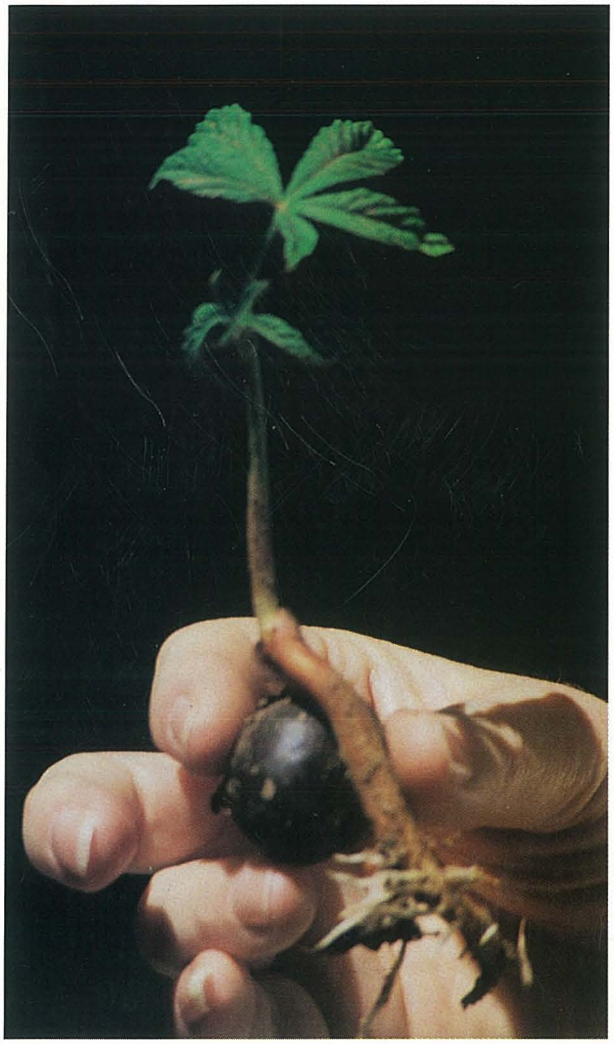
Cover Story

Troubles in the Rhizosphere



The root of this horse chestnut grows first from the energy in the seed. Roots cannot make their own energy. The root "pumps" start first and the top "pumps" follow.

By Dr. Alex Shigo

Rhizosphere Wars

The rhizosphere is the absorbing root-soil interface. It is the zone, about one millimeter in width, surrounding the epidermis of living root hairs and the boundary cells of mycorrhizae as well as hyphae growing out from some mycorrhizae.

The rhizoplane is the boundary where soil elements in water are absorbed into the tree. Under an electron microscope, the rhizoplane appears as a jelly where microorganisms and tree cells mix, making it impossible to tell which side is tree and which is soil.

A constantly changing mix of organisms inhabit the rhizosphere and surrounding soil. Bacteria, actinomycetes, fungi, protozoa, slime molds, algae, nematodes, enchytraeid worms, earthworms, millipedes, centipedes, insects, mites, snails, small animals and soil viruses compete constantly for water, food, and space.

The rhizosphere is a battleground and the wars are continuous. Amoebae are eating bacteria. Some bacteria are poisoning other bacteria. Fungi are killing other fungi. Nematodes are spearing roots. Fungi are trapping nematodes. Earthworms are eating anything they can find. Sometimes the victors benefit the tree and sometimes they do not.

Every tree treatment affects the rhizosphere in some way. The more you know about the rhizosphere, the better the chances are that your treatments will lead to benefits rather than harm.

Declines and the Starving Rhizosphere

Go anywhere in the world and you will learn that some local trees have a "new" decline problem. Declines usually mean the trees are sick because there is a problem in the rhizosphere.

Trees die, as all organisms do, in three basic ways: depletion, dysfunction and disruption. Disruption means wounding, severe mechanical impacts and fracturing. Dysfunction means some parts and processes of the living system have developed problems that retard or prevent their functioning and growth. Depletion means that the basic substances for life

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A mycorrhiza back-lit to show the fungus hyphae extending out from the organ. This is the world of the rhizosphere.

begin to wane, declines follow.

Trees are dependent on the light energy from the sun for their energy, water and 14 elements from the soil for their building blocks of life. Some trees decline when incorrect treatments or abiotic injuries lead to starvation of organisms in the rhizosphere. When there are troubles in the rhizosphere, there will be troubles with the tree.

Energy & Root Exudates

Microorganisms compete in the rhizosphere, an area rich in exudates from the tree. The exudates contain carbohydrates, organic acids, vitamins and many other substances essential for life. From 5 percent to 40 percent of the total dry matter production of organic carbon from photosynthesis may be released as exudates! When trees begin to decline, the amount of organic carbon released as exudates increases. Mineral deficiencies, low amounts of soil air and severe wounding are major causes for the increase. Another way to say this is that an increase in exudates would be caused by over-pruning, construction injury, planting too deeply, over-watering, compaction and planting trees in soils that have a pH too high or too low for their optimal growth.

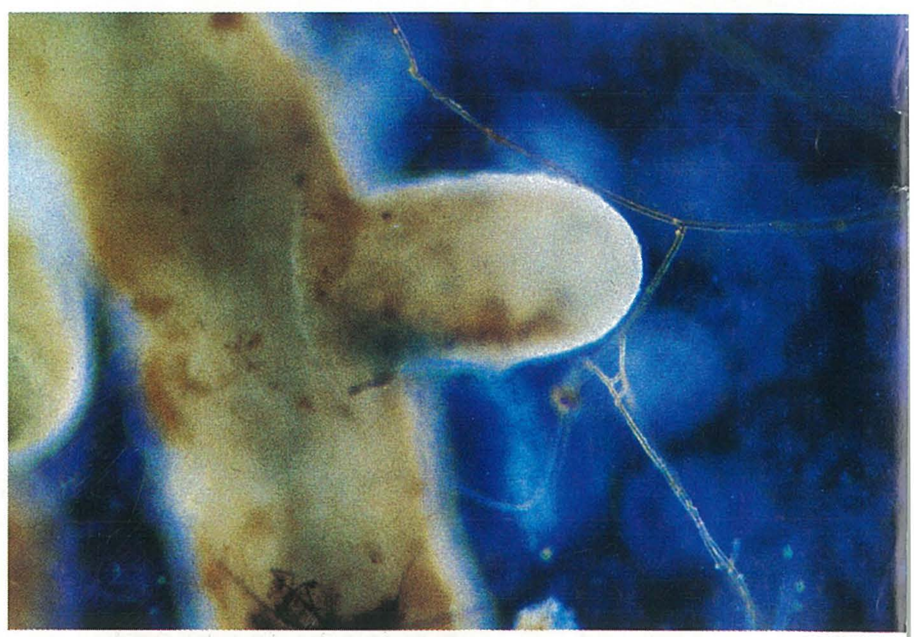
You would think that a tree in decline would decrease not increase exudates. A possible explanation might come from the self-thinning rule of ecology, which states that when energy input into a site equals output, there will be no further growth unless some trees die. As many suppressed trees die, a much fewer number continue to grow bigger. Simple. Or, on the basis of the mass-energy ratio law, as some trees on a site get bigger, many smaller suppressed trees will die. As the suppressed trees decline, they contribute a higher percentage of their soluble carbohydrates to the rhizosphere. The increase in exudates from a declining tree with a defense sys-

begin to decrease to the point where injury and death are certain. One of the ways depletion injures organisms is by starvation.

Soils and wood share a common problem: They are thought of as dead substances. This has come about because wood-products research gained an early lead over research on wood in living trees. With soils, many texts still define soils as "loose material of weathered rock and other minerals, and also partly decayed organic matter that covers large parts of the land surface on Earth."

Sapwood in living trees has many more living cells than dead cells. In upper layers where most absorbing roots of plants grow, soils have more soil organisms than grains of weathered rock. In great disrespect, most people still refer to soil as dirt! When researchers first discovered the great value of soil microorganisms for human antibiotics and profit, the living nature of the soil began to emerge.

A more correct definition of soil should be that it is a substance made up of sands, silts, clays, decaying organic matter, air, water and an enormous number of living organisms. Survival of all living systems depends greatly on synergy and efficiency to optimize the functioning of all processes and to keep waste as low as possible. When synergy and efficiency



Mycorrhizae form when mycorrhizal fungi infect newly forming non-woody roots as shown here. Note the tube-like structure of the hyphae.

Mycorrhizae covered by hyphae. Water and elements often are absorbed into the hyphae and then the tree. The hyphae extending from the mycorrhizae greatly increase the area for absorption.

tem weakened by low energy reserves would give root pathogens an advantage over other soil organisms. When the tree dies, its dead wood adds a great amount of carbon to the soil, thus benefiting all soil organisms. If this scenario is correct, then the codes for the increase of exudates as trees decline would have been set in the genes of the forest trees. Then, even after trees are taken out of their groups in forests and planted as individuals, the genetic codes for increasing exudates as the tree declines for reasons other than crowding would still be in effect.

A tree does not "know" why it is dying. In a crowded, young, growing forest, the self-thinning rule of ecology does benefit tree survivors and all soil organisms. But, when one or two trees in a yard, city or park start to decline, their early death may benefit only the root pathogens. And even worse, since the tree will be cut and removed from the site, there would be no benefits from added carbon to the soil.

A Closer Look at Roots

Woody tree roots are organs that support the tree mechanically, store energy reserves, transport water and the substances dissolved in it and synthesize substances such as growth regulators, amino acids and vitamins that are essential for growth.

Trees have different types of root systems. For example, mangroves along coastlines have stilt roots. Many trees growing in tropical areas have aerial roots that become prop roots when they grow into the soil. Other trees have strangling roots that eventually kill the host tree that first supported their growth. Trees in sandy soils can have roots that grow downward over 90 feet. Palms have roots that are adventitious and grow from meristematic regions in their base. Many tree species have deep roots when they are young and more shallow roots later. It would be nearly impossible for the strongest person to pull out young saplings of beech, oak or hickory from forest soil.

Woody roots have cells with walls of cellulose, hemicellulose and lignin. Lignin is that natural "cementing" substance that gives wood its unique characteristic for strength. Woody roots also have an outer bark or periderm made up of three layers: the phellogen, phelloderm and phellem. The phellogen is the bark cambium. The phelloderm is a thin layer of cells on the inner side of the phellogen. The phellem is the outer corky layer. Phellem cells are impregnated with a substance called suberin, which is a fatty substance that prevents water absorption.

Some characteristics of woody roots are:

- They do not absorb water.
- They have no pith.
- Their conducting elements are usually wider than those in the trunk.
- They have a greater proportion of parenchyma cells than is usual for trunks. The living parenchyma store energy reserves, usually as starch.

A soft cortex without chlorophyll may be in the bark. In some tree species that thrive in wet soils or have deep roots, the cortex may have many open spaces that act as channels for air to reach the living cells in the roots. It is important to remember that the parenchyma in the woody roots store energy reserves, and root defense is dependent on energy reserves. When reserves are low, defense is low. When defense is low, weak or opportunistic pathogens attack. It is nature's way.

Non-Woody Roots

Non-woody tree roots are organs that absorb water and elements dissolved in it. The two basic types of non-woody roots are:

1. Root hairs on non-woody roots are extensions of single epidermal cells. Common on seedlings, root hairs grow to maturity in a few days. They function for a few weeks and then begin to die. On mature trees, they are usually not abundant. When they do form, they do so when soil conditions are optimum for absorption of water and elements. I have found root hairs growing in non-frozen soils beneath frozen soils in winter.

2. Mycorrhizae are the other type of non-woody roots. Mycorrhizae are organs made up of tree and fungus tissues that facilitate the absorption of phosphorus-containing ions and others essential for growth.

The fungi that infected developing non-woody roots to form mycorrhizae were very "biologically smart." Rather than competing with other microorganisms in the rhizosphere for exudates from the tree, the mycorrhizal-forming fungi went right to the source inside the tree. And, even more to their advantage, many of the mycorrhizal fungi grew thread-like strands of hyphae—long, vegetative tubes of fungi—out from the mycorrhizae. This inside and outside presence gave the fungi a distinct advantage over other microorganisms in the rhizosphere.

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A block of frozen soil several inches deep was lifted away to reveal these mycorrhizae and strands of litter-decomposing fungi. Note the cavities surrounding the mycorrhizae.

1. With their extended hyphae, mycorrhizae not only greatly extend the absorbing potential into the soil, but the hyphae may connect with other hyphae on other trees. In this way, the mycorrhizae serve to connect trees of the same or a different species. This leads to the conjecture that the natural connections that developed over long periods in the natural forest may have some survival value. That is why forest types are often named for the groups of species commonly found growing together. For example, we speak of the birch-beech-maple forest, or the pine-oak forest. From a practical standpoint, when trees are planted in cities and parks, there may be great survival advantages by planting groups of trees made up of the species that are normally found together in natural stands.

2. The mycorrhizae have been shown to provide some resistance against root pathogens. It may be that the pathogens would have difficulties in building their populations in the rhizosphere dominated by the mycorrhizal fungi.

3. Perhaps the most important feature of the mycorrhizal fungi is that their boundary material is mostly chitin. Chitin is slightly different from cellulose by the replacement of some cellulose atoms by a chain of atoms that contain a nitrogen atom. This slight change in some way makes chitin a material better suited for absorption of elements. Remember that the fungus hyphae gain all their essentials for life by absorption through their boundary substance.

There are other advantages to the chitin and the tube-like hyphae that ramify the soil in the rhizosphere and beyond. When the hyphae die, they add a nitrogen source for other organisms. Also, when the hyphae are digested, they leave tunnels in the soil that are about eight to 10 microns in diameter. For the bacteria, these small tunnels may mean the difference between life and death. The bacteria quickly colonize the tunnels. The survival advantage here is that the major threats to their survival are protozoa that are usually much larger than 10 microns. So the hungry amoebae are not able to get at the bacteria inside the eight-micron tunnels.

A common treatment for compaction is to fracture the soil and add water. The fracturing allows air to penetrate the soil, but does not provide any eight-micron tunnels for the bacteria. The only way to bring back the tunnels is to bring back the fungi in well-composted wood and leaf mulch, as nature does, or by inoculating the mulch with mycorrhizal fungi.

Who Was First?

I do not know if the fungi were the first to grow into the root to get first chance at exudates or whether it was the bacteria. Regardless, bacteria and their close relatives, the actinomycetes, also infect non-woody roots to form organs that serve for the fixation of atmospheric nitrogen. Fixation means that the nitrogen that makes up almost 80 percent of our air is converted to a soluble ionic form by the action of the bacteria and actinomycetes within the nodules on the roots. (Some free-living soil bacteria can also fix nitrogen.) An enzyme called nitrogenase is the catalyst for the reaction that will take place only under very exacting conditions. There must be soluble molybdenum and iron and no free oxygen available. These conditions are present within the nodules. Here again, the microorganisms benefit the tree by providing a source of soluble nitrogen, and, in turn, the bacteria and actinomycetes get first chance at exudates. Even more importantly, the nodules protect them from foraging protozoa.

Infections that result in benefits to both parties are called mutualistic. When the benefits are greater than the sum of the parts, the association is called synergistic.

Species of legumes commonly have bacterial nitrogen-fixing nodules and mycorrhizae. The mycorrhizae facilitate absorption of elements, and the nodules provide a nitrogen source. Many species of trees have actinorhizae, which are the nodules formed by the root infections by actinomycetes. Species of *Alnus* have very large nodules. The actinorhizae are common on tropical and subtropical trees, and especially on trees that have adapted to soils low in available elements essential for life.

On some subtropical and tropical trees, such as the macadamia, multi-branched clusters of non-woody roots called proteoid roots form. The proteoid roots alter the rhizosphere by acidification processes that facilitate the absorption of phosphorus-containing ions. When I examined the roots of dying macadamia nut trees in an orchard in Hawaii, I could not find proteoid roots, yet only a few days earlier I had found them on macadamia nut trees growing in the wild. I learned later that the orchard where trees were dying

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An iodine stain (I_2-KI) was poured on half of the sugar maple stem section, left, and root, right. The iodine stains starch purple. Note the greater density of purple in the root over the stem. The iodine stain is a very effective way to determine vitality of a tree. Small cores can be removed with care and checked for starch. The cores should be removed only when a determination of vitality is essential for a treatment. The stain can be poured on small cut woody-root tips to check vitality of trees selected for planting.

was heavily fertilized on a regular basis with phosphorus.

Another type of nodule forms on species of cycads. These nodules harbor blue green algae, or cyanobacteria, that have the ability to fix atmospheric nitrogen.

My point is that many different synergistic associations have developed in, on and about non-woody roots that provide elements, not an energy source. These associations are of extreme benefit to all connected members. At the same time, the conditions that provide for the associations are very delicate and exacting. It does not take much to disrupt them.

It Does Not Take Much to Disrupt Them

This statement deserves repeating and repeating. The delicate "threads" that hold these powerful associations together need to be recognized and respected. Trees in cities grow only so long as these "threads" remain connected.

Trees grow as large oscillating pumps, with the top trapping energy and pumping it downward. The bottom absorbs water and elements and pumps them upward. The

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pumps have developed over time to work on the basis of many synergistic associations that maximize benefits for all connected members and to minimize waste.

Many of life's essentials for the bottom associates come from the top of the tree. And, the top works only because the bottom works. Energy is required to move things, and elements and water are required to build things.

Tree Treatments and the Rhizosphere

When trees are over-pruned, the top will be injured first. When it is injured, it will not serve the energy requirements of the bottom. Soon root diseases start and are blamed for the decline or death of the tree. Where over-pruning is common, so are root diseases.

Compacted soil blocks air and water to the bottom and crushes all the micro-cavities where the microorganisms live. In nature, decomposing wood and leaves keep conditions optimal for the rhizosphere inhabitants.

Over-watering stalls the respiration processes in the roots. When respiration stops, carbonic acid is not formed. When carbonic acid is not formed, ions necessary for the absorption process do not form. When absorption is down, the tree system is in trouble. Fertilizers can be of great benefit to trees growing in soils low in or lacking elements essential for growth.

Elements or molecules made up of a few to many different atoms enter the roots as ions. An ion is a charged atom or molecule. Ions with a positive charge are cations, and those with a negative charge are anions. Each particle or granule of fertilizer is a salt made up of a lattice of anions and cations, just as ordinary table salt is made up of a grand lattice of connected sodium cations and chloride anions. When salt as sodium chloride dry granules is poured into water, the sodium and chloride ions separate. When they separate, they carry electrical charges and are called the sodium ion and the chloride ion. When a cation enters a root, another cation must exit. This is very important, as we will see. When nitrogen enters a root as nitrate anion, an anion of bicarbonate ion from carbonic acid exits. The bicarbonate ion is probably the second most important compound in nature, next to water, because it drives the absorption process. When a bicarbonate ion exits into the rhizosphere, the pH increases.

When urea is used in fertilizers as the nitrogen source, the pH in the rhizosphere could increase to 2 or more pH units. The chemistry behind this is complex, but here I present only the conclusion, because a common problem with trees in some high pH soils is chlorosis. There is no easy field method for measuring the pH of the one millimeter wide rhizosphere. The rhizosphere could be pH 8, and the bulk soil would measure pH 6. As pH increases, the availability of elements such as iron and manganese decreases. In soils, it is one thing to have an element present and another to have it in a form available to the plant as an ion. As pH increases, iron and manganese elements form molecules that precipitate in water rather than ionize. If they are not available as ions, they will not be absorbed. And, if they are not absorbed, several of the enzymes essential for chlorophyll formation and photosynthesis will not form.

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When the energy flow from the top of the pump is blocked, then the bottom does not get enough energy for growth and defense. The pathogens invade, and the tree declines. This scenario does not mean that every time you use urea, trees will decline from chlorosis. But the use of urea could be a contributing factor where trees with genetic codes for growth on low pH soils are planted in high pH soils. If fertilization is a desired treatment, then a fertilizer that has nitrogen in a positive charged ion, such as an ammonium ion, would help to reduce the rhizosphere pH. When the ammonium ion enters the root, a proton of positive charge will exit. The protons in rhizosphere water will bring about more acidic conditions, so there is a way out.

In summary, fertilizers can be very beneficial for healthy survival of trees planted outside their forest homes. How beneficial will depend greatly on an understanding of many of the points mentioned here, and some basic chemistry.

Primary Causes of Diseases

It is often very difficult to have people recognize the importance of small organisms in small places doing big things. Blame for the death of a tree is often placed on big things that can be seen or felt. Most pathogens are opportunistic weaklings waiting for a defense system to decrease. Many small disrupting events often lead to the decrease in a defense system. Then after the tree has been weakened, the final agent comes along and gets the full blame for the cause. A perfect example is the cankers on honey locust. Flush pruning is usually the real cause.

Pumps and Food

Trees are oscillating pumps. When the pump begins to wobble, some parts will begin to weaken. When they weaken to the point where some other agent causes a part to break, the pump will stop.

It is very difficult to determine where problems start in an oscillating pump. Symptoms may be in the bottom, but the cause may have been in the top. Or, it could be the other way around.

I go back to two points that may be part of the answer: exudates and the self-thinning rule of ecology. All living things require food and water for growth. Leaves and photosynthesis provide the energy at the top of the pump. The non-woody roots and the rhizosphere provide the elements and water at the bottom. Photosynthesis will not work without water and elements, and the absorption processes will not work without an energy source.

Trees became trees growing in groups in forests where the self-thinning rule had strong survival value. Not only did exudates provide quick energy for the rhizosphere organisms, but the carbon in the wood of the trees that fell to the ground also provided a long-lasting energy source for a succession of organisms.

Reports from some countries indicate an abundance of soluble nitrogen compounds in runoff water and even in ground water. This is a strong indication

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that the carbon-nitrogen ratio has been disrupted in the soil. It is well established from studies of the physiology of fungal parasitism that the degree of parasitism is often determined by the carbon-nitrogen ratio. It is probably similar for other organisms.

The organisms in the rhizosphere and surrounding soils have many different ways to weather rocks and to get nitrogen and other elements essential for their growth. What they cannot get in the soil is a sufficient energy source. Yes, some small animals die and provide carbon, and some microorganisms can get energy by chemosynthesis, but the requirements for carbon are much greater than what could be supplied by those sources alone. Carbon must come from the top of the pump. When the energy source from the top begins to decrease, the rhizosphere organisms will begin to starve.

The oscillating pump model soon takes on the form of a circle, because now it could be said that the top did not work efficiently because the bottom had a problem first, and this could be so. My point is that the energy problem does play a key role in declines. If a single tree is already very low in energy reserves, it cannot contribute much to the rhizosphere even if the genetic codes rule that exudates should increase as a tree begins to decline. Soon we will be faced with the chicken or egg problem.

I believe there is a way to decrease the potential starvation problem. In forests, more wood should be left on the ground, and in cities, more composted wood and leaves should be added in correct quantities to the soil about the base of trees. Incorrect treatments of pruning, watering, planting and fertilizing should be corrected, because they often start the pumps to wobble. If these simple adjustments can be made, rhizosphere starvation will decrease and our trees will lead healthier and longer lives. TCI

Dr. Alex Shigo is the owner of Shigo & Trees, Associates. He will be the keynote presenter at TCI EXPO '96.

Author's Note

Much of the information presented here has come from several books that I found very helpful in preparing for this article. I recommend these few books to people who want more information.

1. Foster, R.C., A. D. Rovira, and T.W. Cock. 1983. "Ultrastructure of the Root-Soil Interface." The American Phytopathological Society, St. Paul, MN.

2. Kilham Ken. 1994. "Soil Ecology." Cambridge University Press. Cambridge, Great Britain.

3. Wild, Alan. 1994. "Soils and the Environment: An introduction." Cambridge University Press. Cambridge, Great Britain.

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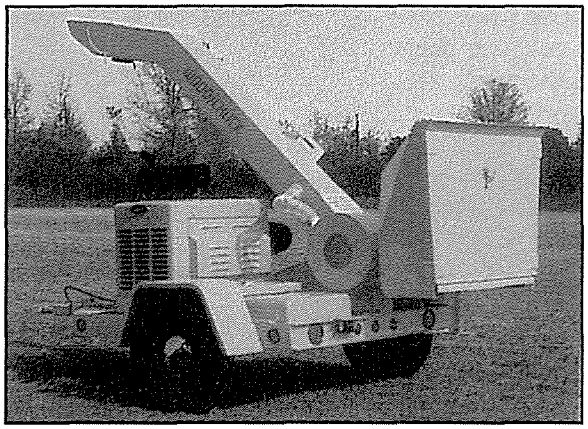

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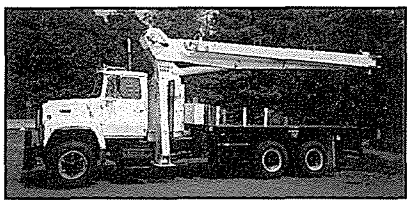

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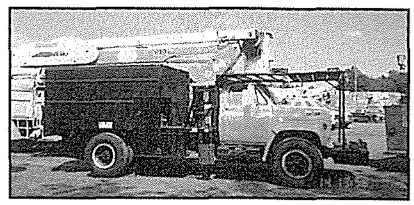

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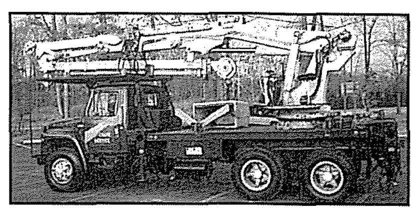

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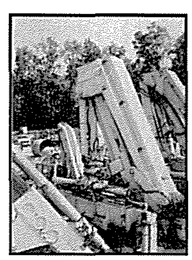

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