CALORIFIC VALUES OF SOUTH GEORGIAN PLANTS

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ABSTRACT. Calorific values are provided for 18 common and widespread South Georgian plants including nine herbs, three shrubs, two pteridophytes and four mosses. The results are compared with available data for related arctic-alpine and sub-Antarctic species.

DUE to severe environmental conditions and restriction of habitats, polar, sub-polar and alpine regions support relatively simple ecosystems in which the diversity of species and the range of life forms are generally small. In any investigation concerning productivity, it is both useful and important to relate biomass to energy flow within the ecosystem, but energy determinations for entire ecosystems, in terms of calorific value, are difficult to achieve. Such data may be obtained for individual species and later applied to the ecosystem as a whole, although this necessitates a detailed analysis of the species composition and cover abundance of the vegetation and/or fauna. Alternatively, the data may be obtained for representative samples of the ecosystem at the community level.

Few calorific data have been published for polar and alpine plant species, although Bliss (1962) has provided results for some alpine tundra species, while Jenkin and Ashton (1970) have given energy values for four sub-Antarctic species from Macquarie Island. The results of a preliminary survey of the energy content of a number of ecologically important phanerogams and cryptograms on South Georgia are thus of value in supplementing the meagre data available from polar regions.

MATERIALS AND METHODS

All of the species were sampled around King Edward Cove, Cumberland East Bay (lat. 54° S., long. 36° W.), during periods of sunshine in mid-growing season between 20 and 24 January 1971. Only living aerial parts were taken for each species, the material being collected from an area *c.* 25 m.^{2} and pooled, so that analyses were carried out on single samples only. Separate determinations were made for individual parts of the deciduous dwarf shrubs and grasses, but the material of the other herbs and the pteridophytes was assessed as a whole. For the mosses, only the apical 1 cm., representing much of the current year's growth, was taken. All material was thoroughly washed and cleaned to remove any soil particles. The samples were then oven dried at *c.* 55° C for several days and stored in paper bags.

Calorific value determinations were made in January 1972 by The Chemical Service, The Nature Conservancy, Merlewood Research Station. Approximately 1 g. of air-dry sample was ground and compressed into pellets each of which was then oven dried and accurately weighed before being ignited in an adiabatic oxygen bomb calorimeter. Corrections were made for unburnt residue, acid formation and fuse combustion, while ash and moisture content were determined separately. The calorific values were calculated on an ash-free basis as well as on a dry-weight basis from the temperature increase, total water equivalent, sample weight and all corrections.

Early calorific determinations were generally expressed only on the basis of dry weight but more recently the ash content of samples has been calculated and the dry weight corrected for this factor (Paine, 1971). The determination of absolute ash contents from bomb calorimetery has, however, been shown to produce both systematic and random errors higher than those found in muffle-furnace determinations (Reiners and Reiners, 1972). Although independent ash determinations are to be recommended if the calorific values are to be used for energy flows in complete ecosystems, ash-free data provide a more accurate calorific value by excluding contaminants such as externally held soil or dust particles not removed by washing, or crystal inclusions within cells.

RESULTS AND DISCUSSION

The calorific values of all species sampled are presented in Table I, both as $J \times 10^3$/g. dry weight and as $J \times 10^3$/g. ash-free dry weight. The difference between the dry-weight and the

TABLE I. CALORIFIC VALUES FOR SOME SOUTH GEORGIAN PLANTS SAMPLED IN MID-GROWING SEASON

Species	*Plant parts sampled*	*Calorific value* ($J \times 10^3$/g.)*	
		Dry weight basis	*Ash-free dry weight basis*
Deciduous shrubs			
Acaena decnmbens	leaves	17·96 (4·29)	19·55 (4·67)
	inflorescences	18·80 (4·49)	19·76 (4·72)
	scapes	18·00 (4·30)	18·80 (4·49)
	woody stem	18·67 (4·46)	19·47 (4·65)
	mean for all aerial parts	18·38 (4·39)	19·76 (4·72)
Acaena decumbens × *tenera*	leaves	18·51 (4·42)	19·76 (4·72)
	inflorescences	18·42 (4·40)	19·64 (4·69)
	scapes	17·58 (4·20)	18·63 (4·45)
	woody stem	18·63 (4·45)	19·26 (4·60)
	mean for all aerial parts	18·30 (4·37)	19·34 (4·62)
Acaena tenera	leaves	19·05 (4·55)	20·14 (4·81)
	inflorescences and scapes	18·84 (4·50)	19·51 (4·66)
	woody stem	18·71 (4·47)	19·09 (4·56)
	mean for all aerial parts	18·88 (4·51)	19·59 (4·68)
Grasses			
Deschampsia antarctica	leaves	19·34 (4·62)	20·39 (4·87)
	inflorescences, seed and culms	18·42 (4·40)	19·26 (4·60)
	mean for all aerial parts	18·88 (4·51)	19·80 (4·73)
Festuca erecta	leaves	18·34 (4·38)	19·26 (4·60)
	inflorescences	19·09 (4·56)	19·93 (4·76)
	culms	18·84 (4·50)	19·34 (4·62)
	mean for all aerial parts	18·76 (4·48)	19·51 (4·66)
Phleum alpinum	leaves	19·01 (4·54)	19·72 (4·71)
	inflorescences and culms	18·71 (4·47)	19·13 (4·57)
	mean for all aerial parts	18·88 (4·51)	19·43 (4·64)
Poa flabellata	leaves	20·18 (4·82)	21·06 (5·03)
	inflorescences and seed	19·30 (4·61)	19·89 (4·75)
	mean for all aerial parts	19·76 (4·72)	20.47 (4·89)

TABLE I—*continued opposite*

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Other herbs			
Callitriche antarctica	leaves, stems and flowers	18·09 (4·32)	19·55 (4·67)
Galium antarcticum	leaves, stems and flowers	18·76 (4·48)	21·31 (5·09)
Juncus scheuchzerioides	leaves and stems	18·67 (4·46)	20·52 (4·90)
Ranunculus biternatus	leaves and stems	17·75 (4·24)	19·64 (4·69)
Rostkovia magellanica	leaves and stems	19·47 (4·65)	20·35 (4·86)
Pteridophytes			
Lycopodium magellanicum	leaves and stems	19·30 (4·61)	20·77 (4·96)
Polystichum mohrioides	leaves, stems and sori	18·67 (4·46)	19·97 (4·77)
Mosses			
Chorisodontium aciphyllum	current year's stems and leaves	19·18 (4·58)	19·51 (4·66)
Polytrichum alpestre	current year's stems and leaves	19·26 (4·60)	19·55 (4·67)
Sphagnum fimbriatum	current year's stems and leaves	17·71 (4·23)	18·25 (4·36)
Tortula robusta	current year's stems and leaves	19·85 (4·74)	20·47 (4·89)

* Values in brackets are in kcal./g.

ash-free dry-weight values for each sample can be used as an indirect measure of the ash content of the species. As indicated in Table I, the ash level in the mosses appears to have been generally lower than in the phanerogams, a conclusion borne out by independent muffle-furnace data. The shoots and leaves of *Galium antarcticum*, *Juncus scheuchzerioides*, *Ranunculus biternatus* and *Acaena decumbens* apparently had comparatively high ash contents and this has also been confirmed by separate ashing experiments. Anatomical studies have revealed the presence of abundant crystals of calcium oxalate and possibly of opaline silica in the leaves of the grasses, *Acaena* spp. and some other species. Since these compounds are not thermo-labile they must contribute significantly to the ash content of the respective samples. The ash content of samples of various living fractions of *Acaena decumbens* were determined separately and it was found that the leaves had a mean ash content of 8·8 per cent of the dry weight, the scape 5·4 per cent and the woody stem 4·7 per cent. Samples of apical segments of the mosses *Chorisodontium aciphyllum* and *Polytrichum alpestre* from the maritime Antarctic have been found to have low ash contents of 2·4 and 2·9 per cent, respectively.

Golley (1961) showed that there can be considerable variation in calorific values both between species and between the various fractions of individual species. The ash-free values for the samples of the three *Acaena* taxa exemplify this point. Comparison of the values for individual fractions of these deciduous shrubs shows that the calorific values for the leaves of the hybrid, *A. decumbens* × *tenera* (19·76 J × 10^3/g. ash-free dry weight) fell between those of its parents, *A. decumbens* (19·55 J × 10^3/g.) and *A. tenera* (20·14 J × 10^3/g.). There was a converse trend in the woody stems and inflorescences, although the differences between the parent species were rather less for these fractions than for the leaves. There was, however, no significant variation in the mean calorific values for the total aerial parts of the three taxa.

The mean calorific value for *Poa flabellata*, and in particular the calorific value of the leaves (21·06 J × 10^3/g.), was considerably higher than the values obtained for the other grasses. The inflorescences of the grasses generally had a lower calorific value than the leaves, possibly due to the majority of them being mature and most of the seeds having been shed. *Festuca erecta*, however, does not set mature seed until fairly late in the season and at the time of

TABLE II. COMPARISON OF MEAN CALORIFIC VALUES FOR RELATED GROUPS OF ARCTIC–ALPINE AND SUB-ANTARCTIC PLANT SPECIES

Species	*Reference*	*Locality*	*Plant parts sampled*	*Mean calorific value as ash-free dry weight** ($J \times 10^3$/g.)
Deschampsis antarctica	This paper	South Georgia	L, S, I	19·85 (4·74)
Deschampsia flexuosa	Bliss, 1962	New Hampshire, U.S.A.	L, S, I, R	18·88–19·09 (4·51–4·56)†
Poa flabellata	This paper	South Georgia	L	21·06 (5·03)
			L	20·18 (4·82) (dry weight)
Poa foliosa	Jenkin and Ashton, 1970	Macquarie Island	L	19·72 (4·71) (dry weight)
Juncus scheuchzerioides	This paper	South Georgia	L, S	20·52 (4·90)
Juncus trifidus	Bliss, 1962	New Hampshire, U.S.A.	L, S, I, R	19·05–19·13 (4·55–4·57)†
Lycopodium magellanicum	This paper	South Georgia	L, S	20·77 (4·96)
Lycopodium annotinum	Bliss, 1962	New Hampshire, U.S.A.	L, S, R	20·72–20·89 (4·95–4·99)†
Huperzia selago	Bliss, 1962 (as *Lycopodium selago*)	New Hampshire, U.S.A.	L, S, R	19·38–20·35 (4·63–4·86)†
Chorisodontium aciphyllum (= *Dicranum aciphyllum*)	This paper	South Georgia	L, S	19·51 (4·66)
Dicranum undulatum	Bliss, 1962 (as *Dicranum bergeri*)	New Hampshire, U.S.A.	L, S	18·67 (4·46)
Polytrichum alpestre	This paper	South Georgia	L, S	19·55 (4·67)
Polytrichum juniperinum var. *alpestre*	Bliss, 1962	New Hampshire, U.S.A.	L, S, C	20·01 (4·78)
Polytrichum piliferum	Bliss, 1962	New Hampshire, U.S.A.	L, S	18·76 (4·48)
Sphagnum fimbriatum	This paper	South Georgia	L, S	18·25 (4·36)
Sphagnum fuscum	Bliss, 1962	New Hampshire, U.S.A.	L, S	18·13 (4·33)
Sphagnum girgensohnii	Bliss, 1962	New Hampshire, U.S.A.	L, S	17·63 (4·21)
Acaena decumbens, *A. tenera*, *A. decumbens* × *tenera*	This paper	South Georgia	L, W, I	19·43 (4·64)
Vaccinium angustifolium, *V. caespitosum*, *V. uliginosum* var. *alpinum*	Bliss, 1962	New Hampshire, U.S.A.	L, W, I, R	20·68 (4·94)

* Values in brackets are in kcal./g.
† First value is for samples collected in June-July; second value is for samples collected in August.
C, capsules; I, inflorescences; L, leaves; R, roots or rhizomes; S, shoots; W, woody shoots and stems.

sampling the flowers were still immature, which may account for their having a calorific value higher than that of the leaves.

The remaining herbs and pteridophytes were not partitioned and the calorific values for these species refer to samples containing both shoots and leaves, although in *Callitriche antarctica* and *Galium antarcticum* a small number of flowers was also present while fronds of the fern *Polystichum mohrioides* had abundant immature sori. Values for the two pteridophytes were high, particularly *Lycopodium magellanicum*. Of the herbs, *Galium antarcticum* had the highest value closely followed by two rushes *Juncus scheuchzerioides* and *Rostkovia magellanica*. *Callitriche antarctica* and *Ranunculus biternatus*, which occupy damp or wet habitats, had relatively low calorific values.

With the exception of *Tortula robusta*, the mosses had relatively low calorific values, particularly *Sphagnum fimbriatum*. Bliss (1962) also found that mosses, and to an even greater extent lichens, have relatively low energy values with the lowest determinations being recorded for species of *Sphagnum*. It is interesting that the two tall turf-forming mosses, *Chorisodontium aciphyllum* and *Polytrichum alpestre*, which commonly associate to form deep peat banks, should have virtually identical values.

Table II compares calorific values of some South Georgian species with those obtained for related species on Macquarie Island (Jenkin and Ashton, 1970) and on Mount Washington, New Hampshire, United States of America (Bliss, 1962). The values of the mosses correspond quite closely and similar results were also obtained for the species of *Lycopodium*. The leaves of *Poa flabellata* and *P. foliosa* have fairly similar values ($20 \cdot 18$ J $\times$ 10^3/g. dry weight and $19 \cdot 72$ J $\times$ 10^3/g. dry weight,* respectively); these species are closely related and occupy the same ecological niche in widely separated sub-Antarctic regions. There is a considerable difference between the corresponding species of *Deschampsia* and *Juncus*. The mean calorific value for the genus *Acaena*, being the only deciduous shrub on South Georgia, is compared with the mean for three species of *Vaccinium*, a genus of somewhat similar growth form and morphology which occupies similar habitats. The values provided by Bliss for nine deciduous alpine shrubs sampled twice during the summer were, with one exception, all higher than those obtained for *Acaena* and ranged mainly from $20 \cdot 1$ to $21 \cdot 8$ J $\times$ 10^3/g. ash-free dry weight.

It should be noted that no attempt has been made to follow seasonal trends in calorific values, although Bliss (1962) and Hughes (1971) have shown that these may be significant, particularly in the reproductive parts. This may be linked with seasonal changes in the lipid content of the plants (Bliss, 1962) and it will be interesting to see whether the high calorific values obtained for *Poa flabellata* leaves and *Galium antarcticum* are associated with high lipid values.

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REFERENCES

BLISS, L. C. 1962. Caloric and lipid content in alpine tundra plants. *Ecology*, **43**, No. 4, 753–57.

GOLLEY, F. B. 1961. Energy values of ecological materials. *Ecology*, **42**, No. 3, 581–83.

HUGHES, M. K. 1971. Seasonal calorific values from a deciduous woodland in England. *Ecology*, **52**, No. 5, 923–26.

JENKIN, J. F. *and* D. H. ASHTON. 1970. Productivity studies on Macquarie Island vegetation. (*In* HOLDGATE, M. W., *ed. Antarctic ecology*. London and New York, Academic Press, 851–63.)

PAINE, R. T. 1971. The measurement and application of the calorie to ecological problems. *Annual review of ecology and systematics*, **2**, 145–64.

REINERS, W. A. *and* N. M. REINERS. 1972. Comparison of oxygen-bomb combustion with standard ignition techniques for determining total ash. *Ecology*, **53**, No. 1, 132–36.

* Ash-free dry weight value not available.