Comparative Physiological Ecology of Arctic and Alpine Populations of Oxyria digyna

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COMPARATIVE PHYSIOLOGICAL ECOLOGY OF ARCTIC AND ALPINE POPULATIONS OF *OXYRIA DIGYNA*

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INTRODUCTION

Tundra environments provide extremely severe conditions for plant growth. They are characterized by a short cold growing season of two to three months and a long bitter winter. In North America, such environments occur from the northernmost parts of Greenland, Canada, and Alaska along the mountain crests as far south as Mexico. Gradients of latitude and elevation throughout this extensive range create significant environmental differences between the arctic tundra of the north and the alpine tundra of the south. Length of photoperiod, amount of ultraviolet radiation received, wind force, and magnitude of diurnal temperature fluctuations are outstanding dissimilarities between the superficially similar environments. Bliss (1956) has called attention to these differences, and many others of a lesser magnitude, in his comparison of microenvironments and plant development in arctic and alpine tundras.

In spite of these environmental gradients, certain arctic-alpine plant species are widely distributed throughout the tundra regions of the northern hemisphere. These plants are low elevation-circumpolar in the north and high elevation-alpine in the great mountain systems of temperate North America and Eurasia.

The question arises, "How are arctic-alpine species able to grow in such diverse environments?" Are they so ecologically plastic that any given member of each population would be able to tolerate all of the possible environmental combinations presented by arctic and alpine habitats? Or, are these species composed of ecological races or ecoclines, each adapted to different aspects of the tundra environment?

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Either solution is theoretically possible, as is a combination of both. Up to now, there has not been enough available evidence to answer either question. However, the results of Turesson (1930) and Clausen, Keck & Hiesey (1948) with wide-ranging species in more temperate environments would tend to favor the second solution.

In an attempt to answer such questions, the environmental requirements of a series of arctic and alpine populations of a selected species, *Oxyria digyna* ("alpine sorrel"), were investigated. The primary emphasis was on possible morphological and physiological differences between these populations under the impacts of different environments. Of particular importance was the study of those physiological characteristics which might be of adaptive significance. Such an approach should be able to determine if the environmental differences between arctic and alpine habitats are reflected, through natural selection, on the physiological responses of the principal biotypes in the local populations of the species.

FIG. 1. *Oxyria digyna* in rocky talus at an elevation of 10,200 ft, Beartooth Mountains, Wyoming.

Oxyria digyna (L.) Hill (Fig. 1), a perennial, herbaceous member of the Polygonaceae was selected for this study for several reasons. (1) It has a circumboreal arctic-alpine distribution of wide latitudinal range. It occurs in the arctic tundra as far north as 83° N, and in North America as far south as Arizona in the mountains. (2) A considerable body of information on the physiological processes of this species, in the field, has been assembled (Wager 1938, 1941; Russell 1940b, 1948; Warren Wilson 1954, 1957, 1959, 1960). These studies were almost entirely confined to arctic populations. (3) The seeds of Oxyria are easily collected and germinate well. Plants can be grown without difficulty and provide excellent material for physiological investigation. (4) There are few taxonomic difficulties associated with this phylogenetically isolated species. Polunin (1940) has called Oxyria one of the few really "good" arctic species, varying from place to place only in size of leaves and height of inflorescences. There is, however, one major difficulty associated with this species. It is not particularly suited for hybridization experiments because of the large numbers of small delicate flowers in the inflorescence. A further complication to such work is the partial apomixis in this species which has been described by Edman (1929).

Utilizing the data of Hultén (1928), the general distribution of Oxyria is arctic-alpine circumpolar, with disjunct locations far to the south in the mountains of Europe, Asia, and North America.

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FIELD METHODS

HABITATS DESCRIPTION

During the summer of 1957 and 1958, a latitudinal series of *Oxyria digyna* plants was collected. These arctic and alpine populations were selected to encompass a wide geographic range of tundra habitats. Elevations ranging from sea level to over 12,000 ft and latitudes extending from 38° N to 76° N were included in the population sites. Accessibility of each collection area necessarily determined its exact locale. The locations of these populations in relation to the North American distribution of Oxyria are shown in Figure 2.

FIG. 2. North American distibution of *Oxyria digyna* from data of Fernald (1933) and Porsild (1957). Numbers refer to areas from which populations were collected: 1. Elephant's Back, California, 2. Loveland Pass, Colorado, 3. Niwot Ridge, Front Range, Colorado, 4. Medicine Bow Mts., Wyoming, 5. Beartooth Mts., Wyoming, 6. Logan Pass, Montana, 7. Highwood Pass, Alberta, 8. Sunwapta Pass, Alberta, 9. Summit Lake, British Columbia, 10. Donjek Mts., Yukon Territory, 11. Eagle Summit, Alaska, 12. Pitmegea River, Alaska, 13. Sagavanirktok River, Alaska, 14. Pt. Barrow, Alaska, 15. Thule, Greenland, 16. Angel Glacier, Alberta.

The site of the most abundant occurrence of Oxyria within each study area was chosen as the local population site. Mass herbarium collections were made and notes on the extent and characteristics of the population were taken. At most sites, the percentage coverage of Oxyria and the associated species was quantitatively determined. This was done for a 5 x 5 m square by crossing two diagonal 7.1 m lines within the microsite. The vegetation was sampled by point intercepts at 5 cm intervals along these lines. This made a total of 283 points along the diagonals of the 25 sq m area.

Seeds and/or live plants were collected at each site. The live plants were sent by airmail to North Carolina for greenhouse culture. Soil samples of the upper mineral soil horizons at each location were collected for later analysis.

Unfortunately, uniformly complete information is not available from all the population sites since the collection of seeds or plant material by some contributors was incidental to other tasks in which they were engaged. However, the available data on sites actually visited by at least one or both of the authors make it possible to get some idea of the environment and associates characteristic of Oxyria populations in widely scattered parts of its range.

FIELD PHYSIOLOGICAL METHODS

During the summer of 1958, it was possible to carry out a few physiological measurements in the field on two alpine Oxyria populations. On one population, Medicine Bow Mts., Wyoming, the carbohydrate content of the leaves and the roots was followed during the course of the growing season. Photosynthesis and respiration rates were measured and leaf chlorophyll content analyzed. On an Alaskan alpine population, Eagle Summit, the carbohydrate content was measured at a single phenological stage and chlorophyll determinations were made.

A Model 29 Liston-Becker Infrared Gas Analyzer (Beckman Instruments, Inc.) was utilized for all photosynthesis and respiration measurements in this study. This model is operated with a six-volt battery, and hence can be used in the field. An Esterline-Angus Model AW direct current milliameter was used as the recording device.

An open system, as described by Billings, Clebsch & Mooney (1960b), was used for field photosynthesis and respiration measurements. The method consisted of making alternate measurements of the CO_2 content of a gas stream passing over a plant enclosed in a plexiglass chamber and of a "free" air stream. Calculations of the photosynthetic and respiration rates were based on the difference between the CO_2 contents of the two streams with the gas flow rate maintained at 80.6 l/hr.

The plant stream was measured for 15-minute periods, alternating with 5-minute periods for measurement of the air stream.

The analyzer was calibrated prior to each test period by flushing the calibration system free of CO_2 by use of an absorbent (Ascarite) in the air stream. Then, definite aliquots of pure CO_2 were injected into the closed calibration system by means of a hypodermic needle. A calibration curve was constructed to indicate mg CO_2/l.

Petioles of 8 to 10 Oxyria leaves (attached to a single rooted plant) were inserted through a slotted plexiglass base plate and sealed in place with Apiezon "Q" type sealing compound. A one liter plexiglass photosynthetic chamber was then sealed on top of the base plate, thus completely enclosing the leaves. During the course of a test period a continuous record of the radiation received was recorded with an Instruments Corporation Recording Pyrheliometer. The temperature was measured at 5-minute intervals inside and outside of the photosynthetic chamber using shielded mercury-in-glass thermometers. Light intensity in foot candles was read on a photoelectric illumination meter (Weston Electrical Instrument Corp.) at 5-minute intervals.

An attempt to control excessive temperature build-up within the chamber was made by placing a Corning infrared glass filter, CS1-69 no. 4600 M-2040, so that it intercepted the direct solar radiation. Also, snow was packed around the base of the chamber, which not only helped in temperature control but prevented moisture condensation on the upper chamber surface.

Two test runs were completed on Oxyria, the first, of 1 hr duration on leaves of a plant in early flower bud stage on July 9, and another of 2 hrs duration on a plant in late flower bud stage on July 22. At the conclusion of each run, the chamber was covered with a black cloth for a ten minute period for determinations of dark respiration.

From the milliameter recordings, calculations of the photosynthetic rate of 1.5 minute intervals were made and expressed on three bases: per gm of fresh weight per hr, per sq dm of leaf surface (twice the area of the leaf) per hr, and per milligram of total chlorophyll per hr.

The procedure used for carbohydrate extraction and analysis has been previously described (Mooney & Billings 1960) and is comparable to the procedures of Russell (1940b) and Warren Wilson (1954). Samples of the upper tap root and leaves were taken at definite phenological stages and analyzed in triplicate for starch and total sugar, the sum of which was considered "total carbohydrate."

Determinations were made of the total nitrogen content of the alcohol-insoluble residues by the method of Block & Bolling (1951) on all the samples taken for carbohydrate analysis.

Samples of Oxyria leaves were collected from the Medicine Bow Mts., Wyoming, and Eagle Summit, Alaska, for chlorophyll determinations. The fresh weight of the sample was taken, the leaf outline traced, and the sample placed in a green vial containing 80% acetone. These were used later for determination of chlorophyll content by the spectrophotometric method of Arnon (1949).

LABORATORY METHODS

All plants used in laboratory experimental work were grown from field-collected seed. The plants were grown in a standard greenhouse soil mixture (two parts loam, one part leaf mold, and one part sand) in 4-inch clay pots. These plants were maintained either in the greenhouse or in especially constructed growth chambers, watered daily, and fertilized with a "complete" liquid fertilizer at regular intervals.

GROWTH CHAMBER DESIGN

Plants utilized for laboratory physiological measurements and for detailed analysis of growth and phenological development were grown in controlled-environment growth chambers. These low-temperature growth chambers constructed from "island-type" display freezer units have been described by Billings, Clebsch & Mooney (1960a). It was possible to control and cycle both temperature and light periods in the chambers enabling a simulation of temperature and light cycles in natural tundra environments.

CHAMBER PROGRAMMING

Three growth chambers were utilized for experimentation. One chamber was used to simulate the diurnal cycle of an alpine environment at a latitude of approximately 41° N. The day temperature was controlled at 65° F for a 12-hr period and the night temperature at 40° F for an equal time. A 15-hr photoperiod was maintained. These values were selected to represent average alpine mid-summer conditions in the Medicine Bow Mts., Wyoming, as measured by Bliss (1956). This simulation of the environment involved control of only thermoperiod and photoperiod.

A second chamber simulated growing season conditions of the Alaskan Arctic Coastal Plain at 71° N. The day temperature was kept at 55° F and the night at 35° F, both for alternating 12-hr thermoperiods. This chamber was constantly lighted.

The two chambers described above will be referred to as the "alpine" and "arctic" chambers, respectively, throughout the text.

A third chamber was used first at a constant 50° F temperature and 12-hr photoperiod. Later, the same temperature was maintained but the photoperiod was changed to 17 hrs. This will be referred to as the "constant temperature" chamber.

CHAMBER UTILIZATION

Two separate sets of plants were placed consecutively in the chambers during the duration of the project. Each set consisted of either 4 or 5 different populations, usually 10 plants to the population, in each of the 3 chambers. At weekly intervals, each plant was scored for phenological development and the inflorescences of fruiting specimens were harvested and pressed. In addition to recording phenological development, growth measurements were made at regular periods on one set of populations.

Almost all plants utilized in the laboratory for physiological measurements were taken directly from chambers for use. Exceptions to this procedure will be noted in the text.

PHOTOSYNTHESIS AND RESPIRATION MEASUREMENTS

For the laboratory, a "closed" system was designed for use with the infrared gas analyzer. It was not possible to utilize the "open" system that was employed in the field because of the rapidly fluctuating CO_2 content of the semi-urban air. A plant was placed in a closed system of known CO_2 concentration and the time was measured for a given amount of CO_2 to be added to or removed from this system. In actual practice, the operating range was .0285 to .0315% CO_2 in the air stream.

In the laboratory, it was possible to control the temperature of the air within the photosynthetic chamber. A thermistor inside the chamber was utilized as the sensing element for a Yellow Springs Instrument Model 71 Temperature Controller. The controller was attached to an ice-water compressor thus maintaining the water at any pre-set temperature. The water from the cooler was circulated around the photosynthetic chamber by use of a water pump.

Four 300-watt incandescent "sealed beam" spot lights were used for both a light and a heat source in the system. Illumination at the base of the photosynthetic chamber could be maintained from 0 to 7,000 fc by use of switches and a rheostat.

The standard air flow rate used in all laboratory gas exchange measurements was approximately 170 l (6 cu ft) per hr.

DESCRIPTIONS OF ARCTIC AND ALPINE *OXYRIA* HABITATS

The similarities and differences of the principal Oxyria habitats investigated throughout a wide range of latitudes are presented in the following section. The location, elevation, exposure, parent material, some of the soil characteristics, and associated species are given for these Oxyria microsites.

GENERAL HABITAT DESCRIPTIONS

Elephant's Back, California. The only Oxyria population collected from the Sierra Nevada was located in Alpine County, California, south of Carson Pass (38° 42′ N, 119° 57′ W). Collections were made at this site on August 15, 1957. Oxyria plants were growing on the very steep northeast-facing talus of Elephant's Back at an elevation of 9,100 ft. The talus, which is composed of volcanic andesitic breccia, is a site of very late snowmelt. The microsite is scantily vegetated with Oxyria as well as *Agropyron pringlei* (Scribn. & Sm.) Hitchc., *Arabis lemmonii* Wats., *Arenaria nuttallii* Pax., *Lupinus lyallii* Gray, *Penstemon heterodoxus* Gray, *Phacelia frigida* Greene, *Ranunculus eschscholtzii* Schlecht. var. *oxynotus* (Gray) Jeps., *Senecio fremontii* T. & G. var. *occidentalis* Gray, and *Calyptridium umbellatum* (Torr.) Greene.

Loveland Pass, Colorado. This population was collected at an elevation of 12,300 ft in the Loveland Pass area of Colorado (39° 40′ N, 105° 53′ W). The microsite is situated on a northwest-sloping (25°) granitic boulder field. Oxyria is restricted to rock crevice areas within the boulder field, although in the general area it is also found on gravelly, otherwise unvegetated areas, such as road fills and drainage ditches. Associated with Oxyria in the soil pockets are *Geum turbinatum* Rydb., *Primula angustifolia* Torr., *Saxifraga rhomboidea* Greene, *Trisetum spicatum* (L.) Richt., and *Selaginella densa* Rydb.

Oxyria was in bloom at the time of collection, and some of the flowers were smutted. These were the only smutted individuals noted in all of the field collections.

Pikas (*Ochotona princeps*), small alpine mammals, were very evident in the site area on the August 5, 1957, collection date.

Niwot Ridge, Front Range, Colorado. The Niwot Ridge population was collected in the vicinity of the University of Colorado Institute of Arctic and Alpine Research Tundra Laboratory on Niwot Ridge in the Front Range of Colorado (40° 04′ N, 105° 38′ W) at an approximate elevation of 12,000 ft. The microsite is located on a north-facing stabilized talus (granite and schist) which has a slope of 25°. Oxyria is restricted to protected crevices within the talus. Abundant Oxyria seedlings were observed on the August 11, 1957, collection date, at which time the mature plants were in flower.

In the protected crevices, *Mertensia viridis* A. Nels. and *Senecio fremontii* T. & G. are prominent. In the more open crevice areas, *Sedum rosea* (L.) Scop., *Cirsium hookerianum* Nutt., *Claytonia megarrhiza* (Gray) Parry, *Trifolium nanum* Torr., *Geum turbinatum* Rydb., and *Trisetum spicatum* (L.) Richt. occur.

Medicine Bow Mountains, Wyoming. The Oxyria population selected from this area is located in the crevices of an essentially level quartzite boulder field. The plants are restricted to soil pockets which are formed, in part, through the intense activity of pikas. The microsite is situated at an elevation of 10,800 ft in the northern Libby Flat area of the Medicine Bow Mts. (41° 20′ N, 106° 19′ W). Oxyria also occurs in the Medicine Bow alpine area on rocky north-facing slopes but is not common.

Associated with Oxyria within the boulder field are *Aquilegia caerulea* James, *Ribes montigenum* McClatchie, *Senecio fremontii* T. & G., and *Cystopteris fragilis* (L.) Bernh.

Observations and physiological measurements were made on this population throughout the 1958 growing season.

Beartooth Mountains, Wyoming. This population is located on the Beartooth Plateau area approximately 4 mi north of Beartooth Pass (44° 59′ N, 109° 25′ W) at an elevation of 10,600 ft. The microsite is located on a gentle north-facing portion of the Wyoming Creek drainage. The area is composed of stream-deposited rock fragments, primarily gneiss, ranging from 2 ft in diameter down to gravel size. In spite of the considerable amount of soil surrounding and underlying the rock, the microsite area is essentially vegetationless with the exception of widely scattered clumps of completely exposed Oxyria and *Deschampsia caespitosa* (L.) Beauv. This relative lack of vegetation is due to normally late snowmelt.

Oxyria was setting and dispersing fruit on the August 25, 1957, collection date. Even at this date, however, it was apparent that the population area had not been snow-free for long.

Logan Pass, Montana. Seed, only, were collected from an Oxyria population growing in the immediate vicinity of Logan Pass, Lewis Range (48° 42′ N, 113° 43′ W), at an elevation of 6,650 ft. The plants were growing completely exposed on a level sedimentary rock substrate. The collection date was August 27, 1957.

Highwood Pass, Alberta. An Oxyria population was selected in the Elk Mountains of Alberta, in the vicinity of Highwood Pass (50° 35′ N, 115° 02′ W). The plants are found locally abundant in a cirque of 8,000 ft elevation at the base of a fossiliferous limestone talus slide. These plants are growing exposed, on an east-facing slope (13°) associated with small rocks, but not in crevices. The thin turf is underlain with broken rock. Oxyria ranged from full flower to fruiting stage at the time of collection, July 28, 1958.

The results of the vegetational analysis here are given in Table 1. Oxyria covers less than 3% of the ground surface, while bare rock has a coverage of over 50%.

Sunwapta Pass, Alberta. Oxyria occurs at the base of a stone-stripe area 1 mi southeast of Sunwapta Pass, Alberta (52° 12′ N, 117° 08′ W). The microsite is located on an east spur of Mt. Athabasca between Hilda Creek and Saskatchewan Glacier at an elevation of 7,200 ft. This late snowmelt habitat is situated on a gentle north-facing slope. Associated with Oxyria are *Silene acaulis* L., *Trisetum spicatum* (L.) Richt., and *Poa alpina* L. Plant cover was less than 1% of the ground. Collections of seed and live plants were made here on August 16, 1958.

Summit Lake, British Columbia. A small colony of Oxyria was found in this area at the base of a large dolomitic rock outcrop and talus. The north-facing slide area (25° slope) is located at an elevation of 5,300 ft near Summit Lake (58° 37′ N, 124° 41′ W). Oxyria is frequent within the microsite area but is limited to the shallow soil pockets in the slide. Even at the relatively early collection date on August 2, 1958, virtually all of the Oxyria fruits had been dispersed.

The percentage cover of the vegetational components is given in Table 1. There is a high percentage of rock cover. Coverage of the site by Oxyria is about 2%. The high percentage of moss cover in the general area is reflected in the figures given for this quadrat.

Donjek Mountains, Yukon Territory. The population site selected in the Donjek Mts. (61° 23′ N, 139° 27′ W) is located on a north-facing solifluction lobe at an elevation of 5,700 ft. The microsite is situated on a 29° slope of the actively flowing lobe where approximately 2 in. of turf overlies a sandy subsoil.

Oxyria is scattered in small clumps throughout the microsite. It is also found in the general area associated with Salix and Cassiope along rocky streamsides down to an elevation of less than 4,400 ft.

Because of the late date of collection at the population area on August 25, 1958, several plant identifications in the quadrat sample could not be carried below generic level. All of the species were in late fruit or had dispersed seed and were showing fall coloration at this date. The results of the vegetational analysis are in Table 1.

Eagle Summit, Alaska. A population of Oxyria was found immediately south of Eagle Pass (65° 28′ N, 145° 24′ W), on the Steese Highway, Alaska. It is situated on a northwest-facing 32° slope, at an elevation of 3,800 ft. The microsite is a semi-stabilized talus with small gravelly soil pockets. The substrate rock is largely mica-schist.

TABLE 1. Vegetational analyses at Oxyria microsites in the middle and northern parts of its North American range. Figures are percentage cover.

Species	Highwood Pass	Summit Lake	Donjek Mts.	Eagle Summit	Pitmegea River	Saga-vanirktok River	Point Barrow
Achillea lanulosa Nutt.	.36	—	—	—	—	—	—
Anemone parvifolia Michx.	.72	—	—	—	—	—	—
Antennaria alpina (L.) Gaertn.	1.80	—	—	—	—	—	—
Arnica cordifolia Hook.	.72	—	—	—	—	—	—
Carex haydeniana Olney	2.88	—	—	—	—	—	—
Castilleja occidentalis Torr.	.72	—	—	—	—	—	—
Deschampsia caespitosa (L.) Beauv.	.36	—	—	—	—	—	—
Draba crassifolia R. Grah.	.72	—	—	—	—	—	—
Epilobium alpinum L.	1.08	—	—	—	—	—	—
Erigeron peregrinum (Pursh) Greene subsp. *callianthemus* (Greene) Cronq.	1.44	—	—	—	—	—	—
Festuca brachyphylla Schultes	.72	—	—	—	—	—	—
Juncus drummondii E. Meyer	.72	—	—	—	—	—	—
Luzula spicata (L.) DC.	.72	—	—	—	—	—	—
Myosotis alpestris Schmidt	.36	—	—	—	—	—	—
Oxyria digyna (L.) Hill	2.88	2.11	.71	23.84	31.54	25.80	22.70
Phleum alpinum L.	.36	—	—	—	—	—	—
Poa alpina L.	5.40	5.26	—	—	—	—	—
Poa epilis Scribn.	.72	—	—	—	—	—	—
Potentilla diversifolia Lehm.	.36	—	—	—	—	—	—
Salix arctica Pall. var. *araioclada* (Schneid.) Raup	2.88	—	—	—	—	—	—
Salix nivalis Hook.	3.24	—	—	—	—	—	—
Saxifraga lyallii Engler	.36	—	—	—	—	—	—
Sibbaldia procumbens L.	1.44	—	—	—	—	—	—
Taraxacum lyratum (Ledeb.) DC.	.36	—	—	—	—	—	—
Antennaria monocephala DC.	—	.35	.36	—	—	—	—
Draba nivalis Liljebl. var. *elongata* S. Wats.	—	1.40	—	—	—	—	—
Erigeron humilis Grah.	—	.35	—	—	—	—	—
Poa leptocoma Trin.	—	1.75	—	—	—	2.47	—
Polygonum viviparum L.	—	1.05	.36	—	—	—	—
Salix arctica Pall.	—	8.77	—	—	—	—	—
Saxifraga punctata L.	—	1.40	—	—	1.79	—	.35
Trisetum spicatum (L.) Richt.	—	5.61	—	.71	6.09	3.89	—
Artemisia alaskana Rydb.	—	—	.71	1.78	—	—	—
Carex sp.	—	—	10.71	3.20	—	—	—
Cassiope tetragona (L.) D. Don	—	—	37.50	—	—	—	—
Dryas octopetala L. subsp. *punctata* (Juz.) Hult.	—	—	.71	—	—	—	—
Oxytropis sp.	—	—	.71	—	—	—	—
Pedicularis sp.	—	—	.36	—	—	—	—
Salix polaris Wahlenb. subsp. *pseudopolaris* (Flod.) Hult.	—	—	16.79	5.34	—	—	—
Salix reticulata L.	—	—	.36	—	.36	—	—
Silene acaulis L.	—	—	3.57	—	—	—	—
Luzula wahlenbergii Rupr.	—	—	—	2.85	—	—	—
Polemonium boreale Adams	—	—	—	1.07	—	—	—
Aconitum delphinifolium DC. subsp. *paradoxum* (Rchb.) Hult.	—	—	—	—	.36	—	—
Artemisia sp.	—	—	—	—	1.43	—	—
Draba sp.	—	—	—	—	.36	—	—
Epilobium latifolium L.	—	—	—	—	2.15	—	—
Equisetum arvense L.	—	—	—	—	.36	—	—
Luzula nivalis (Laest.) Beurl.	—	—	—	—	2.87	—	—
Poa arctica	—	—	—	—	24.01	—	25.53
Salix phlebophylla Ands.	—	—	—	—	8.24	—	—
Stellaria monantha Hult.	—	—	—	—	2.51	—	—
Carex lachenallii Schk.	—	—	—	—	—	.35	—
Salix rotundifolia Trautv.	—	—	—	—	—	2.12	.72
Saxifraga cernua L.	—	—	—	—	—	.71	.35
Cochlearia officinalis L.	—	—	—	—	—	—	5.32
Ranunculus nivalis L.	—	—	—	—	—	—	10.64
Taraxacum alaskanum Rydb.	—	—	—	—	—	—	1.42
Lichens	.36	—	3.57	2.85	—	6.71	.35
Mosses	5.76	28.42	6.43	8.90	12.90	38.16	22.34
Liverworts	—	1.05	—	—	—	—	—
Total vegetational cover	37.41	57.54	82.86	50.53	94.98	80.21	89.72
Bare soil	8.99	6.67	17.14	—	5.02	19.79	10.28
Rock	53.60	35.79	—	49.47	—	—	—

Oxyria is extremely abundant in the microsite as is shown by the vegetational analysis in Table 1. It comprises almost a fourth of the total cover. However, it appears to be mainly of local occurrence, appearing in rock slides and also along the road cut.

The roots of Oxyria here were infested with woolly aphids, the only such infestation noted in the field collections.

The collared pika, *Ochotona collaris*, was very active in the rock slide at the time of collection on August 14, 1958.

Pitmegea River, Alaska. An Oxyria population was selected at the mouth of the Pitmegea River on the Arctic Ocean (68° 56′ N, 164° 38′ W), on the northern coastal plain of Alaska. This site is situated at the base of a north-facing shale bluff with a slope of 24°. The combined talus and solifluction lobe is a site of late snowmelt. Oxyria is very abundant in the microsite, constituting over 30% of the cover (Table 1). Collections were made here on August 18, 1958.

Unfortunately, a number of herbarium specimens of the associated plants were lost in transit, hence some of the identifications are to the generic level only.

This station, and the remainder to be discussed, are all arctic tundra sites; those previously discussed have been located along a south to north alpine tundra environmental gradient.

Sagavanirktok River, Alaska. A population of Oxyria was chosen in the Franklin Bluffs section of the Sagavanirktok River (69° 50′ N, 148° 40′ W), on the Arctic Coastal Plain of Alaska. The microsite is located on a terrace with a very gentle (1°) west-facing slope which evidently has late-lying snow. The elevation of this site is under 500 ft.

Oxyria is abundant in the sample, constituting 25% of the cover (Table 1). Mosses, however, comprise an even greater portion of the sample.

In the general area, Oxyria is frequently found in late snowmelt areas. Collections were made at this site on August 13, 1958.

Pt. Barrow, Alaska. In the Pt. Barrow region (71° 17′ N, 156° 47′ W), there are occasional concentrations of Oxyria on the eroding surfaces of the dissected sea cliffs. At such microsites where snow accumulates and melting is slow, Oxyria may be very abundant although quite dwarfed and with flowering stalks uncommon.

Such a concentration of Oxyria was chosen as a collection site on August 21, 1958. The population area is less than 50 ft in elevation and is south-facing with a 25° slope.

Although Oxyria is quite abundant in the microsite area, comprising over 20% of the cover (Table 1), it becomes rare at a distance of only a few hundred meters inland.

SOIL ANALYSES

Only limited analyses were carried out on the soil samples collected in the field: percentage of sample greater than 2 mm in diameter, pH, and total nitrogen. Total nitrogen was determined by the Kjeldah method, and pH determinations were made by th method of Metson (1956). The results of the limite soil survey are presented in Table 2 as averages o duplicate determinations.

TABLE 2. Soil analyses for Oxyria population area

Location	Percent over 2 mm diam.*	Percent total N	pH
Loveland Pass	38.5	.37	5.30
Niwot Ridge	3.7	.30	5.35
Medicine Bow Mts.	3.4	.43	5.50
Beartooth Mts.	51.8	.07	5.60
Highwood Pass	3.6	.78	7.00
Summit Lake	5.0	.32	7.80
Donjek Mts.	39.0	.20	6.25
Eagle Summit	44.0	.11	5.85
Pitmegea River	41.0	.21	7.35
Sagavanirktok River	40.4	.21	7.75
Pt. Barrow	17.5	.29	6.25

* Fraction over 2 mm diameter and total nitrogen are on an air-dry weight basis.

All of the soils from Oxyria habitats in the Yukon Territory and Alaska have a high percentage of gravel while those of the southern alpine stations usually have low gravel percentages. Loveland Pass, where the population occurs in crevices of severely weathered granite, and the Beartooth Mts., where the observed population grows on stream-deposited gravels, are the two alpine locations where the soil has a high rock and gravel content.

The total nitrogen values are generally high, which may be related to the high incidence of small mammal activity coincident with Oxyria populations. The only low value is from soil of the Beartooth stream gravels. With this exception, the southern alpine soils exhibit higher nitrogen values than those of northern soils.

The pH values range from acidic to basic, demonstrating the broad tolerance of Oxyria as a species in regard to reaction of the substrate.

Russell (1940a) presents pH and total nitrogen values for various Oxyria habitats on Jan Mayen Island. The pH there ranged from 7.2 to 7.6 and the total nitrogen from 0.10 to 0.17%, values which are in keeping with those given here for arctic stations. However, Warren Wilson (unpublished data) found a wider range in soil nitrogen in Oxyria habitats on Jan Mayen, with values extending from 0.008 to 1.091%.

HABITAT SUMMARY

Throughout the range of the present work, the southern and northern alpine areas, and the Alaskan Arctic, habitats of Oxyria generally appear to have late snowmelt as a common denominator. Oxyria in the south is usually associated with crevices or rock in some form: talus, streamside gravel, boulder field, or shallow fractured rock substrate. As a result of such rocky surfaces, alpine Oxyria sites are very

TABLE 3. Analysis of certain morphological characteristics of Oxyria populations as exhibited under field, controlled environment, and greenhouse conditions

Location	AVERAGE LEAF LENGTH/LEAF WIDTH RATIO						AVERAGE INFLORESCENCE BRANCH NUMBER			
	Field		Chambers		Greenhouse		Field		Chambers	
	N	Ratio	N	Ratio	N	Ratio	N	Branch number	N	Branch number
Elephant's Back, Calif.	—	—	19	.77	—	—	—	—	19	6.6
Loveland Pass, Colo.	13	.77	19	.88	—	—	5	8.0	14	8.0
Niwot Ridge, Colo.	15	.78	—	—	—	—	13	5.2	—	—
Medicine Bow Mts., Wyo.	6	.69	20	.81	5	.80	2	8.5	20	5.7
Beartooth Mts., Wyo.	24	.75	—	—	9	.86	13	2.0	—	—
Logan Pass, Mont.	—	—	20	.89	9	.84	—	—	13	5.0
Highwood Pass, Alta.	24	.70	10	.81	8	.71	15	2.5	4	3.8
Angel Glacier, Alta.	—	—	—	—	9	.62	—	—	—	—
Summit Lake, B. C.	25	.57	—	—	—	—	12	2.5	—	—
Donjek Mts., Yukon	9	.67	19	.57	9	.63	11	1.7	6	2.5
Eagle Summit, Alaska	29	.59	20	.53	9	.69	31	2.5	7	3.5
Pitmegea River, Alaska	14	.64	20	.52	—	—	19	3.0	—	—
Sagavanirktok River, Alaska	12	.58	19	.60	9	.66	21	1.2	10	2.6
Pt. Barrow, Alaska	27	.46	—	—	9	.63	19	1.1	2	1.5
Thule, Greeland	—	—	—	—	5	.64	—	—	—	—

Location	FIELD Number of plants with stamen number of:			CHAMBERS Number of plants with stamen number of:			FIELD Number of plants with / without rhizomes:		CHAMBERS Number of plants with / without rhizomes:	
	2	variable	6	2	variable	6	with	without	with	without
Elephant's Back, Calif.	—	—	—	0	3	16	—	—	0	19
Loveland Pass, Colo.	12	1	0	14	0	0	0	7	0	20
Niwot Ridge, Colo.	10	1	2	—	—	—	0	8	—	—
Medicine Bow Mts., Wyo.	0	0	3	2	0	18	0	5	0	20
Beartooth Mts., Wyo.	1	6	0	—	—	—	0	20	—	—
Logan Pass, Mont.	—	—	—	0	1	13	—	—	0	20
Highwood Pass, Alta.	0	0	14	0	0	4	2?	4	0	10
Angel Glacier, Alta.	—	—	—	—	—	—	—	—	—	—
Summit Lake, B. C.	0	0	6	—	—	—	1?	1	—	—
Donjek Mts., Yukon	0	0	1	0	0	6	9	2	1	9
Eagle Summit, Alaska	0	0	23	0	0	7	7	4	6	4
Pitmegea River, Alaska	0	0	12	—	—	—	18	0	2	8
Sagavanirktok River, Alaska	0	0	16	0	0	11	17	1	7	3
Pt. Barrow, Alaska	0	0	17	0	0	2	14	0	4	0
Thule, Greenland	—	—	—	—	—	—	—	—	—	—

thinly vegetated. Unstable fine-grained substrates such as eroding silt bluffs and solifluction lobes assume importance as Oxyria sites in Alaska and the Yukon. Vegetational cover in such sites is relatively high. Oxyria is not found in such habitats in the southern part of its range.

In general, the vegetational coverage of Oxyria microsites increases from south to north. The typical Oxyria habitat in the central Rocky Mountains or Sierra Nevada is a barren rocky talus, cliff, or bouldery morainal material. These "rock piles" have very little vegetation other than scattered Oxyria plants. For this reason, no quantitative vegetational sampling of Oxyria habitats was done south of Highwood Pass. The associates of Oxyria vary throughout its range in North America. At lower latitudes, southern alpine endemics are of importance. Toward the north, circumpolar species increase in frequency. *Trisetum spicatum,* an arctic-alpine species of wide distribution, is often associated with Oxyria in both southern and northern habitats.

ANALYSIS OF MORPHOLOGICAL VARIABILITY BETWEEN POPULATIONS

The mass field collections[1] and the plants grown from seed in the greenhouse and in the growth chambers were analyzed to determine whether or not any patterns of morphological variability were associated with the geographic locations of the various populations. The following characteristics were measured: (1) maximum leaf width and length (top of petiole to apex of blade) of the largest leaf of a specimen; (2) number of primary branches of the largest inflorescence; (3) stamen number; (4) presence or

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[1] All herbarium material, including mass collections, is deposited in the Duke University Herbarium.

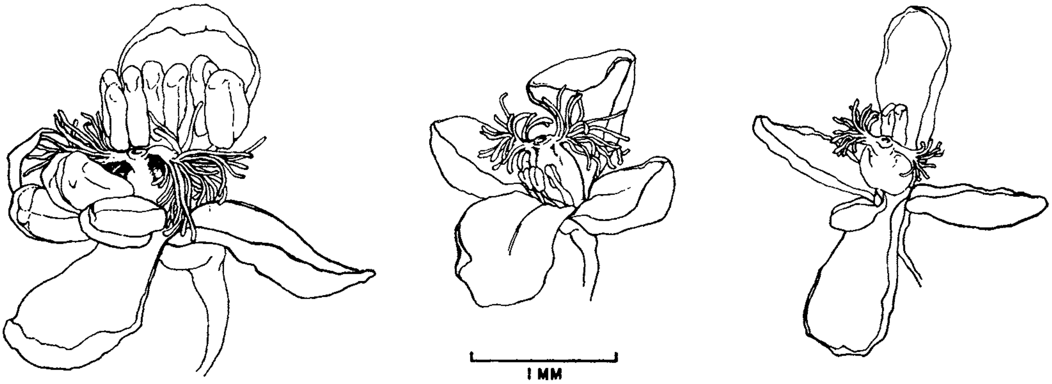

FIG. 3. Oxyria flower types. Flower on left has normal stamen development and is from a Sagavanirktok River, Alaska, plant. Center flower with aborted stamens is from a Logan Pass, Montana, plant. Two-stamen flower on right is from a Medicine Bow Mts., Wyoming, plant.

absence of rhizomes (Table 3). Also noted, was the number of flowers with stamens completely aborted in an inflorescence.

The average ratios of leaf length to leaf width appear to indicate the existence of two population groups: a northern one, made up of all the populations from Thule, Greenland, to Angel Glacier, Alberta, and a southern one, from Highwood Pass, Alberta, southward. Although the absolute magnitudes of the ratios are slightly altered by environmental conditions, the two groups are apparent under all treatments.

The average inflorescence branch number decreases from south to north. Plants of the far southern alpine populations are strikingly more branched than the northern forms, again suggesting two population groups rather than a cline.

Among Oxyria plants, certain individuals have unusual flowers which have only two stamens instead of the normal six. The inflorescences of these plants can be distinguished by their gross appearance. Other plants have inflorescences which have flowers with variable stamen numbers up to the full complement of six. Also, there are inflorescences containing from a few to all of the flowers with stamens completely aborted. The abortion of stamens does not appear to be directly related to the character of variable stamen number since the total complement of six undeveloped stamens can always be distinguished in such flowers. The principal flower types are illustrated in Figure 3.

Table 3, shows that the two-stamen character is limited to the far southern populations. The presence of two-stamen or variable-stamen forms also appears to separate the populations into southern and northern groups. In this instance, the separation occurs between Logan Pass, Montana, and Highwood Pass, Alberta.

Presence of rhizomes is another distinctive character of certain populations, which is not always easily noticed in the field, but is readily apparent in cultivated Oxyria plants. Some populations have plants which produce rhizomes, while other populations lack this character entirely. In Table 3, it may be seen that at the extremes of the range investigated, rhizomes are either completely present or completely absent. The presence of rhizomes is frequent in plants of the northern populations, while plants of the south lack rhizomes. The relatively low percentages of rhizomatous forms in some northern populations grown in the environmental chambers may be a function of their lack of age when scored for this character. Young cultivated plants, when excavated,

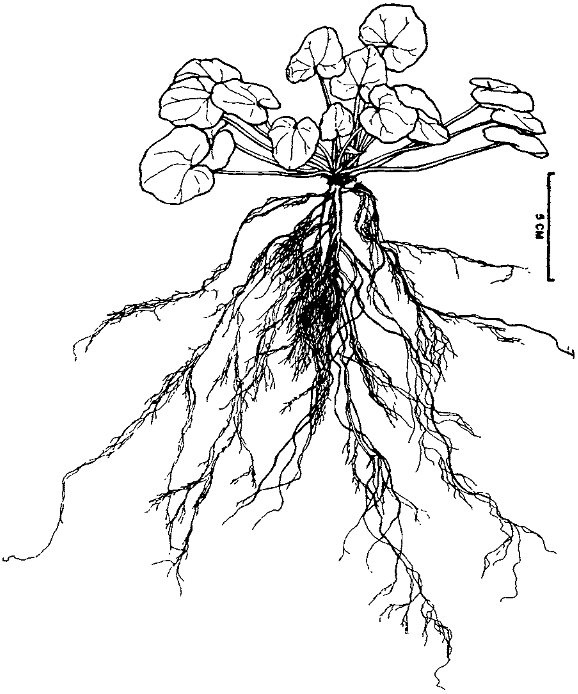

FIG. 4. Non-rhizomatous Oxyria plant grown from seed in the greenhouse. Seed collected from Beartooth Mts., Wyoming.

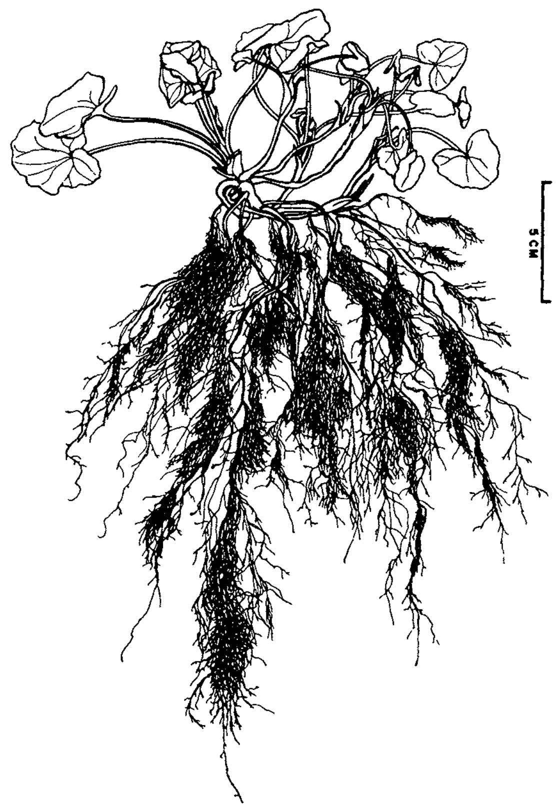

FIG. 5. Rhizomatous Oxyria plant grown from seed in the greenhouse. Seed collected from Sagavanirktok River, Alaska.

were often found to have rhizomes which were not yet apparent above the ground surface.

Figure 4 shows a pot-grown greenhouse-cultivated Oxyria from the Beartooth Mts., Wyoming, population. This nonrhizomatous form may be compared with a plant from the Sagavanirktok River, Alaska, population grown under the same conditions which is illustrated in Figure 5. The rhizomes originate at the base of the stem.

CHROMOSOME NUMBER

Published chromosome counts to date indicate that *Oxyria digyna* has 2n equaling 14 throughout its range. In Europe, counts have been made on material from Norway (Knaben 1950), France and Switzerland (Larsen 1954), as well as from the Kola Peninsula (Böcher & Larsen 1950). Counts have also been made on plants from Spitzbergen (Flovik 1940) and Iceland (Löve & Löve 1956). In North America, 2n equaling 14 has been found in Greenland and Canadian plants by Böcher & Larsen (1950). Other Greenland counts have been made by Holmen (1952) and Jørgensen, Sørensen & Westergaard (1958).

In the present work, flower buds were taken from plants grown under greenhouse and chamber conditions and meiotic figures counted on the following populations: Elephant's Back, Medicine Bow Mts., Logan Pass, and Sagavanirktok River. All of these counts showed n equaling 7. This provides further evidence that Oxyria probably has the same chromosome number throughout its total range.

GERMINATION

A series of experiments was done to determine if there were any differences in the characteristics of seed germination among the various populations of Oxyria. All germination studies were made in duplicate on moist filter paper in petri dishes. Seeds were exposed to light during the course of all experiments unless otherwise noted. Results are expressed as the averages of the duplicate tests. Since no differences were found in the percentage of germination between achenes when either contained in, or removed from, the fruit, the single-seeded fruit was used as the test unit.

After-Ripening

To find out if Oxyria seed has an after-ripening requirement, fresh fruits were collected from inflorescences in several populations of cultivated plants and immediately placed in petri dishes, watered, and kept at 20° C. Additional seeds of some of the populations were stratified on moist filter paper for one week at 3° C before being placed at the 20° C temperature.

There was rather high viability (40 to 80%) in most of the populations even though the seeds were not allowed to dry and after-ripen. Although the seeds of these same populations when dried and stored in a freezer at —10° C for periods up to 2 yrs have slightly higher germination percentages than the fresh seed, there does not seem to be any appreciable after-ripening requirement. Cold-stratification of the freshly harvested seed results in only slightly higher germination percentages.

Light and Dark Effects

To determine if Oxyria seeds have a light requirement for germination, replicate sets of field-collected seeds were placed in each of the following conditions: light at 20° C and dark at 20° C. The average percentage germination after 8 days is given in Table 4.

TABLE 4. Percentage germination in light and dark

Population	Light	Dark
Elephant's Back	82.5	2.5
Medicine Bow Mts.	35.0	2.5
Beartooth Mts.	52.5	15.0
Logan Pass	92.5	50.0
Highwood Pass	80.0	50.0
Donjek Mts.	85.0	35.0
Eagle Summit	70.0	25.0
Pitmegea River	100.0	72.5
Sagavanirktok River	90.0	32.5
Pt. Barrow	67.5	35.0
Thule, Greenland	37.5	30.0

In all instances, there was higher percentage germination in the light than in the dark. The percentage increase of light germination over dark was variable for the different populations with little apparent pattern. However, the divergence between light and dark percentages was greatest for the far southern alpine populations.

EFFECT OF CONSTANT TEMPERATURE ON GERMINATION

Equal numbers of field-collected seeds of representative populations were placed in a graded series of constant temperatures, 3° C, 10° C, 15° C, 20° C, 25° C, and 30° C. After a two week period, no germination had occurred at 3° C and these seeds were moved to 20° C. The average relative germination (where the highest number germinating for a given population at any treatment equals 100%) at 14 days is given for all temperatures and populations in Table 5. Also shown is the germination of the 3° stratified seeds after one week at 20° C as a percentage of the maximum unstratified germination.

TABLE 5. Percentage germination of maximum at graded temperatures

Population	3°C	10°C	15°C	20°C	25°C	30°C	20°C stratified
Elephant's Back.......	0.0	17.1	80.0	100.0	62.9	28.6	94.3
Medicine Bow Mts.....	0.0	45.5	72.7	100.0	45.5	36.4	154.5
Beartooth Mts.........	0.0	3.8	53.8	100.0	46.2	19.2	103.8
Logan Pass...........	0.0	32.4	100.0	97.3	67.6	48.6	102.8
Highwood Pass........	0.0	62.1	69.0	100.0	93.1	72.4	69.0
Donjek Mts...........	0.0	34.5	89.7	100.0	72.5	65.5	113.8
Eagle Summit.........	0.0	28.0	76.0	100.0	72.0	64.0	132.0
Pitmegea River........	0.0	29.4	100.0	100.0	67.6	55.9	117.6
Sagavanirktok River...	0.0	11.1	74.1	100.0	77.8	55.6	129.6
Pt. Barrow............	0.0	7.7	80.8	100.0	73.1	50.0	107.7
Thule, Greenland......	0.0	7.7	69.2	100.0	46.2	53.8	76.9

Several generalizations may be made from this table. In all but the Logan Pass population, the maximum germination occurs at 20° C. Germination is less at 10° C than at 30° C in all but the Medicine Bow Mts. population. Lastly, in most populations, the germination of stratified seeds was higher than the maximum germination percentage of unstratified seeds after 2 weeks at 20° C.

EFFECT OF ALTERNATING TEMPERATURES ON GERMINATION

A more natural situation was provided for germination by placing equal numbers of seeds of two alpine populations and two arctic populations in the alpine and in the arctic growth chambers where they were subject to the influence of alternating temperatures. The average percentage germination at 3 weeks for these populations in the 2 chambers is shown in Table 6. In all instances, germination was lower in the arctic chamber than in the alpine. However, it may be significant that the germination of the arctic populations was less reduced than those of alpine populations in the arctic chamber, with its colder day and night temperatures.

TABLE 6. Percentage germination in ''arctic'' and ''alpine'' diurnal temperature cycles

Population	"Arctic"	"Alpine"	Arctic as percent of alpine
Elephant's Back........	12.5	42.5	31.0
Logan Pass.............	32.5	87.5	37.2
Pitmegea River.........	65.0	80.0	81.4
Sagavanirktok River....	40.0	70.0	57.0

GROWTH AND DEVELOPMENT

EFFECT OF CONTROLLED ENVIRONMENTS ON GROWTH

Laboratory measurements of rates of petiole elongation, leaf expansion, and leaf production were made on 5 Oxyria populations: Loveland Pass, Highwood Pass, Donjek Mts., Eagle Summit, and Pitmegea River. These rates were measured on 10 individuals of each population in each of the two growth chambers, arctic and alpine. All of the plants were grown from seed and were 2 months old at the time of first measurement. The initial and final measurements for a 10-week period are given in Table 7.

TABLE 7. Growth measurements of Oxyria plants under controlled regimes*

Population and regime	MEAN PETIOLE LENGTH		MEAN LEAF WIDTH		MEAN LEAF NUMBER	
	Initial	Final	Initial	Final	Initial	Final
Loveland Pass						
Alpine chamber.........	1.7	9.9	0.9	4.0	4.2	27.1
Arctic chamber..........	1.6	7.2***	1.0	3.5	4.0	23.2
Highwood Pass						
Alpine chamber.........	1.6	5.2	1.0	2.9	6.0	45.8
Arctic chamber..........	1.8	7.2	1.1	3.0	6.6	45.9
Donjek Mts.						
Alpine chamber.........	1.9	3.7	1.3	2.2	4.8	17.0
Arctic chamber..........	1.8	7.2***	1.2	3.3***	4.7	27.1**
Eagle Summit						
Alpine chamber.........	1.6	3.0	1.1	2.0	4.5	12.9
Arctic chamber..........	1.4	5.3***	1.0	2.4	4.5	13.6
Pitmegea River						
Alpine chamber...... ...	1.7	2.3	1.0	1.5	3.8	11.4
Arctic chamber..........	1.9	4.8***	1.0	2.0***	4.9	14.6

* [illegible]
** [illegible] level).
*** [illegible] (1% level).

The average initial petiole length in all populations was essentially the same. The final petiole length on plants in the alpine chamber decreased progressively from the southern to the northern populations. On the other hand, the terminal measurements on populations in the arctic chamber fell into two groups. Plants from the 3 southernmost populations had identical averages, 7.2 cm, while the 2 northernmost populations averaged 5.3 and 4.8 cm. The Loveland Pass population, of far southern alpine origin, was the only one to have longer petioles in the alpine chamber than in the arctic; this difference was significant at the 1% level.

Initial measurements on leaf width were similar for all of the populations, although Eagle Summit plants had slightly wider leaves. The final measurements on leaf width showed the same trends as those shown by petiole length. In the alpine chamber, the widths decreased from south to north. In the arctic chamber, there were two groups: the 3 southernmost populations had average measurements in the 3 cm region, whereas the 2 northern populations had averages in the 2 cm region. Again, Loveland Pass was the only population with larger measurements in the alpine chamber.

Later, evidence will be presented which indicates that the comparison of the populations in the alpine chamber is actually an expression of a clinal growth response to photoperiod. On the other hand, in the arctic chamber where all of the populations had an ample photoperiod for growth and flowering, the differences between populations are an expression of genetically based morphological differences.

A comparison between treatments of the averages of leaf width and petiole length shows that, in the southernmost alpine population, the maximum development in these characters was in the alpine chamber. For the other populations, the opposite was true, with greater development in the arctic chamber. The Loveland Pass population was the only one in this experiment which came from an environment with a maximum photoperiod of less than 15 hrs, the photoperiod regime of the alpine growth chamber. This may explain the growth trend reversal for this population in comparison with the others.

The data on leaf number are similar in all respects to those of leaf expansion and petiole elongation with one major exception. The Highwood Pass population had a very high number of leaves in both treatments, almost twice that of any other population in either treatment. This aclinal variant somewhat obscures, but does not negate, the trends already discussed.

In Figure 6, representatives of the populations are arranged with the southernmost on the left extending latitudinally to the northernmost on the right. These plants had all been in the arctic or alpine chambers for three months at the time of the photographs, not long enough for most populations to flower. The clinal growth rate from south to north is well-illustrated.

EFFECT OF CONTROLLED ENVIRONMENTS ON PHENOLOGICAL DEVELOPMENT

A second group of populations was grown in the controlled chambers and the plants were scored at weekly intervals for phenological development.

In this group of populations were Elephant's Back, Medicine Bow Mts., Logan Pass, and Sagavanirktok River. Ten members of each population were placed in each of the arctic, alpine, and constant growth chambers. These chambers had the following temperature and light regimes: alpine chamber, 15-hr photoperiod, 12-hr day temperature of 65° F and a 12-hr 40° F night temperature; arctic chamber, 24-hr photoperiod, 12-hr temperature period of 55° F and a 12-hr temperature of 35° F; constant temperature chamber, 12-hr photoperiod and a 24-hr thermoperiod of 50° F.

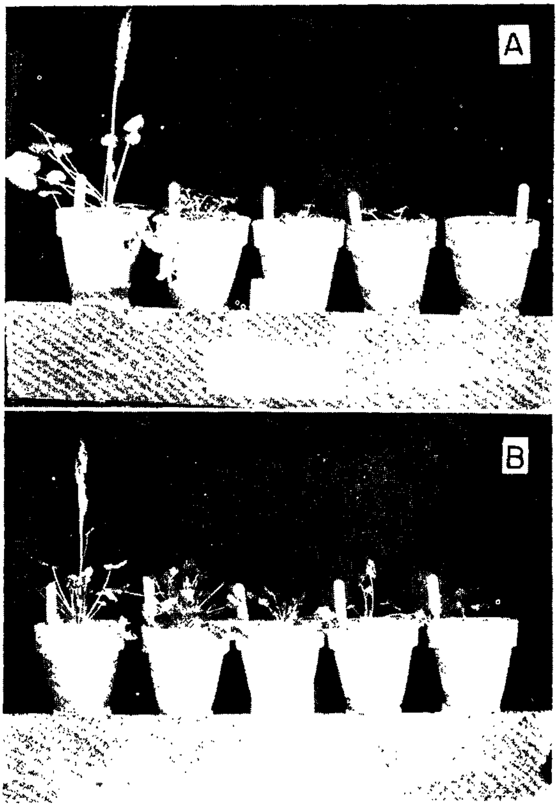

FIG. 6. Aspects of plants from a latitudinal collection of populations grown under uniform conditions. Origin from left to right: Loveland Pass, Highwood Pass, Donjek Mts., Eagle Summit, Pitmegea River. Photograph A is from the alpine chamber; photograph B from the arctic chamber. Plants had been under controlled conditions for only 3 months, not long enough for most populations to produce flowering plants.

At the beginning of the experiment, all plants were 4 month old pre-floral seedlings. The first plants started coming into flower after being in the chamber for 2 months. In Table 8 are given the weekly flowering or fruiting percentages of each population in each of the 3 chambers.

Both the Elephant's Back and Medicine Bow Mts. populations occur in environments which have a maximum photoperiod of 15 hrs or less. Logan Pass has a natural maximum photoperiod of approximately 16 hrs, and Sagavanirktok River has over 2 months of continuous light in midsummer.

In the constant temperature growth chamber, while it was set on a 12-hr photo-period, no plants of any population flowered.

In the alpine chamber (both Elephant's Back and Medicine Bow Mts. populations quickly attained a 100% flowering condition. Most of the Logan Pass

TABLE 8. Percentages of plants in four populations flowering or fruiting at end of weekly intervals

Time in weeks	ELEPHANT'S BACK		MEDICINE BOW MTS.		
	Alpine	Arctic	Constant	Alpine	Arctic
1	0	0	0	0	0
2	0	0	0	10	0
3	30	10	0	30	0
4	60	20	0	30	30
5	80	60	0	30	30
6	90	60	0	80	70
7	90	80	0	80	80
8	100	80	0	80	100
9	100	80	0	90	100
10	100	80	0	90	100
11	100	80	0	100	100
12	100	100	0	100	100
13	100	100	0	100	100
14	100	100	0	100	100
15	100	100	0	100	100
16	100	100	0	100	100
17	100	100	0	100	100
18	100	100	0	100	100

Table 8 (continued)

Time in weeks	LOGAN PASS			SAGAVANIRKTOK RIVER		
	Constant	Alpine	Arctic	Constant	Alpine	Arctic
1	0	0	0	0	0	0
2	0	0	0	0	0	0
3	0	0	0	0	0	20
4	0	0	10	0	0	30
5	0	10	10	0	0	40
6	0	10	30	0	0	70
7	0	20	60	0	0	80
8	0	20	90	0	0	100
9	0	20	90	0	0	100
10	0	20	90	0	0	100
11	0	30	90	0	0	100
12	0	30	90	0	0	100
13	0	40	90	0	0	100
14	0	50	90	0	0	100
15	0	50	100	0	0	100
16	0	50	100	0	0	100
17	0	50	100	0	0	100
18	0	50	100	0	0	100

plants were considerably retarded. Only 50% of the individuals had reached a flowering condition 4 months after the first plants of any populations had flowered. The Sagavanirktok River population failed to flower or fruit at all in the alpine chamber.

Thus, in the alpine chamber there appeared to be a latitudinal ecotypic response to a 15-hr photoperiod. Those populations which have a natural photoperiodic maximum of 15 hrs or less, produced flowers and fruits normally. The Logan Pass population, originating from an area which has a natural maximum photoperiod of 16 hrs, has some members which do flower and others which do not flower and fruit normally at the 15-hr photoperiod. Finally, the Sagavanirktok River population, whose natural environment has a maximum photoperiod considerably in excess of 15-hrs, completely fails to flower or fruit under so short a photoperiod.

In the arctic chamber, which had a continuous

FIG. 7. Plants from Elephant's Back, California, population grown under controlled alpine (A) and arctic conditions (B).

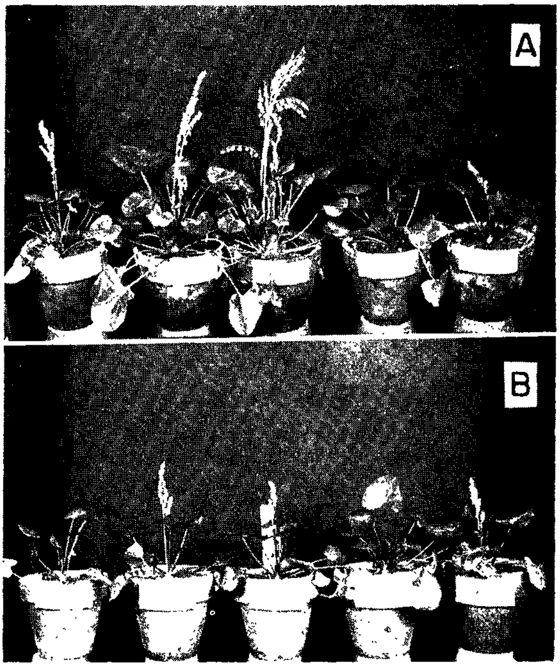

FIG. 8. Plants from the Medicine Bow Mts., Wyoming, population grown under controlled alpine (A) and arctic conditions (B).

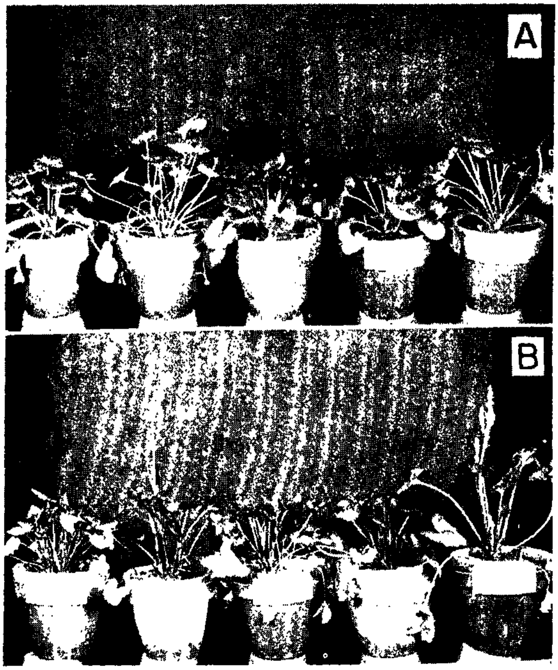

FIG. 9. Plants from the Logan Pass, Montana, population grown under controlled alpine (A) and arctic conditions (B).

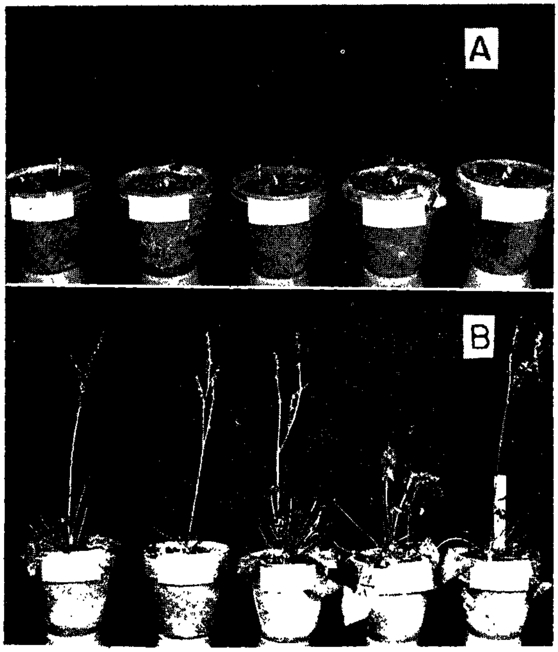

FIG. 10. Plants from the Sagavanirktok River, Alaska, population grown under controlled alpine (A) and arctic conditions (B).

photoperiod, all populations came into flower relatively quickly.

The general aspect of the plants grown during this experiment in the arctic and alpine chambers is shown in Figures 7, 8, 9, and 10. These photographs were all taken on the same day, immediately prior to the first date of inflorescence harvest.

Although there is evidence that temperature may limit photoperiodic induction in some plants (Thomas 1956), there was probably no significant difference in such induction between Oxyria plants in the arctic and alpine growth chambers due to temperature alone. There was only a 5° F difference in the minimum daily temperatures of the two chambers and 10° in the maximum. There is no way of evaluating the temperature effect on photoinduction from the present data. However, the fact that flowering in most populations did *not* occur in the higher mean temperature (52.5° F) of the alpine chamber but did occur in the lower mean temperature (45° F) of the arctic chamber, does appear to indicate that low temperature was not limiting.

At the conclusion of the first experiment, the photoperiod of the constant growth chamber was shifted from 12 to 17 hrs, but the temperature was maintained at 50° F. While the plants were on the 12-hr photoperiod, they all formed perennating buds at the soil surface but maintained functional leaves; in effect, they rosetted. Near the conclusion of the 12-hr photoperiod experiment, the temperature of the constant chamber accidentally dropped to 15° F for a 12-hr period. This low temperature damaged the functional leaves but not the perennating buds. When this chamber was switched to a 17-hr photoperiod, the plants very rapidly broke bud dormancy and became vegetative. In 3 weeks time, the first plants had come into flower.

The populations represented in the constant chamber included the Medicine Bow Mts., Logan Pass, Eagle Summit, and Sagavanirktok River. Thus, the group differed from the one present in the arctic and alpine chambers by lacking Elephant's Back and having the additional Eagle Summit population. The flowering percentages of each population during the 17-hr photoperiod experiment in the constant chamber are given in Table 9. Only the 2 southern populations displayed flowering activity. The 17-hr photoperiod of the constant growth chamber was nearest to the natural 16-hr photoperiod of the Logan Pass

TABLE 9. Percentage of plants in flower at weekly intervals in the constant chamber under 17 hour photoperiod

Time in weeks	Medicine Bow Mts.	Logan Pass	Eagle Summit	Sagavanirktok River
1	0	0	0	0
2	0	20	0	0
3	0	60	0	0
4	0	80	0	0
5	0	80	0	0
6	0	80	0	0
7	20	100	0	0
8	60	100	0	0

population. The fact that this population flowered first in this chamber indicates how closely adjusted these populations are to the natural summer day-length at their respective latitudes. The Medicine Bow Mts. population, with a natural maximum photoperiod of 15-hrs, although flowering, was significantly delayed in comparison to the Logan Pass plants.

INFLORESCENCE PRODUCTION

The total inflorescence production of the populations in the first group was tabulated for a 5-month period (Table 10). The data are expressed as the average number of inflorescences harvested per plant during the total time period and do not represent the number present on a plant at any given time. The production was tabulated only for plants in the arctic chamber where all populations had an ample photoperiod for flowering. The 5-month period commenced with the time of appearance of the first inflorescence in the whole group of populations.

TABLE 10. Inflorescence production of selected populations in the arctic chamber over a five-month period

Population	Average number of inflorescences produced per plant
Elephant's Back	24.9
Medicine Bow Mts.	21.2
Logan Pass	10.3
Sagavanirktok River	7.7

There is a distinct decrease in inflorescence production from southern to northern populations. This trend in inflorescence production would be considerably magnified if the data were converted to relative seed production. This is because of the south to north decrease in inflorescence branching which was discussed earlier in the analysis of morphological variability.

In the field, there appears to be a decrease in the importance of seed production in the north. At the far northern end of its range, in Peary Land, Greenland, Oxyria was not observed to set fruit (Holmen, 1957). The trend of increased rhizome production in the north has already been shown and likely compensates to some extent for reduced seed production.

It should be pointed out that the 5-month span of observation would constitute at least two growing seasons in the field. Thus, the production during such a prolonged growing period is not an index to actual field production, but shows at least a probable genetic difference between populations.

The fact that plants were kept in a continuously flowering condition for periods of up to a year in the growth chamber indicates that there is no inherent seasonal periodicity in the reproductive process.

DORMANCY

Under a 12-hr photoperiod, in the growth chambers, perennating buds were formed. Functional leaves, however, were retained until the advent of subfreezing temperatures.

A similar situation prevailed in greenhouse-grown plants. In the fall, Oxyria plants produced perennating buds and maintained this condition throughout the winter in spite of warm greenhouse temperatures. Several or no functional leaves were retained on these plants. Oxyria could be brought out of this dormant state by extending the photoperiod to 24 hrs without altering the temperature regime. During the winter, in the greenhouse, the temperature never fell below 38° F. However, plants kept outside under a 24-hr photoperiod and subjected to night temperatures as low as 24° F did not break dormancy until warmer temperatures prevailed.

A short photoperiod, then, will induce perennating bud formation even under the influence of relatively high temperatures. Long photoperiods will bring the plants out of this dormant state unless they are subjected to unfavorably low temperatures.

PHOTOSYNTHESIS AND RESPIRATION

FIELD RATES

The rate of apparent photosynthesis of intact Oxyria plants was measured twice in the field. Both test periods were made at mid-day during July, 1958, in the Medicine Bow Mts. at an elevation of 10,800 ft.

There was a rather wide fluctuation in the photosynthetic rate and also in temperature and solar radiation which were measured simultaneously. Such variation is rather typical for such regions where variable afternoon cloudiness during the summer is a regular occurrence. The maximum observed photosynthetic and respiration values for both test periods are given in Table 11, expressed on fresh weight, square decimeter, and milligram of total chlorophyll bases.

TABLE 11. Maximum observed field rates of photosynthesis and respiration

	Per gm fw/hr	Per dm²/hr*	Per mg chlorophyll/hr	Chamber temperature (°C)	Light (f. c.)
Photosynthesis					
July 9	3.65	5.79	9.73	31	8,700
July 22	3.74	7.39	7.52	25	9,000
Respiration					
July 9	0.85	1.35	2.27	21	0
July 22	0.18	0.35	0.35	14	0

* Leaf areas throughout this study were calculated as the sum of both upper and lower surfaces.

To find out if it was possible to distinguish roughly between light and temperature effects on photosynthetic rate, all of the 5-minute interval rates from both the July 9 and July 22 test periods were pooled and plotted against the chamber temperature and are presented in Figure 11. With the exception of several apparently aberrant values, a rough temperature-dependent photosynthetic curve is formed. The aberrant values all represent photosynthetic rates occurring at light intensities of 1,800 fc or less, and may, therefore, represent light-dependent values, at least for the temperature range examined. Since 2,000 fc values fall into the temperature-dependent curve, photosynthetic light saturation in the field apparently occurs at approximately 1,900 to 2,000 fc.

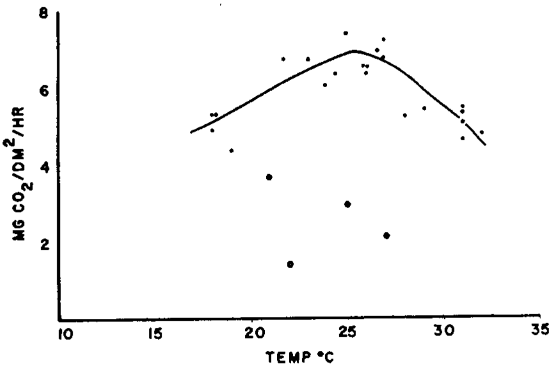

FIG. 11. Relationship between field photosynthetic rate and chamber temperature. Open circles are photosynthetic values occurring at 1,800 fc or less.

Wager (1941) reports a maximum observed photosynthetic rate for this species in East Greenland as 9.0 mg/dm^2 (leaf surface)/hr which is a little above the 7.4 mg/dm^2/hr peak observed in the Medicine Bow Mts. The estimated average light saturation value from Wager's light curves is approximately 1,800 fc, which is comparable to the estimated value from the Medicine Bow Mts. Wager also gives respiration values for Oxyria on a gram fresh weight basis for 0° C, 10° C, and 20° C, which are respectively 0.10, 0.31, and 0.52 mg/gfw. The two respiration values given in Table 11 for the Medicine Bow Mts. fall above and below the expected magnitude by interpolation into Wager's curve.

Field Chorophyll Measurements

The averaged chlorophyll values on a fresh weight and a leaf area basis are given in Table 12 for populations from the Medicine Bow Mts., Wyoming, and Eagle Summit, Alaska. The Medicine Bow values represent an average of 5 determinations. There were only 2 determinations from Eagle Summit, since some samples were lost in transit. From these limited data, it appears that plants from the low elevation, more northerly, Eagle Summit population have a higher total chlorophyll content on both a fresh weight and leaf area basis than plants from the high elevation populations of the Medicine Bow Mts. far to the south.

Laboratory Rates

A primary objective in the laboratory gas exchange measurements was to determine if differences in photosynthesis and respiration rate potentials exist among Oxyria populations. A secondary concern was the evaluation of the effects of the controlled alpine and arctic environments on these particular processes.

TABLE 12. Chlorophyll contents of field-collected leaves

	Medicine Bow Mts.	Eagle Summit
mg. C/gm. f.w.	.387	.636
mg. C/dm^2	.674	.867

All photosynthetic values presented here are of apparent or net photosynthesis which is equal to gross photosynthesis minus the "light" respiration value.

Two types of compensation points are considered. One, the light compensation point, is that light value, at a given temperature, where the net photosynthetic rate is equal to zero, i.e., the gas exchange is balanced. The other, the temperature compensation point, is used here in the sense of Transeau, Sampson & Tiffany (1940), as that temperature, at a given light intensity, where the apparent photosynthesis rate intersects or equals the dark respiration rate. Actually, on any given temperature-dependent photosynthetic curve, there would be two such compensation points, the upper and the lower. No lower temperature compensation points were determined in this study. The upper temperature compensation point, as used here, is not actually a true compensation point since the gas exchange is not balanced in the photosynthetic organ; gross photosynthesis is progressing at twice the respiration rate. The upper temperature at which gross photosynthesis and respiration are equal (the true temperature compensation point) would presumably be near the lethal temperature limit for the plant and would be difficult to determine.

EFFECT OF CONTROLLED ENVIRONMENTS ON PHOTOSYNTHESIS AND RESPIRATION

A series of determinations of photosynthesis at 20° C and dark respiration at 15° C were made on even-aged plants from both the alpine and arctic growth chambers representing four populations: Elephant's Back, Medicine Bow Mts., Logan Pass, and Sagavanirktok River. All the plants in this series from the arctic chamber had flowered, as had those from the alpine chamber with the exception of the Alaskan population, which was held in a non-flowering condition by the 15-hr photoperiod.

The 20° C determinations are expressed on a leaf area basis and are presented in Figure 12 as averages of three or four determinations, each from a different plant. In all instances, the photosynthetic rate of plants in the arctic treatment was less than that of similar plants in the alpine treatment. This difference is, in all probability, a response to the high leaf carbohydrate status of the plants grown in the arctic chamber.

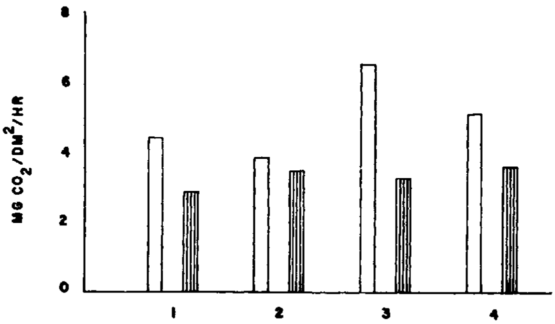

FIG. 12. Average laboratory-determined photosynthetic rates at 20°C on a leaf area basis. Unshaded bars for plants grown in the alpine chamber; shaded bars, plants grown in the arctic chamber. Numbers refer to the following populations: 1. Elephant's Back, California, 2. Medicine Bow Mts., Wyoming, 3. Logan Pass, Montana, 4. Sagavanirktok River, Alaska.

The average photosynthetic rates at 20° C of plants from all populations in the arctic chamber were surprisingly constant, varying between approximately 3 to 3.5 mg CO$_2$/dm^2/hr. There was, however, considerable variation in the values from the plants in the alpine chamber. Although these plants were even-aged, they were not equally developed since the Logan Pass plants were considerably retarded in flowering and those from Sagavanirktok River were not fruiting at all because of the relatively short photoperiod. It may be that the difference observed in the average photosynthetic rates of plants from the alpine chamber were responses to their unequal developmental stage which in turn was an ecotypic response to short (15 hrs) photoperiod.

These same results, when expressed on a milligram of chlorophyll basis, show a striking reduction in the average Assimilation Number (photosynthetic rate on a unit chlorophyll basis) of the Sagavanirktok River population, irrespective of treatment, as illustrated in Figure 13. This will be discussed at greater length when the results of the leaf chlorophyll contents of the various populations are presented.

FIG. 13. Average laboratory-determined photosynthetic rates at 20°C on a chlorophyll basis. Unshaded bars refer to average population rates of plants grown in the alpine chamber. Shaded bars refer to average rates of plants grown in the arctic chamber. Numbers refer to the following populations: 1. Elephant's Back, California, 2. Medicine Bow Mts., Wyoming, 3. Logan Pass, Montana, 4. Sagavanirktok River, Alaska.

The determinations of the dark respiration rates at 15° C represent averages of 5 replications on each population from each treatment, and also include an additional Alaskan Population, Eagle Summit. The results are shown in Figure 14, where the averages are expressed on a mg CO$_2$/gfw/hr basis.

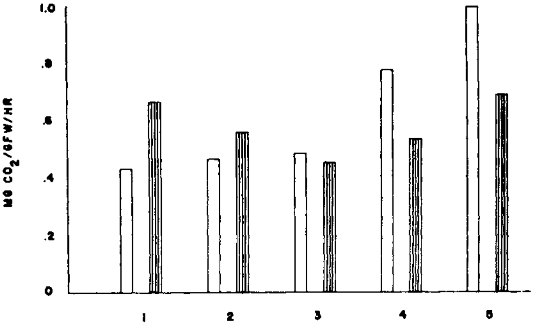

FIG. 14. Average laboratory-determined respiration rates at 15°C on a fresh weight basis. Unshaded bars refer to average population rates of plants grown in the alpine chamber. Shaded bars refer to average rates of plants grown in the arctic chamber. Numbers refer to the following populations: 1. Elephant's Back, California, 2. Medicine Bow Mts., Wyoming, 3. Logan Pass, Montana, 4. Eagle Summit, Alaska, 5. Sagavanirktok River, Alaska.

The results of the respiration measurements are somewhat difficult to interpret. Alpine chamber plants from the two Alaskan populations showed markedly higher respiration rates than southern plants from the same chamber. In the alpine chamber, respiration rate increased latitudinally from southern plants to northern plants. The real difficulty lies in explaining the effect of either treatment in respect to the other. The results may be viewed, perhaps, as a respirational imbalance produced by environmental displacement. The 3 southern alpine populations had a slightly increased respiration rate when grown in the arctic chamber. The two northern or Alaskan populations had an increased respiration rate when grown in the alpine chamber. Apparently, the greater the geographical displacement, the greater the imbalance. A complicating factor may have been the differential development of the plants, since the two northern populations in the alpine chamber remained in a vegetative condition.

EFFECT OF CONTROLLED ENVIRONMENT ON CHLOROPHYLL CONTENT

After being used in the gas exchange determinations, the leaves of plants from the arctic and alpine chambers were analyzed for total chlorophyll. The averaged values in milligrams of chlorophyll are given both on a per gram fresh weight and a leaf area basis in Table 13. The trend among popula-

TABLE 13. Leaf chlorophyll content of Oxyria plants grown under controlled conditions

Population	ARCTIC CHAMBER		ALPINE CHAMBER	
	mg/gm	mg/dm²	mg/gm	mg/dm²
Elephant's Back	.32	.50	.33	.62
Loveland Pass	.30	.67	—	—
Medicine Bow Mts.	.32	.53	.45	.65
Logan Pass	.30	.56	.64	1.10
Donjek Mts.	.34	.74	—	—
Eagle Summit	—	—	1.38	1.90
Sagavanirktok River	.52	.97	1.27	1.89
Pt. Barrow	.50	.85	—	—

tions appears comparable using either basic unit. The results, therefore, will be discussed in general terms.

In comparing chlorophyll contents under the two treatments, the difference between chambers was greater in the northern populations which had higher values in the alpine chamber. This effect is probably related to the non-flowering condition of the arctic populations in the alpine chamber. Among the populations that flowered in both chambers, there was little difference in chlorophyll content.

A comparison among populations within either chamber showed higher average chlorophyll content in the northern plants. In spite of the higher concentration of chlorophyll in the northern populations, there was little difference in the photosynthetic rate at 20° C on a leaf area basis. This results in an apparent decrease in assimilation number, or decrease in photosynthetic efficiency per unit of chlorophyll, in these populations.

COMPARISON OF FIELD AND LABORATORY RESULTS

Extrapolation of laboratory results to field situations should be made with great care. A minimum requirement for such extrapolation should be an analysis of the relative effect of the laboratory environment on the basic physiological responses of the organism as compared to the effect of the natural environment. An attempt has been made to assemble data of this sort in the present study.

PHOTOSYNTHESIS AND RESPIRATION

Table 14 shows the maximum rates of photosynthesis and dark respiration observed in the field and in the laboratory for plants of the Medicine Bow Mts. population. The laboratory rates are from 20° C determinations, which approximates the temperature of the field determinations. The photosynthetic rates agree very closely on both a gram fresh weight and milligram of chlorophyll basis. The laboratory rate on the basis of a square decimeter of leaf area is less than that from the field. There is very close agreement between the respiration rates from the field and the laboratory.

Although caution must be exercised in the use of such single values by themselves, they do indicate that the laboratory photosynthesis and respiration rates of Oxyria plants grown in simulated environments are of the same order of magnitude as those of Oxyria plants in their native habitat.

TABLE 14. Maximum observed rates of photosynthesis and respiration in field and laboratory in Oxyria plants from the Medicine Bow Mountains

	mg CO_2/gfw/hr	mg CO_2/dm²/hr	mg CO_2/mg chlorophyll/hr
Photosynthesis			
Field	3.74	7.39	9.73
Laboratory	3.98	5.60	10.29
Respiration			
Field	0.83	1.13	—
Laboratory	0.85	1.35	—

Both Russell (1940b) and Warren Wilson (1959, 1960) have published net assimilation rates for Oxyria from Jan Mayen Island based on carbohydrate increase in detached leaves. Russell gives a figure of 0.30 g/dm²/wk. Warren Wilson using leaves from a single source reports 0.34 g/dm²/wk for leaves exposed on a windswept summit and 0.46 g/dm²/wk for those in a sheltered hollow. His other measurements, using Oxyria from various habitat types, range from 0.54 g/dm²/wk to 0.66 g/dm²/wk. Most measurements on Jan Mayen were made in late August on plants which probably were in fruiting or post-fruiting condition.

These Jan Mayen net assimiliation results were compared with an approximated value calculated from photosynthesis and respiration rates of plants of the Eagle Summit and Sagavanirktok River populations grown in the arctic chamber. A photoperiod of 17.5 hrs was selected for the calculations. This photoperiod approximates that at latitude 71°N on the 21st of August. Average net photosynthesis at 10°C was used to approximate day-time gain. To calculate night time loss, 5°C dark respiration values were used. Warren Wilson (1960) reports mean maximum and mean minimum August temperatures from Jan Mayen as 8.8°C and 4.9°C, respectively. Warren Wilson (1957) also gives temperatures for a similar period in August for Resolute, Cornwallis Island, 4° in latitude north of Jan Mayen Island. Air temperatures 1 cm above the ground for a diurnal period at Resolute had an approximate maximum of 6°C and a minimum near 2°C. Bliss (1956) gives mean 4 a.m. air temperatures of 2°C for late August and noon values at 8°C for 5 cm above the ground in an arctic habitat (Umiat, Alaska) 3° in latitude south of Jan Mayen. If anything, then, the temperature values selected for calculation are a bit high. Seventy per cent was used as the conversion factor for converting CO_2 fixed to carbohydrate produced.

The net assimilation rate of our laboratory grown plants was calculated to be 0.53 g/dm²/wk. This is very close to the quoted field rates. Single-surface leaf area was used as the basis in this instance so as to conform with the techniques used on Jan Mayen.

Both Russell and Warren Wilson emphasize the approximate nature of their field-determined net assimilation rates. Russell says that these values should be considered as a minimum of the actual potential. Yet, the agreement between the calculated and field rates is quite good.

CHLOROPHYLL CONTENT

The average field values for leaf chlorophyll in plants of the Medicine Bow Mts. population were 0.39 and 0.67 mg on a gram fresh weight and a square decimeter of leaf area basis, respectively. The average chlorophyll values from cultivated plants of this population from the alpine chamber were 0.45 and 0.65, respectively. The close agreement between the field and laboratory chlorophyll values is obvious.

The Eagle Summit chlorophyll contents from field-grown plants, 0.52 mg C/gfw and 0.97 mg C/dm^2, can be compared with the values of 0.67 and 0.87 from Sagavanirktok River plants grown in the arctic chamber. There are no available arctic chamber chlorophyll values for Eagle Summit. Again, the agreement is fairly close but not so close as in the Medicine Bow Mts. chlorophyll contents.

POPULATION DIFFERENCES IN PHOTOSYNTHESIS AND RESPIRATION RATES IN RESPONSE TO TEMPERATURE

A somewhat more detailed study of the apparent differences between the rates of photosynthesis and respiration of the populations was made by constructing temperature curves for these processes. To insure equally developed plants, even-aged fruiting specimens from the arctic chamber were utilized. Determinations were made at temperatures ranging from 0° C to over 40° C. Unfortunately, at the 2,100 fc light intensity utilized for these determinations, 10° C was the lowest temperature that could be maintained for photosynthetic measurements. This was due to the inadequacy of the chamber cooling system.

The general shapes of the photosynthesis-temperature curves were similar for the three southern alpine populations, with maximum rates occurring at the same temperatures. The photosynthesis curves for the two northern populations had peaks at lower temperatures than those of the alpine plants. The actual average photosynthesis rates of the different populations were somewhat variable at any given temperature. In order to present more representative average rates without affecting the characteristics of the curve, the results from the 3 southern alpine populations were pooled and those from the two Alaskan populations were also pooled. Determinations within 5° C intervals were considered as a class. The values derived, representing in some instances as many as 9 separate determinations, are presented in Figure 15.

A number of important differences are apparent in a comparison of the curves for the southern and northern populations. First, the photosynthetic peak in the northern populations is at a lower temperature, although the maximum photosynthetic rate is essentially the same in both groups. Second, the respiration rate in the northern population is considerably higher, particularly at the higher temperatures.

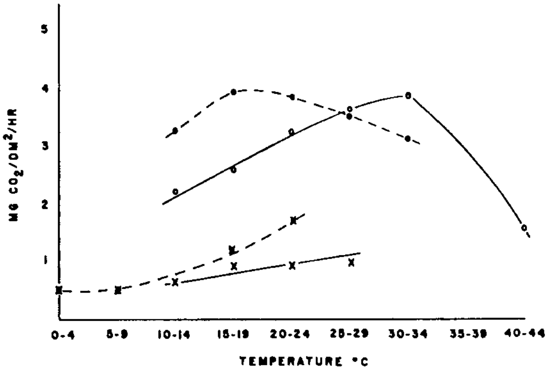

FIG. 15. Average photosynthetic and respiration rates of a southern alpine population group (Elephant's Back, Medicine Bow Mts., and Logan Pass), and of a northern population group (Eagle Summit and Sagavanirktok River), at different temperatures. Solid circles refer to average photosynthetic rates of the northern group; open circles, average photosynthetic rates of the southern group; circled X's, average respiration rates of the northern group; X's, average respiration rates of southen group.

The separated photosynthetic peaks and the different respiration rates result in a difference in the upper temperature compensation points. This may be seen by extrapolation of the curves. Actual determinations of the upper temperature compensation point yielded an average of 35° C (4 determinations) for the southern alpine group and 27° C for the northern populations (2 determinations). These actual determinations thus confirm that the compensation points are quite different.

To investigate further the apparent dissimilarity between northern and southern groups, two additional populations were tested. Temperature curves

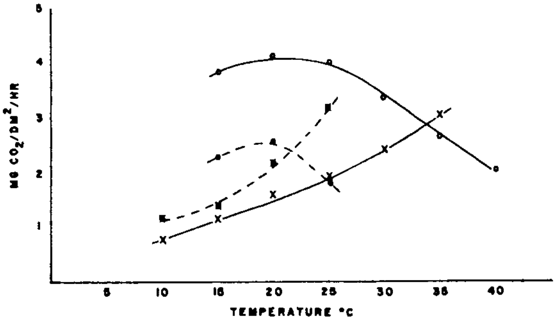

FIG. 16. Average photosynthetic and respiration rates of a southern alpine population, Loveland Pass, Colorado, and a northern population, Donjek Mts., Yukon Territory, at various temperatures. Average photosynthetic rates: solid circles, plants from the Donjek Mts.; open circles, plants from Loveland Pass. Average respiration rates: circled X's, plants from the Donjek Mts.; X's, plants from Loveland Pass.

were plotted from gas exchange measurements on even-aged pre-floral plants grown in the arctic chamber from Loveland Pass, Colorado, and the Donjek Mts., Yukon Territory. The average results of triplicate analyses for each series are given in Figure 16 on a mg $CO_2/dm^2/hr$ basis.

Although the plants were of the same age, they had exhibited a marked inequality in growth rate, which was probably a reflection of the differences of the photosynthetic rates. Aside from this, the essentials of the curves for the two population types are the same as presented earlier, that is, different temperatures for maximum photosynthetic rate, and a large difference in respiration rate. As a result, the upper temperature compensation points are decidedly different; the northern race reached compensation at about 22° and the southern race at 35° C.

POPULATION DIFFERENCES IN PHOTOSYNTHETIC RESPONSE TO LIGHT

Duplicate determinations of photosynthetic rate were made for an arctic and an alpine population at light intensities ranging from 55 to 5,200 fc. The determinations were made at 20° C on plants from Loveland Pass and the Donjek Mts. The resultant photosynthesis-light curves are presented in Figure 17.

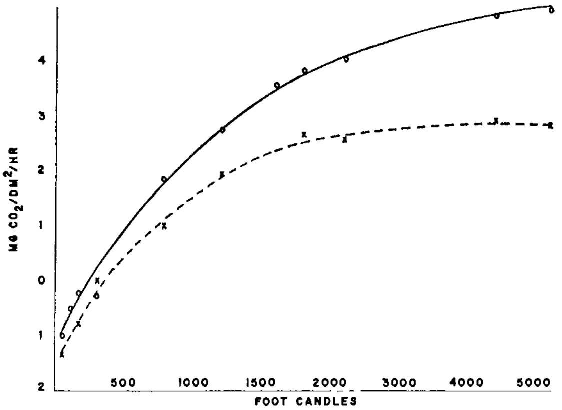

FIG. 17. Photosynthetic light curves at 20°C for a southern alpine population, Loveland Pass, Colorado, and a northern population, Donjek Mts., Yukon Territory. Open circles refer to average photosynthetic rates of plants from Loveland Pass. X's refer to average photosynthetic rates of plants from the Donjek Mts. Note change in light intensity scale between 2,000 and 3,000 fc.

There was little difference in the light compensation points for the two populations. Both were located between intensities of 250 to 350 fc. However, there was a marked difference in the light-saturation figures. The high altitude Loveland Pass population did not become completely light-saturated even at 5,200 fc. On the other hand, the Donjek population attained apparent saturation at approximately 2,000 fc.

FREE AMINO ACIDS, SUGARS, AND PHOTOSYNTHETIC PRODUCTS

Leaves from plants of 4 populations were analyzed for free amino acids, sugars, and photosynthetic products. The leaf material was taken from greenhouse-grown pre-flowering plants in May.

A detached leaf was placed in a photosynthetic chamber with its petiole in a vial of water. The chamber was then sealed and 20% lactic acid was injected into a sidearm of the chamber which contained 50 micro-curies of $NaHC^{14}O_3$. After a 5-minute period, during which the leaf was illuminated at the 2,000 fc level, the leaf was extracted in alcohol for several minutes, the alcohol decanted, and an extraction made in boiling water. The supernatants were combined and brought to volume. Aliquots of the extract were chromatographed two-dimensionally with phenol and butanol-proprionic acid as solvents. Three chromatograms were made of each sample. One was developed for amino acids with ninhydrin, the second for sugars with anisidine, and the third was used to make a radio-autograph. Activity of the photosynthetic products, as shown by the radio-autograph, was measured and expressed as a percentage of the total activity.

The above procedure was followed for leaves from 2 plants from each of the following populations: Thule, Greenland; Eagle Summit, Alaska; Highwood Pass, Alberta; and Medicine Bow Mts., Wyoming. Table 15 lists the presence of free amino acids and sugars in the leaf samples of the 4 populations.

TABLE 15. Presence of free amino acids and sugars in Oxyria leaves

	THULE		EAGLE SUMMIT		HIGHWOOD PASS		MEDICINE BOW	
	a	b	a	b	a	b	a	b
Cysteic acid	+	+	+	+	+	+	+	+
Aspartic acid	+	+	+	+	+	+	+	+
Serine	+	+	+	+	+	+	+	+
Glutamic acid	+	+	+	+	+	+	+	+
Threonine	+	+	+	+	+	+	+	+
Glutamine	+	+	+	+	+	+	+	+
Alanine	+	+	+	+	+	+	+	+
γ-aminobutyric acid	−	−	+	−	+	+	+	+
Leucines	−	−	+	−	+	−	+	−
Proline	−	−	−	−	−	+	−	−
Tryptophane ?	−	−	+	+	+	+	+	+
Sucrose	+	+	+	+	+	+	+	+
Fructose	−	−	+	−	+	+	+	+

No pattern was evidenced that distinguished or separated these populations with the possible exception of the relative lack of γ-aminobutyric acid in the arctic populations.

The analysis of the photosynthetic products present in the various populations yielded similar information. Table 16 lists the products and their percentage activity.

TABLE 16. Photosynthetic products—percent activity

	THULE		EAGLE SUMMIT		HIGHWOOD PASS		MEDICINE BOW	
	a	b	a	b	a	b	a	b
Phosphate area	34.3	36.7	34.6	33.2	37.6	30.2	34.9	25.1
Fructose	.3	T	.3	.2	T	1.1	1.5	.3
Sucrose	16.3	11.7	8.9	17.2	18.1	10.6	12.1	11.4
Maltose	.6	.9	.7	.9	—	.5	.8	.6
Glucose Glycine Serine Aspartic acid	35.4	39.2	41.5	25.5	22.9	42.3	29.8	29.1
Alanine	6.8	4.7	7.0	7.6	14.4	8.2	9.9	13.3
Glutamine	T	T	—	.3	1.7	—	.6	.3
Citric acid	.8	.5	.7	1.0	1.5	.9	1.0	1.9
Malic acid Glyceric acid	5.4	5.6	6.0	10.2	3.8	6.0	7.9	16.1
Cysteic acid	.3	.3	.4	.3	—	.3	.3	.6
Glutamic acid	—	—	—	.3	—	—	—	1.3
Glycolic acid	—	—	—	.3	—	—	.4	—
Tyrosine	—	—	—	—	—	—	.2	—
Leucine	—	—	—	—	—	—	.7	—
Sedo-heptulose	—	—	—	1.2	—	—	—	—
Lactic acid ?	—	—	—	—	—	—	T	—
Unknown	—	.4	—	—	—	—	—	—

CARBOHYDRATE AND NITROGEN CONTENTS

FIELD CARBOHYDRATE MEASUREMENTS

The results of the field carbohydrate analyses of Oxyria plants in the Medicine Bow Mts. made during the 1958 growing season are plotted in Figure 18. Those given by Russell (1940b) for Oxyria on Jan Mayen Island in the Arctic are also plotted. Although his sampling times are not completely comparable to ours, Russell's values are shown in approximate phenological relationship to those from the Medicine Bow alpine area.

Both sets of data are comparable in general aspects; that is, surplus carbohydrate levels were maintained throughout. There was a depletion of carbohydrate reserves during rapid vegetative growth, followed by an increase of stored products. The gradual increase in root starch reserves continued throughout the season.

The primary differences shown by the Jan Mayen series are: (1) depletion of total carbohydrate reserves in the root extended until fruiting, (2) higher carbohydrate levels were attained in the leaves, and (3) of most significance, the amplitude of the root carbohydrate cycle was not nearly as great as that in the Medicine Bow series. The trend in the latter series is more like the cycles for several other alpine species in the Medicine Bow area (Mooney & Billings 1960). In Oxyria and other alpine species in that mountain

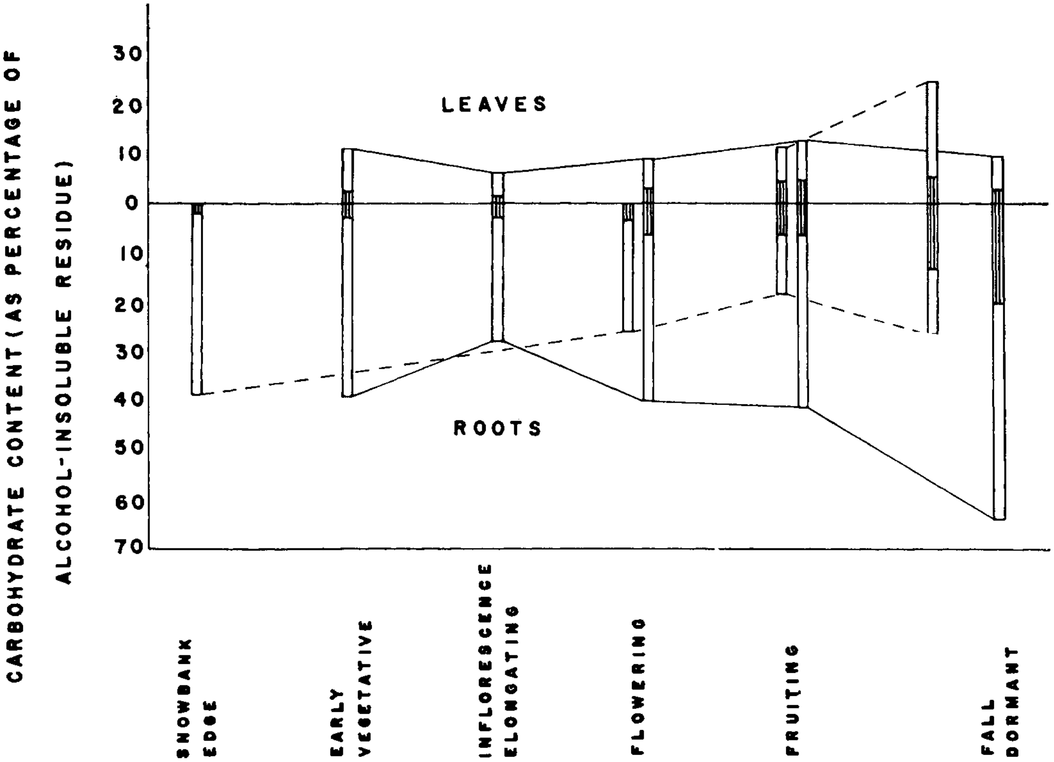

FIG. 18. Seasonal carbohydrate trend in Oxyria. Total length of bar indicates total carbohydrate present. Shaded portion represents percent starch. Solid lines connect Medicine Bow Mts., Wyoming values. Dashed lines connect Jan Mayen Island values as determined by Russell (1940b).

range, the depletion of root reserves extended only to the pre-flowering stage. The apparent discrepancy between the root carbohydrate levels at fall dormancy and at early vegetative growth is attributed to respirational loss under the snow. In this instance, the difference may have been partially due to losses during early developmental activities after release from snow but before the first samples were taken.

Samples taken in August, 1958, at Eagle Summit, Alaska, of Oxyria in late fruit, yielded mean root carbohydrate values of 28.96% starch, 24.87% total sugar, and 53.50% total carbohydrate, which indicates a carbohydrate cycle of apparently greater amplitude than that of the Jan Mayen arctic series.

FIELD NITROGEN MEASUREMENTS

Mean nitrogen contents of the field samples are given in Table 17 with the phenological stage at the time of collection. In the leaves, and to a lesser extent in the roots, of plants in the Medicine Bow series, there was a definite decrease in total nitrogen in the course of the growing season. The Eagle Summit values were slightly lower than those from the Medicine Bow at a comparable phenological stage. Warren Wilson (unpublished data) found maximum leaf nitrogen values of 4.1% in Oxyria plants at mid-season on Jan Mayen Island. There is an indication, then, of possible lower nitrogen content in arctic Oxyria plants as compared to alpine forms.

TABLE 17. Seasonal total nitrogen content in Oxyria plants*

	Leaves	Roots
Medicine Bow Mts., Wyoming		
Early vegetative	6.76	3.26
Inflorescence elongating	6.37	2.31
Flowering	5.61	1.95
Fruiting	5.27	2.30
Fall dormant	4.55	2.01
Eagle Summit, Alaska		
Fruiting	4.87	1.60

* All values as a percentage of alcohol-insoluble residue.

EFFECTS OF CONTROLLED ENVIRONMENTS ON CARBOHYDRATE AND NITROGEN CONTENTS

Analyses were made of the carbohydrate and nitrogen contents of roots and leaves of plants grown in the arctic and alpine chambers. Composite samples were taken of two plants from each population in each treatment and duplicate determinations were made. Leaf samples were taken from the Elephant's Back, Medicine Bow Mts., Logan Pass, and Sagavanirktok River populations. For root analyses, the northern population, Eagle Summit, was also included. All plants utilized were even-aged fruiting specimens with the exception of those from the two northern populations grown in the alpine chamber. As explained earlier, these did not flower in the alpine treatment because of short photoperiod. The averaged results of these analyses are shown in Table 18.

TABLE 18. Carbohydrate and nitrogen contents of Oxyria plants grown in controlled environments*

Population and treatment	Total sugar	Starch	Total Carbohydrate	Nitrogen
Leaves				
Elephant's Back				
Alpine Chamber	4.52	3.09	7.61	6.01
Arctic Chamber	7.28	16.95	24.23	5.33
Medicine Bow Mts.				
Alpine Chamber	3.96	2.03	5.98	7.79
Arctic Chamber	7.69	5.81	13.50	5.50
Logan Pass				
Alpine Chamber	5.88	1.07	6.95	7.49
Arctic Chamber	15.84	14.69	30.53	5.06
Sagavanirktok River				
Alpine Chamber	2.65	1.56	4.21	6.76
Arctic Chamber	5.31	3.85	9.16	7.43
Roots				
Elephant's Back				
Alpine Chamber	21.92	30.08	51.89	1.75
Arctic Chamber	17.49	41.19	58.68	1.49
Medicine Bow Mts.				
Alpine Chamber	24.43	36.60	61.01	1.93
Arctic Chamber	25.04	42.14	67.17	1.12
Logan Pass				
Alpine Chamber	21.45	17.25	38.70	3.01
Arctic Chamber	23.74	36.58	60.32	1.33
Eagle Summit				
Alpine Chamber	8.41	10.01	18.42	4.16
Arctic Chamber	10.55	45.07	55.62	1.42
Sagavanirktok River				
Alpine Chamber	5.39	10.29	15.68	3.93
Arctic Chamber	7.97	34.98	42.95	1.70

* All values as a percentage of alcohol-insoluble residue.

In the leaves, the percentage of total carbohydrates was two to four times higher in plants from the arctic chamber than in those from the alpine chamber. Compared to the levels in the alpine chamber, there was a much greater increase in total leaf carbohydrate in the alpine populations than in the arctic population when both types were grown in the arctic chamber.

In the roots, the general carbohydrate and nitrogen trend was the same as in the leaves, but there were usually higher values for all carbohydrate fractions. Also, there appears to be a definite geographic trend in the total carbohydrate values. The two southernmost alpine populations had the least spread in values between the two treatments. There was a greater difference in the two values for the delayed-fruiting Logan Pass population, and a still greater divergence in the two Alaskan populations. This divergence was a result of the differences in starch values rather than of sugar contents. The root nitrogen values were inversely proportional to the total carbohydrate trend. That is, high carbohydrate corresponded with low nitrogen, and vice-versa. Low C/N ratios were characteristic of the delayed or non-fruiting samples.

Analyses of soils taken from the pots of plants grown in the arctic and alpine chambers showed little, if any, variation in nitrogen content. The values were, respectively, 0.16 and 0.15% of dry weight. Hence, the different nitrogen contents of the plants from these chambers must have been a result of climatic differences between their environments, rather than the result of soil differences.

CARBOHYDRATE AND NITROGEN CONTENTS OF GREENHOUSE-GROWN PLANTS

Carbohydrate and nitrogen analyses were made on plants transplanted from the field to the greenhouse. These plants were brought into flower by using a 24-hr photoperiod. Samples were taken at the end of March when all were in fruiting condition except the Eagle Summit, Alaska, specimens which had aborted inflorescences. In addition to the Alaskan population, samples were taken from 4 southern alpine populations: Elephant's Back, Loveland Pass, Niwot Ridge, and Beartooth Mts. The results of these analyses are given in Table 19.

TABLE 19. Carbohydrate and nitrogen contents of greenhouse-grown plants*

	Total sugar	Starch	Total Carbohydrate	Nitrogen
Leaves				
Elephant's Back....	1.71	0.90	2.61	7.38
Loveland Pass.....	5.64	3.87	9.51	7.98
Niwot Ridge.......	6.71	1.99	8.70	8.30
Beartooth Mts.....	4.36	1.92	6.28	7.13
Eagle Summit......	1.56	1.82	3.37	7.57
Roots				
Elephant's Back....	6.98	21.51	28.48	2.77
Loveland Pass.....	24.97	6.42	31.39	2.13
Niwot Ridge.......	9.04	3.12	12.12	2.67
Beartooth Mts.....	16.20	3.42	19.63	2.78
Eagle Summit......	4.98	20.29	25.27	3.92

* All values as a percentage of alcohol-insoluble residue.

There was considerable variation in values in both the leaves and the roots. This variation may be indicative of a nutritional inbalance which did not become fully apparent until two months after the sampling date when large numbers of Oxyria plants began to die, apparently due to high summer temperatures.

If only fruiting plants are considered, the four alpine populations of the greenhouse series may be compared only with the arctic chamber series or with the Elephant's Back or Medicine Bow populations in the alpine chamber. In making this comparison, the most striking difference is in the low level of root carbohydrate reserves in the greenhouse-grown plants. This suggests either a large depletion of such reserves or that high reserve levels were never attained under the relatively high temperatures of the greenhouse.

COMPARISON OF FIELD AND LABORATORY RESULTS

Carbohydrate and nitrogen contents of mountain-grown fruiting Oxyria plants from the Medicine Bow Mts. were compared with results of similar analyses of fruiting plants of the same population grown in the alpine chamber. An analogous comparison was made between fruiting plants of the Eagle Summit population from the field and from the arctic chamber. The results of these comparisons are listed in Table 20.

TABLE 20. Comparison of field and laboratory carbohydrate and nitrogen contents*

	Total sugar	Starch	Total Carbohydrate	Nitrogen
Medicine Bow Mts.				
Leaves				
Field........	7.35	5.90	13.25	5.27
Laboratory..	3.96	2.03	5.98	7.79
Roots				
Field........	35.38	5.66	41.04	2.30
Laboratory..	24.43	36.60	61.01	1.93
Eagle Summit				
Roots				
Field........	24.87	28.96	53.50	1.60
Laboratory..	10.55	45.07	55.62	1.42

* All values as a percentage of alcohol-insoluble residue.

The total carbohydrate content in the roots of the cultivated plants was either similar to or in excess of that in field-grown plants. This is evidence that the cultivated plants were not operating at a carbohydrate deficit. Furthermore, the conditions of the laboratory enabled the plants to maintain the high carbohydrate reserve which is characteristic of many arctic and alpine species in the field (Russell 1940b, Mooney & Billings 1960).

The root nitrogen content of plants grown in the field was slightly higher than the root nitrogen of those plants grown in the laboratory. The reverse was true of leaf nitrogen contents. Environment apparently has a strong influence on the nitrogen balance of Oxyria, as has been shown earlier in the comparison of analyses of plants grown in the arctic and alpine chambers.

HIGH TEMPERATURE TOLERANCE

During the warmest part of the summer of 1959 in Durham, North Carolina (latitude 36° N), several hundred greenhouse-grown Oxyria plants died. It is significant that the high death rate in Oxyria occurred during a period when populations of other arctic-alpine species (*Poa alpina, Silene acaulis,* and *Trisetum spicatum*), growing under the same conditions, though affected, were not killed in large numbers. From June through August, the weekly maxima in the greenhouse ranged from 35° C to 43° C. During July and August, the greenhouse temperature never fell below 21° C.

The percentage of total population dead at given time intervals during the summer is plotted in Figure 19 for two northern and two southern populations of Oxyria. These results appear to indicate a difference

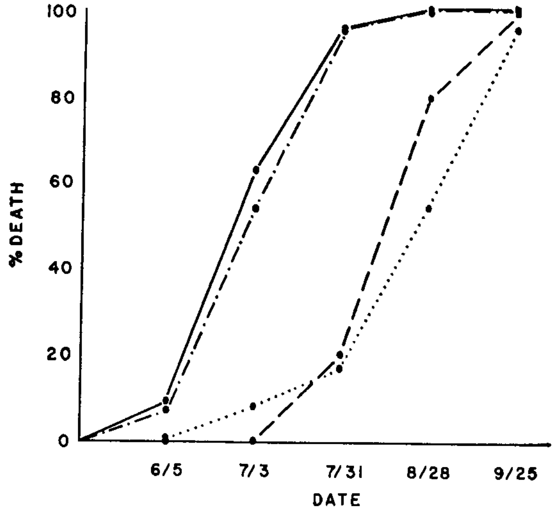

FIG. 19. Summer death rate of plants of two northern and two southern Oxyria populations under greenhouse conditions in Durham, North Carolina. ———— Donjek Mts., Yukon Teritory, —.—.— Pitmegea River, Alaska, — — — — Medicine Bow Mts., Wyoming, ... Logan Pass, Montana.

in tolerance to high temperatures between northern and southern populations. An experiment was designed to evaluate these apparent differences.

Seedlings of a southern population, Logan Pass, Montana, and a northern population, Donjek Mts., Yukon, were germinated in sand and grown at a constant 20° C under 24-hr light. After 2 weeks, the seedlings were individually washed free of sand and transferred to green vials containing complete Hoagland's solution. Each plant was held in place by a paraffined split cork and cotton. For 10 days the young plants were kept at a constant 20° C to become established. Then they were placed for 12 hrs alternately in a dark incubator at 40° C and in a lighted constant temperature room at 20° C. Daily observations were made on 10 plants from each population. These were scored for percentage of plants with all leaves wilted, and percentage of plants with all leaves dried. The results of this experiment are presented in Figure 20. These data indicate that plants from the southern population had a decidedly greater tolerance of high temperature in the dark than did those from the northern source.

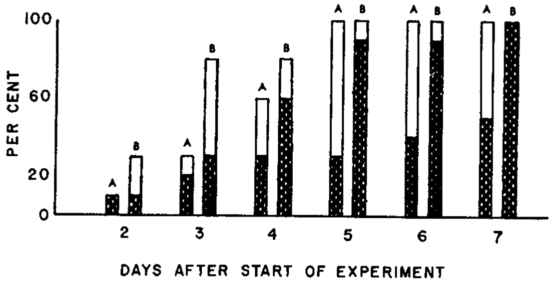

FIG. 20. Experimental heat tolerance. A, Logan Pass population, B, Donjek Mts. population. Shaded areas, plants with all leaves dried; unshaded areas, plants with all leaves wilted.

DISCUSSION

The primary objective of this research was to determine how *Oxyria digyna* is able to grow successfully in such a wide array of severe habitats, ranging from the northern arctic tundra to southern alpine locations. We now have some information which may help to explain this wide distribution. For example, when different geographic populations of Oxyria are grown together under uniform conditions, morphological and physiological differences between the populations become readily apparent. Many of these differential characteristics appear to be of direct adaptive significance in either arctic or alpine environments and thus can be considered as ecotypic modifications. The question now becomes, "How are these ecotypes related to their respective environments?" The following discussion will attempt to answer this question, at least partially, by examining each of the principal kinds of modifications.

RHIZOME FORMATION

The presence of vegetative reproduction in arctic Oxyria plants has been reported for Alaska (Wiggins 1951), the Canadian East Arctic (Gelting 1934, Holm 1922, Savile 1959), and Greenland (Sørensen 1941). Our results indicate that rhizome formation is genetically controlled. Only plants of the northern populations produce rhizomes.

Two possible explanations may be offered as to why rhizome production is important in northern habitats but not in southern alpine locations. First, rhizome production may have survival value in the unstable substrates of the northern habitats where vegetative reproduction could be of competitive advantage. Disturbed habitats resulting from soil movement may be revegetated more rapidly by rhizomes or rhizome fragments than by plants from seed. This possibility has been discussed by Wiggins (1951). Secondly, it has been shown here that seed production is reduced in the northern Oxyria populations. Vegetative reproduction may compensate for this reduction and insure survival of the species even though there may be unfavorable periods for flowering and seedling development.

ADAPTATIONS TO LIGHT

The light climates of arctic and alpine habitats differ considerably from each other. They vary not only in duration but also in intensity and equality of light. It appears that any given Oxyria population is well-adjusted to the specific light climate of its habitat through adaptations in growth and flowering response, perennating bud formation, leaf chlorophyll content, and photosynthetic light saturation.

Definite growth responses to different photoperiods have been shown for Oxyria populations in the present study. Under a 15-hr photoperiod, maximum growth was observed in populations originating from a region where the maximum natural day-length is 15 hrs. The further north the geographic origin of the population, the smaller was the amount of vegetative growth made under short photoperiod.

Related to the clinal growth response of Oxyria populations is a similar cline of flowering response. The latitudinal populations have variable photoperiodic requirements for flowering which agree closely to the maximum photoperiod of their natural habitat. However, a given geographic population appears to have some members whose physiological responses are like those of adjacent geographic populations, thus giving ecological amplitude to the population. These slightly different biotypes could allow limited north-south migrations with changing climates. It would appear easier, because of minimum photoperiodic requirements, for migration to take place from south to north, rather than the reverse.

Population differences in photoperiodic requirement for flowering are of considerable ecological significance. The maximum photoperiod in any arctic or alpine habitat coincides with the onset of favorable temperatures for growth. Late snowbed plants even though released at a period later than June 21 receive their maximum photoperiod at the *beginning* of their growth period.

Photoperiod is also important in the stimulation of the formation of perennating buds in Oxyria. A photoperiod below that necessary for flowering results in the formation of a perennating bud. Although the populations were not scored for critical thresholds, it was established that a 12-hr photoperiod causes all of our populations to form perennating buds even at relatively high temperatures. It would appear then, that toward the termination of the growing season, perennating buds would be formed under the stimulation of the decreasing photoperiod in the natural habitat. It would not be surprising if the differences in photoperiodic requirement for perennating bud formation were more nearly the same for the various latitudinal populations than are the photoperiodic requirements for growth and flowering. The difference in length of photoperiod between a southern alpine habitat and an arctic one is greatest at the beginning of the growing season and becomes much less toward the end and, of course, the difference becomes zero for a short period in September.

Quantitative differences in the photoperiodic requirement for breaking dormancy were not determined. It was established, though, that under the influence of a 24-hr photoperiod, dormancy was broken in all populations unless subfreezing temperatures prevailed.

It appears, then, that in Oxyria, the whole series of events from the breaking of dormancy, through flowering, and to the formation of perennating buds is strongly under the influence of photoperiod, subject to modification by temperature. Quantitative differences, between the populations, in photoperiodic requirement for growth and flowering have been demonstrated; they probably exist also for perennating bud formation.

Differential phenological response of a series of latitudinal races to photoperiod has been shown for several kinds of plants (Olmsted 1944, Larsen 1947, McMillan 1959, Vaartaja 1954, 1959) and is probably a common, but not universal, phenomenon in widely distributed species.

There is also some evidence that there is ecotypic variation in Oxyria in response to the light intensity of the environment. The photosynthetic light curves which were plotted at a constant temperature for a northern population and a southern population of Oxyria show that the latter or high altitude population approaches photosynthetic light saturation at a much higher light intensity than does the northern or low altitude population.

The latitudinal cline in chlorophyll content may be related to these differences in photosynthetic light saturation. Low latitude, high elevation populations have a lower chlorophyll content than the high latitude, low elevation populations. A similar latitudinal cline in chlorophyll content is known for races of *Pinus sylvestris* (Gerhold 1959).

There is, perhaps, additional adaptive significance to the differences in chlorophyll contents of the various populations. Reduced chlorophyll content in leaves of alpine populations would result in less visible light absorption and perhaps a more favorable energy balance. Billings & Morris (1951), for example, found that in plants from high light intensity environments there was greater reflectance from the leaves than occurred from leaves of plants growing in shaded habitats.

ADAPTATION TO TEMPERATURE

Northern Oxyria populations show characteristics which indicate that they are adapted to lower temperatures during the growing season than southern populations. They appear to carry on photosynthesis at a higher rate at lower temperatures and, furthermore, attain their maximum rate at a lower temperature. Also, in contrast to the situation in southern Oxyria populations, the respiration rate increase with temperature in northern populations is more rapid and the rate is higher at all temperatures.

Beljakoff (1930) found similar photosynthetic differences in two morphologically distinct races of barley. A northern race, "Vegakorn," cultivated in Sweden from 62° to 66° N latitude, was found to have a temperature optimum for photosynthesis of 20° C. A second race, "Gullkorn," is grown from 62° N southward. The latter race was found to have a temperature optimum for photosynthesis 10° C higher than that of "Vegakorn."

The higher respiration rate may enable plants of a northern Oxyria population to develop as rapidly in the colder arctic environment as do plants of a southern population at higher temperatures. Such a respiratory temperature compensation has been investigated by Scholander & Kanwisher (1959) in northern and southern populations of nine sub-arctic plant species. They found significantly higher respiration rates in northern populations of two of the species, *Lycopodium annotinum* and *Equisteum sylvaticum.*

Pisek & Winkler (1958) indicate that there may be an altitudinal cline in the respiration rate of *Picea excelsa* similar to the latitudinal cline in Oxyria. They found considerably higher respiration rates in spruce during the summer at timberline at 1,840 m than in trees of the same species in a botanic garden at 600 m or in lowland spruce forests at 580 m.

Our evidence indicates that the southern Oxyria populations are more tolerant of high temperatures than are the northern Oxyria populations. They were more resistant to abnormally high summer temperatures and to experimentally controlled high temperatures. This higher temperature tolerance may be related to the higher temperature compensation points of plants of the southern populations. Such characteristics in southern populations would tend to conserve high carbohydrate reserves which are of considerable importance to the survival and rapid growth of arctic-alpine plants.

In general, the characters measured on the mass collections and on the chamber- and greenhouse-grown plants indicate a northern and a southern morphological population group. The Highwood Pass population form Alberta is aligned in some characteristics with the southern group and in other characteristics with the northern group. In other characteristics, it is intermediate. There are also physiological differences associated with these two population groups.

The approximate boundary between the northern and southern population groups coincides geographically with the extent of maximum Pleistocene glaciation. At present, most areas which were covered by continental glaciation are occupied by populations with apparent northern affinities. The morphological and physiological differentiation between the northern and southern population groups may have been accentuated by separation of the two groups by continental ice during the Pleistocene. It would appear that recolonization of the continentally-glaciated northern Cordilleran region was almost entirely by photoperiod-tolerant biotypes from arctic populations. On the other hand, the alpine populations of the central and southern Rocky Mountains and the Sierra Nevada seem not to have migrated very far north into Canada. These populations may have been confined to these southerly mountain ranges by post-Wisconsin aridity barriers.

Although Oxyria apparently is composed of ecological races which react differently to environmental influences, the overall responses of plants from several populations make possible some inferences concerning the tolerances of an arctic-alpine species. The primary restrictive factor limiting the distribution of Oxyria appears to be relatively high summer temperature. The low photosynthetic economy of plants of this species at high temperatures causes a depletion of carbohydrate reserves. This depletion, perhaps coupled with malfunction of certain enzyme-substrate systems, results in consequent death. The results of Müller (1928) on arctic plants and Dahl (1951) on alpine plants support this hypothesis that high summer temperature determines to a large degree the southern or lower altitudinal limits of a tundra species.

SUMMARY

1. A comparative study was made of the morphological and physiological variation between geographically-separated populations of *Oxyria digyna*, a widely distributed arctic-alpine species. A latitudinal series of North American populations was studied ranging in origin from Colorado and California to Thule, Greenland, and Pt. Barrow, Alaska. The habitat and associates of each population are described.

2. Analysis of mass collections and plants grown under controlled conditions indicate two primary morphological groups within the range studied. One morphological group encompasses all the populations from southern Alberta southward in an area largely to the south of maximum Pleistocene continental glaciation. The other group includes all of the northern populations. The major morphological differences between these groups are in stamen number, inflorescence branch number, and presence or absence of rhizomes.

3. Measurements of field photosynthesis and the seasonal carbohydrate cycle of a Wyoming alpine population were compared with published results of these processes in arctic populations. Comparable photosynthetic rates were found, although the amplitude of the alpine carbohydrate cycle was greater than in the arctic plants.

4. A series of arctic and alpine populations was grown in controlled environment chambers which simulated either alpine growing conditions at 41° N latitude or arctic growing conditions at 71° N. The growth and development, photosynthesis and respiration rates, leaf chlorophyll contents, and leaf and root carbohydrate and nitrogen contents were measured on plants of these populations.

5. In these "arctic" and "alpine" conditions, it was found that photosynthetic rate, and chlorophyll and nitrogen contents were depressed while carbohydrate content was generally increased in plants of most populations under arctic treatment. In the arctic chamber, all plants flowered. In the alpine chamber, there was a cline in growth rate from a maximum rate in the southern populations to a minimum in the far northern populations. Flowering of *all* plants

in a population occurred in only those populations which received a photoperiod corresponding to the maximum photoperiod of their natural habitats.

6. A comparison of the physiological responses between populations when grown under suitable conditions for flowering showed the following:

a. There is a north to south cline of increased flower production. From south to north, there is increased rhizome production.

b. Leaf chlorophyll content increases with latitude.

c. Plants of northern populations have a higher photosynthetic rate at lower temperatures and attain the maximum rate at lower temperatures than do plants of the southern alpine populations.

d. Plants of northern populations have higher respiration rates at all temperatures than do plants of southern alpine populations.

e. High elevation, low latitude plants attain photosynthetic light saturation at a higher light intensity than do low elevation, high latitude plants.

7. The response of the various populations to photoperiod is reflected in their latitudinal origin. There was a clinal increase in photoperiodic requirement for flowering from the southern to northern populations. Formation of perennating buds was also found to be under photoperiodic control.

8. Although all populations were found to be intolerant of abnormally high summer night temperatures, the southern alpine populations displayed a somewhat greater tolerance than did the northern ones.

9. From these results, it is concluded that the continued existence of *Oxyria digyna* throughout a wide range of arctic and alpine conditions is due in large part to differences in metabolic potential among its component populations.

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