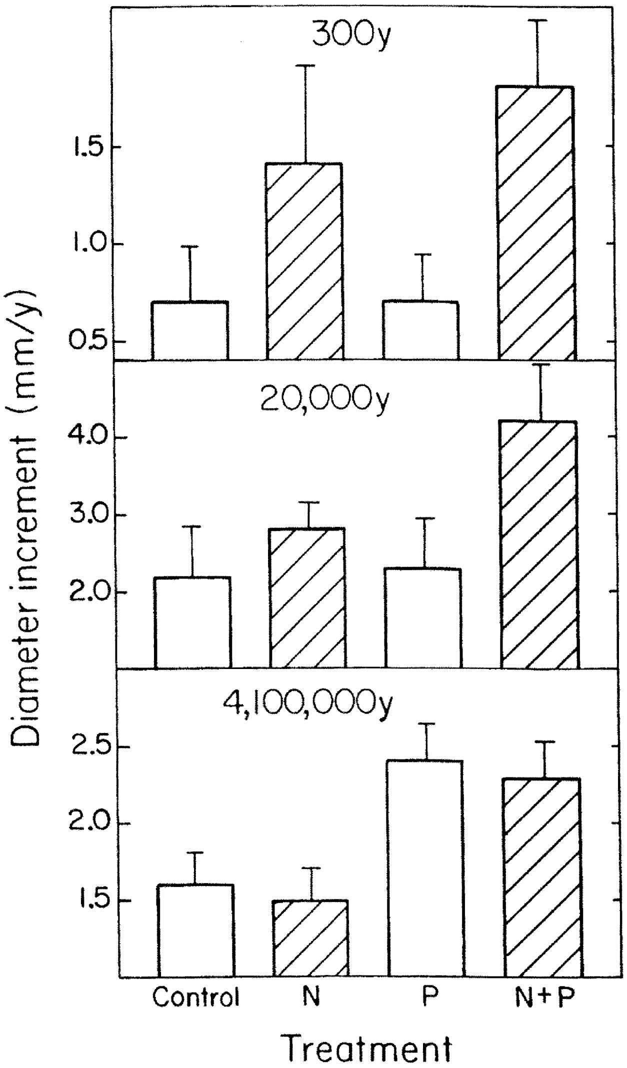

Figure 1. Mean diameter increment (in mm/y, with standard error bars) of *Metrosideros polymorpha* trees in three fertilizer experiments arrayed along a gradient of substrate age in Hawaiian montane rain forest. The top figure is recalculated from Vitousek et al. (1993); the bottom figure is redrawn from Herbert et al. (submitted).

in part to reallocation of resources from belowground, that in itself reflects a reduction in nutritional constraints to growth.

While we are not aware of comparable analyses of nutrient limitation during long-term soil and ecosystem development, nutrient availability and cycling across a developmental sequence have been evaluated carefully at

Glacier Bay, Alaska (Crocker & Major 1955; Lawrence et al. 1967; Bormann & Sidle 1990; Chapin et al. 1994). The entire sequence is relatively short (ca 200 y) there – time enough for successional changes and *N* accumulation, but not for extensive weathering of more recalcitrant primary minerals. Chapin et al. (1994) carried out bioassays of nutrient limitation to seedling growth at Glacier Bay using soil from four stages of development. They grew spruce or alder seedlings in pots filled with field soil and amended with *N*, *P*, or *N* + *P*. Spruce seedlings grown in soil from the two oldest sites responded to added *P*; no other significant responses were observed. Differences in experimental design and in the sequences themselves (their oldest site is younger than our youngest) make direct comparisons with Hawai'i difficult; Chapin et al. (1994) concluded that the *P* limitation they observed reflected recent and massive inputs of *N* by biological fixation.

On a broader scale, the pattern of nutrient limitation on this Hawaiian age sequence is consistent with observations of widespread *N* limitation to forest growth in north-temperate and boreal forests (cf Tamm 1990; Aber et al. 1995), in that glaciation and/or periglacial processes such as loess deposition maintain relatively young substrates at high latitudes. Our results also are consistent with agricultural experiments and with indirect evidence based on soil and plant chemistry in natural ecosystems that suggest that *P* limitation is widespread on old tropical soils (Lathwell & Grove 1986, Vitousek & Sanford 1986). We know of no fertilization experiments of forests on lowland Oxisols or Ultisols, except that Cuevas and Medina (1988) determined that root growth in an Amazonian forest on an Oxisol responded positively to spot additions of *P* and *Ca* but not *N*. The other fertilization experiments we know of in tropical regions, in which at least *N* and *P* were applied separately, have been carried out in montane forests in Jamaica and Venezuela (Tanner et al. 1990, 1992). There, tree growth responded most strongly to added *N*; the developmental state of the soils in those sites is not known.

Overall, our analysis of the Hawaiian developmental sequence suggests that the Walker and Syers model can be extended to explain patterns of nutrient limitation during long term soil and ecosystem development. This result suggests that the model is a good place to begin global evaluations of the distribution and consequences of nutrient limitation. Identifying which nutrients are limiting to forest growth is of more than academic interest; the consequences of environmental change can differ substantially depending which nutrient (if any) constrains production and other ecosystem processes. These differences are most obvious for evaluating the effects of enhanced *N* deposition on species composition and *C* storage in *N* versus *P* limited forests (cf Schindler & Bayley 1993; Galloway et al. 1995), but they may be equally important in predicting ecosystem responses to elevated CO_2 and/or changes in climate (Melillo et al. 1993; Schimel et al. 1994; VEMAP 1995).

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