

ENERGETICS OF A SUBURBAN LAWN ECOSYSTEM¹

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Abstract. A study of the energetics of a suburban lawn was conducted in 1972-73 in Walnut Creek, California USA. Several major components of the annual primary and secondary production were measured, including man's role as manager and experimenter in the system.

The system was extremely productive with net productivity of 1,020 g/m² per yr compared to cornfields with productivity of 1,066 g/m² per yr and exceeding tall grass prairie values of around 1,000 g/m² per yr. Homopterans, with maximal values of 19 mg/m² were plentiful; other typical grassland species, like Araneida, were scarce, representing only 1% by weight of the total invertebrate population. Food utilization per unit area by suburban birds considerably exceeded natural grassland bird utilization (46 kcal/m² per yr vs. 1.01-2.33 kcal/m² per yr); lawns are ideal foraging sites for open area adapted, flock-feeding species.

Man was the dominant consumer in the community, accounting for 10% of the herbivory and nearly 100% of the scavenging. Energy inputs (labor, gasoline, fertilizer, etc.) amounted to 578 kcal/m² per yr, equalling or exceeding corn production for a comparable net productivity, but not necessarily utilitarian return.

Key words: California; energetics, lawn; grassland management; lawn ecosystem, urban and suburban; productivity, lawns.

INTRODUCTION

An increasing percentage of terrestrial sites throughout the United States are being converted by man into lawns and turfs, i.e., grasslands of uniform height and of constant species makeup. No city, suburb, or rural community is devoid of these grasslands, and an estimated 16.5 million acres exist nationally (Hawkes 1969, Nutter and Watson 1969). A science and industry of turf management has developed, one result of which is the nearly uniform species composition of lawns throughout much of the United States (Schery 1961, Hanson and Juska 1969); most lawns are selected varieties of blue grasses and fescues. Exceptions occur in the extremely Southern and Gulf states, parts of California, and the Southwest.

A characteristic complement of broadleaf weeds, such as *Taraxacum*, *Plantago*, and *Trifolium* (Beale 1931, Muenscher 1955, Schery 1961, King 1966), and of invertebrates, especially Isopoda, Aphididae, Cicadellidae, and Chloropidae (Bohart 1947, Kelsheimer and Kerr 1957, Schread 1964, Hanson and Juska 1969), are found associated with lawns. There is extensive literature concerning virtually every aspect of lawns relevant to management (Beale 1931, Bohart 1947, Anonymous 1960, Schery 1961, Barnard 1964, Hanson and Juska 1969, Youngner and McKell 1972), but detailed information concerning

the community ecology of lawns is virtually non-existent.

This study had two primary objectives: (1) to measure several major components of the annual primary and secondary production of a lawn ecosystem, and (2) include man's activities, as manager and experimenter, into the energy flow equation. By calculating all measurements in kilocalorie per square meter per year the diverse roles of man, birds, grasses, and insects could be quantitatively compared within the lawn system and between other grassland and man-managed systems.

STUDY AREA

The study was conducted from September 1972 through September 1973 on a lawn planted in 1964 in suburban Walnut Creek, Contra Costa County, California. Total area of the lawn was \approx 110 m² and was bordered on two sides by concrete walkways, on a third side by a vegetable garden and on the fourth side by concrete blocks. The lawn was a typical bluegrass-fescue turf containing a mix of *Poa pratensis* L. (Kentucky bluegrass), *Festuca rubra* L. (creeping red fescue), and *Festuca rubra* var. *commutata* Gand. (Chewings fescue). Total weed cover never exceeded 6.5%. The most common weed species were the grasses *Digitaria sanguinalis* (L.) Scop. (crabgrass) and *Holcus mollis* L. (German velvetgrass) and the Broadleaf weeds *Oxalis corniculata* L. (oxalis), *Picris echioides* L. (bristly ox-tongue), *Taraxacum officinale* Weber (dandelion), *Sonchus asper* L. (thistle), *Euphorbia maculata* L. (spotted spurge), *Anagallis arvensis* L. (scarlet pimpernel), *Dichondra donnelliana* Tharp & Johnst. (dichondra),

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Medicago polymorpha L. (California bur clover), and *Baccharis pilularis* (coyote bush).

An American elm (*Ulmus americana* L.), a palm-like tree (*Cordyline australis* Hook), and a Chinese toyon (*Photinia serrulata* "Nova" Sieb. & Zucc.) were present on the lawn. The trees intercepted solar radiation, dropped litter onto the lawn, and absorbed nutrients and H₂O. The litter was removed by raking and mowing; light, H₂O, and nutrients were assumed not to be limiting factors for the lawn.

The climate of this part of California is typically cool and wet in winter, hot and dry in summer. In 1972–1973 rainfall was considerably above normal, and both winter and summer temperatures were well below average (the winter of 1972–73 included the longest cold spell in this area in over 100 yr).

METHODS

Vegetation sampling

Plant biomass was determined after every mowing. A gasoline powered rotary lawn mower was used to cut the grass, leaving a 4-cm high stubble of grass. The grass was cut weekly or biweekly (except during winter when it was mowed once a month). Prior to mowing, all litter (including tree litter and old grass clippings) was removed by raking and weighed. After the vegetation was harvested, new clippings were immediately weighed (fresh weight), and four samples extracted by randomly reaching into the grass bag and removing a handful of clippings. The new clippings were again weighed to determine amount removed. Each of the four samples was sorted into three categories: living material (grass and weeds), dead material (grass and weeds), and miscellaneous material (tree leaves, twigs, animal hairs, etc.). The samples were oven-dried at 98°C for 24 h, and were weighed to the nearest 0.1 mg. Besides mowing, the lawn was fertilized twice, once with a commercial all-purpose brand (Best's Super Six®) that also contained herbicides and insecticides, once with manure.

Random core samples were taken six times throughout the year to determine root biomass and aboveground biomass left after mowing (Dahlman and Kucera 1965, Heady, *personal communication*). Cores were 5.2-cm diam. and 7.6 cm long and contained nearly 100% of turf roots. Four core samples were taken immediately following mowing. All aboveground materials were removed from the core, sorted, and processed as described for the grass samples above. The cores were washed and roots separated using the technique described by Williams and Baker (1957). The roots were then dried at 98°C for 24 h, weighed to the nearest 0.1 mg, ashed at 600°C for 6 h in a muffle furnace, and again weighed to the nearest 0.1 mg. Cores were ashed in order to deter-

mine the amount of dry weight attributable to soil clinging to root hairs.

Invertebrate sampling

Invertebrates were initially sampled five times per week, later twice per week, for 1 yr using a modified quick trap method (Turnbull and Nicholls 1966). The 0.25 m² trap was suspended on a tripod and released at a predetermined time with a rip cord. The trap was placed randomly in the site and was set up at least 24 h before release. Sample days were determined by a random selection of dates. Sample times were chosen arbitrarily to represent the entire 24-h day, but the majority of samples were taken during diurnal hours. All collections were made with a modified commercial electric broom (vacuum cleaner). Samples were run through a Berlese funnel and spot-checked by hand. Insects were identified to family or superfamily, other invertebrates to order or phylum. Samples were dried at 98°C for 24 h and weighed to the nearest 0.01 mg.

Vertebrate sampling

Observations of all vertebrates (primarily birds) on the lawn were made from a blind bimonthly for the duration of the study. Prior to each month, observation days were chosen at random. Observations were made from 30 min before sunrise until 30 min after sunset. During this period, the time and nature of every interaction was recorded. Bird weights were estimated using data from the literature or museum records. No evidence of rodent (other than squirrel) or mole activity was seen (baited museum live traps were used).

Management records

All management and experimenter input into the lawn was recorded. Dates, time (measured to nearest ½ minute), and type of activity (lawn mowing, watering, etc.) of all human input were noted. All managerially introduced energy sources were measured and recorded. The total amount of irrigation and fertilizer added to the lawn was recorded. Management and experimenter induced energy drains (e.g., clippings and leaves removed) were measured separately.

Respiration and caloric values

All respiration and caloric values used in this study were based on formulas or values found in the literature.

Daily respiration of vegetation was assumed to be 33% of gross production (Gaastra 1963, Army and Greer 1967, Loomis et al. 1967). A value of 4,350 cal/g (dry weight) was used for live aerial parts of grasses and forbs; 4,257 cal/g (dry weight) for

dead aerial parts; and 4,394 cal/g (dry weight) for roots (Wiegert and Evans 1964). Miscellaneous litter (*Ulmus*, *Cordyline*, and *Photina* leaves, stems, and fruits), was given a value of 4,298 cal/g (dry weight) (Golley 1960).

As a generalization, 79% of all energy assimilated by invertebrates is metabolized; for vertebrates, the value is 98% (Golley 1968). Arthropod metabolism was estimated using Van Hook's (1971) formula. This equation corrects metabolism for temperature and body size, approximating field conditions. The total caloric value of the oxygen consumed was calculated by multiplying microliters O_2 per milligram per hour by the thermal equivalent of O_2 (0.0048 cal/ μ l), assuming a respiratory quotient of 0.82 as suggested by Brody (1964) and Van Hook (1971). Mollusk respiration was assumed to be 86% of production (Teal 1962).

Vertebrate metabolism was estimated using data from Consolazio et al. (1963), Brody (1964), Ludwick et al. (1969), and Kendeigh (1970).

Net primary production was calculated using a formula derived from discussions by Milner and Hughes (1968) (units are kilocalorie per square meter per year).

$$NP = B_i(A) + B_{\max(s)}\theta_s + B_{\max(r)}\theta_r, \quad (1)$$

where $B_i(A)$ = standing crop at the i th sampling period (all aerial plant parts above 4 cm), $B_{\max(s)}$ = maximum standing crop of stubble, θ_s = stubble turnover rate, $B_{\max(r)}$ = maximum standing crop of roots, and θ_r = root turnover rate. Turnover rate was calculated from the ratio of annual growth to total stubble (or root) mass (Dahlman and Kucera 1965). Gross production was calculated from the following equation (Woodwell and Whittaker 1968) (units are kilocalorie per square meter per year)

$$GP = NP + R, \quad (2)$$

where GP = gross production, NP = net primary production, and R = respiration.

Secondary production for invertebrates was assumed to be 21% of assimilation. Vertebrate secondary production was calculated using Wiens' (1973) assimilation and production estimates for grassland passerines, and Ludwick et al. (1969) figures for squirrels. The assumption was made that the net energy intake for other vertebrates (cat, dog, and human) was equal to zero. Production at the consumer level was calculated using the following equation (Petrusewicz and Macfadyen 1970) (units are kilocalorie per square meter per year)

$$P = A - R, \quad (3)$$

where P = net secondary production, A = assimilation, and R = respiration.

RESULTS AND DISCUSSION

Vegetation component

The maximum standing crop occurred in August (1,809.7 g/m² oven-dry weight). Live biomass was greater than dead biomass throughout the year due to constant removal of older aerial parts. This is in contrast to natural grasslands where the dead standing crop normally equals or exceeds that of the living crop over an entire year (Golley 1960, Wiegert and Evans 1964, Van Hook 1971). When live standing crop was greatest, dead standing crop was least and conversely. Aboveground live biomass (above 4 cm) ranged from a low of 1.3 g/m² for the 77-day period, 3 December 1972 through 18 February 1973, to a high of 53.1 g/m² for the 77-day period 18 March 1973 through 3 June 1973. Monthly standing dead biomass was consistently < 0.3 g/m², and except for September 1972 and July 1973 was below 0.2 g/m² (above 4 cm).

Stubble biomass was highest in the early spring at 114.8 g/m² and lowest in the early fall at 59.4 g/m². Turnover rate was slightly greater than twice yearly ($\theta_s = 0.49$). Total stubble mass was calculated to be 237.5 g/m² per year.

Belowground biomass showed a maximum in the summer with 1,609.8 g/m² root mass and a minimum in the spring with 911.3 g/m². This result agrees with the timing of maximum and minimum found by Dahlman and Kucera (1965) for native prairie. Turnover time was roughly once every 2.4 yr, $\theta_r = 0.42$. Dahlman and Kucera (1965) found a root turnover value of 3.85 for tall prairie grass, a turnover time of two-thirds the time found in this study. Total root mass was calculated to be 676.1 g/m² per yr. Stubble and root data are summarized in Table 1.

Annual net primary production equaled slightly more than 1,020 g/m² or 4,467.5 kcal/m². This may be compared with maximal values for grasslands of around 1,000 g/m² and minimal values in the range of 200–300 g/m² for desert grasslands (Woodwell and Whittaker 1968). Van Hook (1971) recorded 3,234.7 kcal/m² (or roughly, 676 g/m²), while Wiegert and Evans (1964) found values of 1,959–6,202 kcal/m² for old fields in Michigan. Tropical grasslands range from 1,500–3,000 g/m² per year (Woodwell and Whittaker 1968), and cornfields have been measured to have an annual net primary production of 1,066 g/m² (Ovington et al. 1963). Rangelands in general show decreased productivity with clipping and removal of mulch (Biswell and Weaver 1933, Heady 1956) since most of the grasses maintain high growing points; an exception being a study reported by Penfound (1964) that showed that clipping and removal of mulch increased the biomass in both prairie and cropland during the growing season in Oklahoma. Turfgrasses, in contrast, have

TABLE 1. Summary of stubble and root data. Total mass calculated using the technique described by Dahlman and Kucera (1965)

	Minimum (g/m ²)	Date	Maximum (g/m ²)	Date	Net increment	Turnover rate	Net productivity g/m ² per yr
Stubble	59.4	24 Sep.	114.8	18 Feb.	55.4	0.49	237.5
Root	675.9	18 Mar.	1,609.8	11 Aug.	933.9	0.42	676.1

been selected to possess thick heavy crowns close to the soil and with extensive rhizomes or stolons. *Poa pratensis* and *Festuca rubra* concentrate a very large percentage of their total weight in the zone extending 5 cm above and 5 cm below the soil surface. Mowing such plants removes relatively little weight, at 2 in roughly 3% (Madison 1971). The net result of clipping turfgrass is to concentrate energies solely into increased vegetative production (as opposed to also reproductive production) and to produce a mat of dense, numerous, short, rapid growing plants (Madison 1971).

Litter weight ranged from a low of 160 g/m² in May to a high of nearly 43,000 g/m² in November and December. The bulk of the litter was *Ulmus* leaves and stems, but a nearly constant quantity of *Photinia* and *Cordyline* leaves were present throughout the year. During the spring and summer months, these two evergreen trees contributed the greatest percentage of the litter biomass. An estimated mean dry weight of 45 g/m² of litter remained after every raking and mowing. Besides raking and mowing, quick trap sampling was also a minor source of litter removal, an estimated 337 g were removed during the study period. In all, > 98% of biomass was immediately removed from the community by man.

Invertebrates

Common herbivores belonged to the families Aphididae, Cicadellidae, Chironomidae, and Chloropidae, and also the order Thysanoptera and the class Isopoda. Common scavengers were Collembola, Dermaptera, Mollusca (snails, primarily), oribatid mites, and the dipteran families Sciaridae, Psychodidae, and Sphaeroceridae. Omnivorous Formicidae and the carnivorous Staphylinidae, Braconidae, Chalcidoidea, and Mesostigmata were also common. Of note was the complementary seasonal distribution of the two common groups of homopterans—Aphididae and Cicadellidae, aphids appearing in April, leafhoppers in June and July. The number of Mollusca varied seasonally while Isopoda numbers were constant throughout the year. Predaceous Chalcidoidea showed a very regular population peak and crash with a 4-mo period. The correlation between weather and invertebrate densities is striking. Every population showed a reduction in abundance during the

unusual cold spell which occurred in December 1972. Most populations also showed a significant decrease during June and July, the two hottest months in 1973, the most notable exception being Cicadellidae which peaked during these months. The Cicadellidae peak coincided with the summer peak in standing dead vegetation, the Aphididae peak matches almost exactly the peak in live grass production in April. The latter correspondence is understandable, but the former may be fortuitous. Decline in Aphididae may have been a more important factor than abundance of dead vegetation in allowing the increase in numbers of Cicadellidae.

Spider populations (Araneida) were relatively constant at a low level. Population densities were much lower than those reported from other grasslands. Turnbull (1966) estimated that spiders comprised 30% of the total arthropod biomass in an overgrazed pasture in Canada. Menhinick (1967) estimated a 13% figure for a *Serica lespedeza* community and Van Hook (1971) arrived at a figure of 15% of total arthropod biomass represented by spiders. In the present study, only \approx 1% of the total arthropod biomass was accounted for by spiders.

Menhinick (1967) found a maximum combined homoptera-hemiptera biomass of 22 mg/m² in a *Serica lespedeza* community. Similarly, Van Hook (1971) found a maximum value of 22 mg/m² in a Tennessee *Festuca/Andropogon* grassland. Wiegert (1964) reported a maximum biomass of 24 mg/m² for the meadow spittle bug *Philaenus spumarius* L. in a Michigan old field. The maximum combined homoptera-hemiptera value in the present study was 19 mg/m². The total homoptera-hemiptera biomass accounted for roughly 2.5% of the total arthropod biomass.

Isopods comprised > 62% of the total arthropod biomass. Paris and Pitelka (1962) found that the isopod *Armadillidium vulgare* (Latr.) was the most abundant macroscopic invertebrate encountered in their 3-yr study of California coastal grasslands. They recorded densities of \approx 500 individuals/m², compared to a maximum of only 40 individuals/m² in this study. Both densities were recorded during the wet, winter months when isopods are normally active at the surface. At other times of the year, a large

percentage of the population is subterranean and therefore impervious to standard sampling techniques.

Van Hook (1971) reports annual invertebrate secondary production from a Tennessee *Festuca-Andropogon* grassland as follows: herbivores 29.09, omnivores 2.96, predators 2.26 (all kcal/m²). Odum et al. (1962) found an annual production figure of 10 kcal/m² for herbivorous orthoptera (the major invertebrate consumers) in a Georgia old field. Odum et al. (1962) extrapolated the total invertebrate consumption at the primary consumer level to be between 75 and 200 kcal/m² per yr. The present study yielded: herbivores—14.4, scavengers 6.0, omnivores < 0.1, and carnivores 0.4 (all kcal/m² per yr). Thus, the estimated production of herbivores in the present study is considerably lower than Van Hook's (1971) and even further below Odum et al.'s (1962) extrapolated values. The comparison of productivity of invertebrate carnivores in this as opposed to earlier studies reveals an even more striking difference. Van Hook's figure is an order of magnitude greater than the figures in the present study.

The 0.05 herbivore utilization efficiencies (Kozlovsky 1968) from the present study generally agree with the 0.01–0.09 values in the literature (Odum et al. 1962, Wiegert 1964, Kozlovsky 1968, Van Hook 1971). Invertebrate predator utilization efficiencies are low (0.09 compared to 0.12–0.33) indicating a small invertebrate predator population. This is consistent with the findings summarized above. The agreement of the herbivore efficiency figures is surprising in light of the management practiced on this lawn. This management included the regular removal of a significant percentage of the potential food resource, and the addition of a pesticide (active ingredients included Carbaryl and methanearsonate). Over 8 kg of poison was applied, or 70.1 g/m². Frequent mowing and trampling were also a constant threat to invertebrate survival. The above practices, although considered minimally significant to the grasses, were potentially a major factor affecting the survival of lawn invertebrates.

In general, the dominant lawn invertebrates fall into one of two categories: (1) very small and mobile organisms which live near the tops of grass blades and avoid danger by rapid escape, or (2) organisms which live in the mulch layer of the soil where they avoid the lawn mower, and where the cushioning effect of the thatch minimizes mortality due to trampling. Lawns have developed a distinctive fauna which includes many common grassland species, but because of unusual selective pressures, other grassland species are absent. Management disturbances appear to be more detrimental to secondary consumers than to primary consumers. It is known, for example, that carnivores are much more

TABLE 2. Calculated invertebrate respiration, production, and assimilation by trophic level (in kcal/m² per year)

Trophic level	Respiration	Production	Assimilation
Herbivores	54.1	14.4	68.5
Scavengers:			
Arthropods	20.8	5.5	26.3
Mollusks	2.3	0.4	2.7
Omnivores	0.1	0.0	0.2
Carnivores	1.3	0.4	1.7
Total	78.6	20.7	99.4

susceptible to nonselective pesticides than are herbivores (Bartlett 1964, Newson 1967).

The pesticide was applied as part of the fertilizer on 18 March, and is assumed to have been slowly released from inert delivery pellets. There is no clear evidence that the pesticide application had any detrimental effect on the primarily aboveground invertebrate population I sampled. The pesticide was intended for subterranean insect forms, though many of these subterranean insects are larvae and eventually emerge aboveground as adults. Since I had no control lawn, true impact was hard to access. Interestingly, Shure (1971) found that herb-stratum arthropod populations were similar on insecticide treated and untreated plots.

Table 2 summarizes invertebrate respiration, production, and assimilation estimates. Experimenter-induced invertebrate consumption (via quick trap and vacuum cleaner) was 0.3 kcal/m² over the year, 97% from the herbivore and scavenger trophic levels.

Vertebrates

All vertebrates observed were considered non-residents, owing to the small size of the lawn relative to typical vertebrate home ranges. With the exception of the Scrub Jay (*Aphelocoma coerulescens* Swarth), no species utilized the lawn continuously throughout the year. Even the Scrub Jays were definitely seasonal, showing a peak of activity in the spring. The absence of other birds during this period was at least partly a result of the aggressive nature of a nearby pair of nesting jays.

Summer months were dominated by mixed flocks of the Brewer's Blackbird, *Euphagus cyanocephalus* (Wagler), Red-winged Blackbird, *Agelaius phoeniceus* (L.), Starling, *Sturnus vulgaris* L. and House Sparrows (*Passer domesticus* [L.]). Flocks varying from three or four birds to over 30 would descend upon the lawn, feeding for periods ranging from a few minutes to 45 min. Brewer's Blackbirds far exceeded all other avian visitors in total time on the lawn, Red-winged Blackbirds logged the second highest amount of time, but their total was an order of

TABLE 3. Management inputs into the lawn system, summarized as kcal/yr

Task	Total time	Energy factor	kcal/yr
Raking (labor)	7 h 26 min	0.686 kcal/kg per 10 min ^a	1,988.7
Irrigation			
Labor ♂	3 h 50 min	0.356 kcal/kg per 10 min ^a	532.2
Labor ♀	2 h 20 min	0.356 kcal/kg per 10 min ^a	249.2
H ₂ O (source-lawn)	340.82 m ³	413.1 kcal/m ^{3b}	140,792.7
Fertilizing			
Labor ♂	27.5 min	0.564 kcal/kg per 10 min ^a	100.8
Manure	10.7 kg	79.70 kcal/lb ^c	1,800.9
Chemical fertilizer ^o	3.63 kg	1,382.15 kcal/lb ^d	11,057.2
Lawn mowing			
Labor ♂	4 h 58 min	0.979 kcal/kg per 10 min ^a	1,983.9
Gasoline	4.73 liters	36,225 kcal/gal ^d	45,281.3
Reseeding			
Labor ♂	6.5 min	0.564 kcal/kg per 10 min ^a	23.8
Seed	326.6 g	1,800 kcal/lb ^d	1,293.7
Miscellaneous labor	16 min	0.686 kcal/kg per min ^a	71.3
Total			205,175.7

^a Consolazio et al. (1963).

^b Hugo B. Fischer (*personal communication*).

^c Extrapolated from Pimentel et al. (1973).

^d Pimentel et al. (1973).

^o Best's Super Six Fertilizer.[®]

magnitude below that of the Brewer's Blackbirds. Mammals also showed seasonal densities, with the majority of activity occurring during the spring and summer months.

Avian daily energy budget in kilocalories per bird-day (a bird-day represents a typical 24-h period, activities vary according to temperature and breeding conditions) was calculated using Kendeigh's Formula 2, using the values $a = 0.2259$ and $b = 0.6210$ for passerines during the warm nonbreeding season; $a = 0.2168$ and $b = 0.6210$ for passerines during the warm breeding and molting season; and $a = 0.2545$ and $b = 0.7545$ for nonpasserines during the warm breeding and molting season (Charles Kendeigh, *unpublished data*). The number of hours/day spent foraging was estimated from time and energy budget studies of Brewer's Blackbird, male Dickcissels, Lapland Longspurs, and male Marsh Wrens (Verbeek 1964, Verner 1965, Schartz and Zimmerman 1971, Custer and Pitelka 1972, T. W. Custer, *personal communication*). (No effort was made to correct for energy needs of fledglings; estimates used are, therefore, underestimates.) Generally, slightly more than 4 h of each 24-h day was spent foraging. To compute avian energy flow, the daily energy budget data was combined with avian interaction time data and with the findings of Wiens (1973). The latter author calculated that assimilation equals 70% of ingestion (egestion equals 30% of ingestion) in grassland carnivores and 69% of ingestion in omnivores (herbivore values were assumed equal to omnivore values), and that respiration equals roughly 99% of assimilation. Avian as-

similation for the year totaled 32.5 kcal/m², while consumption equaled 46.6 kcal/m². Bird invertebrate consumption comprised 40 kcal/m², or nearly 2× the computed available invertebrates. This apparent discrepancy probably results from the failure of the invertebrate sampling technique used to sample adequately the subterranean organisms eaten by Brewer's Blackbirds and Red-winged Blackbirds during the months of June, July, and August (i.e., larval vs. adult lepidoptera).

Observations from the blind, supported by data from Bohart (1947) and Orians and Horn (1969), indicate that lepidopteran larvae would have been the main food items for these two blackbirds during the summer months (Brewer's and Red-winged Blackbirds accounted for 80% of all the invertebrates consumed by birds).

The microlepidopterans present all would have concave survivorship curves in which mortality is very high during young stages; only 2%–5% of large microlepidopteran larvae survive to adults (Morris and Miller 1954, Varley et al. 1974). Thus, my data on adults would indicate that the standing crop of large lepidopterous larvae during the months of June, July, and August would have been more than enough (roughly 50 kcal/m²) to support all of the blackbird consumption during these months.

All of the energy consumed by the bird population was either respired, excreted, or converted to new bird tissue (production). All production was considered exported, since no birds nested or died on the lawn. A portion of avian consumption (roughly 30%) was egested on the lawn and is con-

sidered in Table 3 along with other miscellaneous energy inputs such as dog and squirrel excreta and walnuts cached by Scrub Jays and squirrels.

Avian energy demand is greatest during the late spring and summer, as also has been demonstrated for several natural grassland sites (Wiens 1973). Annual estimated energy intake on the lawn was very high, 46.6 kcal/m², compared to the range of 1.01–2.33 kcal/m² for the five grassland populations cited by Wiens. At least two factors might account for the discrepancy. Wiens used sample plots of 10.6 ha with a 150 m buffer zone of similar vegetation around each plot. This would be a sample area > 3,500 times greater than the lawn used in this study. In a natural grassland, a bird can forage in virtually the entire area. In contrast, prime foraging areas in a suburban area may be only a small percentage of the total (the remainder being areas of very low productivity such as houses, streets, sidewalks, driveways, etc.), forcing birds to feed in an area representing a small percentage of their total range. Assuming the prime urban foraging area to be only 15% of the total area, the average energy consumption by birds in this study would be ≈ 7 kcal/m², which is still three to seven times the intensity of consumption in natural grasslands.

Another important consideration in assessing the high utilization per square meter of lawn relative to natural grassland is the feeding behavior of the birds. Nearly all the birds listed in Wiens' study are territorial, nonflocking species. In contrast, four of the seven major avian consumers in the present study (Brewer's Blackbirds, Red-winged Blackbirds, White-crowned Sparrows and House Sparrows) are gregarious and feed in flocks. In a study of an Arizona urban bird community, Emlen (1974) also found a very high proportion of gregarious species (species with "Type B territories"). In the present study, flock feeding birds accounted for 90% of all avian consumption. Compared with solitary feeding, flock feeding is probably more efficient, i.e., it results in a larger quantity of food removed per unit area per unit time (Schoener 1968, Cody 1971).

Important, also, is the relatively flat, uncomplicated structure of lawns. Lawns provide ideal feeding sites for birds adapted to feeding in open areas. A bird could theoretically cover every square centimeter while maintaining an unobstructed view of approaching danger (plus easy access to safe roosting sites in the event of danger). An analogous situation would be a tidal mud flat, which also encourages intense utilization by mixed flocks of gregarious feeding birds.

The combination of highly localized food resources, an easily searched habitat and highly efficient utilization (flock feeding) probably explains

the high consumption per square meter observed in the present study. In fact, one could argue that lawns act as islands of concentrated food resources for suburban bird populations and can thus support extremely high populations of properly adapted (gregarious flock feeding) bird populations in an often otherwise sterile environment.

Mammalian influence was minimal. More energy was put into the system by mammals in the form of cached walnuts and excreta, than was removed. Lawn damage by dogs (scratching and urination) was also minimal. Treading damage by all vertebrates was considered negligible.

Management

Management inputs are shown in Table 3. By far the greatest energy inputs were in irrigation, primarily in terms of external energy resources used, though labor inputs were also large. Lawn mowing was the second largest management input. This is not a surprising result for this part of the United States. Proper irrigation, more than any other factor, determines the year-round success of most California lawns. Mowing, fertilizing, raking (or dethatching), and reseeding inputs are important but can be much more lax and still yield an acceptable turf. Where irrigation is necessary in crop production, it often requires 20 times the energy inputs needed for field operations.

Management exports resulted in the removal of close to 63,000 g (dry weight) of vegetation (living and dead) by raking and mowing from the system, or 271,000 kcal during the year. This nutrient drain was partially compensated for by adding 14,334 g (wet weight) of fertilizer and manure. This is equivalent to $\approx 1,720$ g N; 430 g P; and 860 g K. Based upon results found for bent grass (Hawkes 1969), the green grass removed contained roughly 2,300 g N; 900 g P; and 1,500 g K. Additional losses were caused by the leaf litter removed: 1,000 g N; 60 g P; and 350 g K (McHargue and Roy 1932). Therefore, a net deficit of 1,580 g N; 530 g P; and 990 g K was created by the management practiced. Natural N input from precipitation would have equalled around 125 g (Buckman and Brady 1969), still leaving a significant deficit. Important to note, however, is the fact that nearly all the N, P, and K input (commercial fertilizer and manure) was in a form readily useable by the plants, whereas that removed would have been largely unavailable on a short-term basis.

Experimenter

Experimenter inputs, Table 4, and exports, Table 5, reveal minimal inputs and large exports; specifically with regard to invertebrates and litter. Ex-

TABLE 4. Direct experimenter inputs in terms of labor and electricity into the lawn system, summarized in kcal/yr

Inputs	Quantity	kcal/unit quantity	kcal/yr
Quick trapping			
Vacuum (electricity)	5 h 8 min	0.83 kcal/sec	15,289.2
Vacuum (labor)	11 h 4 min	0.410 kcal/kg per 10 min	1,769.6
Core sampling (labor)	1 h 12 min	0.862 kcal/kg per 10 min	403.4
Vertebrate census (labor)	24 days	0.0/day	0.0
Total			17,462.2

perimenter export is actually underestimated, since vegetation removal for the purpose of estimating production was considered as part of management.

An analysis of experimenter impact reveals that the experimenter "consumed" a total of 1,774 kcal (16 kcal/m² per yr) of vegetation. This represents 0.5% of the total available production. The experimenter also "consumed" 30.3 kcal of invertebrates (0.3 kcal/m² per yr) which represents about 1% of the total available invertebrate production. One percent or 0.5% may seem to be an acceptably low level of disturbance, but such an evaluation does not accurately reflect the true impact upon other consumers in the community. Using the technique described by Falk (1974), a more accurate picture of experimenter impact is revealed by comparing experimenter consumption to the consumption of other consumers feeding at the same trophic level.

Experimenter impact at the primary consumer level, about 0.5% was probably insignificant considering the enormous quantity of vegetation removed by the manager. The invertebrates removed, nearly 3% of the total consumed, most likely was significant. The sample size was reduced from 1.25 m²/wk to 0.50 m²/wk after a few months in order to minimize impact. Any sampling will produce impact, and reduced sample size to avoid impact must be weighed against increased sample size in order to yield a

more accurate estimate of the population being studied.

An annual invertebrate consumption of 30.3 kcal would be roughly equivalent to the invertebrate consumption of a Scrub Jay (as determined in this study). By comparison, H. T. Odum (1957) in his study of Silver Springs, Florida accounted for 2% of the total secondary consumption, which was equivalent to increasing by 50% the numbers of the largest top carnivores in the community (Falk 1974). On the other hand, Van Hook's (1971) experimental consumption was only 0.05% of the total invertebrate secondary consumption.

Energetically, man was clearly the dominant animal in the community—as a "herbivore," man "consumed" roughly 10% of all the net primary production, and as a "scavenger," man accounted for nearly 100% of all the litter "consumed." All of this was at a human metabolic cost (not including energy costs of irrigation, gasoline, etc.) equal to less than one-half of the metabolic energy of the rest of the consumers in the community combined. When external energy sources are included (gasoline, irrigation and fertilizer production), the energy input dwarfs the rest of the consumer system. Figure 1 graphically shows that the major pathway of energy in the community is via man and his tools. Man accounted for 4% of the measured energy inputs in the system, and nearly 11% of the energy losses. In comparison, all other aboveground animals together accounted for only 0.3% of the total energy losses. A total of 1,865 kcal/m² per yr in labor, gasoline, fertilizer, etc., were used to produce a reasonably attractive suburban lawn. In contrast, 715 kcal/m² is required to raise a corn crop (Pimentel et al. 1973). Corn production in the United States is of intermediate energy intensiveness. A corn crop requires about 130–140 days (H. F. Heady, *personal communication*) or \approx 40% of the year if nongrowing season inputs are considered. Reducing the lawn maintenance estimate by 60% yields 746 kcal/m², a value comparable to that for corn production. Even excluding lawn irrigation (vital to California, but not totally necessary for Eastern lawns) total management inputs equal 578 kcal/m² per yr. For roughly the same energetic effort ex-

TABLE 5. Experimenter impact on a lawn system expressed as energy exports (kcal/yr)

Exports	Quantity	cal/unit quantity	kcal/yr
Quick trap			
Invertebrates removed			
Arthropods	3,967.0 mg	5.2 cal/mg	20.6
Mollusks	2,094.0 mg	4.6 cal/mg	9.6
Litter removed	337.0 g	4,298 cal/g	1,448.3
Core samples ^a			
Aboveground			
Green	4.7 g	4,350 cal/g	20.6
Brown	4.9 g	4,257 cal/g	20.7
Litter	2.3 g	4,298 cal/g	9.9
Belowground	62.5 g	4,394 cal/g	274.7
Total			1,804.4

^a Soil replaced.

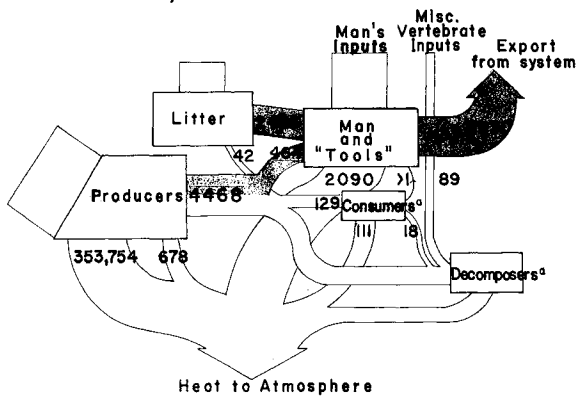


FIG. 1. Generalized energy flow diagram of above-ground primary and secondary production of a lawn ecosystem. Special attention is paid to man's role in the system. No attempt is made to round out the diagram by quantifying belowground invertebrate decomposer and radiation components of the system. The shaded area highlights man's interactions with the vegetation components of the system. Consumers category excludes belowground invertebrates, these are lumped pictorially with decomposers.

pendent on suburban lawns, every home owner could raise vegetables (the net primary production being equivalent also). Most people intuitively know that lawns require a lot of energy, and as energy as well as commodities like vegetables become increasingly expensive, perhaps the future will see a reversal in the trends towards ever-increasing turf coverage in the United States and abroad.

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