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TROPHIC EXPLOITATION AND ARCTIC PHYTOMASS PATTERNS

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The hypothesis of exploitation ecosystems (Fretwell 1977; Oksanen et al. 1981) predicts that natural grazing pressure is light in extremely unproductive ecosystems (because there is very little to forage on) and in productive ecosystems in which grazer densities well below the carrying capacity are exploited by efficient predators. The hypothesis predicts that between these two types of ecosystems there exists a realm of "two-link ecosystems." Within this productivity interval, the plant community provides enough resources to allow the existence of grazers, but only at densities below the hunger threshold of efficient predators. It is predicted that herbivore grazing will keep the plant community depleted. Increased primary productivity should thus only increase the abundance of grazers, whereas the aboveground phytomass should show no correlation with primary productivity. Instead, variation in aboveground phytomass should reflect differences in grazing conditions and the impact of geographical isolation and human disturbance upon the grazer community.

In their review of arctic and antarctic phytomass and productivity data, Oksanen et al. (1981) found drastic differences in the phytomass of moderately unproductive communities apparently related to the presence or absence of key grazers: from the massive (9 kgm^{-2}) moss banks of a grazer-free antarctic island to the modest (100–200 gm^{-2}) phytomasses on the snowbeds of Hardangervidda, Norway. Truelove Lowland (Devon Island, Canada) had an interesting intermediate position. Except for the low vascular phytomass in the polar desert, the aboveground vascular phytomasses stayed at a constant level of about 100 gm^{-2}, a value which was also obtained for the snowbeds of Hardangervidda, in spite of an order-of-magnitude difference in productivity. The total aboveground phytomasses of Truelove Lowland, however, showed an apparent positive trend with increased primary productivity and had generally much higher values (about 1 kgm^{-2}) than Hardangervidda.

Oksanen et al. (1981) claimed that this pattern is exactly what their hypothesis predicts. Grazers of vascular plants inhabit both Truelove Lowland and Hardangervidda whereas the genus *Lemmus,* adapted to utilize moss (see Kalela 1961, 1971; Batzli et al. 1980), occurs only in the latter area. The problem with this interpretation is that only four data points remained for testing the prediction that

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TABLE 1

CLIMATOLOGICAL DATA FOR BARROW AND TRUELOVE LOWLAND

	$\bar{t}$	$\bar{t}_j$	$\bar{p}$	$\bar{p}_{72}$	$\bar{p}_s$
Barrow	−13° C	+4 ° C	124 mm	137 mm	58 mm
Truelove Lowland	(−16° C)	+5° C	(130 mm)	116 mm	59 mm

NOTE.—$\bar{t}$ = mean annual temperature; $\bar{t}_j$ = mean July temperature (estimated on the basis of microclimatological maps for Truelove Lowland); $\bar{p}$ = mean annual precipitation; $\bar{p}_{72}$ = mean precipitation for the period May 1972–April 1973; $\bar{p}_s$ = mean precipitation for June–August. The values in parentheses refer to data from Resolute Bay (the meteorological station nearest to Truelove Lowland).

SOURCES.—Tieszen 1978; Courtin and Labine 1977.

moderately unproductive communities with all key grazers have a steady level of aboveground phytomass. Of these four, two are suspect: a sphagnum bog in Swedish Lapland and a lichen tundra on Hardangervidda. In the former community, the concept of aboveground phytomass is ambiguous and in the latter, the wild reindeer population is managed in order to prevent severe depletion of lichen grounds (Gaare and Skogland 1975), i.e., the very situation predicted to be the natural state of moderately unproductive tundras. This leaves two early snowbeds as references; of them, one is so productive that its appropriateness in this context is questionable.

The publication of phytomass and productivity data from Barrow, Alaska (Miller et al. 1980), where brown lemmings are present, allows examination of a steady level of aboveground phytomass. With a productivity interval of 79–294 gm^{-2} yr^{-1}, the communities of Barrow are comparable to the meadows of Truelove Lowland (productivity 97–280 gm^{-2} yr^{-1}, Bliss 1977). Except for the *Luzula* and *Salix* heaths and the *Cochlearia* meadow, the Barrow communities are also comparable to the meadows of Truelove Lowland with regard to site and successional status. Also the climates of Barrow and Truelove Lowland seem similar (table 1). The interpretation of Oksanen et al. (1981) implies that there must be a significant difference between the aboveground phytomasses of these comparable Truelove Lowland and Barrow communities and that a combination of the data from Barrow and the less productive communities on Hardangervidda must not show any significant correlation between aboveground phytomass and primary productivity.

If the existence of massive moss banks in high-arctic and antarctic areas is attributable to the absence of *Lemmus* spp., it also follows that in areas with brown or Norwegian lemmings, the moss phytomass must be highly dynamical, with rapid increases during times of low lemming densities. This prediction can be tested by means of annual moss phytomass data from Kilpisjärvi during 1972–1978 (Kyllönen and Laine 1980).

TEST PROCEDURE

The aboveground phytomasses of Hardangervidda, Truelove Lowland, and Barrow were obtained from the final IBP reports (Kjelvik and Kärenlampi 1975;

Wielgolaski 1975; Bliss 1977; Miller et al. 1980; notice that the values used by Oksanen et al. [1981] were based on preliminary data). The field layer of the birch forest of Hardangervidda was included separately in order to see whether the steady phytomass level is also obtained for communities not dominated by graminids. (According to Fretwell [1977], different layers in strongly stratified vegetation can be treated as separate communities, because a herbivore of a given type is probably not efficient in utilizing several vegetational layers. Mountain birch forests are at least close to meeting this criterion.)

The difference between the aboveground phytomass of meadows on Truelove Lowland and comparable Barrow meadows (*Carex-Poa, Carex-Onchophorus, Dupontia, Carex-Eriophorum,* and *Arctophila*) was tested by means of the *t*-test (df = 7). The existence of significant correlations between the aboveground phytomass and primary productivity was examined from the data points for Truelove Lowland (df = 6) and those from Barrow and Hardangervidda with productivity values less than 600 gm^{-2} yr^{-1} (df = 9). In the annual data of Kilpisjärvi, the existence of significant correlation between the moss phytomass of the high altitude communities and the time elapsed from the lemming peak and crash 1970–1971 was examined and the magnitude of the change was estimated by means of linear regression. The low altitude communities were excluded, because some of them were probably outside the productivity interval of two-link ecosystems.

The following sources of error or bias should be noted. (1) The variables in the model (gross primary productivity, living phytomass) are only approximately reflected by the measurements available (net primary productivity, phytomass which includes dead tissue). This will cause deflated production estimates and inflated biomass estimates for plant communities with much woody tissue and a relatively high percentage of heterotrophic phytomass. In this study the two communities of Hardangervidda with the highest phytomass values, a birch wood and a willow thicket, are most likely to be affected by this bias.

2) Growing conditions on the tundra are extremely variable from year to year (Gjaerevoll 1956; Kyllönen and Laine 1980). Especially for communities with a snowbed character, productivity estimates obtained during a few growing seasons have wide margins of error.

3) The great difference between preliminary and final phytomass estimates for Truelove Lowland suggests that moss phytomasses are very difficult to estimate. Hence, minor differences in data obtained by different study teams cannot be regarded as biologically significant.

RESULTS AND DISCUSSION

The mean for the aboveground phytomasses of meadows on Truelove Lowland (918 gm^{-2}) is vastly greater than the corresponding value for Barrow (151 gm^{-2}, $t = 8.116^{***}$), in spite of the greater average productivity of the meadows at Barrow (242 gm^{-2} yr^{-1} vs. 178 gm^{-2} yr^{-1} on Truelove Lowland). It was pointed out by L. C. Bliss (personal communication) that the estimates of moss phytomass create the seemingly implausible implication that annual production is about 45% of the phytomass. In his opinion, this implies a gross underestimation of moss

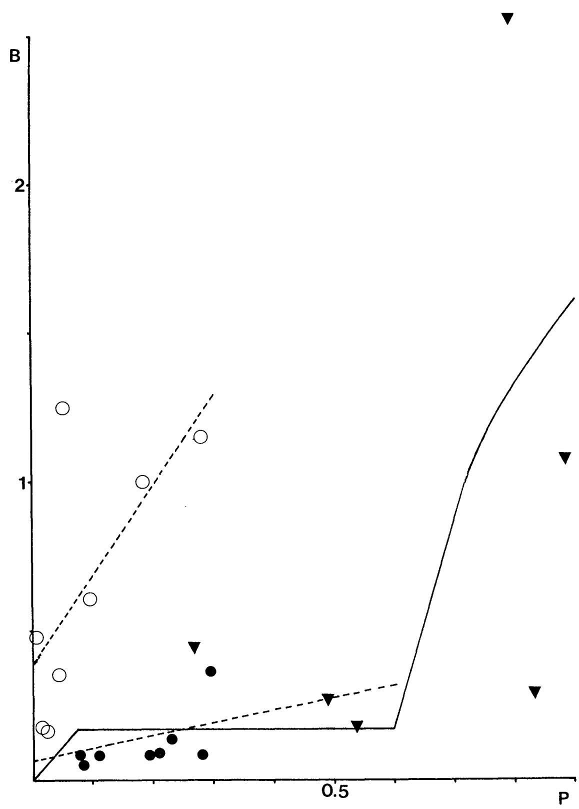

FIG. 1.—Maximum aboveground phytomass (B, kgm^{-2}) and primary productivity (P, gm^{-2} yr^{-1}) for tundra communities on Truelove Lowland (open circles) at Barrow (solid circles) and on Hardangervidda (triangles). Solid line = predicted pattern. Dashed lines = regressions for Truelove Lowland data and combined data for Barrow and Hardangervidda communities with annual productivity less than 600 g/m^2.

phytomasses (but see fig. 2). Even if the estimates of moss phytomasses at Barrow were increased by 100%, the mean for the aboveground phytomasses would only increase to 192 gm^{-2}, and a highly significant difference (t = 6.771***) between the meadows of Barrow and Truelove Lowland would remain.

The correlation between aboveground phytomass and productivity obtained from the preliminary data for Truelove Lowland (r = .906**, df = 5) seems to be present even in the final data (fig. 1, open circles, r = .644°). Conversely, the combination of Barrow data (fig. 1, dots) and Hardangervidda data points (fig. 1, triangles) with productivity below 600 gm^{-2} yr^{-1} shows no indication of significant correlation between the two measures (r = .463, $.2 < P < .4$). The two communities with the highest aboveground phytomass values are the lichen tundra whose dependence on reindeer management has already been mentioned and the *Carex-Poa* meadow of Barrow which occupies centers of raised polygons (Webber 1978). Winter grazing of lemmings is concentrated in troughs between

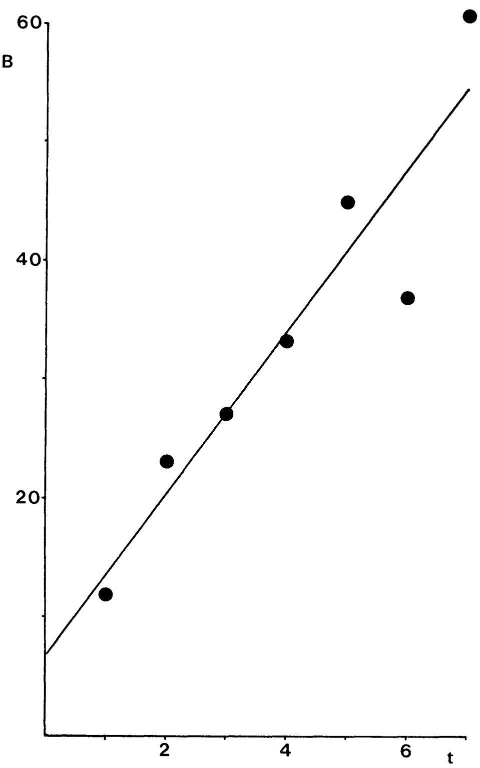

FIG. 2.—Moss phytomass (B, gm^{-2}) in relation to time elapsed from lemming crash 1970–1971 (t, in yr) in high altitude communities at Kilpisjärvi, Finnish Lapland. Solid line = regression.

the polygons (Batzli et al. 1980), probably because of the less favorable snow conditions in polygon centers. The snow cover of elevated sites tends to be thin and crusty, thus being hard to excavate and giving little protection against cold (Dahl 1956; Hiltunen 1980). For the rest of the data points, the semblance of a positive trend is caused entirely by the difference between the Barrow and Hardangervidda phytomasses; this may be an artifact resulting from different operational definitions for moss phytomass.

The correlation between the moss phytomass on the high altitude sites at Kilpisjärvi and the time elapsed from the lemming peak is highly significant (fig. 2, $r = .9378^{**}$). The regression line suggests that an 8.4-fold increase took place during the period 1971–1978 and that the seemingly implausible productivity/phytomass ratio reported for the moss cover at Barrow might actually be realistic immediately after a lemming peak. Data on changes in moss biomass at Kilpisjärvi during the lemming peak of 1978 (see Henttonen and Järvinen 1981) are not yet available. In the tundra plateau of adjacent Finnmarken county, Norway, reduction of moss coverage on tundra heaths and snowbeds (between 96% and 60% for *Dicranum*-type mosses, between 93% and 47% for tall mosses) occurred in 1978 and 1979 (Oksanen and Oksanen 1981). The prediction on the dynamical nature of moss phytomasses on the tundra seems thus to be amply corroborated. A still more critical test could be performed by introducing brown lemmings into Truelove Lowland. The reverse of such a test, an exclusion of lemmings from a piece of Fennoscandian or Alaskan tundra, is less practical. With the rate observed at Kilpisjärvi, it should take 150 yr to reach the phytomass values of Truelove Lowland.

Although the data fully corroborate the predictions of Oksanen et al. (1981), it must be noted that the existence of strong herbivory in moderately unproductive ecosystems can be explained in several other ways (e.g., that the effectiveness of plant defenses depends on the energy balance of plants, as proposed by Haukioja and Hakala [1975] or that the social regulation of herbivores is only effective at moderately high population densities, as proposed by D. Chitty [personal communication]). To distinguish between these propositions and the hypothesis of Fretwell (1977) and Oksanen et al. (1981), data concerning herbivory on productive islands without efficient predators and experimental manipulations of the predator communities are needed. Moreover, some aspects of the hypothesis of Oksanen et al. (1981) can be rejected on a priori grounds. The impact of grazers on the vegetation is unlikely to be only a matter of day-to-day population dynamics. It must be expected that evolutionary trade-offs between the ability to build up high phytomass and the ability to tolerate grazing also occur (see Rosenzweig 1973; Armstrong 1979). The high ratios of belowground to aboveground production obtained for vascular plants of tundra meadows in all three areas may be such an evolutionary response to grazing pressure. The stability analysis of Oksanen et al. (1981) ignores the destabilizing impact of seasonality and the dependence of this impact upon the life history characteristics of grazers (L. Oksanen and T. Oksanen, MS).

Thus, the corroborating data discussed here must not be regarded as evidence for the absolute correctness of the hypothesis of exploitation ecosystems. What the corroboration may suggest is that some elements of the hypothesis might be useful in future studies on community structure.

SUMMARY

Aboveground phytomasses of tundra communities and changes in moss phytomass after a lemming peak were reviewed to test the prediction of the hypothesis of exploitation ecosystems that herbivory limits the aboveground phytomasses of moderately unproductive plant communities. Aboveground phytomasses of arctic meadows on Truelove Lowland where brown lemmings do not occur are about five times as great as corresponding values from Barrow which is within the range of the brown lemming. The combination of Barrow data and data from tundra communities on Hardangervidda with primary production less than 600 gm^{-2} yr^{-1} shows no significant correlation between aboveground phytomass and primary productivity, whereas a weak positive trend is obtained from Truelove Lowland where the herbivore trophic level is impoverished. Data from Kilpisjärvi suggest an 8.4-fold increase in moss phytomasses during 7 yr of low

lemming densities. Both the geographical patterns and the short-term dynamics at Kilpisjärvi are in full agreement with the predictions of the hypothesis.

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