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SPIDERS IN DECOMPOSITION FOOD WEBS OF AGROECOSYSTEMS: THEORY AND EVIDENCE

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ABSTRACT. The involvement of spiders in decomposition food webs has the potential to affect agricultural productivity through two quite different types of interactions: (1) cascading, top-down effects of spider predation on rates of nutrient mineralization—spider-initiated trophic cascades in the detrital food web that could alter rates of decomposition and release of nutrients to plants; and (2) a bottom-up linkage, through spiders, between decomposition and grazing food webs—energy from the detrital web contributing to elevated spider densities, which in turn might reduce pests and enhance net primary production. Scant experimental evidence exists to refute or support either hypothesis. The first set of interactions is most likely to be of significance in no-till and conservation tillage farming. In theory, spiders have the potential to enhance productivity by increasing rates of mineralization, but theory also predicts that spiders, by preying on important detritivores and fungivores, depress rates of litter decomposition. Field experiments by Kajak and her colleagues have uncovered such negative effects of spiders in mown pastures. Although this negative effect could reduce plant growth, the expected time lags in most types of crops suggest that the overall impact of spiders on plant production will be determined more by the interactions comprising the second hypothesis. However, the later hypothesis, that bottom-up control processes in the decomposition web affect crop productivity via energy subsidies to spiders and other generalist predators in the grazing web, remains conjecture without clear experimental confirmation. This hypothesis should be tested in agroecosystems in which detritus-based food webs can feasibly be manipulated.

A major goal of agriculture is to maximize net primary production, which is the ultimate source of energy for both grazing and decomposition food webs. Biocontrol practitioners have focused on the grazing web because agricultural pests and humans compete directly for the living products of photosynthesis. Thus, research on the roles of spiders in agroecosystems has focused primarily on the extent to which these predators suppress densities of grazing herbivores. Spiders also belong to decomposition food webs of agroecosystems, yet arachnid connections to such webs have stressed acarine cousins; and spiders have been largely ignored. Is this neglect justified, or might knowledge of how spiders function in decomposition food webs be utilized to increase agricultural yields?

Two quite different sets of interactions between spiders and the detritus-based food web are potentially relevant. The first set involves cascading, top-down effects of spider predation on rates of nutrient mineralization—spider-initiated trophic cascades in the detrital food web that could affect rates of decomposition and release of nutrients to plants. The second set of interactions relies on a linkage, through spiders, between decomposition and grazing food webs—energy from the detrital web contributing to elevated spider densities, which in turn might cause lower pest numbers and enhanced net primary production. Here we examine the evidence that these two different sets of interactions affect, or have the potential to influence, agricultural productivity.

TOP-DOWN TROPHIC CASCADES AND RATES OF DECOMPOSITION

Theory.—Decomposition food webs are often categorized as ''donor-controlled'' systems (Pimm 1982) because the rate at which detritus is consumed does not immediately influence the rate of supply of this energy to the system, but the amount of detrital input can influence densities of detritivores and their

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predators. Viewing detrital food webs as primarily donor-controlled leads to the conclusion that bottom-up control processes predominate in such webs, i.e., that most linkages of indirect effects are responses to changes in rates of input at the base of the food web. This view is an over-simplification for at least two reasons. First, the rate at which the primary decomposers—the bacteria and fungi, collectively known as the microflora—decompose detritus depends on their population growth rates, which in turn are potentially influenced by their natural enemies (Swift et al. 1979). The second oversimplification is that, ultimately, decomposition processes affect net primary production by altering rates of mineralization, i.e., the rates at which nutrients locked in detritus become available to autotrophs. As a consequence, spiders that feed on detritivores have the potential to influence indirectly the growth of autotrophs by generating trophic cascades in the decomposition food web, thus affecting rates at which nitrogen and other nutrients required by plants enter the nutrient pool.

Such linked indirect effects most likely occur in those agroecosystems in which a substantial fraction of litter decomposition occurs on the soil surface, and in which the major consumers of detritus and the microflora are preyed upon by spiders. Ploughing disrupts the litter layer and distributes organic matter throughout the soil; thus, cultivation encourages below-ground, bacterial-based decomposition food webs (Hendrix et al. 1986). The role of spiders in such webs is likely insignificant. Under no-till and conservation tillage conditions, however, litter accumulates above ground, fungi are a major component of the microflora, and microarthropods, primarily mites and Collembola (springtails), are major detritivores/fungivores (Hendrix et al. 1986; Stinner & House 1990; Robertson et al. 1994). Spiders readily consume Collembola, which constitute a substantial portion of the diet of many species (Hallander 1970; Schaefer 1975; Yeargan 1975; Wingerden 1975, 1978; Greenstone 1980, 1983; Nentwig 1987; Döbel & Denno 1994; Nyffeler et al. 1994). Hence spiders are most likely to exert a trophic cascade affecting mineralization in no-till annual crops; and in orchards, pastures and other perennial crops

Spiders have the potential to generate either positive or negative impacts on rates of mineralization, even if one ignores interactions between spiders and other predators. The simplest abstract food chain in a spider-influenced system would consist of three effective trophic levels: detritus, Collembola (realizing that other detritivores play roles similar to Collembola, but Collembola appear to be ubiquitous and abundant), and spiders. The indirect effects of spiders in such a food chain would be to enhance the standing crop of detritus, i.e., to retard the rate of litter decomposition (Fig. 1A). This model, however, is greatly oversimplified. Fungi play a critical role in decomposing plant litter; and although Collembola consume plant material, many Collembola species are primarily fungivorous (Peterson 1971; Chen et al. 1996). Thus a four-level food chain model is more realistic (Fig. 1B). In grazing food chains of four trophic levels, predators can induce a trophic cascade that negatively impacts the base trophic level—the primary producers. Reasoning by analogy, one might predict that an increase in spider density should lead to a decrease in the amount of detritus, i.e., an increase in decomposition rate, by relieving predation pressure on fungi (Fig. 1B). However, does an increase in fungal biomass always lead to increased rates of mineralization? Not necessarily, because nutrients can become immobilized in senescent fungal hyphae. Thus, Collembola at intermediate densities can enhance rates of mineralization by consuming senescent fungal hyphae (Parkinson et al. 1977; van der Drift & Jansen 1977; Warnock et al. 1982; Finlay 1985; Verhoef & de Goede 1985; Visser 1985). Collembola also enhance decomposition by more indirect pathways, i.e., by comminuting the litter (Anderson et al. 1984). Therefore, depression of Collembola populations by spiders could negatively impact rates of litter decomposition and mineralization (Fig. 1C).

It is clear that the potential relationship between spider densities and mineralization rates is complicated because links between Collembola density and rates of litter decomposition are complex. Field experiments in which spider densities are reduced is the most direct way to determine which of the competing hypotheses about possible spider-induced trophic cascades is correct.

Evidence.—Kajak and her colleagues have

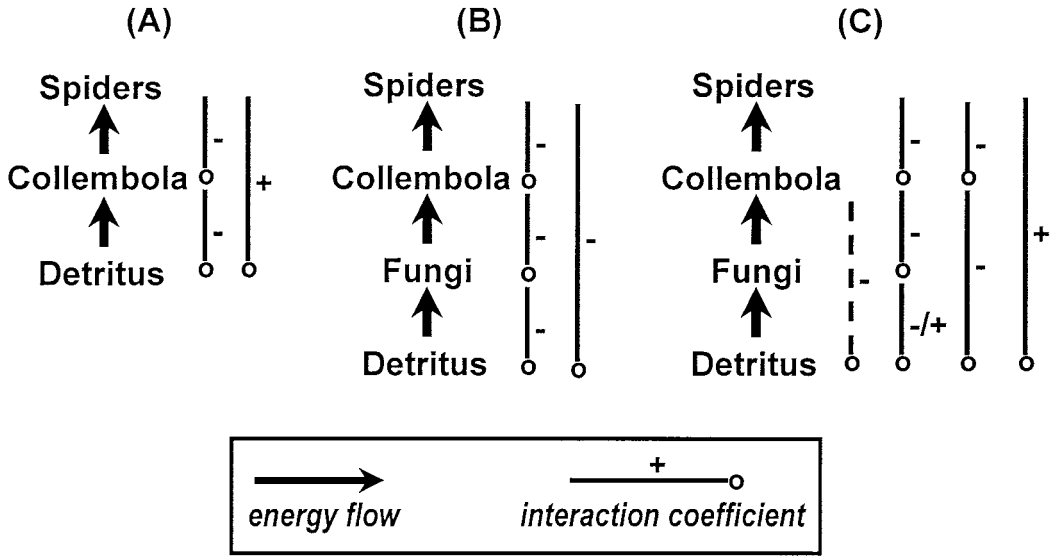

Figure 1.—Three different hypothesized sets of trophic cascades in which predation by spiders on Collembola might either enhance or retard rates of litter decomposition. (A) A 3-level food chain in which indirect effects of predation by spiders retard decomposition, indicated by a net + influence of spiders on the amount of detritus [(−) × (−) = (+)]. (B) A simple food chain of 4 trophic levels in which spider predation enhances litter decomposition, i.e., decreases litter amount [(−) × (−) × (−) = (−)]. (C) A more realistic food chain model, in which indirect effects of spider predation are predicted to retard decomposition rate. This model incorporates the positive non-trophic effects of Collembola feeding, such as litter comminution, on rates of fungal growth; and the fact that the relationship between fungal density and rates of fungal breakdown is non-linear.

studied the impact of spiders and other generalist arthropod predators—primarily carabid beetles—on rates of litter decomposition in mown meadows (Kajak & Jakubczyk 1975, 1976 1977; Kajak & Kaczmarek 1988; Kajak et al. 1991; Kajak 1997). Their basic approach has been to exclude epigeic macrofauna from small field cages, and then compare trapping rates of predators; densities of Collembola, other fungivores/detritivores, and the microflora; and rates of litter decomposition, with corresponding rates and densities in partially open cages or open areas.

In some of their studies not all differences were statistically significant, and some variation occurred between experiments conducted in different meadows and different years. Nevertheless, a clear pattern emerges. Excluding macrofaunal predators, of which spiders comprise a substantial fraction, frequently causes an increase in Collembola and other mesofauna and an increase in rates of litter decomposition. Thus ambient densities of spiders and other macrofaunal predators inhibit rates of decomposition in grasslands.

These studies were conducted in a managed system in which the diversity of vegetation, fauna and microflora probably is more similar to that of more natural ecosystems than to highly disturbed crop systems. To date available evidence supports the hypothesis that spiders inhibit rates of decomposition and mineralization (Fig. 1C); and evidence does not support the alternative hypothesis, that spiders increase crop productivity through trophic cascades within the decomposition food web. Clearly more experiments of the type conducted by Kajak and her colleagues are needed in a variety of agroecosystems.

DETRITAL SUBSIDY OF THE GRAZING FOOD WEB

Theory.—Spiders, because they prey upon both detritivores/fungivores and herbivores, simultaneously belong to decomposition and grazing food webs. The connection of spiders to both webs opens the possibility that increased input of detritus to the agroecosystem could enhance detritivorous and fungivorous prey of spiders, leading to elevated spider

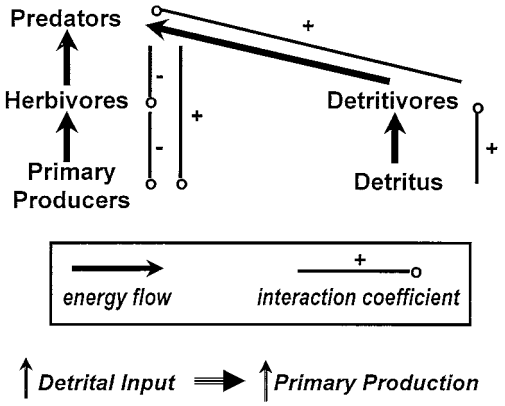

Figure 2.—If decomposition and grazing food webs are linked by common top predators, it is possible that increased input of detritus could elevate the biomass of primary producers through a complex linkage of trophic interactions (i.e. apparent competition between detritivores and grazing herbivores). Because in this model the predators are feeding on more than one trophic level and there is an external input of energy to the grazing food chain, this type of effect on the grazing food web has been termed an *allochthonous energy subsidy via multichannel omnivory* (Polis 1994; Polis & Strong 1996).

densities which in turn would increase pressure on herbivores, thereby enhancing rates of net primary production. In this way increased input of detritus could, in principle, make spiders more effective biocontrol agents by introducing an energy subsidy to the grazing food web. This complex series of indirect effects involving bottom-up control processes in one food web and top-down processes in another is an example of an *allochthonous energy subsidy* via *multichannel omnivory* (Polis 1994; Polis & Strong 1996; Fig 2). An example from non-agricultural systems is the input of detrital energy from the marine environment that leads to elevated densities of spiders and other predators in coastal areas, with subsequent declines in herbivores and reduced plant damage (Polis & Hurd 1996). Food-web interconnections in tropical rice fields, in which detritus is both allo- and autochthonous, constitute a probable example from agricultural systems. Settle et al. (1996) argue that abundant populations of detritivores and planktivores early in the season maintain high densities of generalist predators, which are then able to suppress pest populations on rice later in the season.

Trophic cascades induced by spiders in a grazing food web via energy subsidies from a decomposition web will occur only if certain conditions are met: (1) Bottom-up control processes in the decomposition web must affect spider densities; i.e., spiders must be food-limited, and fungivores/detritivores must be readily consumed by spiders if numbers of the former increase; (2) Increased availability of prey in the decomposition web must not cause spiders to switch from feeding on herbivorous prey, or if such changes occur, the increased numbers of spiders must compensate for this dietary shift; (3) Spider-generated trophic cascades in the grazing food web must be strong enough to enhance crop yield.

No direct experimental evidence exists to support the hypothesis that energy subsidies from decomposition food webs enhance crop yield via multichannel omnivory in agroecosystems. In the absence of direct evidence, the only alternative is to evaluate the evidence that the proposed conditions for such a detrital subsidy are satisfied. Below we summarize briefly some of this evidence, which comes from a mixture of studies with non-agricultural and agricultural systems.

Evidence.—Field experiments have demonstrated that spider populations frequently are food-limited (Wise 1993). Although most studies have been conducted with grazing food webs, some experiments have demonstrated bottom-up limitation of spider numbers in decomposition food webs in non-agricultural systems (Spiller 1992; Chen & Wise 1999). The importance of Collembola numbers in influencing spider population dynamics is particularly crucial to the argument. Experimentally enhancing detrital input to the forest-floor increases densities of Collembola and other fungivores, which is accompanied by a doubling of densities of many families of spiders (Chen & Wise 1999).

Indirect evidence suggests that Collembola help maintain high densities of spiders and other generalist predators in some agroecosystems. For example, two species of wolf spiders in Swiss wheat fields feed predominantly on Collembola ($>$ 35% of their diet) early in the season. As the season progresses, however, Lepidoptera larvae and cereal aphids gradually become the spiders' main prey

(Nyffeler 1982). Field experiments have demonstrated that carabids and spiders can limit aphid numbers in cereal crops (Chiverton 1986; Edwards et al. 1979). Although this pattern supports the hypothesis that a detrital subsidy promotes top-down control in the grazing food web, the relationship between decomposition and grazing food webs in cereal crops is likely complex. In addition to subsidizing spider populations and inducing trophic cascades, high numbers of alternative prey from the decomposition web might weaken such a cascade because some aphid species are low-quality food for spiders (Toft pers. comm.; Toft 1995); and spiders might shift from aphids to higher-quality alternatives. However, although spiders can develop aversions to low-quality prey, limited consumption of suboptimal food provides nutritional benefits to these predators (Toft 1995). Hence spider predation on aphids at low prey levels, common early in the season, may limit aphid outbreaks if the presence of superior-quality prey boosts spider numbers enough to ensure that the overall impact of spider predation on aphids is high (Toft 1995). An additional complicating issue is the finding that not all Collembola are high-quality prey for spiders (Toft & Wise 1999a, b). Clearly more information is needed before accurate predictions can be made about the general impact of increased densities of Collembola and other fungivores/detritivores on the total predation pressure exerted by spiders on agricultural pests.

Increasing evidence suggests that spiders can depress densities of agricultural pests in several types of crop; however, effects on crop yield have not been widely documented. Enough evidence exists to implicate spiders as potentially important biocontrol agents to justify research into the question of whether or not a detrital subsidy could increase their effectiveness. No experimental evidence exists to support the prediction that such a detrital subsidy could be used to enhance the biocontrol effectiveness of spiders. Experimental studies are needed with agroecosystems in which a detrital subsidy is likely to have an impact. Below we discuss one such system.

Vegetable crops.—Field experiments of Riechert & Bishop (1990) have revealed that spiders can limit densities of pest insects in vegetable gardens. Their use of fencing to exclude spiders could have also reduced carabid beetles, which are abundant predators in agroecosystems. We have recently expanded their experiments to examine explicitly the combined impacts of spiders and carabids, their separate impacts, and whether or not intraguild predation limits their effectiveness in biocontrol.

In one set of experiments we employed fence barriers, pitfall trapping and hand removal to reduce densities of ground spiders, foliage spiders and carabid beetles (Tuntibunpakul & Wise unpubl. data). In the first experiment, conducted in mixed-vegetable gardens, reducing spiders and carabids led to elevated densities of squash bugs in cucumbers and Colorado potato beetles (CPB) in potatoes. The presence of beetles and spiders marginally increased total cucumber yield, significantly improved the individual weight of marketable cucumbers, and marginally increased the yield of one of two varieties of potato. In an experiment conducted the following year, manipulating spiders and carabids in a garden planted solely in potatoes had no impact on densities of CPB, which were higher than the previous year, and did not affect potato production.

In another set of experiments, densities of wolf spiders and carabids were manipulated together and separately by continuously altering rates of immigration into fenced plots in conjunction with removal by pitfall trapping (Snyder & Wise in press). In the first year, simultaneously decreasing lycosids and carabids had no impact on pests or yield of cucumber in a spring garden; however, reducing colonization by spiders and carabids of a summer squash garden harmed squash production (Snyder & Wise in press). In the second year (unpubl. data) we manipulated immigration rates of lycosids and carabids both singly and together in order to separate their impact as biocontrol agents and to uncover effects of intraguild predation on their total biocontrol effectiveness. In the spring garden carabids did not affect cucumber production, but in the fall garden of squash they reduced squash bugs and increased fruit production. Lycosids increased cucumber production by feeding on striped cucumber beetles. In marked contrast, in the summer garden wolf spiders harmed squash production by causing an increase in squash bugs at the critical early stage of squash growth. This indirect negative effect of

lycosids likely was caused by their feeding on important insect predators of squash bug nymphs. In the summer gardens, allowing carabids to immigrate into the plots compensated for the negative impact of lycosids on yield, so that the combined effect of the assemblage of wolf spiders and carabid beetles was to increase squash production.

Thus spiders and carabids have the potential to depress pest numbers and increase yield in potatoes and cucurbits, but the pattern is complex. Densities of immigrating spiders and carabid beetles may not always be high enough either to reduce pest numbers or to lower them enough to improve yield. Furthermore, lycosids can substantially reduce crop production by preying on other predators of insect pests. Whether or not the enhancement of spider numbers will improve vegetable yield depends upon both the densities and phenologies of pests and other predators.

Enhancement of spider numbers, and the provision of alternative prey to reduce their feeding on other predators of insect pests, has the potential to increase the impact of spiders in vegetable systems. Providing straw mulch increases the density of spiders ca. 10× compared to plots with bare ground (Riechert & Bishop 1990; Tuntibunpakul & Wise unpubl. data). Similarly, the use of straw refugia in soybeans can dramatically elevate the abundance (20–30×) and diversity of resident spider fauna (Halaj, Cady & Uetz unpubl. data). Such effects could be due primarily to altered structure of the physical habitat; however, some of the increase in spider numbers could have resulted from an energy subsidy derived from the decomposition food web based on the added straw. This effect could be particularly important later in the season, after the mulch has partially decomposed, enhancing detritivore populations.

It would be worthwhile to devise field experiments in which the rate of input of detritus to the decomposition food web of vegetable gardens is explicitly manipulated in order to test the hypothesis that a detrital subsidy can enhance the biocontrol impact of spiders (Fig. 3). Increased detritus could improve plant productivity simply by providing more nutrients, so a complete test of the hypothesis would require documentation that the detrital subsidy does in fact cause higher spider numbers and higher densities of Collembola and other fungivores, and that increased productivity of marketable vegetables can be explained as the result of decreased feeding by insect pests. The impact of a detrital subsidy could be investigated most directly by experimentally introducing high quality detritus to the system (e.g., Chen & Wise 1997, 1999). Support of the detrital-subsidy hypothesis would then justify detailed studies of how farming techniques could be modified to encourage the decomposition food web in vegetable production.

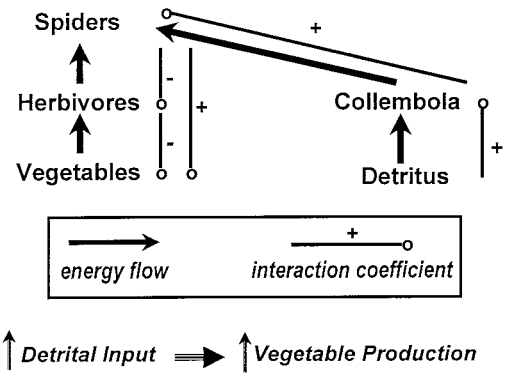

Figure 3.—Hypothesized increase in vegetable production via a detrital energy subsidy of a grazing food web in which spiders are top generalist predators.

CONCLUSIONS

In theory, spiders have the potential to enhance productivity by increasing rates of mineralization through cascading top-down effects on rates of decomposition. Such cascading indirect effects are most likely to be of significance in no-till and conservation tillage farming. The actual impact of spiders on mineralization rates is difficult to predict. It is possible that spider predation also could negatively impact the rate of litter decomposition, as has been demonstrated for grassland systems. Such an effect might lower rates of plant production, but the expected time lags before such an effect would be expressed suggest that the overall impact of spiders on plant production will be determined more by their interactions in the grazing food web.

It is more likely that bottom-up control processes in the decomposition web can affect crop productivity via multichannel omnivory. Energy subsidies from the decomposition subsystem may cause spider-induced trophic cas-

cades that are strong enough to increase crop production. This conjecture remains a hypothesis, but well worth testing in agroecosystems in which detritus-based food webs can feasibly be enhanced.

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