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I. Study: Dead Cicadas Help the Soil

EILEEN PUTMAN, *Associated Press (AP)*, November 25, 2004

WASHINGTON - Even in death, the 17-year cicadas made their mark. Their decaying carcasses gave a super-size boost in nutrients to forest soil and stimulated seed and nitrogen production in a plant important to the forest ecosystem, researchers reported in Friday's issue of the journal *Science*.

The findings might explain why tree growth increases for several years after a major cicada emergence, experts said.

Bard College professor Felicia Keesing likened it to someone pouring a pound of fertilizer per square yard over the forest floor. She co-authored an article accompanying the research paper on the impact of cicada carcasses on soil and plants.

Louie H. Yang, a graduate student at the University of California, Davis, conducted the studies in 2002, 2003 and 2004 in cicada-infested areas in the eastern United States.

Last summer's infestation was the largest, with 17-year cicadas known as Brood X inundating the mid-Atlantic region and filling forests from Georgia north to Pennsylvania and west through the Ohio River Valley to the Mississippi.

The beady-eyed insects spawned a public fascination - along with a multitude of cicada recipes and worries about the insects' impact on trees, plants, pets and even driving visibility.

While most worries weren't borne out, scientists have long been concerned about the impact of such outbreaks in which there is a sudden hyperabundance of organisms with potentially vast consequences for ecosystems.

Andrew Sugden, *Science's* international managing editor, said in an interview from Cambridge, England, that Yang's research was significant because "it quantifies for the first time what is likely to happen when you get large outbreaks of insects all at once," like the swarms of locusts that recently hit portions of Africa.

In his field studies, Yang experimented with naturally occurring densities of cicada carcasses of as much as 300 bugs per square yard. For each density he measured the soil's nitrogen and bacterial and fungal growth over varying periods of time after carcasses were applied.

Soil content of a form of nitrogen used by plants was many times higher - 199 percent to 412 percent - in ground littered with cicada carcasses. Bacterial and fungal growth also increased.

Yang also measured the nitrogen content in the leaves of bellflower plants, with and without cicada carcasses applied to their soil, as well as bellflower seed production. The bellflower is a forest floor plant common to the geographic range in which cicadas occur.

He found bellflowers supplemented with cicada carcasses produced seeds 9 percent larger and foliage with a nitrogen content 12 percent higher than bellflowers without cicadas.

"The nitrogen itself has an unusual isotopic signature that suggests it's actually from the cicadas themselves," Yang said in an interview.

Yang's findings that decaying cicada carcasses apparently stimulate a rush of soil nutrients might explain why other analyses have shown that tree-ring growth among oaks in areas infested with 13-year and 17-year cicadas increased for the first four years after cicada emergence, Keesing said.

Cicadas spend most of their time underground as nymphs, sucking on tree roots and diverting some of the nitrogen that would otherwise go to the plant. In their last few months they emerge from the ground, crawl up trees and shed their hard skins. Over the next few weeks they sing to attract a mate.

The sheer number of such cyclical cicadas overwhelms potential predators, and only about 15 percent of the insects are eaten. The rest fall to the ground, leaving massive numbers of carcasses left to decay.

"The death of the adult cicada is returning some of the nitrogen to the soil the nymphs took up," Yang said.

II. Cicadas, an Elixir for the Earth

HENRY FOUNTAIN, *New York Times*, November 30, 2004

Those buzzing hordes of cicadas that come up from underground every 13 or 17 years may be a nuisance for people, but for birds and small animals they are an all-you-can-eat buffet. Even so, millions and millions of the insects are left uneaten (the cicadas' strategy, after all, is to emerge in such abundance that some of them survive to reproduce).

Cicadas that manage to avoid becoming a predator's tasty repast eventually die, after about six weeks. That raised some questions for Louie H. Yang of the Center for Population Biology at the University of California at Davis. "One that seemed like it would be worth trying to answer," he said, "was, 'What happens to all the dead cicadas?'"

Mr. Yang found that the dead bugs act as fertilizer. In the journal *Science*, he describes how cicada carcasses provide a brief jolt of resources -- what ecologists call a resource pulse -- to a forest.

Mr. Yang collected dead cicadas in the mid-Atlantic region over the last three years. He placed carcasses on forest plots at densities that might normally occur in a major cicada emergence -- up to about 240 per square meter. He found that microbial activity and soil nitrogen increased, both indications that the bugs were decomposing. He also noted that a typical forest plant, the American bellflower, produced larger seeds and leaves with more nitrogen in cicada-enriched plots.

"After they die, all those bodies decompose and they fertilize the forest," Mr. Yang said. This spike in nutrients, he said, may explain previous studies that showed an increase in tree growth in the first few years after a cicada emergence. Resource pulses like this are not uncommon; examples include synchronized heavy seeding by trees and mass deaths of salmon after spawning. "Resource pulse dynamics are occurring in a lot of ecosystems," Mr. Yang said. "Cicadas are just a very clear example."

In effect the bugs are responsible for two pulses: one in life, feeding animals and birds, another in death, feeding soil. Ecologically, he said, "they can be just as important dead as they are alive."

[Illustration]

Drawing (Drawing by Felipe Galindo)

III. Death deluge makes forest mulch

BBC, November 27, 2004

The nutrient boost given to North American forests when trillions of cicadas die en masse is explored in a new study in Science magazine.

The insects emerge from below ground and swarm over the landscape every 13 or 17 years to briefly sing and mate.

Their decomposing carcasses will increase bacteria, fungi and nitrogen in forest soils, Louie Yang shows.

This may explain why trees grow faster following cicada emergences, the University of California scientist says .

"This observation doesn't necessarily mean the pattern comes from cicada 'fertilisation'; it's one possible hypothesis," Yang told BBC News.

"Another explanation says adult cicadas cause damage to trees that makes more light available in certain parts of the forest; but it's certainly a very interesting pattern."

Soil changes

The eastern states of the US have several broods of periodical cicadas (*Magicicada* spp).

The insects spend most of their lives as juveniles, feeding on the xylem in tree roots and growing slowly.

Then, timed to perfection, huge populations come out together to reproduce.

May and June of this year saw the emergence of the so-called Brood X, which swarmed over more than 10 US states, including Georgia, Indiana, Kentucky, New York and Ohio.

The cicada onslaught lasts only a few weeks - but is deafening. The males sing to their partners with high pitched trills, made by vibrating abdominal drums called timbales.

The mass emergence can be extraordinarily dense; up to 350 insects per square metre. It provides a feast for a host of other animals - including birds, raccoons, foxes and skunks - but they cannot hope to eat all the cicadas and most will simply die and drop to the floor to rot.

Louie Yang set up experimental plots to examine the impact on the forest system of this death deluge.

His work demonstrates how the mass of carcasses leads to a dramatic increase in fungal and bacterial decomposers in the soil. This in turn triples soil ammonium, and more than doubles soil nitrate concentration.

Seed size

"We can see a trend which shows that increasing the density of dead cicadas increases the amount of soil nitrogen in the ecosystem - it creates a pulse of nitrogen in the soil," Yang said.

This rush of soil nutrients can be seen in the fillip it gives to a forest-floor plant, the American bellflower (*Campanulastrum americanum*), which grows across the range of the cicada emergences.

The plants in Yang's plots took up more nitrogen and increased the size of their seeds by 9%.

The cicadas are, of course, just returning nitrogen they "stole" when they were sucking on plant roots as nymphs. And the cycle will always show something of a deficit because of the substantial numbers of cicadas that are lost to the system through predation.

Nonetheless, it is an eye-catching observation that tree-ring growth data appears linked to the insects' cycle.

"A couple of studies have found a robust result that there is a decrease in the growth of trees during cicada emergence years, but one of the results in more recent research suggests there may be increases in the growth rate of trees in some of the years following cicada emergence."

He added: "There's an awful lot we don't know about the ecology that happens in our backyard - and these are insects that truly do occur in our backyard; this year they were flying into our cars and bumping into us as we crossed the street.

"These are insects that are everywhere but there is still a great deal we don't know about them."

IV. Cicadas leave bounty of nutrients for forests: Even in death, insects help ecosystem thrive

MARSHA WALTON, CNN, November 25, 2004

(CNN) -- Every 17 years, billions of cicadas cause a loud stir in almost one third of the United States. Scientists now say the insects also leave a lasting and positive impact after they die.

"Even as dead bugs they are still influencing these forest ecosystems," said Louie Yang, whose research is published this week in the journal "Science."

Benefits of the cicadas-as-fertilizer include faster growing trees, and bigger seeds in some flowers for several years following the cicadas emergence.

Scientists call short, dramatic bursts of new resources, like the billions of cicada carcasses, "resource pulses." But unlike other pulses, such as those that occur randomly after El Nino year rainfalls, researchers can predict the appearance of cicadas almost to the day. That makes this phenomenon a lot easier to study.

"I think these are pretty charming and mellow insects," said Yang, a graduate student in ecology at the University of California at Davis. "They don't move very quickly, they don't sting or bite, and for the most part they are very easy to handle and to touch to observe in nature," he said.

Cicadas have a strange and fascinating life cycle. While flies and mosquitoes live for just a few weeks, cicadas, depending on species, spend either 13 or 17 years below ground in the nymph stage, feeding on plant roots.

During the few weeks they are above ground, there's a loud and frantic effort for the insects to mate, and for the females to deposit their eggs in trees.

"When you get thousands, or millions or billions of them together in one spot, it is a fantastic, deafening chorus," Yang said.

The most noted cicada population, known as Brood X, emerged last spring and summer in the eastern United States, from Georgia north to Pennsylvania, west through the Ohio River Valley. When the eggs hatch, the nymphs fall to the ground and burrow up to two feet below ground for their very long growth period.

While they are above ground, they become an unbelievably abundant food source for birds, lizards, snakes and fish. The massive number of cicadas means that predators can only eat about 15 percent of them.

As part of his research, Yang and others gathered tens of thousands of insect carcasses to see what impact they would have fertilizing bellflowers, a plant that's found in roughly the same region as the cicadas.

"What we found was that these plants are actually taking up nitrogen that comes from cicadas," said Yang. The seeds of the insect-fertilized plants were also 9 percent bigger than those in a control group.

Yang said recruiting field volunteers to gather insect carcasses can be a challenge. He's recruited family, friends, high school students, and strangers, who responded to a newspaper ad. And he says they soon become fans of the small creatures.

"These cicadas are everywhere, so everyone knows them. All the people on the street know your bug, and they often know the different species. The people I meet know a lot about the insects, and they often ask me really challenging questions about cicada biology," Yang said.

It's the safety in numbers that has kept the cicada population thriving since the last Ice Age. As individuals, Yang says they can be somewhat klutzy.

"They are not very agile fliers, and they don't seem to be very skilled at avoiding predators," Yang said.

Especially with such an intriguing insect, Yang says it is important to study their entire life cycle, because they are fertilizing both below ground food webs as well as above ground populations.

"When things die a lot of people stop paying attention to them," he said.

V. Cicada infestations boost nutrients for forests

CBC NEWS ONLINE STAFF, *CBC*, November 29 2004

WASHINGTON - Insects that emerge every 17 years in the eastern United States provide valuable nutrients to forest ecosystems when they die, an ecologist says.

The Brood X cicadas emerge from their burrows on a regular cycle, sing to attract a mate and lay eggs before dying on the forest floor.

Last spring, the insects swarmed forests, raising concerns about their effects on the ecosystem.

Scientists had noticed forests tended to have higher levels of the nutrient nitrogen in their leaves after cicadas emerged and tree growth tended to increase.

The infestation gave researchers a chance to test the impact of cicada carcasses on soil and plants.

Researchers at the University of California, Davis, studied cicada-infested areas in the U.S. in 2002, 2003 and 2004.

In an experiment, Louie Yang measured the levels of nutrients in plots with cicadas compared to control plots without extra insects.

The type of nitrogen used by plants jumped 199 per cent on average in soil littered with cicada carcasses, Yang's team found.

Populations of bacteria and fungi also increased, the researchers said in Friday's issue of the journal *Science*.

Plants appeared to benefit from the extra nutrients. Bellflower, a plant that commonly grows on the forest floor in cicada territory, produced seeds that were nine per cent larger.

The plants also produced leaves containing 12 per cent more nitrogen than those that grew in cicada-free soil.

The nitrogen from the cicadas came in a unique form, which allowed the researchers to trace it to the insects.

VI. Perspectives: Oh the Locusts Sang, Then They Dropped Dead

RICHARD S. OSTFELD and FELICIA KEESING*, *Science*, November 26, 2004

The Bob Dylan song "Day of the Locusts" [HN1] refers to the cacophony from the 1970 emergence of 17-year cicadas (*Magicicada* spp.), which happened to coincide with his acceptance of an honorary degree from Princeton University. These cicadas [HN2], which dutifully reappeared aboveground in 1987 and then again this year, are a quintessential case of a resource pulse--a transient, multiannual episode of resource superabundance. On page 1565 of this issue, Yang (3) [HN3] describes the ramifying impacts that massive pulses of cicada carcasses have on forest soils, microbial biomass, nitrogen availability, and reproductive success of understory plants.

Resource pulses typically are associated with reproductive events in plants, such as synchronized heavy seed production (mast-seeding) [HN4] within populations of oaks or bamboos, and even more spectacularly, across dozens of genera of paleotropical dipterocarp trees (2) [HN5]. Plant populations that synchronize seed production achieve high reproductive success because seed predators can only consume a fraction of the hyperabundant resource ("predator satiation") (3), and most of the escapees germinate. Similarly, so many periodical cicadas are involved in the dissonant mating swarms that their predators--principally birds--can consume no more than 15% of the peak numbers (4). The remainder die after reproducing and drop to the forest floor.

Although much is known about the evolutionary causes of synchronized reproductive events, only recently have ecologists begun to analyze the consequences of resource pulses for ecosystems (5). The predominant type of resource pulse--mast seeding--occurs in grasses, annual forbs, shrubs, and trees, across at least four continents and from deserts to tropical rain forests. Generalist consumers--often rodents--are the most immediate beneficiary of this superabundant resource, and they respond with population outbreaks of their own. These rodent irruptions, in turn, result in severe impacts on their alternate prey, such as songbird eggs (6), their avian and mammalian predators (7), and their parasites and pathogens (5, 8). In these cases, the pulsed resource is quickly converted into consumer biomass, and the direct and indirect consequences for ecosystems follow this consumer pathway.

The research by Yang demonstrates a new pathway by which resource pulses can affect ecosystems--through the action of decomposers (1) [HN6]. Unlike seeds, which germinate following escape from predation, periodical cicadas die and rot. These insects are a high-quality fertilizer indeed (about 10% nitrogen), delivered at a rate of up to 0.5 kg m⁻². Within a month of a simulated cicada irruption, biomass of both fungal and bacterial decomposers in the soil increased dramatically, and this in turn resulted in a tripling of soil ammonium, and a more-than-doubling of soil nitrate concentration [HN7]. As with other fertilizers, the cicada-induced flush of soil nutrients ultimately boosted nitrogen concentration and seed mass in the American bellflower (*Campanulastrum americanum*) [HN8], an understory plant.

Periodical cicada nymphs spend 16-plus years attached to tree roots sucking on xylem (9) [HN9], resulting in a persistent, long-term deflection of soil-derived nitrogen from leaves into insect biomass. Upon emergence, the cicadas then transport this stolen nitrogen aboveground. From there, a little ends up in avian or mammalian consumer tissue, and another fraction goes to cicada egg production, but most becomes fertilizer, first for soil microbes and then for understory plants like bellflowers. Because the nitrogen-enriched bellflower tissues die and decompose themselves, the trees would seem to be the ultimate recipients of the prodigal nitrogen's return underground (see the figure).

Analyzing radial tree-ring growth [HN10] of oaks within the geographic ranges of 13-year and 17-year cicadas, Koenig and Liebhold (10) [HN11] found a ~4% decrease in tree growth during the year of emergence, which they attributed to the damage caused by oviposition wounds in twigs. However, some of Koenig and Liebhold's analyses also demonstrated a ~1% increase in tree radial growth during the first 4 years after emergence, for which they had no explanation. The fertilization effect of cicada carcasses reported by Yang might account for this apparently compensatory stimulation of growth after emergence.

Spectacular resource pulses like the emergence of periodical cicadas constitute one of the more obvious demonstrations that ecological systems rarely exist in equilibril states, but instead are in constant flux. By tracing the responses of populations or entire trophic levels [HN12] to resource pulses, ecologists can assess the extent to which resources versus consumers control abundance or biomass--in other words, whether control is bottom-up or top-down. They can also determine the strength and nature of interconnections between species or trophic levels. A trophic cascade [HN13] occurs when top-down effects permeate through three or more trophic levels (11), and we suggest that the cicada-decomposer-plant system, which represents the penetrance of bottom-up effects through three trophic levels, be considered a "trophic fountain." The bottom-up metaphor, of course, refers to the effects of lower trophic levels on higher ones. In a more physical sense of the metaphor, Yang's work demonstrates how organisms and materials flow inexorably from bottom to top and back again.

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VII. Cicada invasion feeds forests: Insect broods kick-start forest ecosystems every 17 years

ROXANNE KHAMSI, *Nature*, November 25 2004

A huge troop of cicadas known as Brood X emerges in the eastern United States every 17 years, covering streets, cars and buildings with a crunchy coating of insects. Although they aren't welcome in the cities, the nutrients from the Magicicada carcasses provide a valuable boost to forest ecosystems, says a California ecologist.

When the insects appear, the adults burrow up from the soil to mate, then lay their eggs inside trees, allowing newborn larvae to travel back underground. Once the mating season ends, these adults die and their bodies litter the forest floor.

The most recent invasion took place last spring, in an area covering eastern states such as Tennessee and Kentucky. Experts estimate that, in affected areas, around 100 insects emerge from each square metre of ground, although this number can vary from fewer than 10 to more than 300.

Scientists had already noticed that in the years following the cyclical emergence of the cicadas, forest plants seem to have unusually high amounts of nitrogen in their leaves. Nitrogen is normally a limiting factor in the plants' growth.

So Louie Yang at the University of California, Davis, decided to investigate further. He measured the levels of nutrients in experimental soil plots to which he had added cicadas, and compared them with control plots that lacked the extra insects.

Bountiful bugs

To Yang, the idea of going into a forest to dispense dead cicadas by hand was anything but tedious. "Putting dead bugs on the ground does not sound like fun for most people, but for me it's really exciting. It will produce results," he says.

Yang found that, a month after adding cicada carcasses, the numbers of bacteria and fungi known to feed on biological material in the soil had been boosted, and the amount of ammonium and nitrate available for plants to use had increased by up to three times.

He added 140 cicadas per square metre to a plot that contained a forest plant called the American bellflower (*Campanulastrum americanum*); the plants later had 12% more nitrogen in their leaves, compared with plots without cicadas, and produced seeds that were 9% larger.

The results directly prove the link between the cicadas and increased levels of nitrogen in plants, says Yang. The insects are generally known for their negative effects on forest plants: they eat large amounts of plant matter and lay their eggs within the trees. But Yang believes the swarms could have a beneficial effect on the ecosystem overall, by kick-starting forest growth every 17 years.

Similar 'resource pulses' are seen in other ecosystems, he points out, including dramatic plant growth after El Niño rainfalls, and the nutrient boost to riverbank communities when large amounts of salmon die after spawning.

VIII. The cicada: More than meets the ear

MICHAEL STROH, *Baltimore Sun*, November 26, 2004

While some Marylanders fled the state last summer to avoid the largest cicada emergence in 17 years, Louie Yang, a population biologist, rushed here from the West Coast with one question in mind: How much do those rotting cicada carcasses impact the environment?

As the University of California researcher reports today in the journal *Science*, the answer is: a lot.

Periodical cicadas spend most of their lives underground as nymphs sucking on tree roots, emerging only once every 13 or 17 years (depending on the brood) to mate. As anyone who has witnessed their arrival knows, it can be an assault on the senses: In wooded areas, 200 nymphs can squirm up from a single square yard. An acre can cough up 1 1/2 million.

In population biology, these massive emergences are known as a "resource pulse."

Some oaks and bamboos, for example, suddenly release enormous quantities of seed to propagate the species, overwhelming the capacity of rodents and other animals to devour them. In the case of cicadas, previous studies have shown that birds snarf down only 15 percent of the bugs. The rest are left to mate and, eventually, die and rot.

Yang wanted to know: then what?

So he spent two years before this summer's emergence scooping up nearly 20,000 periodical cicadas around the East Coast. He buried them in experimental soil plots to see how much nitrogen was released and what its effect would be on the seed output of the American bellflower, a plant he used as a stand-in for the rest of the forest flora.

Sure enough, the rotting cicadas caused a big spike in the quantity of nitrogen-producing bacteria in the soil. And his bellflowers produced larger than normal seeds. Other scientists have noticed that trees grow faster in the years after a cicada pulse. The noisy, annoying bugs live only a few weeks, but "their effects don't stop after they die," says Yang.

IX. Forests flourish under carpet of dead cicadas

New Scientist, December 4, 2004

FOREST trees in the eastern US grow quicker in years after large numbers of cicadas have emerged, and we may have found the reason why.

Cicadas spend most of their lives underground, where they consume tree root juices, depriving leaves of valuable nutrients. Some periodical species then emerge en masse every 13 or 17 years and feast on tender tree branches before laying their eggs and dying. Now Louie Yang at the University of California at Davis has established that, in dying en masse in this way, the insects provide a deluge of compost that fertilises forest soils and helps trees grow faster.

Using insects collected from broods of periodical cicadas that emerged in 2002 and 2003, Yang applied various densities of dead cicadas to 1-metre-square forest plots. After a month, plots laden with a typical 240 cicadas contained more microbes, three times the concentration of available ammonium and 2.5 times the concentration of nitrates compared with untreated plots. And bellflowers growing on soil enriched with cicadas had a higher concentration of nitrogen in their leaves and seeds - 9 per cent greater than those growing on control plots (*Science*, vol 306, p 1565).