

Bootstrapping in ecosystems.

by D.A. Perry, M.P. Amaranthus, J.G. Borchers, S.L. Borchers and R.E. Brainerd

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Bootstrapping in Ecosystems

Positive feedback is being increasingly recognized as an important component of ecosystem dynamics (DeAngelis et al. 1986, Gutierrez and Fey 1980, Pastor and Post 1988). Within the constraints of resource supply or other environmental factors, the biological system characterized by strong positive feedback among its components is in many respects self-generating - its productivity and stability determined largely through its internal interactions. "The idea of a system... generating [itself] in a self-consistent loop of explanation is reminiscent of the story of the boy who fell into a bog and hauled himself out by pulling on his own bootstraps, so... such modes of explanation [are called] 'bootstrapping'" (Davies 1983).

A bootstrapping view, neither reductionist nor holistic in its basic orientation, can yield useful insights into ecosystem processes, particularly as they relate to stability and resilience. Systems characterized by strong, positive interactions among their components can be complex, productive, and quite stable under conditions to which they are adapted, but when key linkages are disrupted they are fragile and subject to threshold changes (DeAngelis et al. 1986).

In this article we review recent work on one particular relationship - reciprocal interactions between plants and soils. We argue that some ecosystems are continually pulling themselves up by their own bootstraps. Through close mutual interactions between plants and soil organisms, these ecosystems create the conditions that allow the systems to persist. Severing the close links between plants and soils has contributed to degradation of many ecosystems, and restoring these links is an important step toward rehabilitation.

The plant-soil system

The importance of soil to primary productivity is well known. Soils are banks of nutrient elements and water, and they provide the matrix for the biological processes involved in nutrient cycling. The role of plants in soil formation is also well known. They provide energy that fuels the biological processes and either directly or indirectly create much of the structure within soils. The picture now emerging is that, at least in some cases, the coupling of plants and soils is both intimate and vulnerable.

Plants allocate a high proportion of photosynthate to roots, and a surprisingly large amount of that photosynthate is either diverted to mycorrhizal symbionts or exuded into the surrounding rhizosphere or mycorrhizosphere. Roots and mycorrhizal fungi account for 70% to 80% of net primary production in Pacific silver fir (*Abies amabilis*) ecosystems (Vogt et al. 1982). Fogel and Hunt (1983) found similar values for Douglas-fir. Studies such as these, because they do not account for root exudates, underestimate the amount of energy diverted below ground by plants. Carbon labeling has shown that 10% to 40% of the total photosynthate fixed by cereals passes from roots into the rhizosphere (Whipps and Lynch 1986). The value for trees is probably similar (Reid and Mexal 1977). Both exudation rates and the character of exudates from a given plant vary, in part according to its nutrient status (Olsen et al. 1981, Ratnayake et al. 1978) and whether it is infected by mycorrhizal fungi (Foster 1986, Meyer and Linderman 1986).

Photosynthate flowing from roots and mycorrhizal hyphae supports a diverse community of soil organisms. Mycorrhizal fungi, symbiotic with roughly 90% of plant species, form a first trophic level and, through influences on the character of exudates, shape the composition of the surrounding rhizosphere community (Meyer and Linderman 1986, Rambelli 1973). Mycorrhizal plants, for example, have fewer pathogens and perhaps more nitrogen-fixers in their rhizosphere than do nonmycorrhizal plants. Bacterial grazing by protozoa, amoebae, nematodes, and microarthropods accelerates release of nutrients in plant-available form (Anderson et al. 1985, Clarholm 1985, Coleman et al. 1984, Ingham et al. 1985).

Of 6507 species of angiosperms that have been studied, 70% are consistently found to be mycorrhizal and 12% are apparently facultatively mycorrhizal, sometimes forming mycorrhizae and sometimes not (Trappe 1987). A high proportion of the world's worst weeds are facultatively mycorrhizal. Coniferous species that have been studied are always mycorrhizal in the wild.

The most common mycorrhizal types are formed by two quite distinct groups of fungi. Ectomycorrhizae (EM), which are characterized by extensive hyphal development external to the root and by (usually) lack of penetration of host cells, are formed by several thousand species in the subdivisions Basidiomycotina and Ascomycotina. Vesicular-arbuscular mycorrhizae (VAM), which penetrate host cells but do not modify the external appearance of the root, are formed by several hundred species in the family Endogonaceae, subdivision Zygomycotina. Trees are the predominant hosts of EM, whereas a wide range of herbs,

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shrubs, and trees host VAM. Some plant species host both types.

Although the role played by mycorrhizal fungi in plant nutrition and defense against pathogens has been much studied, little is known about the cost-benefit relations of energy loss from plant roots under field conditions. A burst of research activity within the past few years, however, has provided evidence that numerous rhizosphere processes contribute significantly to the health of both individual plants and the ecosystem as a whole (Bowen 1980, Coleman 1985, Janos 1980, Linderman 1986, Malloch et al. 1980, Perry et al. 1987, St. John and Coleman 1982). Among the important processes occurring in the rhizosphere or mediated by rhizosphere organisms are nitrogen fixation; production of hormones, antibiotics, and metal chelators; grazing-enhanced nutrient turnover; material transfer between plants through mycorrhizal hyphae; and creation and maintenance of soil structure through the production of humic compounds and polysaccharide glues. Of course not all rhizosphere organisms benefit plants, nor do they necessarily provide the same, benefits at all times. The healthy rhizosphere is likely to be characterized by dynamic balance rather than rigid structure.

What happens when the energy that fuels rhizosphere processes is eliminated, as, for example, when a forest burns or is clear-cut or a wheat field is harvested? The same thing happens as when any open, nonequilibrium system is cut off from its energy source: entropy increases and, if the energy source is not restored, the system eventually reaches a new state that is likely to be quite different from the original. In soils, organisms that use root exudates for energy either are replaced by saprophytes, become saprophytic themselves, or enter a resting state. Rhizosphere organisms do not, in general, appear to switch successfully from living plant substrates to detritus, hence they decline in the absence of plants.

Composition of the bacterial community clearly differs between rhizospheres and soil not influenced by living plant roots. Rhizobacteria have quite different nutritional requirements than those of open soil (Atlas and Bartha 1987). Populations of both mycorrhizal fungi and *Rhizobium* sp., the nitrogen-fixing partners of legumes, decline rapidly in the absence of hosts (Corman et al. 1987, Janos 1988, Perry et al. 1987). Fungi and some rhizobacteria do produce resting stages, but unless they are protected in some fashion, for example in large soil aggregates, these organisms are vulnerable to consumption by saprophytes and to loss by soil erosion.

Eliminating energy inputs may significantly affect the physical as well as the biotic structure of soils. Various

microbes, including mycorrhizal fungi, produce extracellular polysaccharides (ECP) that glue mineral particles together into water-stable aggregates, 0.25 - 10 mm in diameter. These aggregates are important components of soil structure (Lynch and Bragg 1985). Unless protected by clays or polyphenols, ECPs are readily metabolized by soil microbes. Therefore, soil aggregation is a nonequilibrium phenomenon, maintained by periodic influx of fresh ECPs to replace those metabolized.

The stability of large aggregates is thought to rely on plants (Tisdall and Oades 1982), and loss of aggregates in this size range - unfortunately little studied - may be quite rapid in the absence of plants. Grassland soils put under fallow lose most of their large aggregates within one year (Low 1955). Large aggregates are diminished in 15- to 20-year-old unreforested clear-cuts in southern Oregon, although we do not know how rapidly this loss occurs (Borchers and Perry 1987).

Recovery of ecosystems after disturbance includes re-establishing the energy source for belowground organisms and processes and therefore stabilizing the soil ecosystem before key elements are lost. This stabilization does not necessarily imply that the species composition of the below-ground community is unaltered. In fact, disturbance probably initiates successional change below ground much as it does above ground, at least for mycorrhizal fungi (Mason et al. 1983). It is not the species composition but the functional aspect of the rhizosphere community - the positive feedback to the plant host - that is critical to maintain.

Diversity stabilizes the

plant-soil system

The source of strength for a bootstrapping system, its strong, self-helping links among system components, is also an Achilles heel. Stress in one part can be rapidly amplified and spread to the whole system through the positive feedback links that tie the system together.

If disturbances and stresses are common features of ecosystems, how does the plant-soil system avoid the continual threat of a small perturbation turning into a disaster? Little research has been done along these lines. However, it seems likely that diversity in both the plant and microbial communities stabilizes the plant-soil system during environmental fluctuations or other periods of potential stress. For example, the mycorrhizal fungal community on a given site is composed of numerous species and genotypes that differ in their environmental tolerances, physiological requirements, and microhabitat

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preferences (Perry et al. 1987, Pirozynski 1981, Trappe 1962). An altered environment frequently results in replacement of one mycorrhizal fungal species by another, but the plant retains a belowground partner throughout its life. Physiologically diverse mutualists are likely to further buffer the plant-soil system by extending the range of environments in which the plant is able to maintain positive net photosynthesis (Perry et al. 1987).

Diversity in the plant community can be quite important in stabilizing belowground mutualists after catastrophic disturbance, and certain plant species appear to form guilds (associations for mutual aid and the promotion of common interests) defined by common belowground mutualists. In forests of Oregon and California, growth of conifer seedlings is significantly enhanced in soils previously occupied by some species of early successional hardwoods (Amaranthus et al. 1987, Amaranthus and Perry in press, Borchers and Perry 1987). This enhancement is not due to inherent site differences between areas with and without hardwoods, but to biological imprints: mycorrhizae, nitrogen-fixing *Azospirillum* sp., siderophore producers, and perhaps other microflora shared between the hardwoods and the conifers (none of the hardwoods were symbiotic nitrogen fixers).

In these systems, bootstrapping becomes a phenomenon of the community rather than a two-way interaction between a single plant species and the soil. The redundancy provided by shared microflora means that any one guild member is able to maintain the soil organisms required by all. In most ecosystems, variability in the nature or timing of disturbance leads to uncertainty in the composition of the pioneering community and such redundancy benefits both individual plants and the community as a whole.

It does not follow from the description above that all species in a community necessarily share the same belowground mutualists. Forests composed of both EM and VAM trees are not uncommon. Mixtures are found, for example, in many forests of eastern North America and also throughout much of southern Africa, where the balance between EM and VAM tree species within a given community is determined by the characteristics of the disturbance regime (Hogberg and Pierce 1986).

Various biotic and abiotic components of ecosystems may contribute to maintaining the links between plants and their belowground mutualists during disturbance and recovery. Mammals that feed on the belowground fruiting bodies of mycorrhizal fungi defecate fungal spores, associated nitrogen-fixing bacteria, and essential yeasts (Li et al. 1986, Malajczuk et al. 1987, Maser et al. 1978, Warner et

al. 1987). After the eruption of Mount Saint Helens, small mammals increased the availability of mycorrhizal spores to pioneering plants by bringing buried soil to the surface (McMahon and Warner 1984).

Partially decayed logs are common in soils of some ecosystems, where they act as water reservoirs for roots and hyphae during drought periods (Harvey et al. 1983). These logs probably protect mycorrhizal fungi and associated microflora during stand-destroying fires; therefore they may serve as foci for re-establishing populations of these organisms. After the extensive wildfires of 1987 in Oregon and California, logs within one stand that had been completely destroyed averaged 150% moisture content ($[\text{wet weight} - \text{dry weight}]/\text{dry weight}$) and contained living mycorrhizae and fungal hyphae. (1)

If for some reason the close links between plants and soils are weakened during disturbance, alteration of the belowground system may lead to poor recovery of the original plant guild, which leads in turn to further reductions in populations of belowground mutualists. Positive feedback then pushes the system rapidly toward some new state.

Breaking the plant-soil link:

an example

A broad band of granitic bedrock caps high elevations of the Klamath Mountains of southern Oregon and northern California. Although the soils are coarse-textured and growing seasons are short and droughty, the granitics support productive forests, some of which were clear-cut in the 1960s. Despite numerous attempts, these clear-cuts have not been successfully reforested (Figure 1).

The clear-cut. One of these sites, Cedar Camp, has been intensively studied over the past few years (Amaranthus and Perry 1987, Perry et al. 1984, Perry and Rose 1983). It illustrates the role of close links between plants and soils in maintaining system integrity. Cedar Camp is a 10- to 15-hectare clear-cut dating from 1968. It is on a 30% southerly aspect with a 1700-meter elevation. The adjacent forest, on the same slope and aspect, is dominated by 80-year-old white fir (*Abies concolor*) and is classed as Site I, or the highest productivity level for that species and elevation. The clear-cut has been planted four times, all failures.

Current vegetation consists of approximately 30% cover of annual grass (*Bromus tectorum*), scattered patches of bracken fern (*Pteridium aquilum*), and an occasional manzanita bush (*Arctostaphylos viridis*). Manzanita are more frequent at the clear-cut forest boundary, where they

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apparently were protected from the slash burning and herbicides used to prepare the site for planting. The only encroachment of natural conifer seedlings from the forest into the clear-cut is in association with manzanita.

Forests of this area regenerated successfully after previous wildfires. The consistent failure of regeneration after clear-cutting is probably related to two factors in the natural system that are not present in the managed area. First, early successional hardwoods of the natural system stabilize important soil organisms, and these hardwoods' cover ameliorates temperature and moisture regimes. Second, standing dead snags (fire-killed trees) also shade the site and dampen temperature fluctuations.

Soil comparisons. Various factors may have contributed to reforestation failures at Cedar Camp, but two in particular seem likely to underlie the inability of seedlings to secure a foothold in the clear-cut. First, loss of aggregation reduced the capacity of soils to store and deliver resources, particularly water. Second, reductions or outright loss of essential rhizosphere organisms diminished the capacity of tree seedlings to exploit sufficient soil volume to compensate for the lowered resource levels per unit of soil volume. Active antagonism by actinomycetes against mycorrhizal fungi and rhizobacteria may have exacerbated the inability of trees to reoccupy the clear-cut (Freidman et al. 1988). These factors are consequences of breaking the link between plants and soil.

Soils under the forest at Cedar Camp are highly aggregated. Scanning electron micrographs show diverse pore sizes (Figure 2a, 3) permitting both water retention and water drainage (therefore aeration), which are important to soil fertility. Clear-cuts soils, in contrast, resemble beach sands, having virtually no pore structure (Figure 2b). Loss of soil structure is not due to differences in total organic matter, which does not differ significantly between forest and clear-cuts soils (Perry and Rose 1983), but apparently to the removal of living tree roots and associated ectomycorrhizal hyphae.

Soil microbial communities differ dramatically between forest and clear-cut at Cedar Camp. The ratio of bacterial to fungal colonies is nearly 10 times greater in the clear-cut, and mycorrhiza formation on planted seedlings is reduced (Perry and Rose 1983). Actinomycetes are a common class of filamentous bacteria that are noted for production of chemicals that inhibit growth of other microbes and of plants (Katz et al. 1987). These bacteria are more abundant in clear-cut than in forest soil, and a higher proportion of colonies express allelopathy in bioassay (Freidman et al. 1988, Perry and Rose 1983). Concentration of hydroxamate siderophores - microbially produced iron chelators that are important in plant nutrition

and resistance to pathogens - are also reduced in clear-cut soils (Perry et al. 1984).

Had the first planting been successful, or had sprouting manzanita not been sprayed with herbicide, soil structure and microbial communities might have been stabilized at Cedar Camp. Without the proper plant guild, however, the system entered a downward spiral in which deterioration within the soil resulted in further planting failures that in turn led to further soil deterioration. Rehabilitation of such a site requires that mycorrhizal fungi and other microbes that interact positively with the trees be re-established.

Soil-transfer experiments. In experiments at Cedar Camp, adding less than 150 ml of soil from the root zone of a healthy conifer plantation to each planting hole doubled growth and increased survival of conifer seedlings nearly 50% in the first year after outplanting (Amaranthus and Perry 1987). By the third year, only those seedlings receiving soil transfers remained alive. Clear-cut and transfer soils did not differ significantly in macronutrient concentrations, and the small amount of soil added to planting holes further suggests that seedlings were not responding to fertilization, but rather to the addition of critical organisms whose numbers had been reduced in or eliminated from the clear-cut soil.

In a similar study conducted on another site in southwest Oregon, improved growth of conifer seedlings after inoculation with soils from an EM hardwood stand was accompanied by significantly enhanced mycorrhiza formation and free-living nitrogen fixation in seedling rhizospheres. This effect was eliminated by pasteurizing transfer soils (Amaranthus et al. 1987, Amaranthus and Perry in press).

Implications of the close links

Close, self-reinforcing links between plants and soil organisms are likely to exist in numerous ecosystems. The importance of belowground mutualists to trees was clearly demonstrated some years ago, when biologists learned that species planted outside of their normal habitat (e.g., trees planted in grasslands or temperate-zone trees planted in the tropics) did not grow well and often did not survive unless inoculated with soil from a forest of the same or similar tree species (Mikola 1970, Shemakanova 1967). Similarly, trees planted on mine spoils frequently do not succeed unless given a suitable below ground partner (Marx 1975). These examples represent rather extraordinary physical disruptions of the plant-soil link.

As our studies at Cedar Camp indicate, the link between plants and soils can also be weakened or severed and sites degraded by other kinds of disturbances to which the

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system is not well adapted. For example, mycorrhiza formation is reduced by pollution (Kowalski 1987), and Meyer (1985) suggested that positive feedback develops in polluted forests: weakened trees lead to fewer mycorrhizae and fewer mycorrhizae lead to trees that are more susceptible to pests and pathogens. Following are three other examples in which disruption of the links between plants and soils may have led to ecosystem degradation.

* In the Miombo woodlands that cover much of southern Africa, sites cleared and burned for cultivation, then grazed or left fallow for as little as one year, no longer support growth of the original tree species. Extensive areas around Lake Victoria are well on their way toward semidesert,(2) whereas throughout northern Zambia such sites return to an open savanna vegetation (Stromgaard 1986).

* In western North America, some annual grasslands, which had been converted from perennial grasslands by overgrazing, no longer support perennial grasses even when planted.(3) Perennial grasses require mycorrhizae, at least when certain nutrients are in short supply, but invading annual grasses probably do not (Reeves et al. 1979). It is reasonable to hypothesize that overgrazing eventually reduces energy flow to mycorrhizal fungi and associated organisms, weakening the link until annuals successfully invade.

* Intensified shifting cultivation (longer periods of cultivation and more frequent return to a given spot than was the historic norm) has converted large areas of moist tropical forest to scrublands (Blaike and Brookfield 1987). As with grasslands, late successional trees in moist tropical forests are mycorrhizal, whereas invaders often are not (Janos 1980).

Under what circumstances is maintaining a strong link between plants and soils likely to be important to ecosystem stability? Clearly, resource availability is a key factor. Where water or nutrients are in short supply, belowground mutualists are particularly important to perennial plants. The mutualists influence resource availability both directly, through gathering and nitrogen fixation, and indirectly, through effects on soil physical characteristics. In coarse-textured soils, mycorrhizal fungi provide much of the structure (Rose 1988) and therefore the capacity to store nutrients and water.

Because of seasonal constraints, some environments have a relatively narrow window during which perennial plants may successfully reestablish after a disturbance. In these situations, maintenance of a strong link between plants and their belowground mutualists is likely to be most critical.

For example, despite their many differences, the high-elevation granitics of western North America and the Miombo woodlands of southern Africa share certain important characteristics. Both have short growing seasons, drought, and under their natural disturbance regime are dominated by EM trees. In the granitics, and probably in the Miombo woodlands, newly establishing seedlings must exploit soil resources quickly to develop sufficient vigor to survive drought and other stresses (e.g., grazing and pathogens). Trees and shrubs are likely to need mycorrhizae and associated organisms, such as nitrogen-fixing bacteria, to satisfy these requirements (Malloch et al. 1980, St. John and Coleman 1982).

It is perhaps a testament to the strength of a healthy link between plants and rhizosphere organisms that, despite stressful environments, these ecosystems are not necessarily unproductive. On the contrary, ring widths on stumps at Cedar Camp showed that the previous forest had grown surprisingly well for that elevation and soil type - probably because of strong, positive feedback links within the tree-soil system.

The biotic, as well as the abiotic, environment bears on the significance of bootstrapping. Some plants, including many annuals and weeds, do not require mycorrhizae (Trappe 1987), hence they may gain competitive advantage when mycorrhizal fungi and associated rhizosphere organisms decline in abundance. Once such plants gain dominance, the weakened links between the original plant community and its belowground mutualists are likely to break, and regenerating the original plant community may require simultaneously reestablishing the proper microbial complex. In the Himalayan foothills of northeast India, inoculation with soils from established forests enhanced rehabilitation of sites degraded by intensified shifting agriculture (Sharma 1983).(4)

Although soil transfer has a long history of success as a means of introducing or reintroducing beneficial organisms to a site, the solution is not always that simple. In southwest Oregon, soils collected from beneath Pacific madrone (*Arbutus menziesii* Pursh) greatly stimulate growth and rhizosphere nitrogen fixation of conifer seedlings when they are planted in association with manzanita, but when seedlings are planted in annual grass meadows, soils from madrone have no effect on growth and actually depress rhizosphere nitrogen fixation (Amaranthus et al. 1987, Amaranthus and Perry in press). Much more knowledge about the dynamics of the belowground ecosystem is needed to explain results such as these. Madrone and manzanita, both EM plants, probably support compatible rhizosphere microbes. In contrast, microbial communities in soils beneath annual grasses (probably nonmycorrhizal, perhaps facultatively

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VA mycorrhizal) are likely to differ from, and perhaps be actively antagonistic to, those that were transferred to the meadow site in the madrone soils.

Bootstrapping and

ecosystem stability

Strong, self-reinforcing links may characterize many interactions in nature. Subsystems comprised of strongly interacting components, termed holons by Koestler (1969), play a central role in hierarchy theory and have long been thought to account for the stability of complex systems (Allen and Starr 1982, O'Neill et al. 1986, Roberts and Tregonning 1980, Simon 1962).

May (1973) argued, "Complex communities contain much more information than can be estimated by counting links in the trophic web." This information appears as structure within the network of community interactions; some interactions are stronger than others, and some are strong enough that the health and often the continued existence of the participants resides in the interaction (i.e., they are bootstrapping relationships). The latter may range from classic mutualisms such as those between plants and mycorrhizal fungi or pollinators, through the extended mutualisms that exist between plants and their rhizospheres, to interactions that may not fit the standard definition of mutualism at all, but nonetheless are characterized by strong positive feedback among the system components (DeAngelis et al. 1986). Though a bootstrapping system may be quite stable, it is also poised; its stability is not that of a ball lying at the bottom of a potential well, but of a dancer in arabesque. Like the little boy in the bog, such a system draws on the strength of its internal interactions to rise above the limitations of its environment and maintain order.

The stability of such a system resides in internal communication: the efficiency with which fluctuating regions are detected and damped (DeAngelis et al. 1986, Prigogine and Stengers 1984). In southwest Oregon and northern California, for example, several plant species with quite different adaptations such as thick bark, buried seed, or sprouting from rootstocks also are capable of stabilizing the same sets of soil mutualists after disturbance. This redundancy minimizes the extent of fluctuating regions - areas where belowground mutualists are lost - after catastrophic disturbance, and it buffers the plant-soil links at least to some degree against uncertainties in the disturbance regime.

Although stable against the disturbances that characterize its environment, the bootstrapping system may be quite vulnerable to foreign disturbances or disturbance patterns.

There are numerous examples of change in the nature or frequency of disturbance resulting in a drastic and rapid alteration of system structure (Amaranthus and Perry 1987, Trapnell 1959, Zedler et al. 1983). Such threshold effects, typical of positive feedback systems whose internal stabilizing mechanisms are disrupted, can be avoided only if we understand and protect the critical interactions that bind diverse ecosystem components into a whole.

Much still needs to be learned, but one conclusion already seems warranted. Diversity - in the plant community, the microbial community, and the ecosystem as a whole - plays a seminal role in buffering against disturbance and maintaining healthy links between plants and soils. Management systems aimed at protecting diversity are an important step toward sustainable resource utilization.

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D. A. Perry is a professor of ecosystem studies and M.P.

Amaranthus, J.G. Borchers, S.L. Borchers, and R.E.

Brainerd are students in the Department of Forest Science, Oregon State University, Corvallis 97331-5704.

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