sumably came from the marine organisms thriving in the overlying surface waters. The average value for these sediment samples is -24.6 per mill, an indication that the sedimentary organic carbon in this area is also enriched in C^{12} relative to the organic carbon deposited in warmer areas, δ being about -20 per mill (*3, 4*). Thus it now appears that the isotopic carbon composition of marine organic sediments can be controlled by two major factors: the amount of terrestrially derived organic carbon, δ being about -27 per mill (*3*), or the amount of cold- or warm-water marine plankton preserved in the sediments, or both.

These plankton isotopic compositions suggest another plausible explanation for the carbon isotope composition of petroleum—average being about $\delta -28$ per mil (*8*). This explanation is that many oils may have been formed with little carbon isotope fractionation from organic carbon of the composition now found in cold Antarctic waters. If some factor other than temperature determines the composition of marine plankton, then perhaps present-day isotopic compositions of cold-water plankton were present in ancient warm seas where most organic carbon sources of petroleum were presumably deposited.

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Polyploidy and Environment in Arctic Alaska

Abstract. *The frequency of polyploidy in the angiosperm flora of the Ogotoruk Creek–Cape Thompson area of northwestern Alaska is correlated with edaphic environmental gradients in the area. These results, when placed in a historical and ecological context, help to clarify the problem of increasing frequency of polyploidy with latitude in the northern hemisphere.*

The observations that the frequency of polyploidy in angiospermous plants increases along a south-to-north latitudinal gradient in Europe (*1*) and that the polyploid members of a euploid complex sometimes occupy environments different from those of their diploid relatives (*2*) have led some workers to claim that polyploidy enables plants to occupy extreme environments. Subsequent investigations (*3*) have not generally supported this conclusion, though some workers maintain (*4*) that the Arctic and sub-Arctic regions are exceptions. The high frequencies of polyploid taxa in these regions have been linked alternatively to the observation (*5*) that polyploids had a marked advantage in colonizing bare ground after the retreat of the Pleistocene ice sheets. With this line of reasoning it is presumed that at more northerly latitudes the initial high frequency of polyploids colonizing the previously glaciated land surface has been largely unaffected by the influx of diploid migrants that have, in later postglacial time, significantly reduced the polyploid frequency in such areas at lower latitudes, the reasons given being an insufficient period of time for migration to occur and the present climatic regime (Reese, *3*).

Both these approaches to the problem of polyploidy and plant distribution require explanations in terms of supposed special genetic attributes in polyploids, but such explanations may provide only partial solutions. Many workers appear to have overlooked the fact that the distribution of polyploids is affected by such things as their time and place of origin, migration routes, past and present climates, location of refugia, and all the other factors (including genetic make-up) that affect plant distribution. The present trend (*6*) of studying the distribution of polyploids within a broader phytogeographical framework should lead to a more complete understanding of the problems.

In 1962, we began cytological studies of the angiosperm flora of the Ogotoruk Creek–Cape Thompson area (68°06′N;165°46′W) of northwestern Alaska. In this report we relate the polyploid frequency of the angiosperm flora to the history and ecology of the area and discuss some of the problems raised above in the light of our data.

The Ogotoruk Creek Valley covers about 110 km^2 of extensive tundra flats and low mountains up to slightly more than 325 m. Mudstone, sandstone, dolomite, limestone, chert, and argillite of Mississippian to Cretaceous age are the most common bedrocks. The area was unglaciated, but unconsolidated Quaternary sediments 6 to 18 m thick cover about 50 percent of the area (*7*).

The climate is typical of the western Arctic; winter temperatures reach −40°C and mean summer maximum temperatures are above 10°C only during July. Precipitation averages about 20 cm, most of it occurring in summer. Snowfall is light and is redistributed into extensive beds of snow by strong winds which average 36 km/hr in the winter. Wind velocities during summer average 22 km/hr (*7*). Permafrost extends to depths over 300 m, and its upper boundary lies close to the soil surface (*7*).

Temperature and precipitation are relatively constant throughout the valley, and plant distribution depends primarily on edaphic factors. Soil texture varies considerably from the lowlands, where fine-grained mineral fractions and organic materials predominate, to the slopes and ridgetops where 20 to 40 percent of the soil mass consists of coarse angular rock fragments (*8*). Other soil characteristics are correlated with the topographic and textural gradients. Soil moisture is high in the lowlands, low on the slopes and uplands (*9*). Permafrost at depths of less than one-half meter maintains low soil temperatures on the valley floor, while on steeper topography, permafrost is deeper (about 2 m) and soil temperatures are higher (*10*). Frost action is correlated with fine-grained soils, low temperatures, and high soil moisture, and is, therefore, most intense in the Quaternary sediments of the valley floor (*8, 11*). In summary, cold, wet, organic, or fine-grained mineral soils of lowland areas in which permafrost and frost action play important roles are found at one extreme of several environmental gradients; at the opposite extreme are the coarse, well-drained, warmer soils of upland areas in which permafrost and frost action are relatively unimportant.

The environmental gradient scale (Fig. 1) is based on both physical and biological data from this area and is supported by data from similar areas (*12*). Points on the gradient scale (Nos. 1–6 in Fig. 1) correspond to places where the data suggest significant environmental discontinuities. These points are usually associated with topographic breaks and are most easily identified in nature by changes in the vegetation. Most of the species at Ogotoruk Creek occupy only one or two points on the gradient scale, and once their distributions have been correlated with environment, they may be used, to some extent, as environmental indicators. For example, the distributions of the following pairs of species correspond to the numbers on the gradient scale: 1, *Andromeda polifolia, Pedicularis pennellii;* 2, *Carex aquatilis* s.1, *Eriophorum angustifolium;* 3, *E. vaginatum, Ledum decumbens;* 4, *Carex bigelowii, Oxytropis mertensiana;* 5, *Dryas octopetala, Arenaria arctica;* 6, *Dryus octopetala, Pedicularis lanata.*

Polyploidy is correlated with distribution and environment (Fig. 1) by grouping the taxa according to their habitats (Nos. 1–6) and then calculating the frequency of polyploidy in each group. We have made similar calculations for plants of habitats which are insufficiently known to place them on the gradient scale, for example, snowbeds, gravel bars, and the marine strand. In general, the frequencies of polyploids in these three habitats correspond to values expected from our incomplete evaluation of their physical characteristics.

The angiosperm flora of the Ogotoruk Creek Valley includes 291 taxa. In our statistical comparisons of polyploid frequencies (Table 1; Fig. 1) we have not included the Cyperaceae (23 species) as is more or less customary in this kind of study because of their exceptional karyology. Of the remaining 266 taxa, 234, or 88 percent, have been examined cytologically; we have utilized chromosome counts from the literature for 24 taxa, while the polyploid levels of 8 taxa are unknown.

There are nine species which some workers consider as diploids, others as polyploids. We have assigned these doubtful cases to polyploid categories for comparative purposes, but the numbers in brackets (Table 1) illustrate their effect on frequency if all are considered as diploids.

Polyploid frequencies in both monocotyledonous and dicotyledonous plants (Fig. 1) are highest in wet lowland habitats and lowest on the well-drained slopes and uplands. The lower polyploid frequency at point two on the gradient scale as compared to point three is due to a small group of diploid dicotyledonous species growing on relatively stable peaty ridges in this environmental regime, a situation which does not occur in habitat three. This emphasizes that our idealized environmental gradient scale can be related to existing conditions in the Ogotoruk Creek Valley.

The polyploid frequency of the Ogotoruk Creek flora is lower than that of any European flora of equivalent latitude yet studied, a point which is probably related to the different Pleistocene histories of the two areas. Northwest Alaska, unlike northern Europe, was never glaciated, and the present flora is probably not fundamentally different from the pre-Pleistocene flora. This, together with the demonstrated high frequency of diploid species in surviving Tertiary floras (*6*), allows us to relate the relatively high frequency of diploid species in the Ogotoruk Creek flora to the survival of a large Tertiary element.

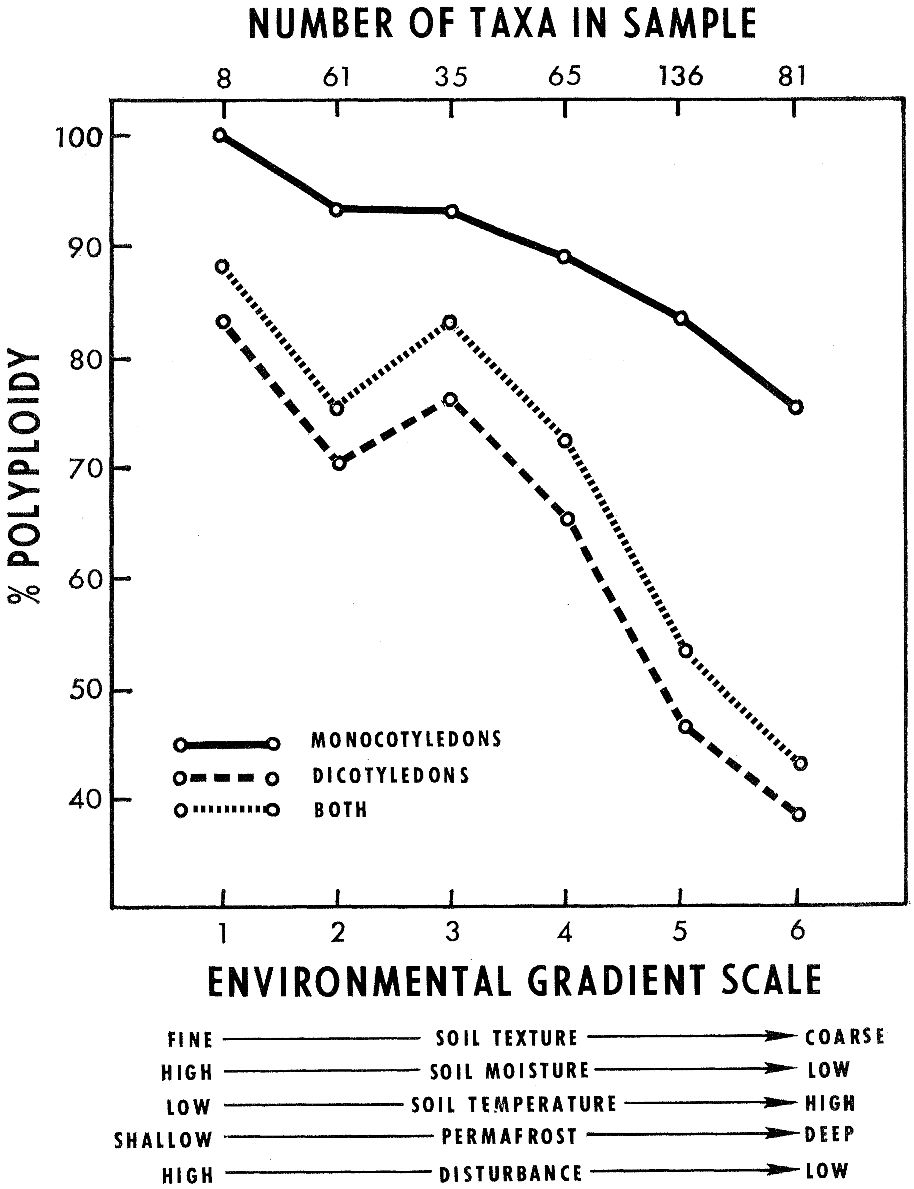

Fig. 1. The relationship of the frequency of polyploidy in the angiosperm flora of the Ogotoruk Creek Valley, Alaska to environmental gradients.

However, if as we suggest, the survival of Tertiary taxa accounts at least in part for the difference in polyploid frequency between northwestern Alaska and northern Europe, it is necessary to explain why the extinction of diploids in northern Europe was relatively greater than that of polyploids. In this connection we regard the historical interpretation of Fig. 1 as highly significant; the interpretation may also provide some indication of why, even in an unglaciated part of the Arctic, polyploid dicotyledons are as numerous as the diploids and polyploid monocotyledons far more abundant than diploids.

The climatic deterioration of the Tertiary Period in the northern hemisphere caused extensive southward migrations of species (*13*). At the same time, species adapted to habitats of restricted distribution, such as alpine fell-fields and bogs (*14*), extended their ranges into qualitatively similar and increasingly widespread habitats as climatic deterioration continued. Habitats which had not previously existed, such as those in which permafrost plays a role (*15*), also appeared. By Quaternary time, the better-known elements of the Arcto-Tertiary Flora and their habitats (*13*) became virtually nonexistent at higher latitudes.

We have shown a close correlation between habitat and frequency of polyploidy (Fig. 1) as has been found in a few previous studies (*16*). At Ogotoruk Creek, the most stable habitats occur on slopes and uplands, which, we suggest, are probably the least modified of all Tertiary habitats in the Arctic. This is supported by the fact that the majority of diploids grow there. Though polyploids grow there too, they occur in their highest frequencies in the cold, wet, unstable soils which we believe to be the most recent habitats, or at least those most modified by Quaternary events. Thus, the frequency and distribution of diploid and polyploid taxa in the Ogotoruk Creek Valley depend on the survival of Tertiary diploid and polyploid species and the more successful exploitation by polyploid species of habitats most directly affected by the climatic deterioration.

In northern Europe, species survived in unglaciated areas, and those least changed by the periglacial climates supported the largest percentage of Tertiary diploid and polyploid species, just as they do today. In areas escaping glaciation but nevertheless severely affected by the climatic and geomorphic changes, the formation of habitats toward the disturbed end of the environmental gradient scale must have occurred. Such conditions favored the survival of polyploid species. If this were the case generally, the preferential survival of polyploids during the Pleistocene must be a significant factor in the high frequencies of polyploidy in northern Europe (*4*). In our opinion, however, the polyploid frequency of glaciated areas has been accentuated by the immigration of newly formed or existing polyploid taxa which were successful pioneers on newly exposed glaciated surfaces. With continued climatic amelioration, diploid and polyploid immigrants from refugia or from south of the glaciations have changed the polyploid-diploid ratio (*5*). Under the present climatic regime where periglacial habitats exist at high latitudes, the latitudinal gradient of polyploidy may have reached equilibrium.

Table 1. Polyploid frequencies in the Ogotoruk Creek Flora. Values in parentheses were calculated by considering all ambiguous cases as diploids.

Group	Species known	Species known cytologically (No.)		Diploids		Polyploids	
		Total	From Ogotoruk Creek	No.	%	No.	%
Monocotyledons	52	52	40	8 (9)	15.4 (17.3)	44 (43)	84.6 (82.7)
Dicotyledons	214	206	194	97 (105)	47.1 (51.0)	109 (101)	52.9 (49.0)
Totals	266	258	234	105 (114)	40.7 (44.2)	153 (144)	59.3 (55.8)

It has been suggested that the superiority of polyploids in exploiting bare ground in the North is due to their greater genetic variability (*4*) or to their greater ecological adaptability (*5*). We believe that a separation of the two is artificial, just as it is artificial to separate diploids and polyploids when considering genetic variability and adaptability. The problem in northern latitudes is, why are there more genetically variable polyploids than comparable diploids? The answer appears to be, as Manton (*17*) suggested, that polyploids are at a selective advantage in those conditions where climatic fluctuations have been frequent and often catastrophic. We would expect new polyploid taxa, in which genetic variability is great as a result of recent hybridization, to be among the most successful in adjusting to changing conditions. In the absence of genotypic adjustment, migration or extinction inevitably occurs. In either case, old established species are eliminated from the affected area, leaving behind only the old species sufficiently rich in biotypes to adjust and the newly formed polyploids.

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