

TABLE I. Average energy values for parts of plants, based on determinations from 57 species (Value g cal/g dry wt)

Part	Number Samples	Average Value	Coefficient Variation
Leaves.....	260	4229	.116
Stems and Branches...	51	4267	.081
Roots.....	52	4720	.092
Litter.....	82	4298	.104
Seeds.....	22	5065	.219

that the values ranged from 4308 g cal/g dry wt for the seed head to 3435 g cal/g dry wt for one of the oldest leaves. The highest values he obtained were for seeds of conifers, which ranged from 5625-7117 g cal/g dry wt.

The seasonal analysis includes vegetative samples from 3 old-field communities: a blue-grass field in Mich., a broomsedge field and young pine stand in Ga. (Table II). Values for the dominant plants in these 3 communities were grouped so that the comparison is between months, irrespective of the species of plants. The analysis of variance showed that significant differences at the 99% level ($F = 2.36$, d.f. = 11 and 272) existed between months. The highest caloric values occurred in the fall and winter, presumably from storage of energy in the roots, culms, and seeds. Morrison (1949) reports that in many plants the per cent of crude protein in the green foliage decreases, that of crude fiber and nitrogen-free extract (mostly carbohydrate) increases, while that of ether extract (partly fat) remains constant through the growing season. Accordingly, the caloric value of the foliage should be higher in the spring than in the fall. However, when considering all parts of the vegetation growing in the community the caloric value per gram total vegetation (including roots and seeds) appears to be greater in the fall and winter.

Caloric data are available for the dominant plants in 9 ecological communities, ranging from tropical rain-forest to alpine tundra. The pine community data furnished by J. D. Ovington are from England. The alpine tundra data obtained by L. Bliss are from New Hampshire. The *Spartina* (analysed by C. Connell), the *Andropogon*, and the old-field herb communities were studied in Ga., the *Poa* community in Mich., and the rain-forest and mangrove forest in Puerto Rico. The values in Table

TABLE II. Average energy values for dominant species in three old-field communities collected at different seasons (Value g cal/g dry wt)

Season	Number Samples	Average Value	Coefficient Variation	Seasonal Average
January.....	18	4039	.152	4099
February.....	17	4225	.022	
March.....	3	4034	.028	
April.....	27	3900	.129	
May.....	24	4127	.070	3981
June.....	24	3917	.088	
July.....	21	4072	.065	
August.....	41	3919	.079	
September.....	38	4197	.061	4063
October.....	20	4192	.066	
November.....	33	4151	.097	4083
December.....	18	3907	.215	

III are mixed-species averages of all the data available for the dominant species; they are not average weighted by the importance of individual species in the phytosociology or biomass composition of the communities. The statistical analysis showed that the average caloric value per gram total vegetation (roots, leaves, and stems) in these communities differed significantly at the 99% level ($F = 11.3$, d.f. = 8 and 343). The tundra estimates were considerably higher than those for the other communities indicating that communities with a long period of nonproduction accumulate a greater energy store than those which grow throughout the year. However, the pine community, with its high resin and turpentine content, also had a high energy value.

TABLE III. Average energy values of dominant vegetation in ecological communities (Value g cal/g dry wt)

Community	Number Samples	Average Value	Coefficient Variation
Tropical rain-forest.....	15	3897	.060
Mongrove forest.....	11	3764	.082
<i>Spartina</i> marsh.....	14	4072	.042
<i>Andropogon</i> field.....	143	3905	.104
Herb old-field.....	35	4177	.096
<i>Poa</i> old-field.....	115	4075	.064
<i>Pinus sylvestris</i> stand.....	14	4787	.078
Alpine meadow.....	3	4711*	.005
Alpine <i>Juncus</i> dwarf heath	2	4790*	.003

* Bliss (pers. comm.) recently reported that the average value for tundra, based on 32 determinations, is 4709 g cal/g dry wt.

The 3 analyses described are not as precise as desired because it was necessary to compare caloric values per gram dry weight rather than values per gram ash-free weight. The large amount of ash-free weight data available for the *Andropogon virginicus* community (Table IV) shows how ash may influence the differences between categories. When the caloric values by plant part and month uncorrected for ash are compared a significant difference exists between parts at the 95% level ($F = 2.74$, d.f. = 4 and 32) and months at the 99% level ($F = 4.07$, d.f. = 8 and 32). However, the same comparison but using calories per gram ash-free weight (Table IV) shows significant differences at the 95% level between seasons only. The average value for parts for all seasons, shown below, illustrates the differences when ash is considered.

Part	cal/g dry wt	cal/g ash-free wt
Green Broomsedge	4231	4377
Standing-dead vegetation	4116	4290
Litter	3902	4139
Roots	3607	4169
Green herbs	3634	4288

ENERGY VALUES OF ANIMALS

Only limited caloric data are available for animals. Seven taxa, including invertebrates and vertebrates, are in Table V. The crabs were especially low in energy content, probably because the calcareous exoskeleton was not separated from the soft parts. E. P. Odum has provided unpublished data on the ash content of crabs from Sapelo Island, Ga., which indicate that the ash is about 51% of the total dry weight. This means that the caloric value per gram ash-free weight for crabs is about 4400 cal. The analysis of variance showed that

TABLE IV. Energy values in an *Andropogon virginicus* Old-field Community in Georgia
(Value g cal/g dry organic matter)

Part	April	May	June	July	Sept.	Oct.	Nov.	Dec.	Jan.	Ave.
Green grass.....	4254	4372	4325	4187	4256	4529	4508	4505	4422	4373
Standing dead.....	4435	4338	4201	4208	4281	4205	4429	4190	4325	4290
Litter.....	3928	4369	4104	4225	4124	4126	4264	4029	4078	4139
Roots.....	4387	4056	4344	4270	4104	4074	4137	4236	3891	4167
Green herbs.....	4477	4157	4088	4212	4399	4429	4265	4375	4193	4288
Average.....	4296	4258	4212	4220	4233	4273	4321	4267	4182	4251

TABLE V. Energy values for animal taxa
(Value g cal/g dry wt)

Taxa	Number Samples	Average Value	Coefficient Variation	Authority
Crustacea				
<i>Daphnia</i>	18	4419	.115	Richman (1958)
<i>Stenonema</i>	29	5596	.048	Trama (1957)
<i>Uca</i> and other crabs	8	2248	.188	Connell (unpubl.)
Mollusca				
<i>Modiolus</i>	3	4600	—	Kuenzler (unpubl.)
Insecta				
<i>Schistocerca</i>	8	5363	.048	Connell (unpubl.)
Annelida				
Earthworms.....	3	4617	.030	French <i>et al</i> (1957)
Mammalia				
Mice.....	8	5163	.157	Golley (1960)

the energy value of the animals, excluding the crabs, did not differ significantly ($F=1.84$, d.f. = 5 and 63). In general, the values for the animals are about 1000 g cal/g dry wt higher than the plant values.

DISCUSSION

Examination of over 600 records of plants has shown that significant differences in caloric value exist between plant parts, between vegetation collected in different months, and between vegetation growing in different ecological communities. When the variation in chemical composition of various cultivated and noncultivated crop plants reported in Morrison (1949) is considered (e.g., fat ranges from 1.0% in *Lespedeza* stems to 38.8% in wild mustard seed) and the fact that Long (1934) found that caloric values varied with light intensity, length of day, amount of nutrients, and type of soil, the observed differences are not unexpected.

Richman and Slobodkin (1960) have emphasized the constancy of the caloric value of animal tissue. Except under starvation or storage conditions animal tissue averages about 5000 g cal/g dry wt. The data in this report are less extensive but support their conclusions. Richman and Slobodkin (1960) point out that when an animal is storing food material before hibernation or a nonfeeding portion of the life cycle, the energy value of the body may increase to 6000 or 7000 g cal/g dry wt. This condition in animals is analogous to the seed stage in the life history of the plant and to the fall condition of many perennial plants which store food in the root, tuber, or rhizomes. This analogy helps to explain why significant differences exist between the plant categories.

The caloric value of a plant or animal is a function of its genetic constitution, nutritive condition, and life his-

tory. Because these factors may vary with species, seasons, and environmental conditions the ecologist making intensive measurements of energy flow through natural systems cannot depend on caloric constants or equivalents. This study shows that the ecologist must determine the energy content under the specific conditions of his particular study. However, those engaged in extensive surveys are probably justified in converting biomass to energy by using the average caloric values in the tables.

SUMMARY

This report summarizes and evaluates the variation between caloric values of plants and animals. Analysis of over 600 records shows significant differences between plant parts, between vegetation collected in different seasons, and between vegetation from different ecological communities. Differences between animal taxa were not significant. It was concluded that ecologists should directly determine the energy content of ecological materials when studying energy flow through natural systems. It is also hoped, however, that the average values presented may be useful for energy estimation in some types of ecological research.

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