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**THE BOREAL
ECOSYSTEM**

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made. Nevertheless, the temperature of the black lichen-covered downed *Picea mariana* twigs was still 50°C, one reason why the fire hazard can become intense in such areas. Temperatures steadily declined toward ground level, and the influence of permafrost not far below the surface (actual depth at the site unknown) can be seen in the 3°C temperature under the roots of a *Picea mariana* tree—a temperature at which physiological activity would obviously be slow. It is apparent, also, that this temperature is rarely if ever exceeded for roots of *Picea mariana* trees growing in the area. Not more than 30 mi to the north, *Picea mariana* trees no longer dominate the landscape, and the species is found only in protected valleys (Larsen, 1965, 1974a; Elliott, 1979). The low temperatures obviously also will have an influence upon the growth and development of the species making up the ground cover and upon the mortality of seedlings, although detailed information on such matters is as yet lacking.

Forest fires occur most often in areas such as this, where temperatures of aboveground plant parts and low atmospheric humidity lead to severe desiccation. Most fires are caused by a lightning flash that ignites both lichen mat and tree branches. The trees are almost always killed, and the lichen mat is consumed. If the fire is intense, or if reburning occurs, the organic layer of the soil will be destroyed. The effect on both vegetation and the physical environment is profound. Rouse (1976), for example, made microclimatic measurements at four sites, burned 0, 1, 2, and 24 years previously, and compared them with measurements for a control site of mature, open *Picea*-lichen woodland. The measurements showed a substantial change in radiation absorbed over the recently burned surfaces, and soil temperatures were much higher at the burn sites during the growing season. Most striking was the decrease in albedo, leading to increased absorption of solar radiation, creating very high temperatures over the burned surfaces. There was a long-term increase in summer surface temperatures of as much as 14°C. The surface temperatures rose as high as 65°C over fresh burns, and diurnal temperature changes were extreme—up to 46°C. Soils of unburned forest start the growing season wetter than the soils of burned areas.

CLIMATE AND SPECIES DISTRIBUTION

All the studies described above point to the fact that minor variations in topography and vegetational community composition and structure can, indeed, be correlated with variations in climatic parameters. It is apparent, furthermore, that studies of the relationships between climate

and vegetational communities yield pertinent ecological information, not only in terms of plant ecology but in terms of the bioclimate of the animal inhabitants of the forest as well. Thus, Pruitt (1957, 1959, 1978), for example, has conducted much work on the bioclimate of the subarctic environment, as well as on the effects of low temperatures and snow cover on larger mammals in northern regions; he states that animals and plants can scarcely be considered separate entities in boreal regions, since changes in plant cover result in habitat modification as a result of the changes in soil temperature. Moreover, successional development of vegetation, especially of a thick moss layer, results in colder soils; frozen soil prevents water percolation, resulting in wetter soils, inhibition of tree growth, and markedly changed conditions for animal life. It seems obvious that temperature is the single most important factor limiting the growth and development of vegetation in boreal regions, and four temperature-dependent physiological processes are most important in this relationship (Warren Wilson, 1967): (1) translocation, which is not greatly affected by temperature under normal temperate-zone conditions but which is markedly checked when plants are chilled to 0°–5°C; (2) water absorption, which is affected similarly; (3) rate of photosynthesis, which increases roughly 50% with an increase in temperature from 0° to 1°C, while an equal increase in photosynthetic rate is achieved only by a 10°C increase in temperature from 20°C; and (4) rate of respiration, which is slow at low temperatures and increases steadily with a rise in temperature. If the rate of respiration exceeds that of photosynthesis, a plant eventually will run out of its store of carbohydrate and will be incapable of further growth or of reproduction. When photosynthesis exceeds respiration, sugar and starches are manufactured, stored, and used in growth, flowering, and production of seed. Temperature must often establish upper limits to growth in northern regions. It is, ultimately, gene structure that establishes the tolerance limits of a plant species, and it seems likely that distribution of a plant species in northern regions is not simply a response to frost but is conditioned by many specific temperature-dependent requirements (Warren Wilson, 1967). Illustrative of the complexity of physiological response to the environment is the work of Hickleton and Oechel (1976, 1977) with the moss *Dicranum fuscescens*, specifically in relation to the acclimation and acclimation potential of the carbon dioxide exchange mechanism in relation to habitat, light and temperature. This and other work indicate the importance of photosynthetic acclimation in the distribution of plant species in arctic and subarctic environments (Kershaw and Rouse, 1971; Larson and Kershaw, 1975; Büttner, 1971; Billings and Mooney, 1968).

on the rates of primary production and energy flow. Plant succession on areas burned by wildfire in southern central Alaska followed a variety of patterns, resulting in the creation of a useful moose winter range for a period of at least 50 years. Under average conditions, stands appeared to furnish good forage for 15–20 years after the fire.

Preliminary analyses of the plant-moose-wolf food chain of Isle Royale National Park show that the weight of vegetation consumed by the herd of moose was about 3000 tons annually and that their wolf predators consumed about 45 tons of moose. From the bottom to the top of the pyramid in terms of energy content, the following was estimated: plants, $11,000,000 \times 10^3$ kcal; moose, $46,000 \times 10^3$ kcal; wolves, 780×10^3 kcal.

Jordan *et al.* (1971) analyzed the population and biomass dynamics of the moose of Isle Royale by constructing a simple model from which calculations were carried out by digital computer. The model assumed that the annual pattern of population and biomass dynamics remained constant throughout the 10-year study period. They concluded that, strictly in terms of the quantity of transfer of flesh from moose to wolves, this represents an inefficient cropping system, because a large portion of biomass is maintained for many years before it is harvested. The observed low ratio of wolf population biomass to moose population biomass is related in part to the slowness of turnover in the moose. While this model did not test the impact of environmental changes or feedback processes, it appears to be a useful tool for summarizing data and for evaluating assumptions about the ecosystem (Table 38).

TABLE 38
Weights of Consumed Vegetation and of the Moose and Wolf Populations of Isle Royale National Park^a

Area of Isle Royale	544 km ²
Wolf population weight (in midwinter)	812 kg (24 average wolves)
Moose population weight (in midwinter)	367,000 kg (1000 average moose)
Weight of moose killed by wolves per year	61,200 kg (taking as a maximum estimate; 90% of moose dying per year are killed or eaten by wolves)
Weight of vegetation eaten by moose per year	22,000,000 kg
Weight of moose killed by each wolf per year	2550 kg (7 kg/day; not all of which is consumed since a large portion—bones, etc.—is inedible)
Portion of vegetation going into wolf population per year	0.003%

^a Data from Jordan *et al.* (1971).

THE WOLVERINE AND WOLF COMPARED

An example of a predator that has probably a minimal influence on the vegetation, even indirectly, perhaps largely because of its low population density, is the wolverine, one of the most poorly known of the larger carnivores of Canada, a fact reflected by the dearth of information in the literature on the species (van Zyll de Jong, 1975). The species is reported to still occur in Labrador, Quebec, western Canada, and Ontario, but there have been no recent reports of wolverines from Labrador or Newfoundland.

Wolverines normally occur at relatively lower densities than other carnivores of comparable size; data on densities are not easily obtained, but estimates for Scandinavia vary from one wolverine per 200–500 km² (approximately 193 mi²). For comparison, estimates of wolf densities in North America vary up to one wolf per 26 km² (10 mi²) for high-density areas. These estimates indicate that wolverines tend to be less abundant than wolves even in optimum habitats. There seems to be a low rate of natural increase incapable of compensating for losses due to human hunting and trapping.

Studies of food habits show that the wolverine is an omnivore in summer, feeding on a large variety of food including carrion, small mammals, insect larvae, eggs, and berries. It is a carnivore in winter. Herbivores, especially caribou, the most numerous large herbivore over most of the wolverine's range, are the most important winter food. Most of the large herbivores eaten are thought to be carrion, resulting from predation by other carnivores or death from other causes.

The wolverine can be regarded as a seasonal scavenger on the fringe of the food web. The distribution and abundance of wolverines in Manitoba coincides with that of the barren-ground caribou in winter (van Zyll de Jong, 1975). In the mountain ranges of Alberta, British Columbia, and the Yukon, wolverines are still common, and large and diverse ungulate populations occur.

Wolves are large and formidable predators. The weight of individual animals varies from 30 to 60 kg. The adult male takes an active part in the rearing and training of the young. Although in summer the wolf supplements its diet with vegetable matter such as grass, roots, and berries, in winter, hunting is the source of by far the largest proportion of the food supply, and several families may join together in a single hunting pack.

The diet of wolves on the winter range of the barren-ground caribou in open spruce forest of southern Mackenzie was estimated by Kuyt (1972) to be made up of about 75% caribou, the staple food, with the remainder consisting of otter, wolf, wolverine, mink, fish, and other

substances. In summer, their diet is somewhat lower in caribou, about 40%, with more birds, rodents, fish, squirrels, and microtine rodents being consumed. Kuyt calculated that a wild wolf will eat about 7 lb of meat a day, on the average, which comes to about 23 average caribou a year. This, on the basis of reports from other sources compiled by Kuyt, can be compared with the diet of wolves of other areas presented in Table 39. Wolf densities of as high as one wolf per 7 mi² occur locally at times in winter in areas where caribou are concentrated.

In the open forest caribou range in northwestern Manitoba, in inhabited areas the density of caribou increased from 14 to 68 animals per square mile from January to April; this occurred as the animals congregated in smaller areas. The highest wolf density was about one wolf per 8 mi², although the average density was about one per 14 mi²; the latter density was in January, when the animals were dispersed over about 3600 mi², and a lowered wolf density was found in April when the caribou range had contracted to about 680 mi². It seemed that the lowered wolf density in late winter, when the caribou were most concentrated, was the result of the wolves being forced to avoid the forest because of deep snow (and stay on lakes or in areas that had been blown clear of snow) or to leave the area to seek denning sites in preparation for the whelping of cubs (Parker, 1973).

ROLE OF INSECTS

At the other extreme from the large carnivores in terms of individual size, but probably far more significant in terms of biomass, are the insect populations of the boreal ecosystem. Insects damage plants in a variety of ways and reduce their photosynthetic capacity, hence net primary production, by sap consumption, consumption of tissues, and damage to reproductive organs, all of which produce effects that are cumulative and lasting, particularly if the insect populations are high and the damage is appreciable. Fortunately, however, except for a relatively few forest pests, most insects occur in comparatively small numbers and have little effect upon the growth of plants. Large numbers of defoliators injure trees by reducing photosynthesis and interfere with transpiration and translocation. In conifers, photosynthesis is affected by the absence of foliage for up to 3 or 4 years. On the other hand, it appears that the rate of normal insect grazing usually does not impair annual plant (primary) production; it may even accelerate growth. Although outbreaks do reduce plant production temporarily, they commonly occur in individual plants or in whole forest systems that have passed peak efficiencies in biomass production (Mattson and Addy, 1975).

TABLE 39
The Diet of Wolves: Data from Various Sources

Region	Source	Ungulate prey	Other
Mt. McKinley, Alaska	Murie (1944)	69 (caribou)	31
Rocky Mts., Canada	Cowan (1947)	80 (big game)	20 (rodents)
Northern Wisconsin	Thompson (1952)	90 (white-tailed deer)	10 (showshoe hare)
Northern Minnesota	Stenlund (1955)	90 (white-tailed deer)	10 (small mammals)
Algoma Park, Ontario	Pimlott <i>et al.</i> (1969)	Mostly white-tailed deer	Secondly beaver
Southern Alaska	Merriam (1964)	95 (black-tailed deer)	5
Northwest Territories	Kelly (1954); Banfield (1954); Kelsall (1960)	Ca. 100 (caribou)	
Mackenzie forest, winter	Kuyt (1972)	75 (caribou)	25 (see text)
Mackenzie tundra, summer	Kuyt (1972)	40 (caribou)	60 (see text)

* Most important item when noted in report.