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Rhizospheric processes influencing the biogeochemistry of forest ecosystems

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Abstract. In the rhizosphere, biotic and abiotic processes interact to create a zone distinct from the bulk soil that may strongly influence the biogeochemistry of forest ecosystems. This paper presents a conceptual model based upon three operationally defined soil–root compartments (bulk soil, rhizosphere and soil–root interface) to assess nutrient availability in the mineral soil–root system. The model is supported by chemical and mineralogical analyses from bulk and rhizosphere soils collected from a Norway spruce forest. The rhizosphere was more intensively weathered and had accumulated more acidity, base cations and phosphorus than the bulk soil. The quantity and quality of organic matter regulate the reciprocal relationships between soil and roots with their associated biota. However, the biogeochemical role of organic matter in the rhizosphere still remains as an area in which more future research is needed. The mechanisms that may regulate nutrient availability in the rhizosphere are also discussed and related to nutrient cycling and adaptation of forests growing under nutrient poor or perturbed conditions. We suggest that the rhizosphere is not an ephemeral environment in the soil, but persists over time and is resilient against perturbation as evinced by consistent differences between rhizosphere and bulk chemistry and mineralogy over wide range of field treatments.

Introduction

Many ecosystem studies are concerned only with structural or chemical measurements of above ground plant parts and bulk soil and humus chemistry, even though 70–80% of the annual net primary production may be allocated below ground (Vogt 1982; Linder & Axelsson 1982). That roots and rhizospheric processes have frequently been ignored has lead some researchers to describe the rhizosphere as 'the hidden half of the hidden half' (Bowen & Roriva 1991) or as one of the areas 'more difficult to study' (Beier & Cummins 1993).

The term rhizosphere was introduced by Hiltner in 1904 to describe the interaction between bacteria and legume roots (Curl & Truelove 1986). Although the term seems self explanatory, *rhizo* from the Greek word for root and *sphere* (Greek, sphaira) the environment in which one acts or exists, the term has many conceptual and operational definitions. Curl and Truelove (1986) described the rhizosphere as 'that narrow zone of soil subject to the influence of living roots, as manifested by the leakage or exudation of substances that affect microbial activity.' According to Lynch (1990), 'the total rhizosphere environment is determined by an interacting trinity of the soil, the plant and the organisms associated with the roots.' Similarly, Ulrich (1987) stated that 'Morphologically, roots and soil, or microorganisms and soil, usually could be clearly separated,' but 'From a functional point of view this clear boundary does not exist.'

Plant roots can be considered as 'biological engineers' in the soil since they create and maintain their own milieu not only by their physical presence but also by actively transforming biotic and abiotic components of the system (Lawton & Jones 1995). Examples of such transformations include the maintenance of microbial communities (Curl & Truelove 1986; Parmelee 1995) and increased weathering of minerals (Courchesne & Gobran 1997; Hinsinger et al. 1992; Richards 1987) due to processes such as exudation of organic acids and enzymes to the rhizosphere. In spite of the small volume the rhizosphere occupies in the mineral soil (Gobran & Clegg 1996), it plays a central role in the maintenance of the soil–plant system. These root effects on soils suggest to some investigators that soil can be considered, in part, as a product of plants and soil biota (Van Breemen 1993).

Interactions between roots, microbial communities and the soil under forest conditions could involve feedback loops driven by photosynthate released by roots (Perry et al. 1989; DeAngelis et al. 1986; Hobbie 1992). Microorganisms that make the rhizospheric community 'continually pull themselves up by their own bootstraps' (Perry et al. 1989) so that nutrient cycling and availability in the rhizosphere is higher than in the bulk soil, thus buffering the ecosystem against disturbances.

We present a conceptual model (Gobran & Clegg 1996) and field results that support the 'bootstrapping' view, and which may help explain how ecosystems can withstand stresses. We also discuss how control of the rhizospheric soil processes can increase forest stand fitness by feedback mechanisms.

Model of rhizosphere properties and processes

The organic layers of forest soils have higher root densities than deeper mineral soil, allowing trees to efficiently recycle nutrients from litter and throughfall. However, 40 to 50% of predominantly mycorrhizal living fine roots are found in the upper 30 cm of the mineral soil (Wood et al. 1984; Persson et al. 1995; Clemensson-Lindell & Persson 1992; Häussling & Marschner

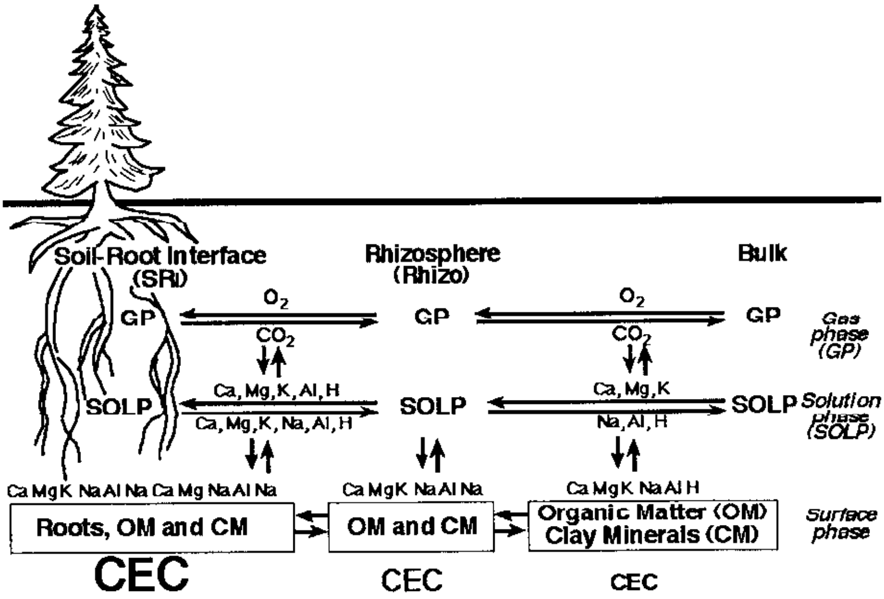

Figure 1. A conceptual model for nutrient availability in the mineral soil–root system.

1989). We developed a conceptual model to assess nutrient availability in the mineral soil–root system (Gobran & Clegg 1996).

In the model we assume that fine roots and their associated organisms maintain a higher level of nutrient availability in the rhizosphere than in the bulk soil. This is accomplished by the release, transport and accumulation of reactive soil organic matter and inorganic compounds in the soil–root interface (SRI) and rhizosphere. The interaction between soil, microorganisms and roots creates a mutually supportive system that can raise nutrient availability by increasing moisture content, mineralization and enriching the pool of cations and anions through increased exchange sites (Figure 1).

According to the conceptual model, the soil–root system can be considered as a multiple-phase system with each soil compartment comprised of a gas phase, a solution phase and a surface phase. In this paper, we focus on the solution and surface phases and discuss chemical and biological processes that cause these phases to differ between the rhizosphere and the bulk soil. The surface phase in the bulk soil occupies a larger volume of soil but has a lower charge per unit mass, and thus a lower cation exchange capacity (CEC), than the rhizosphere and SRI with their higher content of organic matter (OM), clay minerals and amorphous oxides (CM). Additionally, soil bulk density is relatively high in the rhizosphere due pressure exerted by growing roots (Greacen et al. 1968; Bruand et al. 1996).

Rhizospheric organic matter probably differs from that in the bulk soil by having a higher proportion of easily mineralizable root material, exudates, mycorrhizae and associated microorganisms. We believe that its living and dead organic constitutes make the rhizosphere and SRI the most dynamic part of the system since they act as both a source and sink for elements, are involved in weathering and act as fuel for biological reactions. Therefore, CEC follows the same trend as organic matter content, increasing from the bulk soil to the SRI (Figure 1). The arrows represent the three major transport mechanisms between the soil fractions and phases; mass flow, diffusion and biological transport by mycorrhizae. Our studies focused on mineralogical and chemical changes in the solution and surface phases that were considered as products of both chemical and biological interactions.

Supporting field results

Field site and soil components

In this section we will show how the conceptual model was supported by our field investigations of bulk and rhizosphere soil. Preliminary data on the SRI compartment are not presented here, but support the conceptual model (Gobran & Clegg 1996). Soil samples were taken from a 30 yr. Norway spruce (*Picea abies* (L.) Karst.) stand in South-West Sweden (Gobran & Clegg 1996). The soil was classified as a Haplic podzol (FAO-UNESCO 1988) with a silty loam texture throughout the profile. Soil samples were collected from four replicate blocks by taking 16 cores from each plot. The cores were split into three horizons, and samples were pooled into composite samples per per plot for each horizon. All samples were analyzed chemically and statistically in a similar way, as described in Gobran and Clegg (1996), Clegg and Gobran (1997) and Clegg et al. (1997). The studies and model were based upon three operationally defined soil fractions or compartments. These were separated by first carefully removing all roots by hand from the field moist mineral soil. The remaining soil was then passed through a 2-mm mesh to give the bulk soil compartment (Bulk). All fine roots (<2-mm) with any adhering soil were gently shaken to separate roots and soil aggregates (0.5–5 mm). The 0.5–5 mm soil fraction is termed here the rhizosphere compartment (Rhizo). This method is similar to that described by Hendriks and Junk (1981). We defined the soil–root interface compartment (SRI) as apparent free space within fine roots and remaining soil still adhering to the root (<0.5 mm thick). This is similar to the rhizocylinder fraction described by Riley and Barber (1969) and Hoffmann and Barber (1971) (see Figure 1). Concentrations of elements were expressed in $\mathrm{cmol_c\ kg^{-1}}$ and not on a volumetric basis since the bulk

Table 1. Chemical characteristics of the bulk and rhizosphere soil fractions in the E horizon. Means followed by different letters are significantly different at the 5% level. Information about chemical analyses can be found in Gobran and Clegg (1996). 'Calcium aluminium balance' refers to log(Ca/Al) where Ca and Al stand for exchangeable fractions in mol_c

	Bulk soil	Rhizosphere soil
Cation exhange capacity ($cmol_c$ kg-1)	4.41^b	12.16^a
Exchangeable base cations ($cmol_c$ kg-1)	0.33^a	1.93^a
Titratable acidity ($cmol_c$ kg-1)	4.08^a	10.23^a
Soluble base cations ($cmol_c$ kg-1)	0.10^b	0.46^a
Calcium aluminium balance	-1.35^a	-1.20^a
Base saturation (%)	7.47^b	16.13^a
Organic Matter (%)	9.80^b	23.03^a

density of the soil compartments varies and is difficult to asses (Greacen et al. 1968; Bruand et al. 1996).

Chemical properties of the rhizosphere

Chemical characteristics of the bulk and rhizosphere soil fractions in the E horizon are presented in Table 1. Similar data for the other soil horizons can be found in Gobran and Clegg (1996). The bulk and rhizosphere soil compartments differed greatly in soil chemistry (Table 1). The rhizosphere had a significantly higher cation exchange capacity than the bulk soil. Exchangeable base cations, titratable acidity and soluble base cations were also increased in the rhizosphere. The relative increases in base cation content exceeded the increase in acidity (Table 1), giving a higher calcium aluminum balance {log (Ca mol_c/Al mol_c)} and a higher base saturation in the rhizosphere than in the bulk soil(Table 1).

We believe that organic matter organic matter quantity (Table 1) and quality plays a major role in controlling the chemical composition of the soil fractions (Figure 1). Some support for this comes from correlation analysis of our samples. Gobran and Clegg (1996) found a more pronounced correlation of organic matter to chemical variables in the horizontal plane (i.e., soil compartments) than in the vertical plane (i.e., horizons). Microbial biomass is probably a main source of organic matter in the rhizosphere, as indicated by the ratio of bacterial counts in rhizosphere soil to those in the bulk soil (R/S), which was found to be 10 to 50 under varying plant species at different stages of development and in different soils and climates (Paul & Clark 1989). Richards (1987) found that R/S is typically 10 to 50 for bacteria and 5 to 10 for fungi.

In the same forest soil under control, drought, irrigated and ammonium sulfate treatments we also found P and K content to be higher in the rhizosphere than in the bulk soil (Clegg & Gobran 1997; Clegg et al. 1997). The organic and inorganic P and soluble and exchangeable K were significantly associated with the organic matter content of the three horizons in the bulk and rhizosphere soil in the control although the effect was more pronounced in control than in treated plots (Clegg & Gobran 1997). This supports the conceptual model for nutrient availability in the mineral soil–root system proposed by Gobran and Clegg (1996). It is also contrary to the traditional view that P and K are normally depleted around roots due to rapid uptake and slow rates of ion diffusion (Barber 1984; Nye & Tinker 1977). At present, there are few rhizosphere field studies of P and K in forest soils. Yet, a number of studies which have used similar rhizospheric separation methods also appear to contradict the absolute depletion concept. For example, Häussling and Marschner (1989) studied seven Norway spruce stands of 60 to 100 years old in Germany. Their results showed that water extractable inorganic P accumulated in rhizosphere samples taken from the mineral soil in five out of the seven sites examined. Chung and Zasoski (1994) and Clemensson-Lindell and Persson (1992) also reported significant accumulation of K and other cations in the rhizosphere when compared to the bulk soil.

Mineral weathering within the rhizosphere

Courchesne and Gobran (1997) compared and contrasted the mineralogical composition of the same bulk and rhizosphere soil compartments as used for the chemical study (Gobran & Clegg 1996). They hypothesized that the weathering of soil minerals is enhanced in the immediate vicinity of roots in forest soils. Two soil profiles were sampled in a control plot. In each profile, samples were collected from the A (0–10 cm), the upper B (10–25 cm) and the lower B (25–50 cm). The mineralogy of the clay-sized particles of both compartments was determined by X-ray diffraction (XRD) after removal of coatings with DCB and H_2O_2. Subsamples were saturated with Mg, Mg-ethylene glycol or K and mounted in preferential orientation by drying 2.0-ml suspensions on a glass slide (Whittig & Allardice 1986). The K-saturated specimens were analyzed when air-dry and also after heating to 300 and 550 °C. The integrated intensity of each mineral (I) was normalized relative to the intensity of the (100) peak (d = 0.426 nm) of quartz (I_{QZ}) to calculate a mineral intensity ratio (I/I_{QZ}). Amorphous solid phases of pedogenic origin were estimated by extracting Fe and Al with acid-ammonium oxalate (Al_O, Fe_O) and analyzing by AAS (Ross & Wang 1993). These solids can accumulate as *in-situ* weathering products or precipitate from solution in Podzols (McKeague et al. 1983).

Table 2. Average (+ standard deviation) mineral composition of bulk and of rhizosphere materials for the six horizons studied

Sample origin		Amphibole	Interstratified Vermiculite	Plagioclase	K-feldspar
			I/I_{QZ}[†]		
Bulk	(n = 6)	0.12a[‡] (0.07)	1.14a (0.70)	2.24a (0.78)	1.29a (0.54)
Rhizosphere	(n = 6)	0.03b (0.04)	0.54b (0.25)	1.73a (0.37)	1.28a (0.28)

[†] Intensity of a mineral divided by the intensity of the 100 quartz peak (*d* = 0.426 nm).

[‡] In a given column, mean values for the six horizons followed by the same letter are not significantly different at the $a \leq 0.10$ probability level (ANOVA).

Abundance of weatherable minerals (I/I_{QZ}) near roots was consistently lower than in the bulk soil (Table 2). The magnitude of changes corresponded to the relative stability of minerals in a weathering environment stimulated by root activity, and followed the order: amphiboles > plagioclases > K-feldspars (Goldich 1938). The rhizosphere contained significantly lower amounts of amphiboles ($a = 0.10$) than the bulk soil (Table 2). Lower amounts of plagioclase were also seen in the rhizosphere samples from five of the six horizons, but the difference from the bulk soil was not significant when all horizons were integrated in the comparison. No rhizosphere effect was detected for K-feldspars. Expandable phyllosilicates were less stable than the plagioclase and K-feldspars (Table 2), in agreement with observations made by Sarkar et al. (1979), but in contrast with Kodama et al. (1994) who an found accumulation of interstratified minerals in the rhizosphere compartment.

Overall, Al_o and Fe_o were systematically higher in the rhizosphere than in the bulk materials although the differences were marginally significant ($a \leq 0.10$) only in the A and upper B horizons (Table 3). These results are in agreement with those of Chung and Zasoski (1994). The depletion of weatherable minerals and the concomitant accumulation of Al_o and Fe_o close to root surfaces indicate that the weathering regime was stimulated by root activity. The accelerated degradation of mineral structures in the rhizosphere zone has been related to a series of root-induced acidifying processes like the exudation of H^+ ions, CO_2, and complexing organic acids (April & Keller 1990). These mineralogical observations, the reported higher organic-matter content, and the higher acidity in the rhizosphere soil at our field site lead to the same conclusion.

Table 3. Amounts of Al and Fe extracted by acid-ammonium oxalate solutions from bulk and rhizosphere samples of the three horizons in profile #1

		Aluminum		Iron	
		Bulk	Rhizosphere	Bulk	Rhizosphere
		mean (SD)†	mean (SD)	mean (SD)	mean (SD)
Horizon		g kg^{-1}			
A1	(n = 4)	6.5a‡ (1.3)	12.5b (3.1)	18.9a (4.1)	25.2b (4.3)
upper B	(n = 4)	14.8a (4.6)	22.9b (5.1)	40.8a (8.6)	54.3b (8.8)
lower B	(n = 4)	50.2a (9.0)	60.2a (12.6)	64.1a (13.2)	76.5a (10.6)

† Standard deviation.
‡ For a given horizon, mean values followed by the same letter are not significantly different at the a $\leq$ 0.10 probability level (ANOVA).

Discussion

The function of mycorrhyzae and organic matter in the rhizosphere

The roots of most soil-grown plants are mycorrhizal and the role of mycorrhizal symbiosis in nutrient transport and uptake has been well documented (Grayston et al. 1996). The large numbers of mycorrhyzal hyphae present within the rhizosphere act to regulate supply and store soluble P (Smith & Read 1997) and other nutrients (Marschner & Dell 1994) in exchange for energy rich compounds from roots. For example, mycorrhizae are rich in exchange sites with high affinity for phosphate (Richards 1987; Bolan 1991; Jakobsen et al. 1992). These exchange sites may behave both as a source and sink for nutrients thus dampening seasonal variations in nutrient supply (Grayston et al. 1996), and shielding plants from the effects of toxic metals, such as Al, Cu and Zn (Wilkins 1991; Marschner & Dell 1994). The excretion of phosphatases also may play an important part in mineralizing the large organic P pool in the rhizosphere (Clegg & Gobran 1997; Marschner & Dell 1994; Häussling & Marschner 1989). Finally, the mycorrhyzal pool of nutrients may also be released when the hyphae die e.g., as a result of grazing by micoorganisms in the rhizosphere (Clarholm 1984) or become detached following disturbance such as sampling (Häussling & Marschner 1989).

Our work on the total organic matter of the rhizosphere (Gobran & Clegg 1996) emphasized a greater effect of organic matter on the soil compartments than in the soil horizons. This is not surprising since organic acids released to the rhizosphere by roots and mycorrhizae play an important part in nutrition of plants (Grayston 1996). The rhizosphere has higher concentrations of reactive organic substances such as low molecular weight organic acids (Fox

& Comerford 1990; Grierson 1992; Szmigielska et al. 1996) and enzymes (Häusling & Marschner 1989). The production of organic acids and enzymes in the rhizosphere has great chemical and geochemical implications for the release of nutrients. Their functions include metal chelation, retention and solubilization of nutrients as well acidification of the rhizosphere (Mench & Martin 1991; Petersen & Bottger 1991). Due to the effects of these acids (e.g., oxalic acid) on the crystallization of Al and Fe oxides (Huang & Schnitzer 1986), they can increase P availability through formation of stable complexes with Al (Martell et al. 1988; Fox & Comerford 1992). Therefore, the origin, quality and quantity of the rhizospheric organic matter plays a decisive role in the regulation of the reciprocal relationships between soil and roots with their associated biota.

Implications of the rhizosphere to forest biogeochemistry

The most active portion of the root system exists as fine roots (1–2 mm). Minirhizotron studies of Norway spruce have shown that fine roots can live for nine months or more (Majdi 1994) and frequently reoccupy old root channels. This indicates that the rhizosphere is not necessarily an ephemeral environment in the soil in time and space. The apparent longevity of roots in forests would allow more time for the establishment of a distinctive rhizosphere than in many experimental and agricultural systems. The re-establishment of rhizospheric conditions in unoccupied root channels may possibly be stimulated due to the priming effects of dead roots. Such effects may include physico-chemical properties such as high porosity, nutritional retention on active surfaces and readily decomposed organic matter (Van Noordwijk et al. 1991) as well as biological priming with the propagules of rhizospheric organisms.

In addition to long-term rhizospheric effects, trees adapted to nutrient-poor sites have low nutrient absorption rates as well as efficient internal cycling (Van Breemen 1995). This strategy of trees under such conditions contrasts with rapidly growing agricultural and ruderal species growing on intensively managed and fertile soils where nutrient supply by mass flow to roots may equal that by diffusion (Binkley 1986). Moreover, a relatively large and long-lived root biomass may benefit from the accumulation of organic matter observed in the rhizosphere (Clegg et al. 1996; Chung & Zasoski 1994) which could act as both a source and sink of available nutrients and potentially toxic ions (Gobran & Clegg 1996). Therefore, P and K availability is not only controlled by diffusion and mass transport but also by surface adsorption-desorption on organic matter, decomposition and dissolution and precipitation of minerals due to root exudates. Additionally, the role of mycorrhizae would be particularly important since they may both transport and store P and K in the rhizosphere as well as release enzymes to facilitate mineralization of nutrients from organic pools (Finlay 1992, 1995).

Certain tree species actively control nutrient availability by complex feedback loops (Perry et al. 1989) between trees, microbial communities and the soil to maintain a competitive advantage (Van Breemen & Finzi 1998). Feedbacks may involve, for example, decreasing the availability of essential nutrients such as P in the bulk soil by acidification (Cole 1995; Van Breemen 1993) or decreasing mineralization rates. This may be achieved by production of secondary metabolites which are leached from foliage and litter (Van Breemen 1995) while simultaneously favoring their own root systems by the establishment of nutrient-rich rhizospheric conditions and mycorrhizal association. It is apparent that accumulation of nutrients in the rhizosphere is a natural result of these many feedback processes occurring under forest conditions.

Due to these regulating processes, the rhizospheric nutrient supply and demand are more carefully balanced in nutrient-poor forests than under agricultural and short-term experimental conditions. It is generally believed that, in infertile soils (e.g., Spodosols), the biota renders the soil less favorable for plant growth (Chapin 1993). Although this observation holds when the bulk soil is considered, it is not supported by examination of the rhizospheric chemical properties. At the scale of the rhizosphere, biota (roots and microorganisms) seem to increase the capacity of the soil to support plant growth in nutrient-poor environments.

Since most mineral nutrients must pass through the rhizosphere before assimilation by plants, this small zone has great potential as a regulator of plant nutrient availability and flux. Yet, in order to have any significant effect on nutrient cycling in forest ecosystems the rhizosphere must be persistent in time and exhibit resilience against perturbation, which are known properties of ecosystem stability (Richards 1987). We believe the rhizosphere has such features, as reflected by the consistent difference between rhizosphere and bulk chemistry and mineralogy regardless of a wide range of field treatments (e.g., drought, irrigation and ammonium sulfate) (Clegg & Gobran 1997; Clegg et al. 1997).

Converging results from chemical and mineral studies emphasize the significance of feedback processes in the rhizosphere zone and the role of roots as dynamic weathering agents. Specifically, the preferential dissolution of minerals at the soil–root interface and the associated cation release to solution could be expected to affect nutrient availability in the vicinity of living-plant roots and thus to increase biological uptake. Accordingly, we believe that rhizospheric processes are of great importance in maintaining forest growth under stress conditions. Rhizospheric processes have not been considered properly in forest ecosystem models (Högberg & Jensen 1994) and inclusion of soil rhizospheric heterogeneity in ecosystem models is needed to realistically describe soil–plant relationships and the feedback processes involved.

Further research is needed to improve our proposed conceptual model, in order to describe the rhizosphere in quantitative terms. To achieve this goal development of small scale sampling and analytical techniques adapted to the rhizospheric environment and allowing the *in situ* monitoring of processes is needed. This would involve characterization and quantification of the soluble and solid phases, preferably on a volumetric basis. Additionally, the rhizosphere effect should be examined under a range of field conditions (disturbed, manipulated and natural) and for a variety of vegetation types especially in ecosystems with a permanent vegetation cover. These experiments are required to support and validate the observations obtained from controlled experiments (laboratory or greenhouse), and to increase the limited amount of information on forest systems, which at present, constrain the scaling of knowledge from the laboratory to the field.

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