RADIONUCLIDE TRACER ANALYSIS OF TROPHIC RELATIONSHIPS IN AN OLD-FIELD ECOSYSTEM[1]

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ABSTRACT

Wild radish (*Raphanus raphanistrum*) and ragweed (*Ambrosia artemisiifolia*), the dominant producers during initial succession in an old field, were labeled with ^{32}P in several trophic-transfer studies. Feeding relationships were determined by correlating the population dynamics and ^{32}P uptake by consumer species with the phenological changes in producer components and isotope distribution in plant tissues. The relative magnitude of consumer pathways was estimated by using trophic-transfer indices.

The first year of old-field succession was characterized by rapid phenological changes in plant-organ availability with related shifts in consumer trophic relationships. The food web of wild radish, the early summer dominant producer, changed rapidly over time resulting in successive pulses of leaf, pollen, and seed feeders. Grasshoppers were the major leaf feeders. Aphids consumed internal juices within stems while flea beetles were concentrated and feeding solely on nutrient-rich seed tissue. Leafhoppers and tarnished plant bugs also consumed internal fluids during wild radish development. The high densities and consumption by plant bugs and aphids, the major consumers of wild radish, resulted in a low food-web diversity for wild radish. Predator-prey relationships during early summer were governed mainly by the aphid infestation. Young ragweed plants and the litter and seed crop of wild radish were major food-web bases in midsummer. Generalized herbivores such as grasshoppers and crickets utilized radish seeds and ragweed tissue during this period. A second phase of specialized feeders entered the old field as ragweed became available. Food-web diversity was highest at this time when many species were present and at low densities.

Ragweed was the dominant producer late in the growing season. Some herbivores utilized ragweed leaves while several species of plant bugs became abundant and were consuming the nutrient-rich fluids being channeled into pollen tissue. Plant bugs were the major ragweed herbivores. The importance of these plant bugs resulted in a decline in food-web diversity near the end of the growing season. Most consumers decreased in numbers and ^{32}P activity as ragweed died back in September. Ragweed litter, however, supported crickets and other components of the detrital food web over the fall season.

Wild radish and ragweed were the major food-web bases during the first year of succession. Over 90% of the arthropods sampled in the old field were food-web components of these producers. Many of these consumers were specialists and sucking forms which peaked in density and ^{32}P activity as nutrient-rich fluids were entering their specific food sources. The synchronal occurrence of consumer population peaks and successive nutrient pulses in host-plant organs thus appears to maximize the energy utilization by these consumers while minimizing interspecific competition for sites of trophic transfer.

Little foliar damage was evident for wild radish or ragweed because of the importance of herbivores with sucking mouthparts. Tracer studies were thus critical in evaluating the role of both producers as food-web bases. The similarity of results in two replicate studies

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confirmed the repeatability and accuracy of tracer techniques for trophic-transfer analysis. However, temporal aspects of food-web structure should be considered in future studies where rapid changes in plant phenology are present.

Introduction

Early studies of energy flow in ecosystems were often based on assumptions concerning food sources and gross estimates of energy transfer between trophic levels. Radionuclide tracers, however, have enabled more accurate determination of food-chain components and show great promise for future energy-flow estimations (Odum and Golley 1963). The basic technique involves labeling a food source in the field and then following the fate of the label through consumer trophic levels.

Several goals have been reached through the development of tracer techniques for ecosystem analysis. Initially, Pendleton and Grundmann (1954) determined insect-plant relationships of the thistle (*Cirsium undulatum*) by using ^{32}P as a tracer. Odum and Kuenzler (1963) used ^{32}P to analyze food chains from major producers in an old-field ecosystem. They identified the trophic positions of consumer species by changes in their activity-density (cpm/mg body tissue) levels. Consumers of higher trophic levels generally showed slower uptake rates of ^{32}P than did herbivore species. Trophic relationships have also been studied in aquatic environments (Whittaker 1961, Ball and Hooper 1963) by introducing ^{32}P in water and following its uptake by biotic components. Next, Marples (1966) worked out the grazing vs. detritus food chains in a salt marsh by separately labeling both living and dead *Spartina*. Wiegert, Odum, and Schnell (1967) labeled concurrently the two major producers in an old field and determined the relative utilization of each by resident consumer species. Their use of trophic-transfer indices represented a new attempt to provide relative estimates of food consumption. Two additional outgrowths from their study were the isolation of an unsuspected producer-aphid-ant food chain (de la Cruz and Wiegert 1967) and the initial focusing on food-web diversity in nature by using radionuclide tracer methods (Wiegert and Odum 1969). Other tracer studies have included a long-term investigation of ^{137}Cs cycling through food chains in a *Liriodendron* forest (Auerbach, Olson, and Waller 1964, Reichle and Crossley 1965, 1969, Waller and Olson 1967), analysis of the trophic dynamics of natural isopod populations (Paris and Sikora 1965, 1967), and a study of the arthropod consumers in a tagged cornfield (Rose, Monk, and Wiegert 1969).

Plant species tagged in past tracer studies were only labeled on single occasions. Little emphasis was placed on replicate studies or possible temporal changes in the trophic relationships that were reported. Marples (1966), however, labeled *Spartina* twice during a single growing season, but made only a few temporal comparisons. Paris and Sikora (1965, 1967) tagged plant species during two successive summers in preliminary and confirming studies on the food sources of *Armadillidium vulgare*. The possible variability associated with tracer studies has remained largely untested, leaving some doubt about their accuracy.

Several objectives were included in the present radiotracer experiments. The basic objective was to determine the food-web components of dominant producers during early old-field succession on the New Jersey Piedmont and to obtain some measure of their trophic transfer. Successional changes in trophic structure of the community were thus followed throughout the initial growing season. Additional objectives included comparing the trophic transfer from a dominant producer in replicate plots, during two successive summers, and at different stages of its development. This permitted analysis of the variability in results when considering either replication or temporal aspects of trophic transfer.

Methods

Study area

The study was conducted in a 3-acre field adjacent to Hutcheson Memorial Forest in East Millstone, New Jersey. The field is on the Piedmont Plateau of New Jersey and is underlain with Triassic red shale of Brunswick Formation (Kümmel 1940). Soil type was primarily silt loam 18–24 inches deep (Ugolini 1964). The field was bordered by a mature oak forest on the south, sycamore (*Platanus occidentalis*) and shrub growth on the north, and by early old fields on the east and west. The patterns of plant (Bard 1952) and small mammal (Pearson 1959, Root and Pearson 1964) succession in the immediate area have been previously reported.

The study area had been planted with orchard grass (*Dactylus glomerata*) from 1962 until 1967 when the research was initiated. The entire 3-acre field was deeply plowed and disced twice during April 1967 and was then subdivided into four subplots, two of which were sprayed on May 5 with an organophosphate insecticide. The effects of the insecticide treatment on the succession that followed have been reported elsewhere (Shure 1971). The field was again plowed, disced, and treated in the spring of 1968 to repeat the initial year of old-field succession.

Herbaceous vegetation

Plant succession was studied in the old field during the 1967 and 1968 growing seasons. Vegetation was sampled by harvesting within four 10- by 20-m quadrats (Shure 1971). Quadrats were established prior to vegetation development and sufficiently removed from the field's boundary to avoid possible edge effects. The same quadrat locations were used both summers.

Twenty ¼-m^2 areas were harvested, five from each quadrat, at 2-week intervals over the growing season. Sample locations were selected by using a table of random numbers. All plants within each sample area were clipped at ground level, bagged, and returned to the laboratory. Each sample was sorted by species, ovendried at 90°C for 24 hr, and weighed for biomass estimations.

Herb-stratum arthropods

Sweep-net removal techniques were used to follow the successional changes in herb-stratum arthropod populations during the 1967 summer. A 10-sweep method (Malone 1969) was employed to sample the arthropods from 1 m^2 of vegetation. Twenty sweep samples were obtained at random from the old field on three sample dates during July and August. A more detailed account of the specific methods has been presented elsewhere (Shure 1971).

Trophic relationships

Five radionuclide tracer studies were conducted to determine the successional changes in trophic relationships in the first-year old-field ecosystem (Table 1). The tracer studies included labeling ragweed (*Ambrosia artemisiifolia*) at its peak biomass in two separate quadrats in 1967. Three additional studies were carried out in 1968 to study the food web of major producers over a 2½-month period. Wild radish (*Raphanus raphanistrum*), the dominant producer in early summer, was labeled in early July as it reached peak standing-crop biomass. Ragweed was again tagged in 1968 both early in development and when it was nearing peak biomass.

The methodology of the tagging experiments followed similar studies by Odum and Kuenzler (1963), Marples (1966), and Wiegert et al. (1967). Equal-sized quadrats (10 m by 10 m) were set up to conduct the tracer studies. Those quadrats run concurrently were separated by at least 50 m. This distance was believed sufficient to prevent mixing of labeled arthropods (Wiegert et al. 1967). Each 100-m^2 quadrat was subdivided into twenty-five 4-m^2 sections in which eight plants were selected for labeling. Two hundred plants were labeled in each experiment.

The plants were labeled with ^{32}P by using a stem well" method (Wiegert and Lindeborg 1964). An equal quantity of ^{32}P was used for all 200 plants in each experiment. This amount varied between experiments, however, depending on plant size and stage of development (Table 1). Stem wells were constructed from plastic tape and then fastened to form a well around the plant base. Incisions were made in the plant stem at the bottom of the well after water had been added. Isotope was then added, and the ^{32}P-water solution was drawn into the plant by transpiration. Wells were sealed to the stem following isotope uptake to prevent direct contamination of consumers or further stem injury.

TABLE 1. Tagging dates and amount of ^{32}P added per plant in the five tracer studies

Plot	Study	Date	^{32}P/plant (μc)
P-1	Mature ragweed	August 7, 1967	18
P-2	Mature ragweed	August 16, 1967	24
P-3	Wild radish	July 9, 1968	15
P-4	Young ragweed	July 26, 1968	15
P-5	Mature ragweed	August 15, 1968	20

Consumer populations were sampled by two methods. Herb-stratum arthropods were collected with a sweep net (30 cm diameter) by taking 10 sweeps while moving systematically through the quadrat. The net was then sealed in a pastic bag charged with carbon tetrachloride as a killing solution. Arthropods associated with the ground or litter layer were collected with cryptozoan boards. Twelve 19- by 47-cm boards were placed in a uniform grid in each 100-m^2 quadrat. Representative samples of cryptozoans were collected from under all boards on each sample date. Some hand sampling of ants, grasshoppers, and occasionally ladybird beetles (1967) was necessary.

Samples were obtained from each quadrat on seven dates over a 41- or 42-day period. All samples were returned to the laboratory and sorted by species. Each species group was then radioassayed with an organic quenched G.M. detector (Baird Atomic, model EWT-64) with a 1.4 mg/cm^2 end window and a decade scaler (Baird Atomic, model 135). Species were considered labeled if the counting rate was at least 10 counts/min over background. Samples were then dried at 100°C for 24 hr and weighed with a semi-micro analytical balance (± 0.1 mg) to obtain activity density (cpm/mg dry wt) estimations. All activities were corrected for background and physical decay of the isotope. No self-absorption corrections were attempted.

Trophic-transfer indices (Wiegert et al. 1967) were used to determine the extent of ^{32}P uptake by consumer species. The formula

TABLE 2. Percentage of available biomass of the producer being tagged that was labeled within each 100-m² quadrat (N_L and B_L are the number and mean biomass, respectively, of labeled plants; N_T and B_T are the number and mean biomass, respectively, of all plants of the tagged species in each quadrat)

Quadrat	N_L	B_L (g)	N_T	B_T (g)	Percentage biomass labeled
P-1	200	21.9	778	21.9	25.7
P-2	200	21.9	841	14.9	35.0
P-3	200	5.0	4320	1.3	17.4
P-4	200	4.7	1257	1.9	39.7
P-5	200	13.2	1051	5.7	43.9

Trophic-transfer index

$$= \frac{\text{Mean activity density consumer}}{\text{Mean activity density plant foliage}}$$

× total consumer biomass (dry wt) sampled represents the mean concentration factor of a consumer species times its population biomass.

Plant samples were collected in each study to determine activity-density levels. Small portions of leaves and reproductive organs were obtained at random from labeled plants on several sample dates. Plant samples were assayed in the same manner as arthropod samples. Plant-component activities were averaged in determining the overall mean activity density of plant foliage for trophic-transfer estimations.

Only a portion of the particular plant species being tagged was labeled in each quadrat. It was thus necessary to estimate the fraction of the available biomass that was labeled to account for feeding by consumers on unlabeled plant tissue. The use of only labeled samples in estimating plant activity density underestimates the mean concentration factor and thus trophic transfer of a consumer species. The mean activity density of plant foliage was therefore multiplied by the fraction of the biomass labeled in calculating mean concentration factors. The fraction of biomass labeled (*FBL*) in each experiment (Table 2) was estimated by the formula

$$FBL = \frac{N_L \times B_L}{N_T \times B_T},$$

where N_L equals the number of plants labeled (200), B_L is the average biomass of labeled plants as estimated by randomly harvesting plants of the size labeled from outside the tracer quadrat, N_T is the total number of ragweed plants inside the quadrat as measured by direct count, and B_T equals the average biomass of those plants as obtained from harvest data from adjacent vegetational sampling areas.

A small study was also conducted in 1968 to determine which cryptozoans were acting as decomposers of ragweed. Plants labeled on July 26, 1968, in an additional study (Shure and Pearson 1969) were harvested, separated into biomass components, dried at 100°C for 24 hr, and later returned to the field as litter. Litter from eight plants (132 g dry wt) was distributed over an approximate 4-m² area. Five cryptozoan boards were placed around the edge of the area to sample for saprophagous cryptozoans. Cryptozoans were collected and assayed for ^{32}P activity on days 4 and 22 after litter had been deposited.

RESULTS

Community succession

Successional changes at the community level were somewhat different over the two summers (Fig. 1). Plant density increased until early July in 1967 and then remained fairly stable during the rest of the growing season. Plant biomass remained low until the end of June in 1967 and then increased rapidly during July and August. A peak biomass of 259.6 g/m² (dry wt) was reached by the end of August. In 1968, however, a greater plant density resulted in the old field and earlier in the growing season. Plant density peaked by late June in 1968 at nearly three times the peak 1967 level and then declined during July. Plant biomass also increased

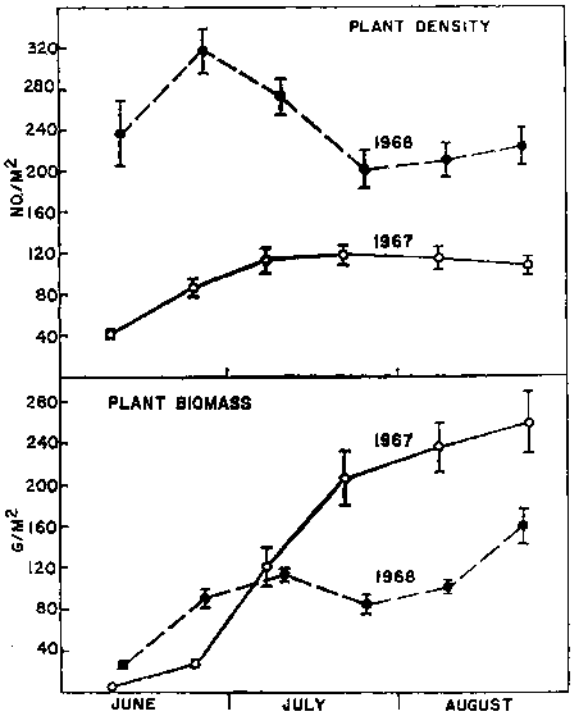

FIG. 1. Total plant density (number/m²) and biomass (g/m²) changes during old-field succession in 1967 and 1968. Means ($N = 20$) plus one standard error are indicated.

more rapidly in 1968, but reached only 159.2 g/m² by late August. It increased until early September, but never reached the 1967 level.

Plant species involved in the successional process were similar both summers (Tables 3 and 4) (Shure 1969). Wild radish was the dominant producer in early summer amounting to about half of the total producer biomass. *Raphanus* began dying back during late July, and only dead plants were present late in the growing season. Hedge bindweed (*Convolvulus sepium*) was also a major producer in early summer and formed a dense vegetative mat near ground level. Ragweed, which was present as seedlings through early July, eventually replaced wild radish as the dominant late-summer producer. Ragweed comprised over half of the community biomass each year at the peak standing crop of the community. Red sorrel (*Rumex acetosella*) and three-seeded mercury (*Acalypha rhomboidea*) were additional major producers which reached their peak biomass late in the growing season. Other important plant species included *Chenopodium album*, *Cyperus sp.*, *Dactylis glomerata*, *Linaria vulgaris*, *Polygonum pennsylvanica*, and *Setaria viridis*. A more detailed analysis of the species composition, density, biomass, and diversity changes in vegetation as well as the insecticide effects on these parameters has been presented elsewhere (Shure 1971).

In 1968 approximately 115 species of arthropods were sampled in the old field during each tracer experiment (42 days). A slightly lower total (101) was present in 1967 late in the growing season. Arthropod density increased in the old field throughout the 1967 growing season (Table 5). Species

TABLE 3. Mean biomass (g/m²) and density (plants/m²) of dominant plant species in an old field on six days in 1967 ($N = 20$)

Dominant species	June 9	June 24	July 7	July 21	August 8	August 23
Raphanus raphanistrum						
Biomass	3.3	12.8	60.6	85.3	48.2	—
Density	19.4	12.6	8.8	10.0	9.2	—
Convolvulus sepium						
Biomass	1.0	4.7	19.9	21.3	4.8	10.7
Density	5.6	5.2	8.0	9.8	6.0	7.6
Ambrosia artemisiifolia						
Biomass	0.2	3.3	27.8	75.2	143.1	218.3
Density	9.2	10.6	10.4	10.8	10.4	10.4
Rumex acetosella						
Biomass	0.1	1.6	4.6	7.6	8.6	2.2
Density	2.0	6.8	6.8	8.2	14.4	14.0
Acalypha rhomboidea						
Biomass	<0.1	0.6	2.4	4.1	4.5	5.5
Density	0.1	17.6	26.4	22.2	14.8	20.8

TABLE 4. Mean biomass (g/m²) and density (plants/m²) of dominant plant species in an old field on six days in 1968 ($N = 20$)

Dominant species	June 11	June 26	July 10	July 25	August 8	August 22
Raphanus raphanistrum						
Biomass	14.0	57.1	58.9	19.1	2.9	2.3
Density	91.4	83.4	47.4	12.2	6.6	3.4
Convolvulus sepium						
Biomass	9.6	20.4	25.7	18.0	21.5	22.0
Density	37.0	46.8	42.6	30.8	25.8	29.2
Ambrosia artemisiifolia						
Biomass	0.3	3.8	7.8	24.1	42.4	85.9
Density	12.4	20.6	18.8	15.6	18.4	18.4
Rumex acetosella						
Biomass	2.2	4.8	12.7	7.5	9.9	10.5
Density	16.2	35.5	31.2	17.6	26.4	36.6
Acalypha rhomboidea						
Biomass	0.3	1.9	3.7	8.9	15.2	20.5
Density	53.0	74.0	75.0	76.4	73.6	76.2

TABLE 5. Density (number/m^2) of major arthropod orders ($N = 20$) in an old field on three days in 1967 (means plus one standard error)

Order	July 6	July 29	August 22
Hemiptera	9.2±1.62	29.4±2.16	102.9±10.70
Homoptera	16.5±1.32	15.5±1.07	24.4± 1.55
Coleoptera	3.9±0.74	15.9±2.61	5.6± 0.67
Diptera	13.9±1.44	16.4±1.54	11.0± 1.23
Hymenoptera	2.9±0.52	5.5±1.23	2.4± 0.39
Orthoptera	0.3	0.3	0.2
Lepidoptera	0.3	0.6	1.1
Arachnida	0.3	1.1	1.7
Total	47.0±3.83	83.9±3.71	147.7±11.34

diversity, however, was highest during July and dropped off during August (Shure 1971). These changes were mainly due to the increased density of a few species of plant bugs (Hemiptera, Miridae) during August. Other insect orders were either fairly stable in numbers throughout July or August or had reached peak levels by the end of July.

Successional changes in arthropod populations were different during 1968. Aphids, flea beetles, and the plant bug *Lygus* were very abundant by mid-July when arthropod density was at its greatest. The rapid buildup and decline in numbers of these insects was associated with the rapid increase in density and biomass of vegetation during 1968. Arthropod density increased again during August, as it did in 1967.

Trophic relationships

Ragweed 1967.—In both tracer studies in 1967 the isotope was translocated to all plant organs but at different activity-density (AD) levels. Two plants harvested from P-2 on day 7 had a mean AD (cpm/mg) of 27.8, 72.8, 52.3, and 12.6 for leaves, inflorescences, stems, and roots, respectively. Further comparisons (Shure 1969) indicated that inflorescences were labeled significantly greater than leaf tissue until the end of the tracer studies. Both flowers and leaves had dropped in ^{32}P activity by the end of each study. A detailed analysis of the phenological changes in ^{32}P activity in ragweed organs has been presented elsewhere (Shure and Pearson 1969).

The food-web components and their trophic transfer from ragweed were quite similar in the replicate studies (Table 6). Species listed accounted for 98.2% (P-1) and 99.0% (P-2) of the total transfer from ragweed. Plant bugs were the major ragweed herbivores in both plots; *Lygus pratensis*, *Reuteroscopus ornatus*, and *Plagiognathus politus* were responsible for 74.5% (P-1) and 74.1% (P-2) of all herbivore transfer. Both immature and adult stages of these species utilized ragweed as a major food source. Other important herbivores in both plots included meadow spittlebugs (*Philaenus spumarius*), red-legged grasshoppers (*Melanoplus femur-rubrum*), and lepidopteran larvae. The remainder of the herbivore transfer was mainly due to several species of leafhoppers. In both studies the major herbivores exhibited a rapid uptake of ^{32}P, reaching peak AD levels by 3 weeks after tagging. Peaks were reached somewhat sooner in P-2 where a greater amount of ^{32}P was used per plant and a greater percentage of available biomass was labeled.

The predatory and cryptozoan components of the ragweed food web were also similar in both quadrats. Major predators included ground (mainly lycosid) and herb-stratum spiders and a species of ladybird beetle (*Coleomegilla maculata*). Cryptozoan consumers included isopods, millipedes, ground beetles, and crickets. The field cricket *Nemobius fasciatus* and two ground beetle species (*Harpalus pennsylvanicus*, *Harpalus caliginosus*) were the major cryptozoan consumers. Most predators peaked in ^{32}P activity about day 20, but ^{32}P uptake by cryptozoan forms was somewhat slower.

Intraspecific differences in ^{32}P uptake between quadrats were attributed to the delay in labeling the second quadrat. Species such as *Plagiognathus politus* and *Scaphytopius frontalis* increased rapidly during late August and were thus sampled more often in plot P-2 when their densities were greatest. Higher trophic-transfer indices resulted (Table 6). *Reuteroscopus ornatus* and damsel bugs (*Nabis alternatus*, *N. americoferus*) declined in numbers during late August and showed the reverse difference.

Wild radish 1968.—Tagging wild radish at its peak biomass enabled a determination of both the grazing and detrital components of its food web. Plants were labeled as seed development was initiated and remained labeled after dying back by early August. Labeled seeds and dead plant material were thus available to consumers during the latter part of the study.

Two plants harvested 10 days posttagging had mean activity densities of 239.5 for stems, 825.5 for seeds, and 167.2 for roots, indicating translocation to all plant organs. A more detailed study (Shure 1969) indicated high activity densities in leaves and seeds by 3 days posttagging. Leaves were nearly absent by day 10 when most phosphorus (nutrients) was apparently channeled into seed production. Seeds remained highly labeled throughout the remainder of the experiment.

Trophic positions and feeding relationships of consumer species were derived from ^{32}P uptake curves in conjunction with field observations of feeding habits. Specific feeding sites of certain herbivores were also identifiable by correlating their uptake curves with phenological changes in plant-nutrient availability. The major arthropod herbivores on wild radish (Table 7) included the tarnished

TABLE 6. Number (N), total dry weight (Mg), mean ^{32}P activity density (AD), mean concentration factor (CF), and trophic-transfer index (TTI) of arthropod consumers from ragweed (*Ambrosia artemisiifolia*) in 1967 (data represent totals (all samples) for the two concurrent studies)

Species	Plot P-1					Plot P-2				
	N	Mg	AD	CF	TTI	N	Mg	AD	CF	TTI
Herbivores										
Lygus (A)[a]	283	504	18.0	1.02	514	148	244	101.0	2.00	487
(N)[a]	221	106	62.1	3.51	374	237	135	196.9	3.91	526
Reuteroscopus (A)	457	237	32.0	1.81	430	347	200	89.6	1.78	356
(N)	251	57	47.8	2.70	154	72	24	108.9	2.16	52
Plagiognathus (A)	453	204	42.9	2.43	495	465	226	139.2	2.76	624
(N)	211	54	60.6	3.43	185	472	129	156.9	3.11	400
Chlamydatus	65	11	30.5	1.72	19	39	9	135.9	2.70	25
Polymerus	21	17	11.9	0.67	12	—	—	—	—	—
Ilnacora	9	7	18.3	1.03	7	1	1	248.3	4.93	3
Macrosteles	43	17	6.0	0.34	6	33	11	30.4	0.60	7
Empoasca	174	32	5.1	0.29	9	134	20	61.8	1.22	24
Scaphytopius (A)	21	16	11.5	0.65	11	80	58	53.6	1.06	61
(N)	15	4	14.2	0.80	3	34	13	218.0	4.32	55
Aceratagallia (A)	—	—	—	—	—	43	18	62.5	1.24	23
(N)	—	—	—	—	—	22	6	34.8	0.69	4
Philaenus	65	241	6.7	0.38	92	64	252	12.3	0.24	60
Stobaera	21	17	15.2	0.86	14	21	11	26.8	0.53	6
Euaresta	50	28	8.2	0.46	13	16	8	41.8	0.83	7
Oscinella	73	8	12.9	0.73	6	38	4	77.3	1.53	6
Trigonorhinus[b]	63	20	18.5	1.05	21	67	22	62.6	1.24	28
Smicronyx										
Gallerucella	5	11	6.9	0.39	4	1	3	31.3	0.62	2
Melanoplus	8	1192	2.5	0.14	167	8	1403	3.1	0.06	84
Oecanthus	2	38	5.2	0.29	11	6	87	39.1	0.78	68
Lepidoptera larvae	19	67	82.4	4.67	315	17	107	146.1	2.90	311
Total	2,530	2,888		1.34	2,862	2,365	2,991		1.79	3,219
Predators										
Nabis	15	31	12.9	0.73	22	1	4	19.0	0.37	1
Coleomegilla	24	92	11.1	0.63	58	23	89	33.4	0.66	59
"Web" spiders	15	32	11.8	0.67	21	23	240	19.5	0.39	94
Ground spiders	18	249	3.9	0.22	55	22	1,458	1.3	0.03	44
Total	72	404		0.56	156	69	1,791		0.36	198
Cryptozoa										
Isopoda	25	260	2.9	0.16	42	30	340	3.2	0.06	20
Diplopoda	27	986	1.3	0.07	69	7	323	3.8	0.08	23
Harpalus pennsylvanicus	27	1,331	0.4	0.09	120	44	2,049	1.2	0.02	48
H. caliginosus	12	2,003	0.2	0.01	16	18	2,978	1.9	0.04	110
Nemobius	78	1,534	1.4	0.08	123	81	1,670	3.9	0.08	129
Gryllus	15	1,223	0.4	0.02	25	26	2,847	1.0	0.02	48
Total	184	7,337		0.07	395	206	10,207		0.05	378
Grand total	2,876	10,629			3,413	2,640	14,989			3,795

[a]Adult (A) and nymphal (N) stages have been separated where so indicated.
[b]Data combined.

plant bug (*Lygus*), a leafhopper (*Macrosteles fascifrons*), an aphid (*Hyadaphis erysimi*), flea beetles (*Phyllotreta chalbeipennis*), and the red-legged grasshopper (*Melanoplus*). Important predators were damsel bugs (*Nabis*), ladybird beetles (*Coccinella novemnotata*), and spiders. Ground beetles (*Harpalus*), soldier beetle larvae (*Chauliognathus pennsylvanicus*), and field crickets (*Nemobius* and *Gryllus*) were the important cryptozoan consumers.

The flea beetle *Chaetocnema elongatula*, a leaf feeder, and the aphids *Mysus* and *Hyadaphis* reached peak uptakes during week 1 (Fig. 2) when leaves were present and liquid nutrients were still circulating through all plant organs. Aphids were highly abundant along the stems of wild radish feeding off internal plant juices. The two aphid species had the highest activity densities and mean concentration factors of any radish herbivores. Aphids shifted to winged forms as the plants dried up and were absent from the old field by day 12. *Chaetocnema*, however, remained abundant in subsequent samples apparently shifting to other plant species for food when radish leaves were unavailable. Lepidopteran larvae and fruit flies (*Euaresta bella*) also reached peak uptake levels quite early, but then declined in ^{32}P activity as leaves and foliar exudates became absent. Large numbers of a second flea beetle species (*Phyllotreta*) became concentrated and

TABLE 7. Number (N), total dry weight (Mg), mean activity density (AD), mean concentration factor (CF), and trophic-transfer index (TTI) of arthropod consumers of *Raphanus raphanistrum* (plot P-3)

Species	N	Mg	AD	CF	TTI
Herbivores					
Lygus (A)[a]	453	901	84.7	0.68	612
(N)[a]	530	336	170.3	1.37	460
Reuteroscopus (A)	21	—	—	—	—
(N)	76	12	7.3	0.06	<1
Chlamydatus	51	14	9.4	0.08	1
Polymerus	16	14	62.6	0.50	7
Nysius	20	14	52.4	0.42	6
Macrosteles	299	97	42.2	0.34	33
Aceratagallia	34	10	191.1	1.54	15
Philaenus	44	170	0.6	0.01	1
Myzus	167	19	170.6	1.38	26
Hyadaphis	1,797	321	304.6	2.46	789
Macrosiphum	19	3	36.1	0.29	1
Phyllotreta					
chalbeipennis[b]	657	182	55.7	0.45	82
P. zimmermanni[b]	19	7	125.5	1.01	7
Chaetocnema	466	103	3.2	0.03	3
Gallerucella	4	10	4.0	0.03	<1
Trigonorhinus	30	12	40.4	0.33	4
Euaresta	75	45	1.6	0.01	<1
Melanoplus	24	674	19.4	0.16	108
Lasius	32	8	52.3	0.42	3
Lepidopteran larvae	32	85	32.7	0.26	22
Phalangida	12	44	24.5	0.20	9
Total	4,878	3,081		0.55	2,190
Predators					
Nabis	14	18	78.2	0.63	11
Orius	8	1	46.3	0.37	<1
Sinea	1	21	5.0	0.04	1
Coleomegilla	3	14	2.0	0.02	<1
Coccinella (A)	15	190	67.6	0.55	105
(Larvae)	49	181	92.8	0.75	136
Harpalus convergens	4	25	11.2	0.09	2
Web spiders	74	89	29.1	0.23	20
Ground spiders	21	492	15.3	0.12	59
Total	189	1,031		0.31	335
Cryptozoans					
Harpalus pennsylvanicus	19	724	8.3	0.07	51
H. caliginosus	6	761	2.5	0.02	15
Chauliognathus	13	218	41.4	0.33	72
Nemobius	106	1,206	26.8	0.22	265
Gryllus	15	1,600	18.0	0.15	240
Total	159	4,509		0.16	643
Grand total	5,226	8,621		3,168	

[a] Adult (A) and nymphal stages (N) are separated for certain herbivores.
[b] Probable species. Identification not positive.

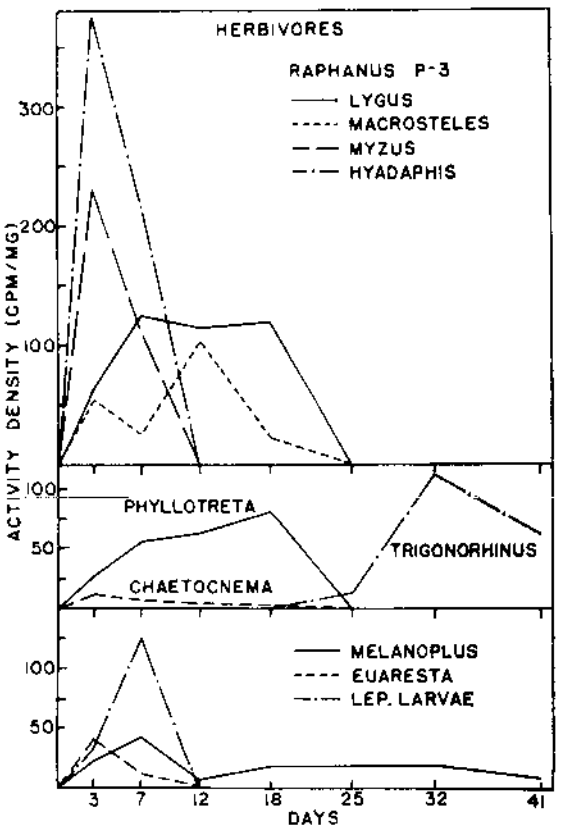

FIG. 2. Uptake curves (^{32}P) of major herbivores of wild radish. Lines connect mean activity-density values for the entire species sample collected on the dates indicated.

were feeding solely on radish seeds during late seed development. *Phyllotreta* peaked in activity density on day 18 and then disappeared from the samples after seeds were deposited by 25 days posttagging. *Lygus* and the leafhopper *Macrosteles* remained labeled until day 25 when internal plant juices were no longer available. The delayed uptake curves for the fungus weevil *Trigonorhinus tomentosus* and the chinch bug *Nysius raphanus* (peaked at day 25) indicated that these species were utilizing seeds or dead radish plants as food sources. Grasshoppers (*Melanoplus*) peaked initially in activity density while leaves were available and then remained labeled throughout the study. Seeds and possibly leaf litter were their food source during the latter part of the study.

Certain predator-prey relationships were determined from the uptake curves of major predators (Fig. 3). Adult and larval *Coccinella* peaked early and reached high activity-density levels, indicating aphids as their food source. The later peak by adult stages is attributed to the pupation of highly labeled larvae which were sampled as they emerged during the second and third weeks of the study. All *Coccinella* were gone from the samples by day 25, leaving the field when the aphids departed. Soldier beetle larvae (*Chauliognathus*) and herb-stratum spiders also peaked early, feeding mainly from aphids. Other prey were also consumed by herb-stratum spiders since they remained labeled throughout the study. *Nabis*, however, peaked on day 18 and remained labeled through day 32, relying more on plant bugs (*Lygus*) or leafhoppers as prey sources. Ground spiders also showed little ^{32}P uptake during the aphid infestation.

Seeds or dead plant material served as a food base for cryptozoans (Fig. 3). The field crickets *Nemobius* and *Gryllus* became highly labeled late

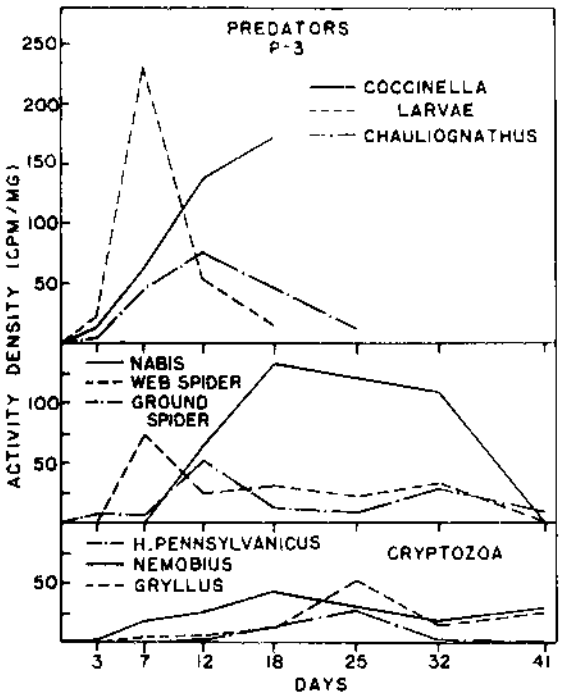

FIG. 3. Uptake curves (^{32}P) of major predator and cryptozoan components of the wild radish food web. Lines connect mean activity-density values for the entire species sample collected on the dates indicated.

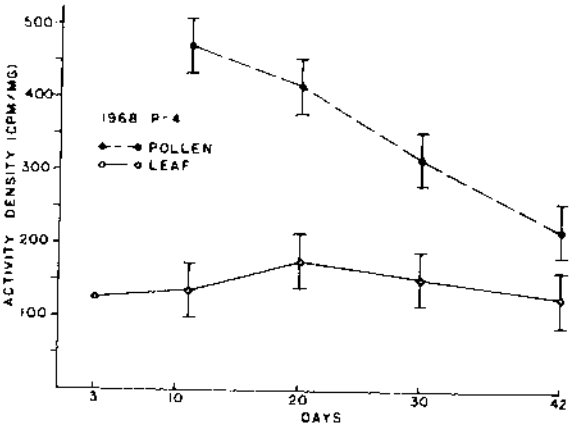

FIG. 4. Activity density in pollen stalks and leaves of young ragweed (P–4). Each mean represents replicate samples ($N = 30$) from 15 plants selected at random on each sample date. Least significant intervals (Shure 1969) were determined from a 4 x 2 factorial design for the analysis of variance (Steel and Torrie 1960).

in the study when seeds were abundant in the litter. Seed remains were often found under cryptozoan boards where crickets aggregated. *Nemobius* was labeled by day 7, however, indicating living or dead leaves as an additional food source. Ground beetles (*Harpalus*) also became labeled after the radish die-off. They either consumed seeds or were predaceous on other labeled consumers such as *Nemobius* or *Chauliognathus*.

Ragweed 1968.—Young ragweed plants were labeled in late July (P-4) at about one-fourth their peak standing-crop biomass. The old field at this time was at a transition stage between the two dominant producers. Leaf activity density remained fairly stable throughout the experiment (Fig. 4). Inflorescences which began appearing during the second week were labeled significantly greater than leaf tissue. The decline in inflorescence activity after day 10 was believed due to a biomass dilution initially (Shure and Pearson 1969), and later losses were attributed to leaching, pollen dispersal, or herbivory.

The major ragweed herbivores in P-4 (Table 8) included the plant bugs *Lygus*, *Reuteroscopus*, and *Plagiognathus*, a leafhopper (*Scaphytopius frontalis*), spittlebugs (*Philaenus*), grasshoppers (*Melanoplus*), and lepidopteran larvae. Damsel bugs (*Nabis*) and spiders were the only important predators. Crickets (*Nemobius* and *Gryllus*) and the ground beetle *H. pennsylvanicus* were the major cryptozoan consumers.

Feeding relationships of consumer species were evident from their uptake curves (Fig. 5, 6). The appearance of highly labeled pollen tissue part way through the study provided two distinct sources of ^{32}P available for consumption. Herbivores feeding only on leaves would peak early in activity density, whereas species consuming pollen or pollen and leaves together should peak at later periods. *Reuteroscopus*, *Scaphytopius*, the leafhoppers *Empoasca erigeron* and *E. alboneura* (mixed), *Melanoplus*, *Lasius neoniger* (ant), and lepidopteran larvae all had rapid uptakes of ^{32}P, indicating leaves or possibly stem tissue as essential food sources. The rapid decline in activity density for these species suggests little or no use of pollen tissue. The plant bugs *Lygus*, *Plagiognathus*, and *Chlamydatus associatus*, however, picked up most ^{32}P late in the study. These species appeared to feed only slightly on leaves, obtaining most food from pollen tissue when available. Snout beetles (*Smicronyx cornicularus*) and fungus weevils (*Trigonorhinus*) also had delayed uptake curves, but were not sampled until midway through the study. These beetles, when present, were observed feeding from pollen tissue. The fruit fly *Euaresta* had a double peak which may indicate the consumption of foliar exudates both from leaves and pollen tissue. The low activity density of this species may reflect a low phosphorus content of foliar exudates (Marples 1966).

Predators became labeled more slowly than prey species (Fig. 6). Spiders most likely fed on various herbivores, while the delayed uptake of *Nabis*

TABLE 8. Number (N), total dry weight (Mg), mean activity density (AD), mean concentration factor (CF), and trophic-transfer index (TTI) of arthropod consumers of *Ambrosia* when tagged at early development (P-4) in 1968

Species		N	Mg	AD	CF	TTI
Herbivores						
Lygus (A)[a]		246	419	19.1	0.21	88
(N)[a]		63	29	135.6	1.50	43
Reuteroscopus	(A)	227	109	100.5	1.11	121
	(N)	336	59	133.3	1.47	86
Plagiognathus	(A)	101	50	80.0	0.88	44
	(N)	265	48	117.4	1.30	63
Chlamydatus		103	27	100.8	1.11	30
Ilnacora		19	13	40.0	0.44	6
Macrosteles		70	20	1.6	0.02	<1
Empoasca		138	18	40.3	0.45	8
Scaphytopius	(A)	32	22	55.3	0.61	14
	(N)	78	25	144.9	1.60	40
Aceratagallia		118	39	23.1	0.26	10
Agallia		22	18	10.0	0.11	2
Philaenus		123	696	7.6	0.08	56
Stobaera		70	21	40.3	0.45	10
P. chalbeipennis		335	98	3.3	0.04	4
Gallerucella		1	3	31.6	0.35	1
Diabrotica		2	13	12.7	0.14	2
Smicronyx		60	25	45.1	0.50	12
Trigonorhinus		55	19	44.2	0.49	10
Euaresta		89	53	14.0	0.15	8
Melanoplus		19	1,027	25.9	0.29	298
Oecanthus		4	52	11.5	0.13	7
Lasius		80	12	17.1	0.19	2
Lepidopteran larvae		46	36	84.6	0.94	34
Phalangida		30	110	15.7	0.17	19
Total		2,732	3,061		0.55	1019
Predators						
Nabis		22	44	42.7	0.47	20
H. convergens		2	13	21.0	0.23	3
Web spiders		83	127	16.9	0.19	24
Ground spiders		11	175	2.7	0.03	5
Total		118	349		0.23	52
Cryptozoans						
Isopoda		10	123	5.1	0.06	7
H. pennsylvanicus		25	1,171	1.5	0.02	23
Nemobuis		110	2,102	2.6	0.03	63
Gryllus		22	2,981	2.4	0.03	89
Total		157	6,377		0.04	182
Grand total		3,007	9,787			1,253

[a]Adult (A) and nymphal (N) stages are separated for certain herbivores.

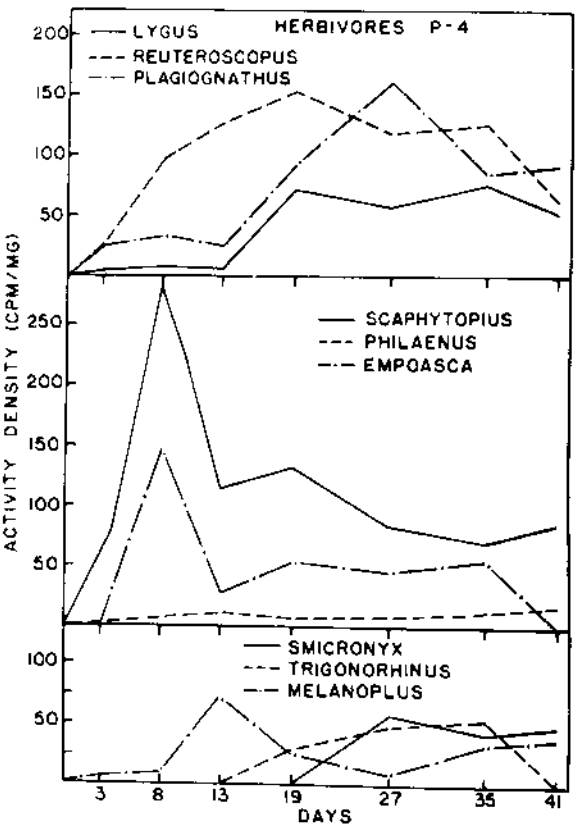

FIG. 5. Uptake curves (^{32}P) of young ragweed herbivores (P–4) during 1968. Lines connect mean activity-density values for the entire species sample collected on the dates indicated.

further suggests *Lygus* or other pollen consumers as major prey species. The cryptozoans *Nemobius* and *Gryllus* both peaked early, probably feeding off ragweed leaves near the ground surface.

Mature ragweed plants were labeled on August 15 (P-5) as they approached peak standing-crop biomass. Changes in ^{32}P distribution in leaf and flower tissue were similar to those found in 1967. Inflorescences were labeled significantly greater than leaf tissue until the end of the study.

Ragweed herbivores were similar both summers and at different stages of ragweed development (Table 9). Major herbivores on mature ragweed in 1968 included *Lygus, Reuteroscopus, Plagiognathus, Philaenus, Melanoplus, Oecanthus quadripunctatus* (tree crickets), and lepidopteran larvae. All herbivores peaked in activity density by day 21; levels declined late in the study (Fig. 7).

Predator-prey relations were altered during 1968 (Fig. 8). Herb-stratum spiders and a few assassin bugs (*Sinea diadema*) were the chief predators on ragweed herbivores late in the 1968 growing season. *Nabis*, a fairly important predator until midsummer, declined in importance near the end of the growing season both summers. The ladybird beetle *Coleomegilla*, an important predator in 1967, was rare and unlabeled in both ragweed studies in 1968. The only predation by ladybird beetles on ragweed consumers in 1968 was by a few *Hippodamia parenthesis* and a single *Coccinella*.

The trophic transfer by cryptozoan species was quite low in the final ragweed study (Table 9). *Nemobius* was the major cryptozoan consumer. The lack of a definite peak in the uptake curve for *Nemobius* indicated omnivorous feeding habits at the end of the growing season. *Gryllus*, important in all other ragweed studies, was barely labeled in the final study. Isopods, millipedes, and ground beetles were also less important consumers in 1968.

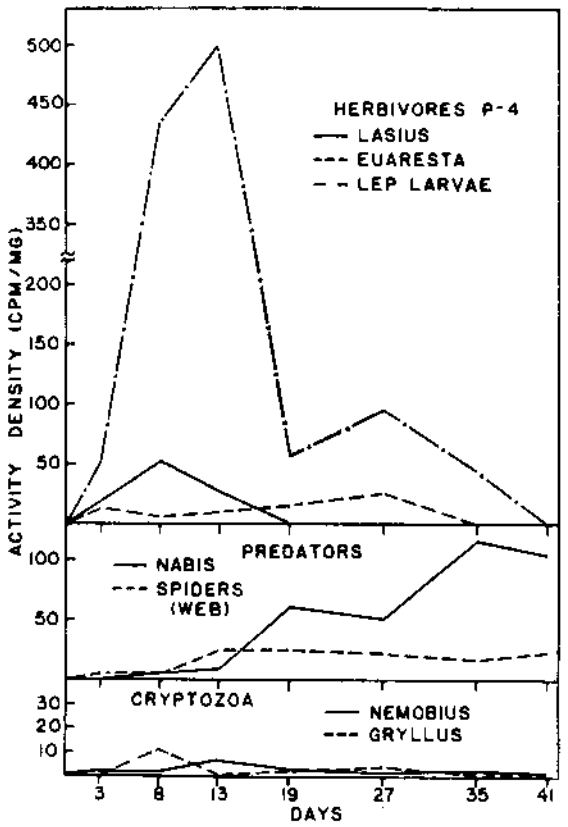

FIG. 6. Uptake curves (^{32}P) of selected components of the ragweed food web during its early development (P–4). Lines connect mean activity-density values for the entire species sample collected on the dates indicated.

The use of labeled litter in a separate study enabled the determination of which cryptozoans fed from ragweed litter. Field crickets (*Nemobius* and *Gryllus*) and isopods were the only species that were labeled in this study (Shure 1969) with most transfer by *Nemobius*. Ground beetles and ants were unlabeled. Only a single unlabeled millipede was collected.

Food-web comparisons

Food-web composition and trophic transfer from the two dominant producers were compared using percentage trophic transfer, percentage similarity (Southwood 1966), and information theory (Shannon 1948). The relative abundance and relative trophic transfer of shared food-web components were used in percentage similarity (Σ min./a,b/) determinations. Relative abundance and percentage trophic transfer of each food-web component were also used as inputs in the Shannon formula ($H' = \Sigma p_i \log_e p_i$) for estimating food-web diversity in each study. Relative comparisons were possible between producer species and for replicate plots, two years, and stages of development of ragweed.

TABLE 9. Number (N), total dry weight (Mg), mean activity density (AD), mean concentration factor (CF), and trophic-transfer index (TTI) of arthropod consumers of mature *Ambrosia* in 1968 (P-5)

Species		N	Mg	AD	CF	TTI
Herbivores						
Lygus	(A)[a]	126	234	183.8	1.71	400
	(N)[a]	235	131	363.6	3.39	444
Reuteroscopus	(A)	397	214	200.2	1.86	398
	(N)	239	54	172.4	1.61	87
Plagiognathus	(A)	191	98	208.5	1.94	190
	(N)	317	73	370.4	3.45	252
Chlamydatus		141	34	186.5	1.74	58
Ilnacora		19	13	53.8	0.50	7
Macrosteles		33	12	21.3	0.20	2
Empoasca		97	14	104.2	0.97	14
Scaphytopius	(A)	39	35	95.4	0.89	31
	(N)	26	8	264.9	2.47	20
Aceratagallia		43	17	87.1	0.81	14
Agallia		11	7	140.0	1.30	10
Philaenus		73	324	32.8	0.31	100
Stobaera		45	18	111.4	1.04	19
Chaetocnema		23	5	10.8	0.10	<1
Diabrotica		7	46	14.3	0.13	6
Smicronyx		64	27	88.9	0.83	23
Trigonorhinus		51	18	68.0	0.63	12
Euaresta		48	28	47.4	0.44	12
Oscinella		19	2	106.3	0.99	2
Melanoplus		23	1,810	45.5	0.42	760
Oecanthus		16	240	55.1	0.51	123
Lepidopteran larvae		45	205	108.9	1.01	208,
Phalangida		5	31	23.4	0.22	7
Total		2,333	3,698		1.13	3,200
Predators						
Nabis		5	7	59.5	0.55	4
Orius		11	1	25.7	0.24	<1
Sinea		2	19	72.3	0.67	13
Coccinella	(A)	1	9	2.4	0.02	<1
Hippodamia parenthesis		3	10	22.4	0.21	2
Web spiders		50	79	55.1	0.51	40
Ground spiders		8	383	0.5	<.01	2
Total		80	508		0.31	62
Cryptozoans						
Isopoda		34	390	2.2	0.02	8
Diplopoda		25	795	2.0	0.02	16
H. pennsylvanicus		37	1,771	0.3	<.01	4
Nemobius		127	2,952	2.4	0.02	59
Gryllus		20	3,112	<.1	<.01	1
Total		243	9,020		0.02	88
Grand total		2,656	13,226			3,350

[a] Adult (A) and nymphal (N) stages are separated for certain herbivores.

Trophic-transfer distribution was nearly identical in the two ragweed studies in 1967 (Fig. 9). In both plots most trophic transfer (63–65%) was by plant bugs which suck up internal plant juices. About one-third of this transfer was due to nymphal stages. Between 5-7% of the total transfer was by homopterans which also utilize internal plant juices. Orthopterans and lepidopteran larvae, however, which feed by chewing, obtained only 8% of the total transfer. In both studies the transfer by predators was about 10% of all herbivore transfer approximating a 10% efficiency of energy transfer between successive trophic levels. Cryptozoans accounted for very little trophic transfer.

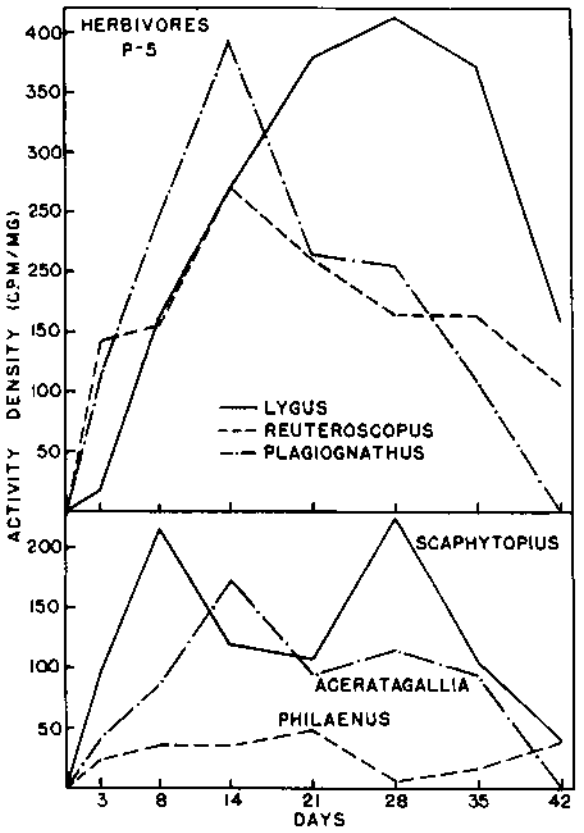

FIG. 7. Uptake curves (^{32}P) of mature ragweed herbivores (P–5) during 1968. Lines connect mean activity-density values for the entire species sample collected on the dates indicated.

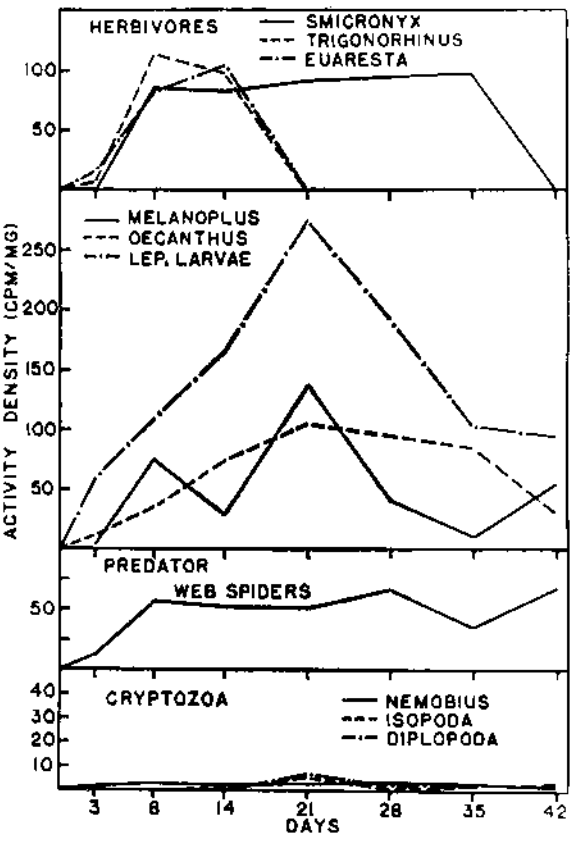

FIG. 8. Uptake curves (^{32}P) of selected components of the ragweed food web (P–5) during 1968. Lines connect mean activity-density values for the entire species sample collected on the dates indicated.

Food consumption from wild radish was more evenly distributed taxonomically (Fig. 10), but involved fewer major consumers than for ragweed. Hemipterans were the greatest consumers with nearly all hemipteran transfer by *Lygus*. Homopterans were also important herbivores on wild radish mainly because of the aphid infestation. Orthopterans and lepidopteran larvae were relatively unimportant consumers in the later stages of radish development. Their importance as consumers was probably greater during early radish growth when leaves were readily available. Predator transfer was high, amounting to 21% of the total transfer by herbivores. Most of this transfer was due to predation on aphids. Cricket consumption on radish seeds was quite high, whereas millipedes and isopods were absent at this stage of the growing season.

In 1968 the distribution of trophic transfer was similar at early and late stages of ragweed development (Fig. 10). Similarities were increased, however, because of the temporal overlap in the two studies. Hemipterans were again the major ragweed herbivores in 1968. They increased in importance as consumers as ragweed approached peak biomass

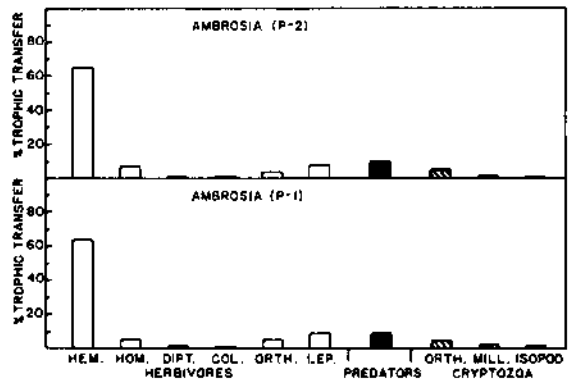

FIG. 9. Trophic-transfer distribution among taxonomic components of the ragweed food web (P–1, P–2) in 1967. Histograms indicate the percentage of total trophic transfer that occurred for each taxon. Arthropod taxons include hemiptera (hem.), homoptera (hom.), diptera (dipt.), coleoptera (col.), orthoptera (orth.), lepidoptera (lep.), and millipedes (mill.).

levels. Homopterans decreased in relative importance as consumers throughout the 1968 growing season. Their importance was similar, however, at the peak production of ragweed both summers.

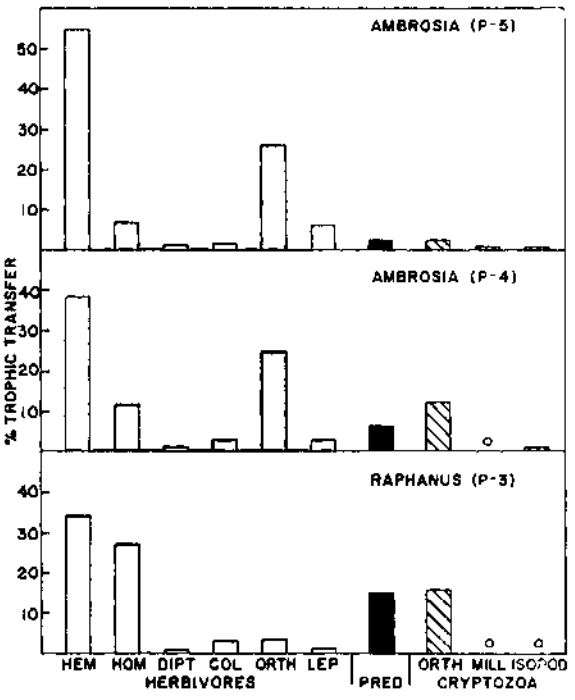

FIG. 10. Trophic-transfer distribution among taxonomic components (see Fig. 9) of the wild radish and ragweed food webs in 1968. Histograms indicate the percentage of total trophic transfer that occurred for each taxon.

TABLE 10. Percentage similarity in food-web components and trophic-transfer distribution from *Raphanus* (P-3) and *Ambrosia* (P-1, P-2, P-4, P-5) (similarities were based on relative abundance and percentage trophic transfer by shared food-web components in each comparison)

Item		P-1	P-2	P-3	P-4
Food-web components	P-2	77.1	—	25.4	63.3
	P-3	29.5	25.4	—	35.6
	P-4	64.0	63.3	35.6	—
	P-5	78.7	72.9	26.9	73.9
Trophic-transfer distribution	P-2	81.3	—	37.9	50.5
	P-3	39.5	37.9	—	30.7
	P-4	57.0	50.5	30.7	—
	P-5	72.2	67.6	32.2	71.4

TABLE 11. Information theory (H') estimates of the diversity of food-web components and of trophic transfer from *Raphanus* (R) and *Ambrosia* (A)

	1967		1968		
Item	A P-1	A P-2	R P-3	A P-4	A P-5
Food-web components	2.364	2.418	2.222	2.904	2.750
Total trophic transfer	2.346	2.353	2.159	2.673	2.274
Herbivore trophic transfer	1.872	1.953	1.344	2.313	2.115

Orthopterans were more important consumers throughout ragweed development the second summer. This resulted mainly from an increased number of grasshoppers in 1968. Predator transfer decreased during ragweed development in 1968, amounting to only 2% of the herbivore transfer from mature ragweed. Crickets were more important consumers during early ragweed development, but millipedes and isopods remained unimportant throughout the 1968 growing season.

Standard sampling techniques enabled absolute comparisons of the total transfer by consumers in each study. Assuming ^{32}P uptake comparable to food consumption, then the grazing pressure by herbivores was similar both years at the peak production of ragweed. Grazing was only one-third as great, however, when tagging was initiated at the early stages of ragweed development. Herbivore consumption from wild radish was only two-thirds that of ragweed, partly because of the short period in which live radish biomass was available. Adding the consumption by crickets, which fed on seeds, increased total consumption to just under the grazing pressure on ragweed.

Percentage similarity in the food-web components of mature ragweed was high between plots in 1967 and between summers (Table 10). A high similarity also existed in the trophic structure of young and mature ragweed in 1968. The food-web components of wild radish, however, were quite different from those of ragweed. These trends were also present when comparing relative similarity in trophic-transfer distribution. The greatest similarity in this respect was between the replicate plots in 1967. Trophic-transfer distribution from radish and ragweed was only slightly more similar than when comparing their food-web components.

Food-web diversity was also nearly equal in the two ragweed studies in 1967 (Table 11). The lowest diversity in both food-web composition and trophic transfer occurred in 1968 at the peak biomass of wild radish. This low diversity resulted from the dominance of aphids and *Lygus*. The greatest food-web diversity occurred at the early stages of ragweed development. The dominance of a few consumer species which occurred at the peak production of both major producers was lacking at this stage of ragweed development. The reduced trophic transfer from young ragweed was thus distributed more evenly among food-web components which were below peak densities at this transition period. As ragweed approached peak biomass the increasing abundance and trophic transfer by plant bugs decreased the diversity (equitability) of food-web composition and trophic transfer.

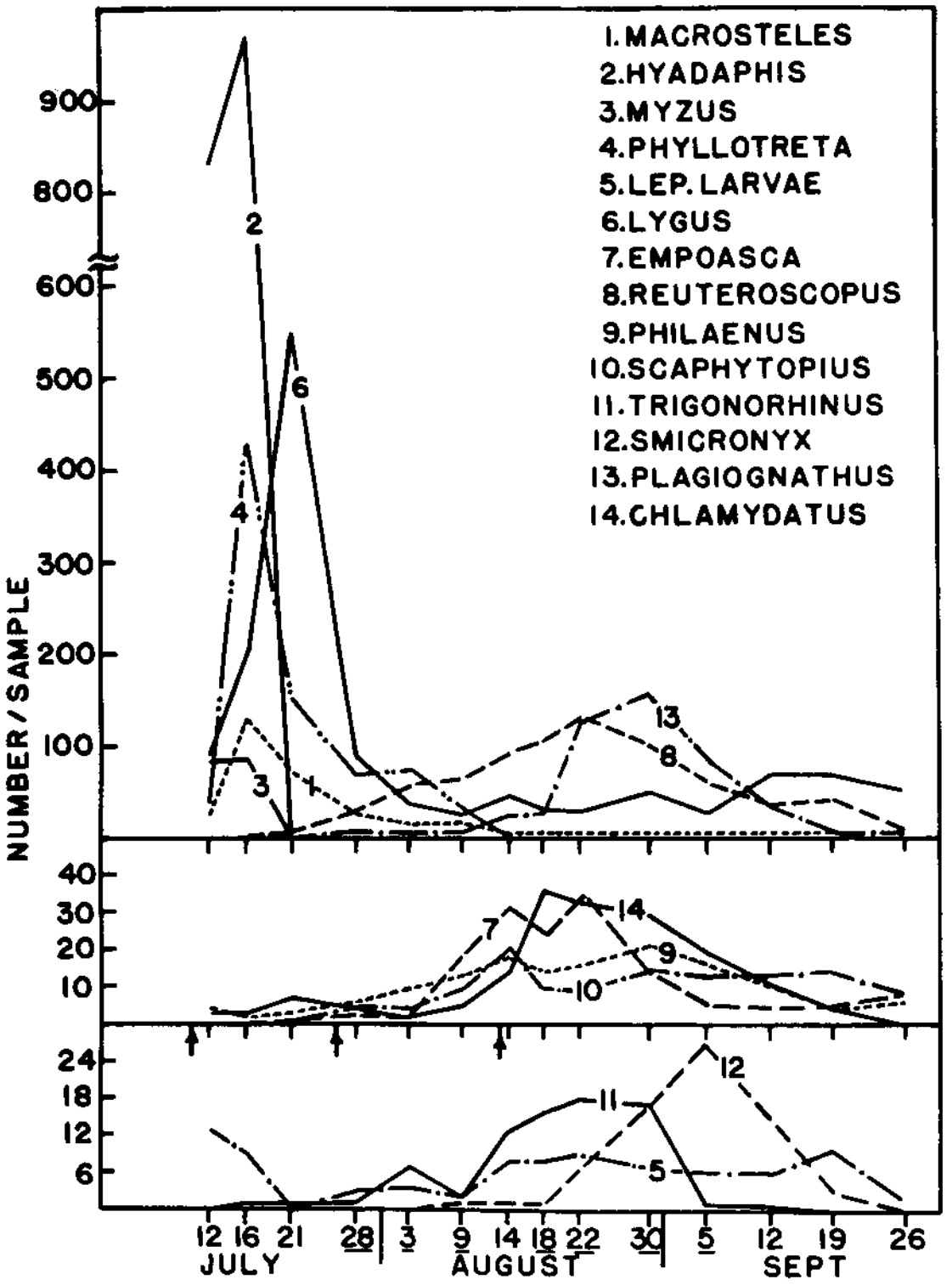

FIG. 11. Relative abundance of major herbivore species over the 1968 summer. Lines for each species connect numbers of individuals collected per tracer sample on the date indicated. Means ($N = 2$) are presented for the dates underlined. Arrows indicate dates when tracer studies were initiated.

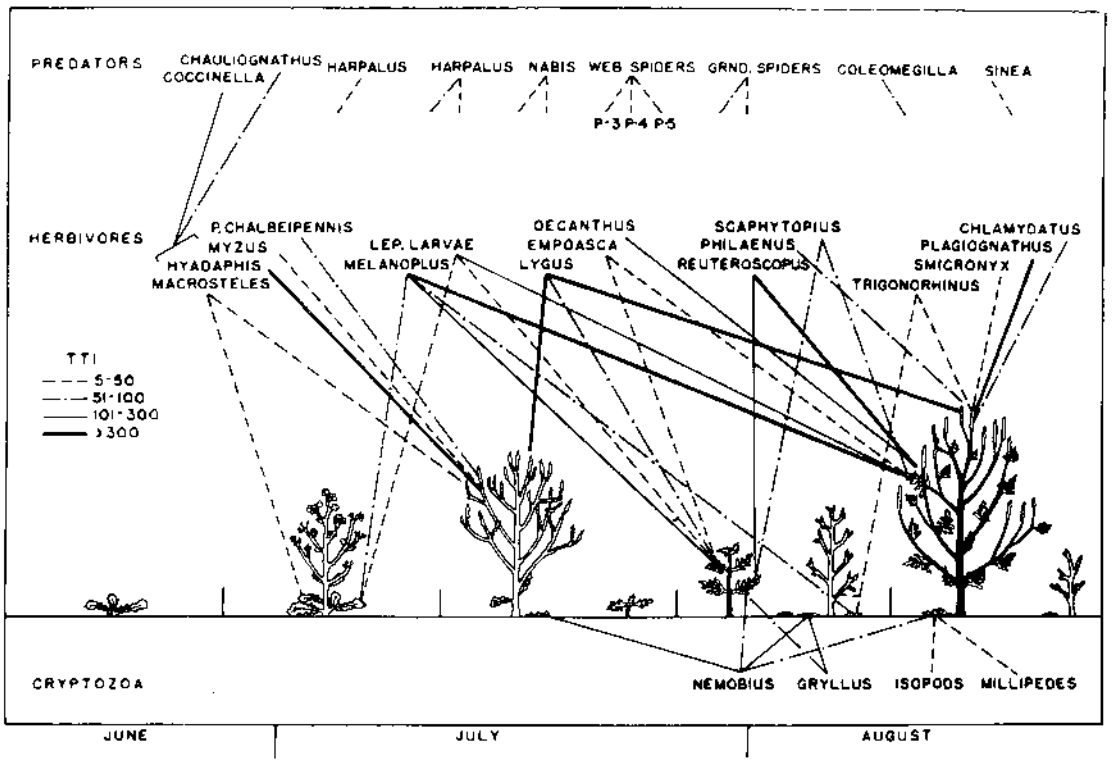

FIG. 12. Trophic relationships during early old-field succession in 1968. Phenological changes in wild radish (light stem) and ragweed (dark stem) have been separated into five major stages. Major herbivore species are included with lines indicating the extent of trophic transfer (TTI) from specific food sources. Lines not connected with specific plant organs indicate nonspecific or undefined feeding locations. Trophic transfer by predators is represented as the total in each study (P–3, P–4, P–5).

DISCUSSION

Successional relationships

Changes in plant phenology, consumer abundance, and trophic structure in the first-year old field are summarized in Fig. 11 and 12. These figures illustrate the interrelationships that exist between host producers and their consumer populations during the 1968 successional process.

Young radish plants constituted the major food-web base during the initial phase of old-field succession. *Lygus*, *Macrosteles*, aphids, and grasshopper nymphs had entered the field by early June and were believed feeding from wild radish before tracer studies were initiated. Consumer abundance and diversity remained low throughout this period.

Succession during July was characterized by rapid phenological changes in plant organ and nutrient availability with subsequent shifts in plant-consumer relationships. The flowering of wild radish in late June and early July brought many nectar-feeding hymenopterans, dipterans, and lepidopterans into the old field for a short duration. These species left the field when flowering terminated. The next shift in successional relationships was triggered by seed development of wild radish. Leaves were drying up by mid-July, and most nutrients were being channeled into seed formation. Aphids consumed internal fluids moving within the stems, and flea beetles utilized the nutrient-rich developing seeds shortly thereafter. *Macrosteles* and *Lygus* were also consuming internal fluids being channeled into seed production. All of these species peaked in abundance at this time (Fig. 12) and then declined in density and ^{32}P activity as seeds and internal fluids became unavailable. Ladybird beetles (*Coccinella*) showed a similar population pulse during July, which was related to the aphid infestation.

Consumer density was greatest in mid-July 1968 because of the abundance of aphids, plant bugs, and flea beetles. Food-web diversity was lowest in the old field at this period. A different situation existed in 1967 when consumer density was low and arthropod diversity was highest during the same stage in the growing season. Low equitability rather than decreased species richness was believed responsible for the low food-web diversity the second summer. Causal mechanisms for the greater abundance of aphids and other species in 1968 are not obvious. Involved, however, may be the greater rainfall in 1968 (Shure 1971) which contributed

to the greater density and biomass of vegetation that had resulted by late June the second summer.

Young ragweed plants and the seeds and litter of wild radish were available for consumption in late July. No major arthropod species peaked in abundance during this transition period (Fig. 12). Radish seeds were the major energy source for grasshoppers, chinch bugs (*Nysius*), and especially crickets. These species were present throughout the summer and were considered generalists in their feeding requirements. No synchronal occurrence of a specialized consumer thus resulted with the addition of radish seeds to the litter.

Trophic relationships changed considerably as ragweed became the dominant producer late in the growing season. Synchronal shifts in plant phenology and consumer responses were also evident for ragweed. Generalized consumers including grasshoppers, ants, lepidopteran larvae, and crickets began utilizing the newly available food source. Other species such as *Reuteroscopus* and the leafhoppers *Scaphytopius* and *Empoasca*, which were nearly absent until late July, increased in abundance in early August (Fig. 12). These species were consuming internal fluids within the rapidly growing ragweed plants prior to flowering.

The appearance of ragweed inflorescences in mid-August afforded a new source of nutrient-rich material for possible consumption. Several specialized species including *Plagiognathus*, *Chlamydatus*, and *Trigonorhinus* peaked in abundance at this time and were believed feeding from the highly labeled inflorescences. *Lygus* had shifted from wild radish and was also consuming fluids from the ragweed pollen. Meadow spittlebugs, however, consumed ragweed fluids throughout the plant's development. The activity-density peaks for this species each coincided with growth pulses of leaves, pollen, and seed development. This fact, plus the relatively low activity density of *Philaenus*, may indicate feeding from xylem fluid, which would experience only limited nutrient pulses. Wiegert (1964) has reported similar feeding behavior in *Philaenus*.

Ragweed was dying back by early September. The abundance and activity density of most ragweed herbivores dropped shortly thereafter. *Lygus* and *Smicronyx*, however, remained abundant and highly labeled in September and were probably consuming nutrients being channeled into seed production. The addition of ragweed leaves and other material as litter provided an energy source for crickets, isopods, millipedes, and other detrital food-web components throughout the fall period.

The diversity and relative importance of predators were reduced during the latter part of the 1968 growing season. This was partly due to the near absence of the ladybird beetle *Coleomegilla* which was a major predator in 1967. The failure of *Coleomegilla* to reestablish in 1968 may be related to the aphid infestation. The large number of *Coccinella* present during the aphid infestation may have prevented the subsequent buildup of *Coleomegilla* through interspecific interactions. Other changes in predator-prey relations in 1968 may have resulted from the instability created by the aphid infestation.

TABLE 12. Total number of species and individuals sampled in each tracer study and the percentage of those total individuals that were from labeled species groups and thus food-web components

Plot	Total number of species[a]	Number of individuals	Individuals from labeled species	Percentage food-web components
P-1	109	3,131	2,836	90.6
1967				
P-2	93	2,804	2,701	96.3
P-3	117	5,537	5,231	94.5
1968 P-4	114	3,660	3,059	83.6
P-5	113	2,974	2,771	93.2

[a]Includes only approximate estimation of hymenopteran, arachnid, and lepidopteran larvae species.

Significance of feeding relationships

Wild radish and ragweed were the major food-web bases during initial succession in the old-field ecosystem (Table 12). In 1968, between 40 and 50 arthropod species were labeled in each study out of the approximately 115 species sampled. The labeled species included all major arthropods in terms of numbers and biomass. Over 90% of all arthropods sampled in each study except P-4 (83%) were from labeled species groups and thus food-web components. The arthropod dependence on the two dominant producers is further supported by the synchronal occurrence of population increases in apparent response to producer changes. Consumer abundances were related either to shifts in producer species or phenological changes in availability of plant components. All major herbivores thus peaked in abundance when their specific food source became available.

Much of the trophic transfer from wild radish and ragweed was by consumers with specialized feeding habits. The nutrient-rich reproductive structures of both plant dominants served as major sites of trophic transfer for these specialized consumers. Specialists entered the old field from surrounding areas. Those species with host plants present in the field (i.e., aphids, plant bugs) increased rapidly in density through their high reproductive potential. Peak population densities of these specialists resulted when nutrients were being channeled into their specific food sources. The significantly higher activity density of these reproductive organs (Shure

and Pearson 1969) indicates this feeding is resulting when and where the greatest nutrient source is readily available. The synchronal occurrence of population peaks and nutrient (energy) pulses in host-plant organs thus appears to maximize the energy utilization by these consumers while minimizing interspecific competition for sites of trophic transfer.

In some studies (Bray 1961, 1964) estimates of primary consumption in forests have been based on percentage of leaf foliage removed by chewing. Most feeding from both wild radish and ragweed, however, was by sucking forms such as plant bugs and aphids which consume internal plant juices. Little evidence of feeding was therefore evident from either major producer, in contrast to species such as *Acalypha* and *Polygonum* which had considerable foliar damage. The tracer studies were thus critical in assessing the role of wild radish and ragweed as food-web bases in the old-field community. Estimates of primary consumption based solely on percentage of foliage removed would be highly misleading in similar situations.

The influence of sucking insects on primary production in different habitats can be quite extensive. Adams and Drew (1969) reported increased yields of 47% for oats and 32% for barley when aphid-infested areas were treated with malathion. Weaver and Hibbs (1952) found that spittlebug infestations reduced alfalfa, red clover, and timothy yields from 13% to 45% below controls, whereas Wiegert (1964) found that spittlebug feeding on plant amino acids decreased the potential photosynthetic fixation of energy by five times the total energy ingested by the insects. Sucking forms can thus have greater effects on plant growth per calorie removed than herbivores chewing on previously developed tissue. Although total primary consumption was not estimated in this study, it seems likely that the influence of primary consumption by sucking forms was quite significant. The consumption of internal fluids being channeled into successive stages of plant development may have exerted an influence similar to that described by Wiegert. The extensive feeding on reproductive tissues of ragweed and radish may have a definite effect on the future germination of these annual species.

Trophic-transfer methodology

Trophic separation solely from the shape of ^{32}P uptake curves of consumer species (Odum and Kuenzler 1963, Wiegert et al. 1967) was not possible for certain species in the old field studied. This result was due to the rapid successional changes in host-plant or plant-component availability with related shifts in consumer populations. Specific trophic positions of herbivore species were determined only by correlating activity-density changes in different plant components with the uptake curves, abundances, and feeding adaptations of consumer species (Shure 1970).

In past studies the activity density of leaf material has generally been used in determining concentration factors and trophic-transfer indices (Wiegert et al. 1967) for consumer species. Herbivores, feeding on plant components other than leaves, may obtain different tracer concentrations, if the producer is differentially labeled. This occurred in the present study where insects utilizing reproductive structures were obtaining significantly higher levels of ^{32}P than leaf consumers. Leaf and pollen-tissue activity density were averaged in obtaining concentration factors in this study since estimates of relative utilization of each plant component by different consumers were lacking. Some errors in trophic-transfer estimation probably resulted in the case of specialized feeders. In the future, however, appropriate plant activity density should be employed in determining concentration factors and plant consumption by consumer species (Shure and Pearson 1969).

Quadrat size presents some limitations in the estimation of trophic transfer by consumer species. Large or motile species may be only temporary residents in the 100-m^2 quadrats, thus preventing accurate estimation of their consumption. Removal of arthropods through sampling may also induce replacement by immigration from surrounding areas. Replacement of unlabeled individuals can decrease the uptake curves and concentration factors of food-web components. Herb-stratum arthropod density in the old field was 147.7 per m^2 on August 22, 1967. Removal of herb-stratum arthropods from plots 1 and 2 averaged 467 per sample ($N = 4$) from August 19 to 27. Therefore, only about 3.2% of the total population was removed by each sample, which should also apply to the 1968 studies. This fraction is less than the 7–12% reported by Marples (1966). Induced immigration was thus believed to be relatively unimportant in the activity-density changes that resulted.

The similarity of results in the two ragweed studies in 1967 attests to the repeatability and accuracy of tracer techniques for trophic-transfer analysis. Differences can result, however, when considering temporal aspects of trophic transfer. Changes in grasshopper density and predator-prey relations were the major differences in the ragweed food web over two successive summers. Trophic relationships were also somewhat different at different stages of ragweed development. These differences were related mainly to availability of plant reproductive structures. Paris and Sikora (1965, 1967) and Marples (1966), using ^{32}P as a tracer, have also reported some temporal differences in trophic re-

lationships. Temporal aspects of food-web structure should thus be considered in future studies particularly where rapid changes in plant phenology are present.

Standard sampling techniques enabled comparisons of grazing pressure, trophic-transfer distribution, and food-web diversity in separate trophic-transfer experiments. The estimation of trophic-transfer indices must be similar, however, if grazing pressure and diversity of energy pathways are to be compared in different geographical areas, at different times, and for different investigators. Mean concentration factors are comparable providing appropriate plant activity densities are utilized. The population-biomass component of trophic-transfer indices, however, is contingent on sampling methodology. Estimation of the approximate percentage of the population removed in each study would enable appropriate corrections for different sampling pressures. The future determination of trophic-transfer indices is more meaningful if absolute comparisons are possible between different studies.

Diversity indices obtained from trophic-transfer data provide a realistic measure of the functional trophic interactions within communities. Most diversity indices, based on the number of species and individuals in communities, only permit an estimation of potential trophic interactions. Wiegert et al. (1967), however, found that considerable differences existed in the number of trophic links and relative usage of the two dominant producers in a South Carolina old-field ecosystem. The use of tracers enabled this unexpected finding, which would have gone unnoticed if conventional diversity measures were used. In the present research the use of information theory to estimate diversity of food-web components and trophic-transfer pathways permitted a quantitative expression of the trophic interactions emanating from two major producers.

Tracer techniques enabled the isolation of specific trophic relationships in this study as well as providing an estimate of the extent of feeding by food-web components. The assumption inherent in these estimates is that ^{32}P uptake is equivalent to food consumption. The actual similarity in these parameters has yet to be fully determined. Phosphorus-32 does translocate well within producers, being available for consumption in accord with expected nutrient levels. If ^{32}P uptake is proportional to food consumption and if bio-elimination rates of beta emitters are obtained for major consumers, then it should be possible to use ^{32}P to obtain tracer estimates of energy flow as well as food-web relationships in natural ecosystems.

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