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Autecological Life History Studies of Two Geraniums, Geranium richardsonii and Geranium nervosum

Becky Lee Green

Utah State University

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AUTECOLOGICAL LIFE HISTORY STUDIES OF TWO GERANIUMS: GERANIUM RICHARDSONII AND GERANIUM NERVOSUM

by

Becky Lee Green

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1973

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Finally, for my husband, Tom, I cannot express my gratitude for his suggestions, encouragement and patience throughout this project.

Becky Lee Green

Becky Lee Green

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ABSTRACT

Autecological Life History Studies of Two Geraniums: *Geranium richardsonii* and *Geranium nervosum*

by

Becky Lee Green, Doctor of Philosophy

Utah State University, 1973

Major Professor: Dr. Martin M. Caldwell
Department: Range Science and Ecology Center

Two perennial species of wild geranium (*Geranium nervosum* Rydb. and *G. richardsonii* Fisch. and Trautv. [Geraniaceae]) which grow throughout the mountainous regions of western North America were studied to determine the factors influencing the life stage development and distribution of these plants. Attempts were also made to provide some information to assist in the taxonomy of this genus.

Geranium richardsonii is found in wet meadows and along streambanks throughout its distribution. *Geranium nervosum* frequents rocky hillsides and drier meadows throughout its range.

Seeds of *G. nervosum* had 65% germination in the stratification pretreatment. *Geranium richardsonii* seeds required scarification to reach 60% germination. Both species germinated in excess of 80% when scarified and stratified.

Overwinter survival experiments indicated that *G. richardsonii* could survive only in a wet meadow environment while

G. nervosum could survive and establish in all three environments examined: wet meadow, dry hillside, and aspen (*Populus tremuloides*) grove.

Both *G. richardsonii* and *G. nervosum* appeared to be limited by the same environmental factors although the degree of response was different. The seedling stage was the most responsive to environmental stress. Both *G. richardsonii* and *G. nervosum* seedlings had an optimum temperature range for survival of 20-25°C although they could and did adapt to lower temperatures. Seedlings of neither species could survive soil water potentials (Ψ_s) of -10 bars or lower. The adult stage of both species was more tolerant of $_s$ stress and *G. nervosum* adults could survive Ψ_s of -25 to -30 bars. *Geranium richardsonii* was less tolerant and appeared to be limited by both Ψ_s and temperature in its distribution at the Forestry Field Station.

The critical factors influencing the distribution of *G. nervosum* and *G. richardsonii* were similiar but the species reacted to them in different ways. *Geranium richardsonii* was able to survive in environments that were highly saturated with water and under heavy cover. *Geranium nervosum,* although limited by temperatures above 32°C, was able to live in drier conditions by virtue of a tap root system. Hence, although the distribution of these two species was similiar, they were seperated by their response to environmental conditions.

Hybridization is possible between *G. nervosum* and and *G. richardsonii*, but the seedlings of these crosses were dwarfed and grew slowly. Crosses between these two species probably do not occur naturally. *Geranium nervosum* and *G. viscossissimum* crosses can occur naturally. Pollinators did not appear to distinguish between species, and seeds which were the result of hand pollination germinated and grew in the laboratory. It is not known whether the hybrids are fertile. *Geranium nervosum* and *G. viscossissimum* were also difficult to distinguish by morphological characteristics where the two species grew together. This indicates that some hybridization may have occurred. *Geranium nervosum* and *G. viscossissimum* also appear to have similiar environmental requirements. This evidence indicates that *G. nervosum* and *G. viscossissimum* are probably not separate species.

(107 pages)

CHAPTER I

Introduction

Ecological life history studies of plants are of fairly recent origin (Pelton, 1953) and can take many forms. Pelton (1961), for example, investigated the ecology of *Mertensia ciliata* with no particular emphasis on any one life stage whereas Nord (1965) studied the ecology of bitterbrush (*Purshia spp.*) including emphasis on insect interactions with antelope bitterbrush (*P. tridentata*) and desert bitterbrush (*P. glandulosa*). Martin (1965) was concerned with morphological variation in *Geranium maculatum* as well as with its autecology.

The life cycle of an herbaceous plant has five major stages of development: (1) seed stage - following dispersal to the point of germination (the emergence of the radicle), (2) seedling stage - from the time of germination to establishment, (3) juvenile stage - that period of vegetative growth preceeding flowering, (4) adult or reproductive stage, and (5) senescent stage (Pelton, 1953). Of these, the seed and seedling stages are probably the most critical to the maintenance of a plant population. Germinating seeds and young seedlings generally have more specific requirements for survival than do adults. It is usually the limitations on seed production, germination, and seedling survival (e.g. lack of pollinators, temperature extremes, length of the growing season) which prevent a species from reproducing in a given area. One of the objectives of this study was to determine the limiting factors for maintenance at each stage in the life cycles of *Geranium richardsonii* Fisch. and Trautv. and *G. nervosum* Rydb.

Geranium richardsonii and *G. nervosum* are herbaceous perennials found throughout the mountainous regions of the western United States and Canada. *Geranium richardsonii* has a wide range which extends from northern British Columbia and Alberta to Montana, Wyoming, western South Dakota, Colorado, Utah, Nevada, and northeastern California (Fig. 1) (Jones and Jones, 1943; Munz, 1963; Shaw, 1952). *Geranium nervosum* is confined to Utah, western Colorado, western Idaho, eastern Washington, and the Modoc County of eastern California (Fig. 2) (Jones and Jones, 1943; Munz, 1963; Shaw, 1952). It is found on drier meadows and hillsides throughout its range.

Hanks and Small (1907) published the first study on the taxonomy of *Geranium* in North America in which they described 64 species, half of which were native to Mexico. The North American species were revised by Jones and Jones (1943); they recognized 18 species. Since that time, Shaw (1952) has done a comprehensive cytological and descriptive study of the genus in the Wasatch Mountains of Utah.

Geranium richardsonii was originally described by

Figure 1. The distribution of _G_. _richardsonii_ in western North America.

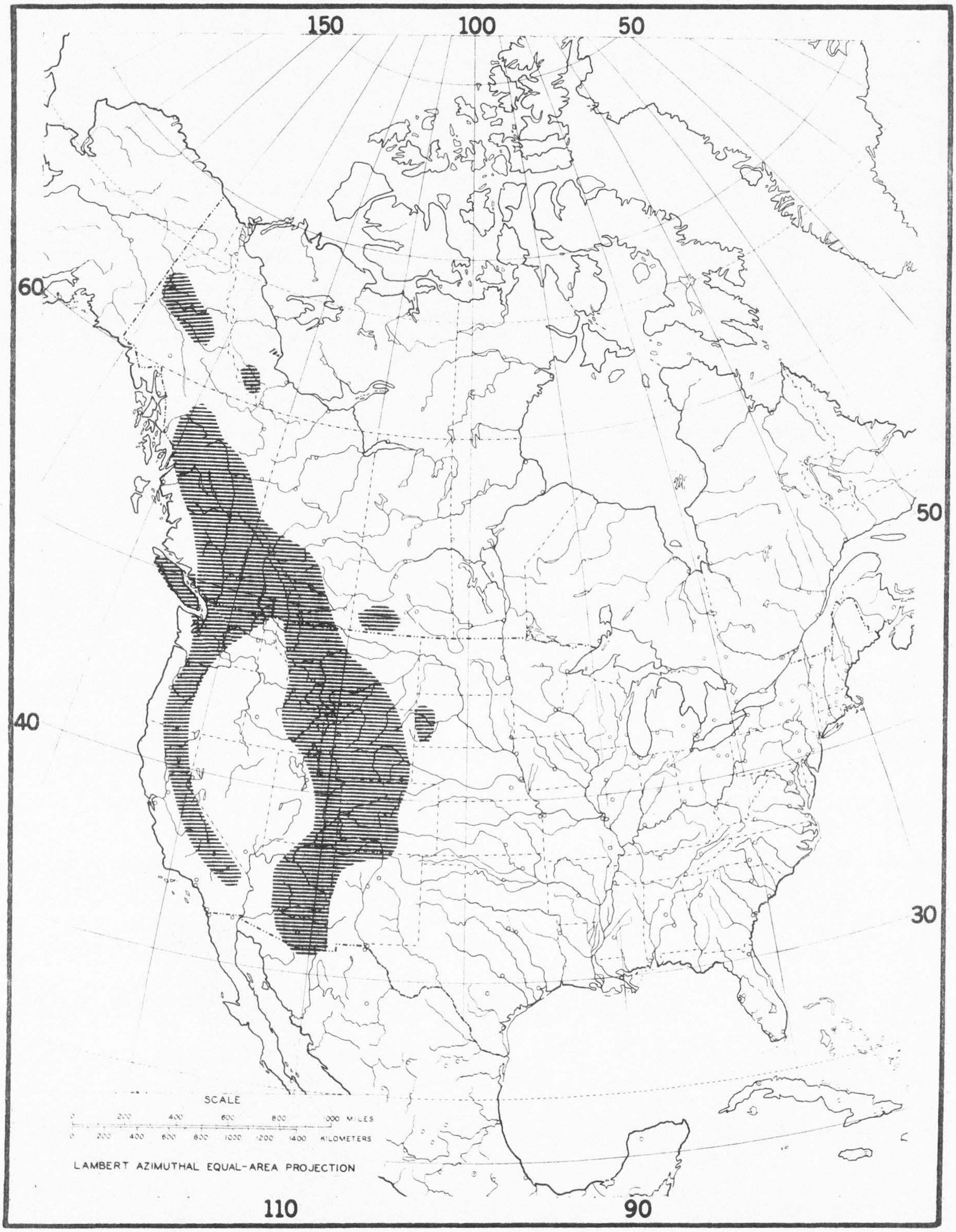
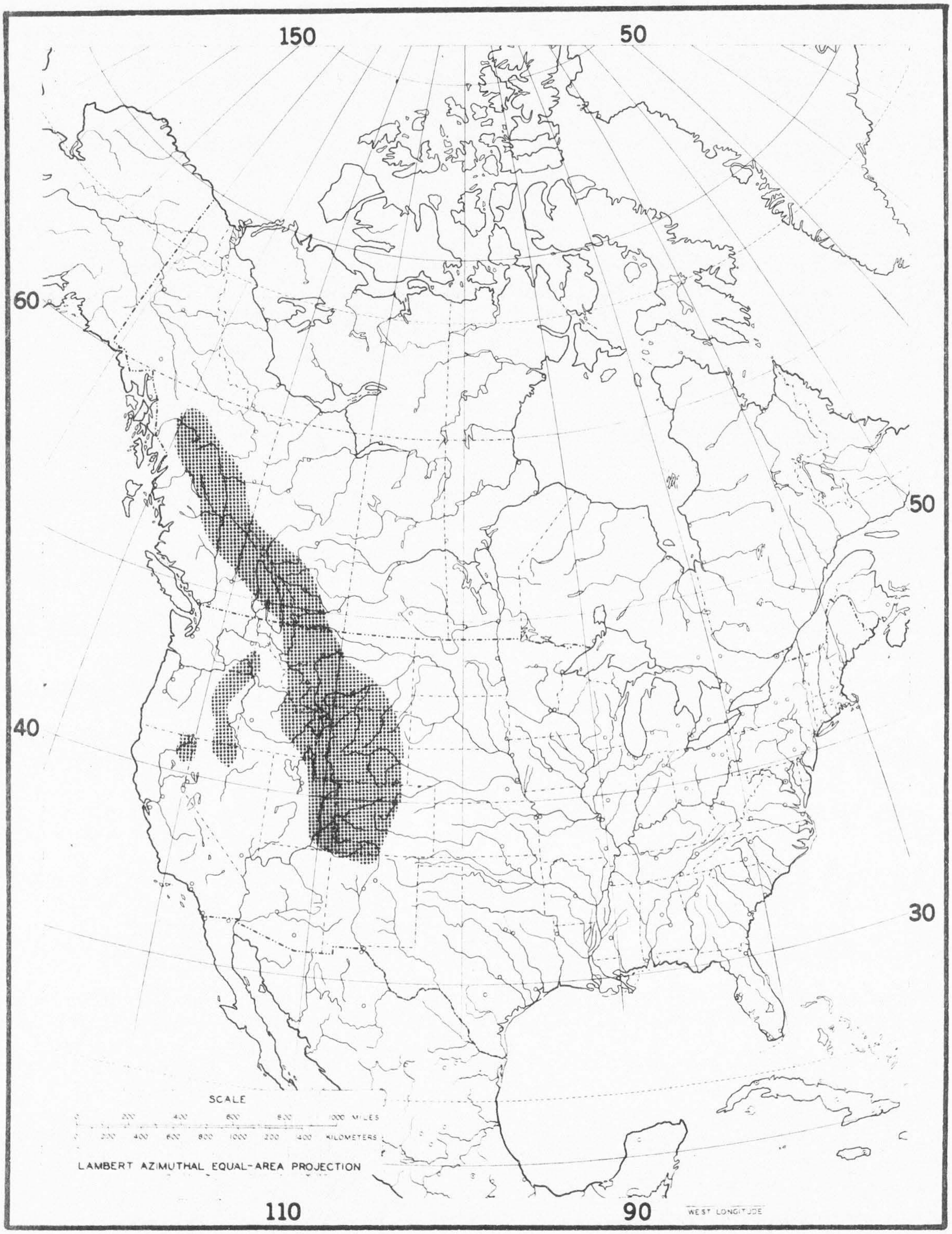

150
100
50
60
50
40
30
110
90
SCALE
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

Figure 2. The distribution of *G. nervosum* in western North America.


150
50
60
50
40
30
SCALE
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
110
90
WEST LONGITUDE

William J. Hooker as *G. albiflorum* in 1930. However, due to the fact that *G. albiflorum* was the epithet of an Asiatic species, a new name had to be given to the North American species. *Geranium gracilentum* Greene and *G. loloense* St. John are relegated to synonymy under *G. richardsonii* (Jones and Jones, 1943).

Geranium nervosum has been variously described as *G. canum* Rydb., *G. incism* of Rydb. not Nutt., *G. strigosius* St. John, *G. strigosum* Rydb. not Burm.f., and *G. viscossissimum* Fisch. and C.A. Meyer var. *nervosum* C.L. Hitchc. (Holmgren and Reveal, 1966). It is commonly confused with *G. fremontii* Torr. ex Gray and *G. viscossissimum*. Shaw (1952) and Jones and Jones (1943) considered *G. fremontii* to be a smaller plant than *G. nervosum* and to be limited to the southern Rocky Mountains. Neither suggested any other differences. *Geranium viscossissimum* is a darker and coarser plant than *G. nervosum* due to the abundant yellowish-green glandular pubescence on the stems, petioles, and, at times, the leaf blades (Jones and Jones, 1943).

The major morphological feature separating *G. nervosum* and *G. richardsonii* is the fact that the petals of *G. richardsonii* are pilose on the inner surface 1/3 to 1/2 their length while those of *G. nervosum* are pilose for only 1/4 to 1/2 their length. Although this characteristic does overlap, *G. richardsonii* has, in general, smaller seeds and flower parts with petals that are 12-20 mm long and milk-white or sometimes tinted pink. *Geranium nervosum* petals are 15-23 mm long and light pink to rose purple with dark purple veins (Jones and Jones, 1943; Shaw, 1952). The vegetative parts of the two species are almost indistinguishable.

Ecological relationships within *Geranium* have been little sutdied. Martin (1965) did an ecological life history study of *G. maculatum* which occurs only in the eastern part of North America. Lewis (1969) studied the leaf morphology of *G. sanguineum*, a European *Geranium*, as it was correlated with distribution of the plant.

Since *Geranium spp.* appear to be forage plants, particularly for sheep, their carbohydrate reserves have been studied (Donart, 1969). It was found that *G. fremontii* could survive under moderate to intense grazing although this reduced its reproductive capacity (Donart and Cook, 1970).

The most noticable fact about these two species is that they rarely, if ever, grow intermingled although populations of *G. nervosum* and *G. richardsonii* may grow sympatrically. This observation led to the questions: (1) What are the critical environmental factors controlling the distribution of these species, and (2) Do these factors affect each species in the same manner? The primary difference appeared to be water availability since *G. richardsonii* was always found in more moist areas than was *G. nervosum*. Other factors may be involved and one of primary concern is temperature. *Geranium richardsonii* may be susceptable to temperature extremes and the moist environment in which it grows may have modified these. Additional factors important in maintaining the spatial distribution of the two species might be germination requirements, i.e. safe-sites (Harper, et al., 1961); soil factors; and flowering mechanics, including pollinators. All of these factors were considered in this study.

Voucher specimens of G. nervosum, G. richardsonii and G. viscossissimum are filed with the Intermountain Herbarium at Utah State University, and all nomenclature follows Holmgren and Reveal (1966).

Objectives

The objectives of this sutdy were as follows:

(1) To determine the limiting factors for maintenance at each stage in the life cycles of G. richardsonii and G. nervosum,

(2) To determine the critical environmental factors affecting the distribution of these species and to see if these factors affect each species in the same manner, and

(3) To contribute to refinements of the taxonomy of the genus Geranium.

CHAPTER II

Study Area

Field investigations were conducted at the Utah State University Forestry Field Station in the Cache National Forest, Cache County, Utah. The Forestry Field Station is located about 34 km northeast of Logan, Utah, at about 41°50' latitude and 111°40' longitude at an elevation of 1854 m in the Wasatch Mountains. This site is typical of the sagebrush (*Artemisia tridentata*) - aspen (*Populus tremuloides*) alternation common in the mountains of Utah (Matthews and Conrad, 1968).

Geranium nervosum was studied in two habitats: (1) aspen grove - an aspen stand with a northwest exposure and a dominant understory of *Delphinium occidentale* and *Senecio serra* and (2) dry hillside - *Artemisia tridentata*, *G. nervosum* and *G. viscossissimum* dominant on a 30% slope with a south exposure. *Geranium richardsonii* was studied in a wet meadow along the Little Bear Creek where the dominant vegetation was a combination of *Agropyron smithii* and *G. richardsonii* (Fig. 3).

Climate

Precipitation data from the weather station at the Forestry Field Station appear in Figure 4. Sixes-type maximum-minimum thermometers which recorded ambient air

Figure 3. Study area at the U.S.U. Forestry Field Station, 34 km northwest of Logan, Utah, on highway 89.

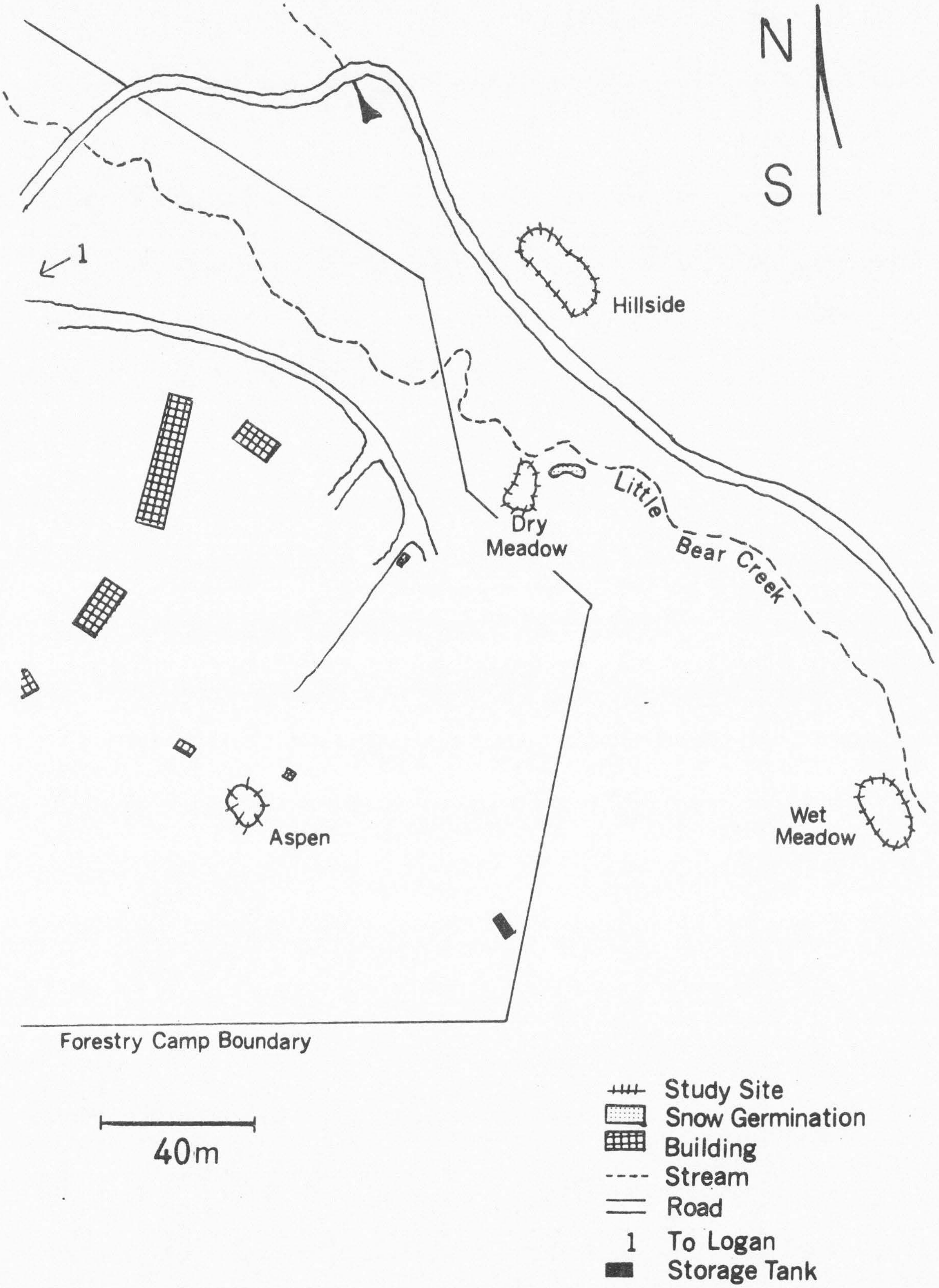
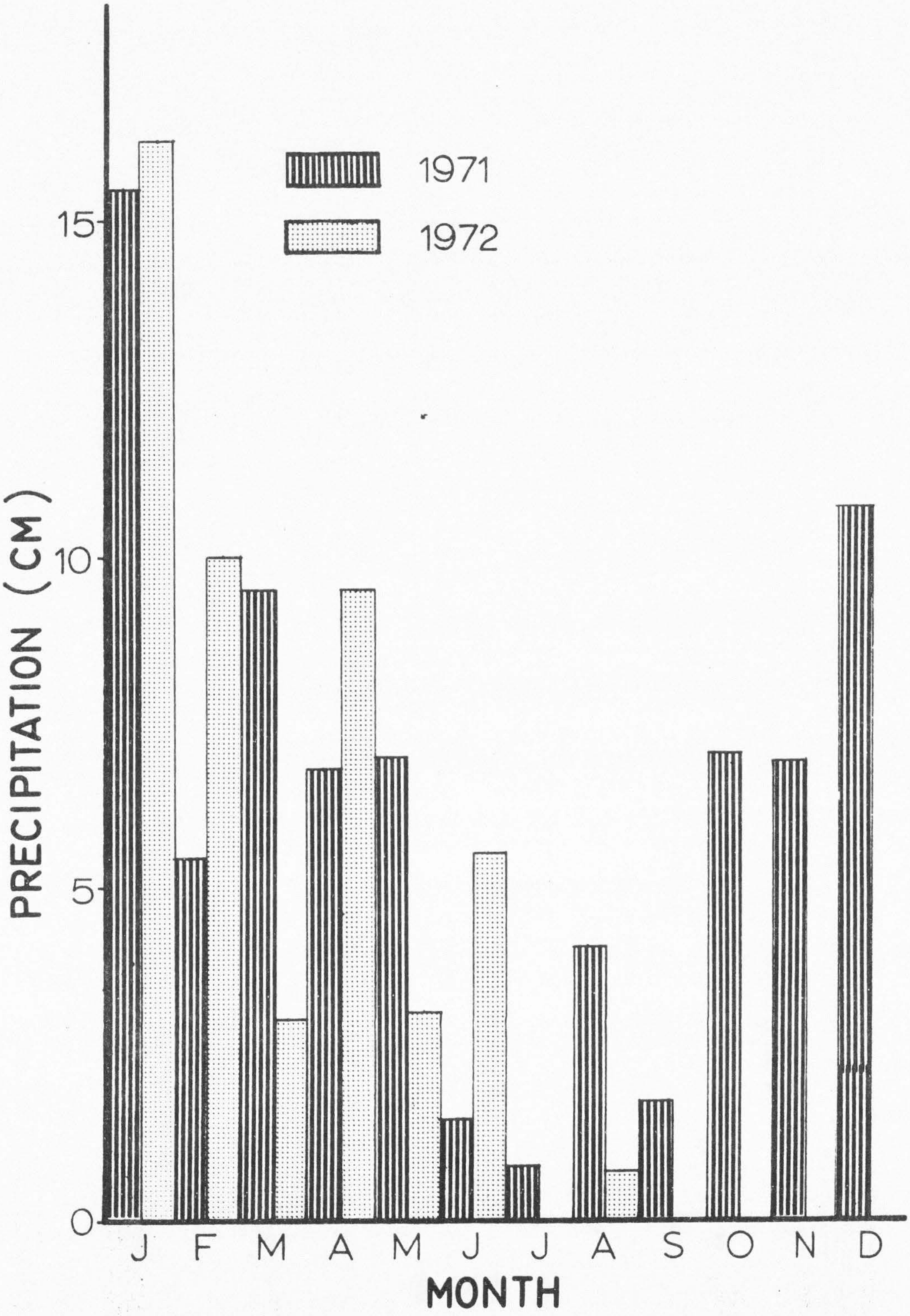

N
S
1
Hillside
Little Bear Creek
Dry Meadow
Aspen
Wet Meadow
Forestry Camp Boundary
40m
Study Site
Snow Germination
Building
Stream
Road
1 To Logan
Storage Tank

Figure 4. Precipitation regimes for 1971 and 1972. No figures were available for September, October, November, and December, 1972.


1971
1972
PRECIPITATION (CM)
15
10
5
0
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

extremes were placed on stakes 10 cm above the ground under reflective, ventilated metal covers. They were utilized in conjunction with Bendix Model 594 hygrothermographs to monitor the total ambient air regime. Soil temperatures were measured by copper-constantan thermocouples placed in the soil at 3 depths: surface, 15 cm, and 60 cm.

The data of Figure 4 indicate that 1972 was a drier year. This was reflected in an earlier snow melt and the appearance of seedlings one week earlier than in 1971. The increased rainfall in June, 1972, is misleading; half of the rain was received in one intense storm, with a high percentage of the water probably being lost in runoff.

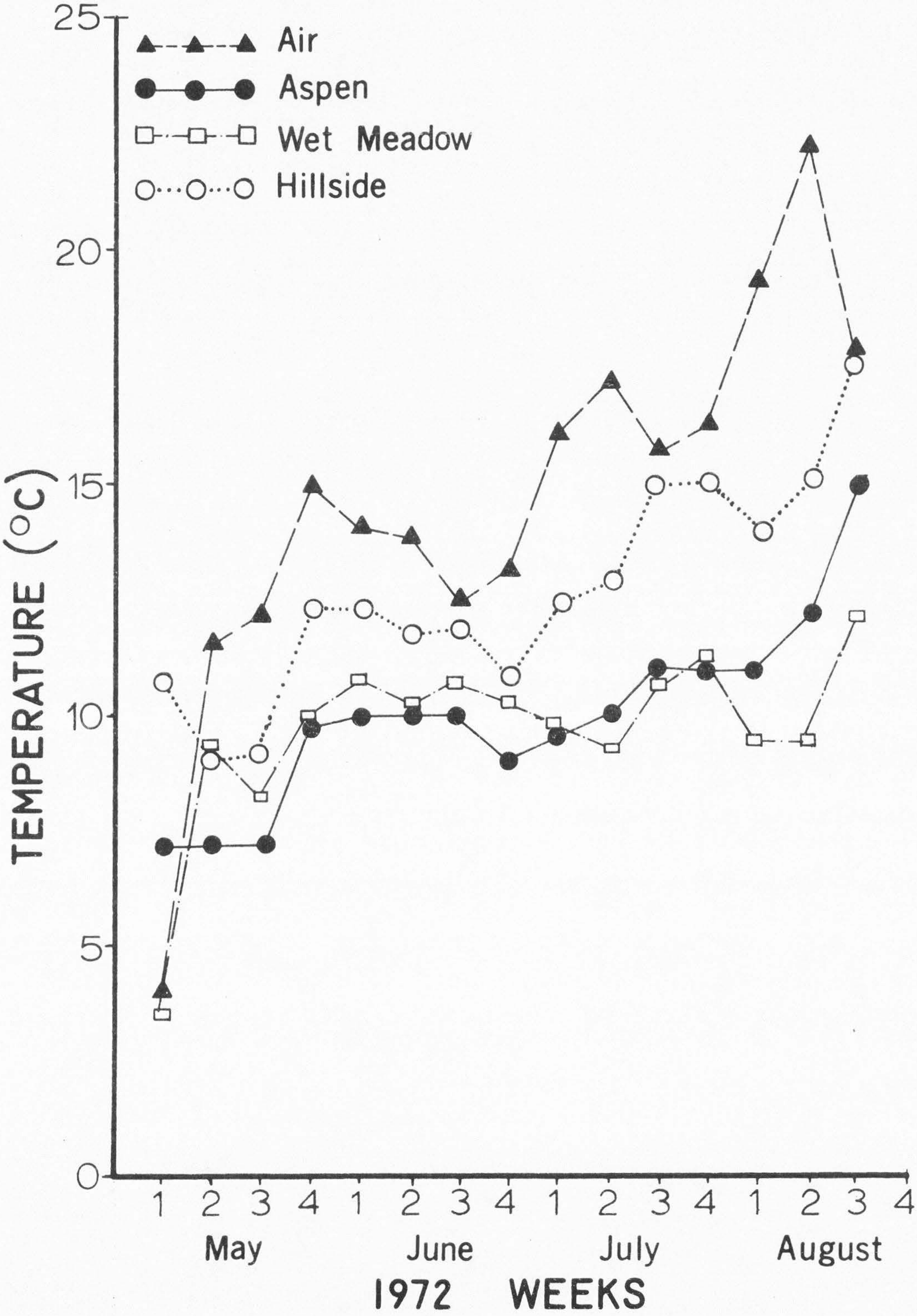
Soil temperatures at 15 cm followed the fluctuations in ambient air temperature with the characteristic lag (Fig. 5). During the period of maximum growth (May-June), soil temperatures were rarely above 12°C and ambient air temperature reached an average of 16°C.

The low temperatures between snowmelt and the last spring frost ranged between -3°C (May 21, 1971, on the dry hillside) and 5°C (June 7, 1972, in the wet meadow). The frost-free period at the wet meadow site was longer than at the other sites: May 21 to mid-September as opposed to June 16 to mid-September.

Soil Moisture

Due to apparent habitat selection characteristics (*G. richardsonii* found along streams and *G. nervosum* on

Figure 5. Soil temperatures at 15 cm and average ambient air temperatures at 10 cm above the ground in the Aspen grove for the summer of 1972.


Air
Aspen
Wet Meadow
Hillside
TEMPERATURE (°C)
0
5
10
15
20
25
1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4
May
June
July
August
1972 WEEKS

dry, rocky hillsides), response to soil moisture conditions may be a significant factor affecting the distribution of these species.

Soil moisture was measured from early May until mid-August by Spanner (Peltier) psychrometers (Brown, 1970; Wiebe, et al., 1971) placed at 2 depths: 15 cm and 60 cm.

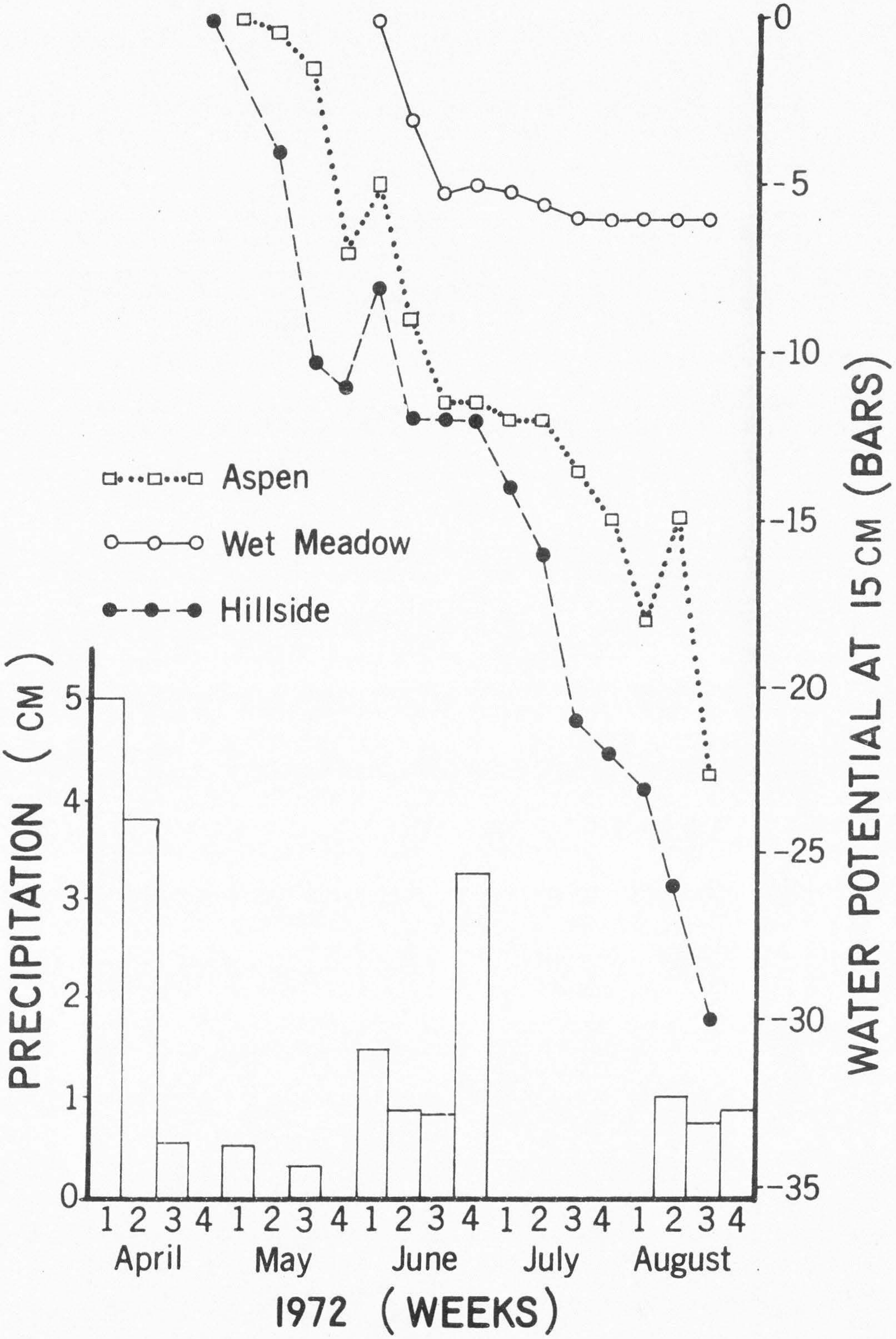
The data in Figure 6 indicate that precipitation may have an effect on the soil moisture in the aspen grove and dry hillside. The first storm in June was sufficient to raise the soil water potential (Ψ_s) in those areas, while the other storms appeared to slow the drop in moisture availability. Overflow from Little Bear Creek covered the wet meadow until the third week in June. The June rainstorms appear to have been sufficient to enable this site to maintain a high moisture content.

Soil

Soil samples from each of the 3 sites were analyzed for saturation percentage, percent nitrogen, percent organic matter, pH, conductivity, phosphorus, potassium, texture, and presence of lime by the U.S.U. Soils Testing Laboratory. These data were intended to be only an indication of soil composition, not a complete survey.

The soil in the wet meadow area was different insofar as the phosphorus and potassium levels were concerned. Both the dry hillside and the aspen grove had greater than 30 ppm phosphorus and greater than 480 ppm potassium, while

Figure 6. Precipitation received vs. soil water potential at 3 sites at the U.S.U. Forestry Field Station in the summer of 1972.


Aspen
Wet Meadow
Hillside
PRECIPITATION (CM)
0
1
2
3
4
5
WATER POTENTIAL AT 15 CM (BARS)
0
-5
-10
-15
-20
-25
-30
-35
1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4
April
May
June
July
August
1972 (WEEKS)

the soil in the wet meadow had only 4 ppm phosphorus and 126 ppm potassium (Table 1). The reason for the extremely low phosphorus and potassium levels in the wet meadow was probably leaching due to the overflow of Little Bear Creek. Potassium is found in the soil as K_2O; phosphorus is most commonly found as fluorapatite ($Ca_{10}(PO_4)_6F_2$) (Bear, 1965). Both of these are readily leached. The running water probably removed the nitrates and nitrites from this area as well as the potassium and phosphorus (Bear, 1965).

The presence of lime was tested by effervescence with 1M HCl (Buckman and Bradey, 1969). Since the degree of effervescence in the hillside and wet meadow soils was so slight, it was concluded that the absence of lime in the soil of the aspen grove was not a significant factor (R.E. Lamborn, personal communication).

Table 1. Soil composition at three sites at the Utah State University Forestry Field Station.

Location	% 2 mm Rocks	Saturation %	% Nitrogen	% Organic Matter	Lime
Aspen Grove	0	55.7	.28	4.62	0
Wet Meadow	0	69.9	.42	8.04	+
Dry Hillside	39.9	50.0	.30	5.57	+

	mmhos/cm EC_e	ppm Phosphorus	ppm Potassium	pH	Texture
Aspen Grove	.4	36	480	7.0	Silt Loam
Wet Meadow	.5	4.0	126	7.6	Silt Loam
Dry Hillside	.3	40	480	6.8	Silt Loam

CHAPTER III

Biological Factors

Germination under snow

To insure the success of any species, the seeds should germinate when environmental conditions are most favorable for survival. In an area like the Forestry Field Station where the summer is the dry season, the best time to germinate would be early in spring (April to May) or under the snow during the winter when the maximum water supply is available, providing it was possible to adapt to cold conditions. To determine when seeds of *G. richardsonii* and *G. nervosum* germinate, whether or not they grow under the snowpack and how many seeds survive as viable but ungerminated at the end of the winter, the following experiment was conducted. Fine nylon mesh was made into 20 cm x 20 cm bags each of which was divided into 2 compartments. Twenty-five seeds of *G. nervosum* were placed on one side, 25 seeds of *G. richardsonii* on the other. The site selected was in a transition zone between *G. nervosum* in a dry meadow situation and *G. richardsonii* along the banks of Little Bear Creek. Ten 1 m stakes with 1 m marker flags attached were placed 1 m apart in 2 rows. Two bags were placed flat on the ground and attached to each stake. At 3 week intervals beginning in January, 1971, 3 stakes were removed and the number of germinated seeds was counted. Seeds that had not germinated were tested with tetrazolium chloride (Machlis and Torrey, 1956) to determine their viability. The radicles of germinated seeds were measured to determine growth.

At each sampling period, the number of seeds which had germinated, remained viable or been destroyed was scored and the results tested by analysis of varience (ANOV) to see if there was a significant difference (at the 95% level) between species.

After January, 1971, there was no apparent increase in the numbers of G. nervosum seeds which had germinated (Table 2). Many of the seeds which had not germinated by that time remained viable. By March, all ungerminated seeds had rotted. On the other hand, G. richardsonii seeds continued to germinate until early March. As in G. nervosum, all ungerminated seeds had rotted. There was no significant difference between species in the number of seeds which had germinated or were destroyed.

In both species, the radicle attained a length of up to 4 cm by March. The radicle continued to grow slowly until the cotyledons emerged.

Field germination and survival

Not all seeds that germinate survive. Mortality factors are legion and can include insects, fungi, temperature, moisture availability, and interference by other plants of the same or different species. To study germination

Table 2. Germination of seeds of G. nervosum and G. richardsonii in packets under snow at the U.S.U. Forestry Field Station. (Germ. = Germination; Dest. = Destroyed.)

	G. nervosum			G. richardsonii		
Date	% Germ.	% Viable	% Dest.	% Germ.	% Viable	% Dest.
Jan. 1971	22	10	68	3	28	69
Feb. 1971	18	9	73	8	10	82
Mar. 1971	20	0	80	15	0	85

and survival in the field and to determine some of the mortality factors involved, the following experimental designs were used. In October, 1970, the effects of competition and scarification on seedling survival were examined. Three 100 x 50 cm plots were established, one each in the aspen, wet meadow and dry hillside sites. Each plot was scraped clean of grass, seeds and other debris and divided into eight 25 x 25 cm squares with 20 seeds in each square. Half the squares were G. nervosum, half were scarified and half were weeded in a 2x2x2 factorial design with no replications. Significance was tested by ANOV at the 95% level. Seedlings which survived the following winter (1971-1972) were observed in early spring of 1972 for overwinter survival. In October, 1971, 3 replications of four 25 x 25 cm squares were established in the same sites. The squares were randomized for species, and 20 seeds were placed in each square.

Squares which were weeded and/or contained scarified seeds in the 1970-1971 plots were not significantly different from squares with untreated seeds so the data were pooled and averaged (Baskin, Schank and West, 1969).

Geranium nervosum and G. richardsonii seedlings first appear 1-2 weeks after snowmelt (middle to end of April). The cotyledons emerge and persist for 4-6 weeks until the first true leaf has appeared and a second is forming. Rarely does the seedling form more than 3 true leaves in its first growing season.

Germination and survival rates throughout one summer did not differ significantly between the two species except in the wet meadow (Figs. 7 and 8). In the summer of 1971, *G. nervosum* had a significantly higher number of seedlings in the wet meadow than did *G. richardsonii*. In 1972, the *G. richardsonii* seedlings were more successful in the wet meadow.

Geranium richardsonii germination and survival rates were significantly greater in the aspen grove and wet meadow than on the dry hillside. *Geranium nervosum* had a significantly higher germination rate in the wet meadow in 1971 but, in 1972, there was no apparent difference in survival between the wet meadow and the aspen grove. The dry hillside was inimical to germination and survival; *G. nervosum* was the only species to survive on it.

The key indicator for successful establishment is overwinter survival ability. Although a seedling may survive until the end of its first summer, it may not have sufficient carbohydrate reserves to sustain it through winter and to initiate growth the following spring. Insufficient reserves may be due to stress. For example, a plant may have to put so much energy, i.e. carbohydrates, into combating competition or lack of water, that it is unable to store any energy for maintenance.

Geranium richardsonii had significantly better survival in the wet meadow than did *G. nervosum*. In the aspen grove and dry hillside plots, *G. nervosum* had significantly greater

Figure 7. Mean number of seedlings/plot of G. richardsonii and G. nervosum at 3 sites at the U.S.U. Forestry Field Station throughout the summer of 1971.

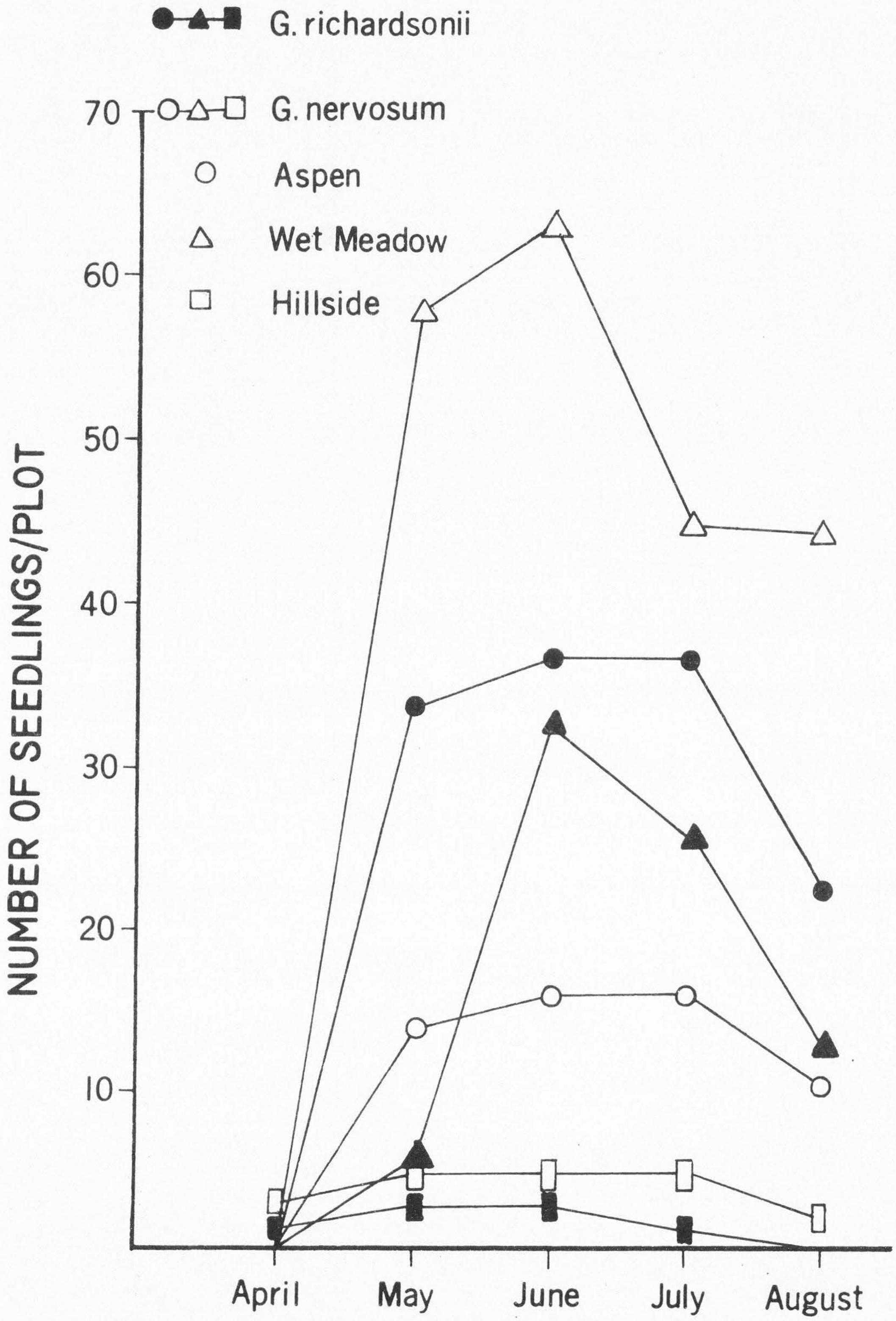
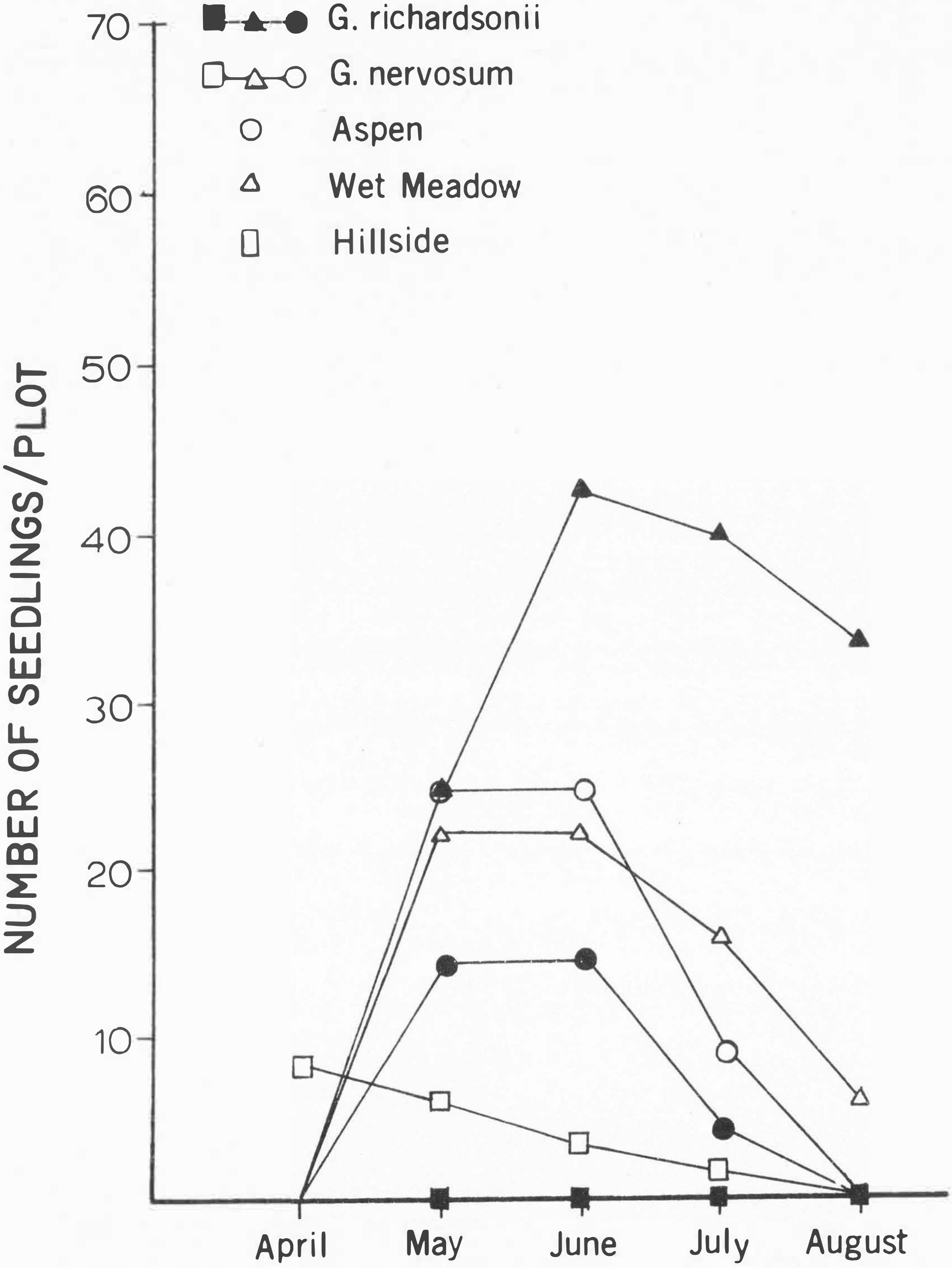

G. richardsonii
G. nervosum
Aspen
Wet Meadow
Hillside
NUMBER OF SEEDLINGS/PLOT
70
60
50
40
30
20
10
April
May
June
July
August

Figure 8. Mean number of seedlings/plot of *G. richardsonii* and *G. nervosum* in 3 sites at the U.S.U. Forestry Field Station throughout the summer of 1972.


G. richardsonii
G. nervosum
Aspen
Wet Meadow
Hillside
NUMBER OF SEEDLINGS/PLOT
70
60
50
40
30
20
10
April
May
June
July
August

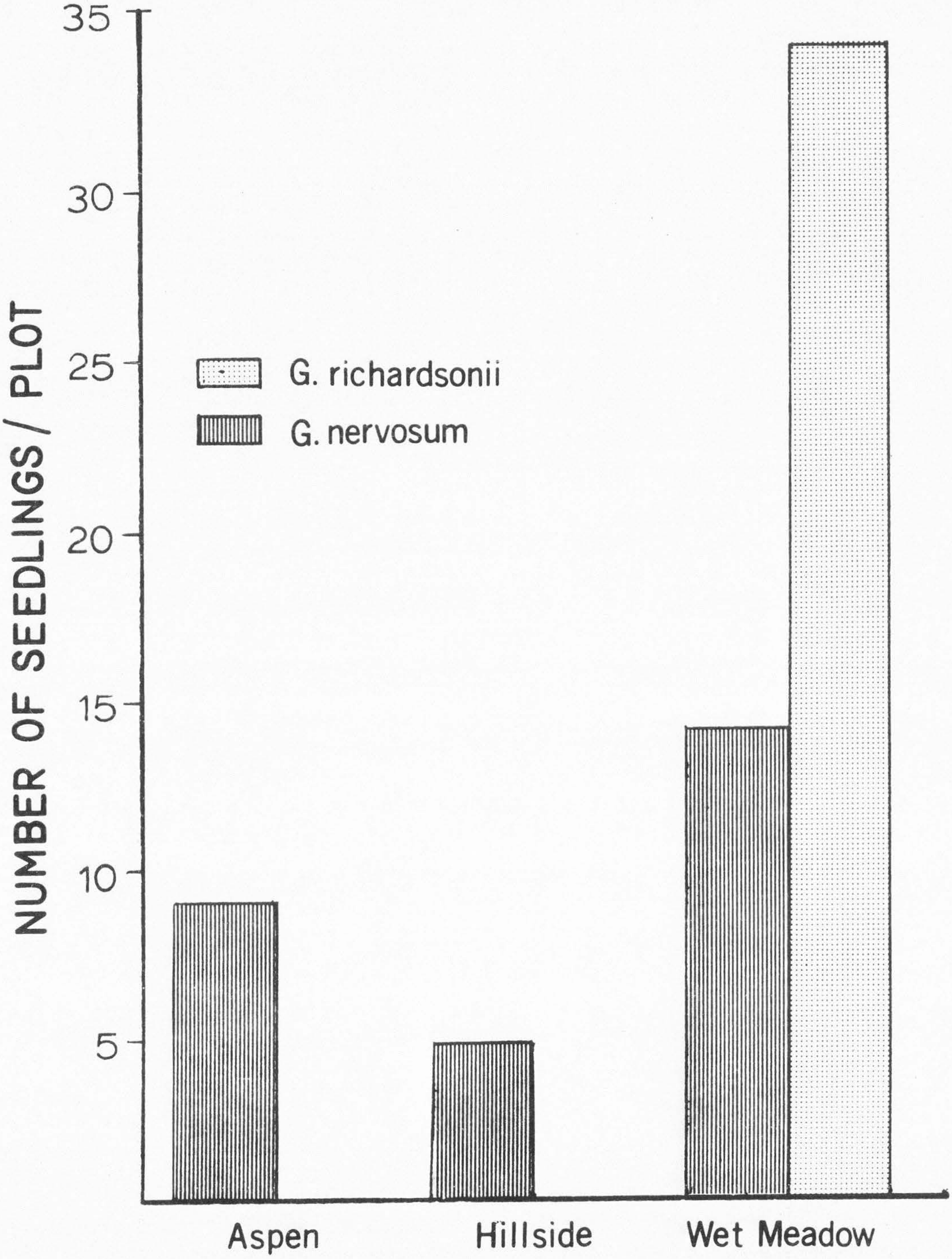
survival than did G. richardsonii. There was no significant difference in overwinter survival for G. nervosum in any of the locations but G. richardsonii had significantly greater success in the wet meadow as opposed to the other sites (Fig. 9).

Potential germination

Dormancy mechanisms are usually responsible for preventing seed germination during periods of unfavorable environmental conditions (e.g. drought). Some of the more common mechanisms are a hard outer seed coat which requires scarification to break it, the presence of an inhibitor which requires leaching or time to destroy it, and embryo immaturity which requires after-ripening (time for physiological maturation). Astragalus tennesseensis, which inhabits cedar glades in Tennessee, for example, combines a hard outer seed coat and an inhibitor in the inner seed coat to insure that germination occurs in the spring only after scarification and leaching which occur in the winter (Baskin and Quarterman, 1969).

A series of germination tests were performed in the laboratory in 1970-1971 to study the dormancy mechanisms of G. nervosum and G. richardsonii. The seeds used were collected from natural populations during August of each of these years and spread in metal trays covered with cheesecloth until the carpels had dried and the seeds were dehisced; this usually occurred within 2 weeks. All tests were con-

Figure 9. Overwinter seedling survival in *G. richardsonii* and *G. nervosum* at the U.S.U. Forestry Field Station from germination in May, 1971, to survival through June, 1972.


NUMBER OF SEEDLINGS / PLOT
35
30
25
20
15
10
5
G. richardsonii
G. nervosum
Aspen
Hillside
Wet Meadow

ducted using 25 seeds of one species which were placed in 9 cm petri dishes on 2 sheets of moistened Whatman #2 filter paper. The petri dishes were stored in 2 lb. (1 liter) coffee cans with plastic lids to prevent evaporation of water. After pretreatment, the coffee cans were placed in a germinator with a 12 hour alternating temperature regime of 5^{o}C and 15^{o}C.

Four pretreatments were examined: (1) scarification only, (2) stratification only, (3) stratification/scarification, and (4) control. Stratification was achieved by keeping seeds on moistened filter paper at 1^{o}C in a large walk-in cooler. Seeds were scarified by nicking the seed coat with a 3-cornered file; the scarification only group was kept at room temperature on dry filter paper for the duration of the pretreatment while the scarification/stratification group was placed directly into the cooler. The control groups were kept on dry filter paper at room temperature (25^{o}C) until it was time to move them to the germinator. Each can contained three replications for each species and, at 4 week intervals, 1 can from each pretreatment was removed to the germinator. The number of seeds which had germinated after 4 weeks was counted and viability of the ungerminated seeds was tested using a tetrazolium chloride solution (Machlis and Torrey, 1956). Germination was considered successful when the radicle emerged. Comparisons between pretreatments were made using ANOV with a level of significance equal to 95%.

Germination after 4 weeks in pretreatment was significantly better for both species when the seeds had been both scarified and stratified (Fig. 10). Germination response to scarification differed between species (Fig. 11). Greater than 20% of the *G. richardsonii* seeds had germinated after 4 weeks in the germinator whereas only 1% of the *G. nervosum* seeds germinated in that same time period. *Geranium nervosum* was significantly more responsive to stratification without scarification than was *G. richardsonii* (Fig. 12). *Geranium nervosum* showed an increase in percent germination with time up to 64% in 10 weeks. At that time, most of the cultures became infected with a fungus (*Rhizopus sp.*). It may be that, had the cultures not become infected, *G. nervosum* would have reached the level of germination (82%) indicated in the stratification/scarification pretreatment (Fig. 10). *Geranium richardsonii* did not show an increase in germination with time until after 10 weeks in the pretreatment. Both species indicated that either stratification or scarification (*G. richardsonii* only) improved germination, while untreated seeds had very low germinability (Fig. 13).

Viability tests performed on ungerminated seeds after 4 weeks in the germinator indicated 99% viability in both species.

Potential seedling survival

The numbers of seedlings growing in the field do not

Figure 10. Percent germination of all pretreated seeds of G. *nervosum* and G. *richardsonii* after 4 weeks in pretreatments.

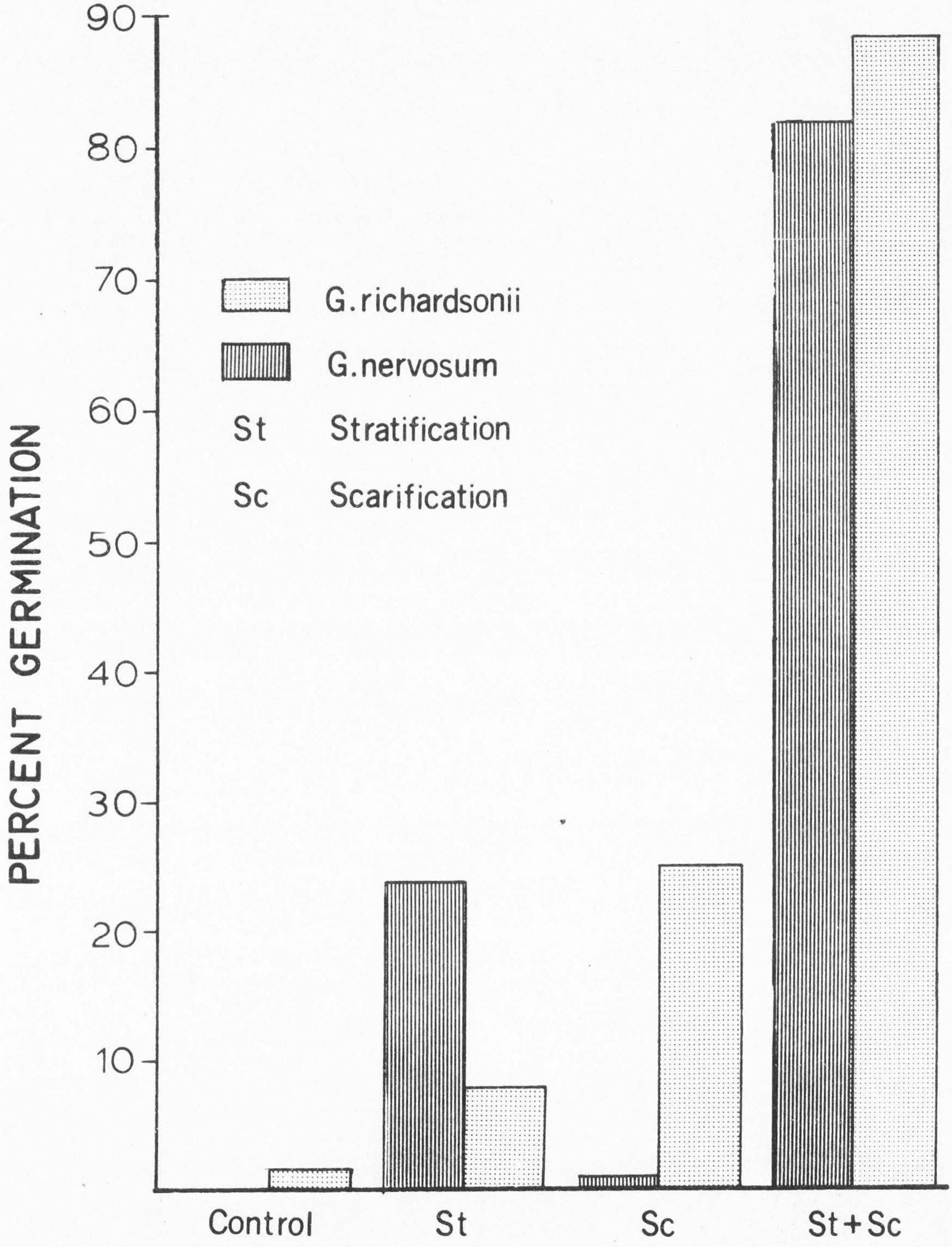

90
80
70
60
50
40
30
20
10
PERCENT GERMINATION
G. richardsonii
G. nervosum
St Stratification
Sc Scarification
Control
St
Sc
St + Sc

Figure 11. Percent germination of G. richardsonii and G. nervosum seeds after scarification and storage at room temperature.

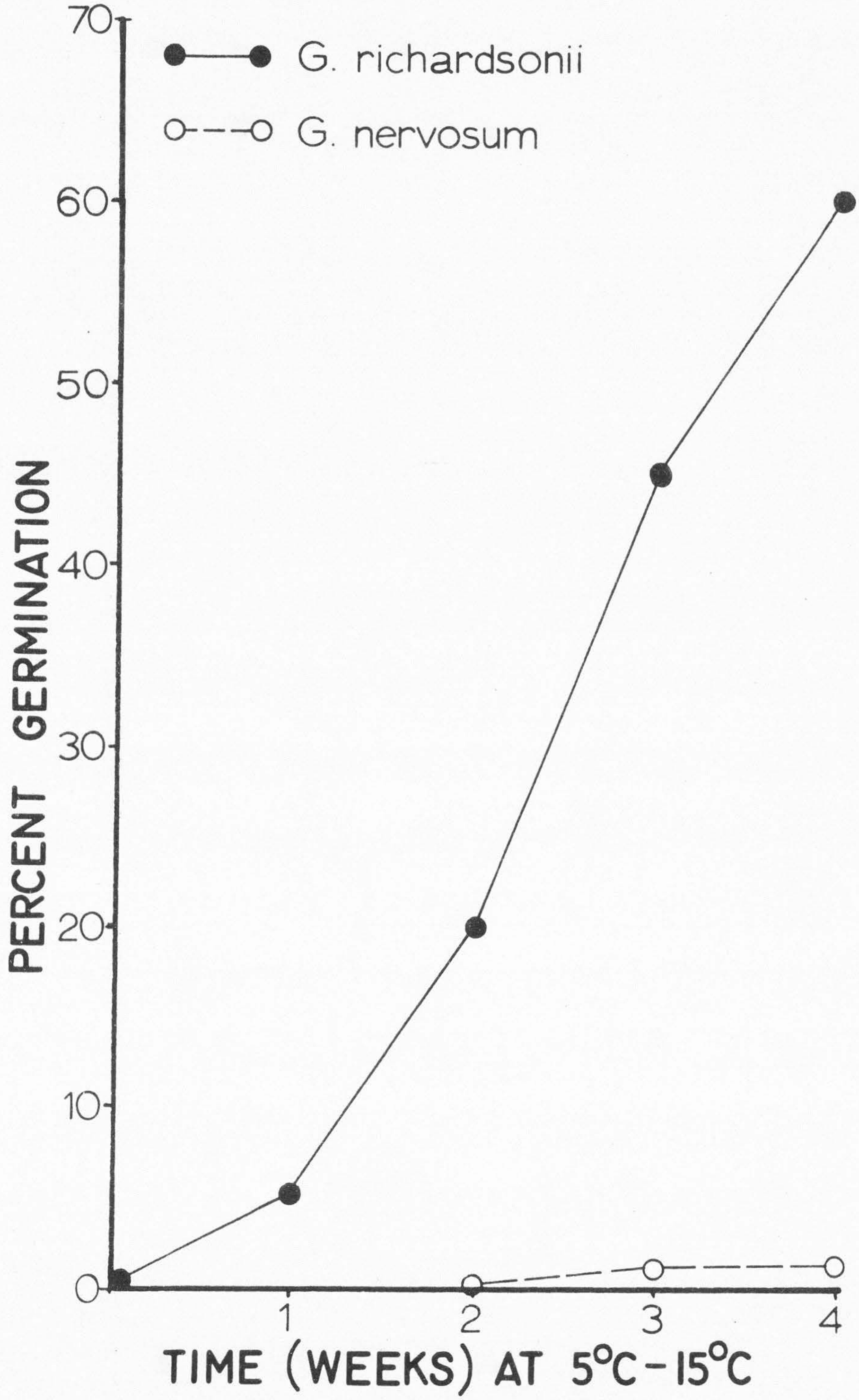

G. richardsonii
G. nervosum
70
60
50
40
30
20
10
0
PERCENT GERMINATION
1
2
3
4
TIME (WEEKS) AT 5°C-15°C

Figure 12. Percent germination of *G. richardsonii* and *G. nervosum* seeds after stratification at 1°C.

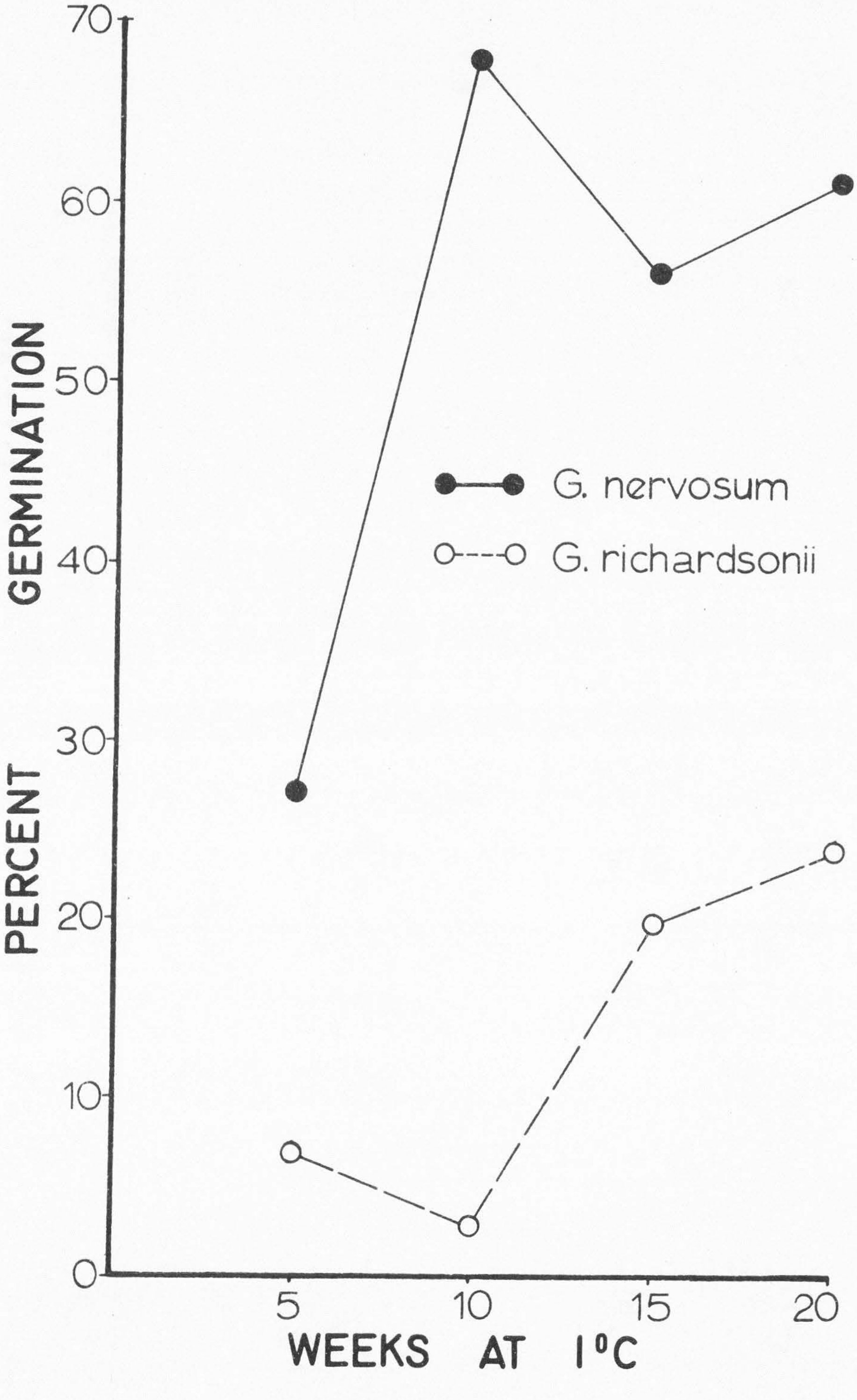
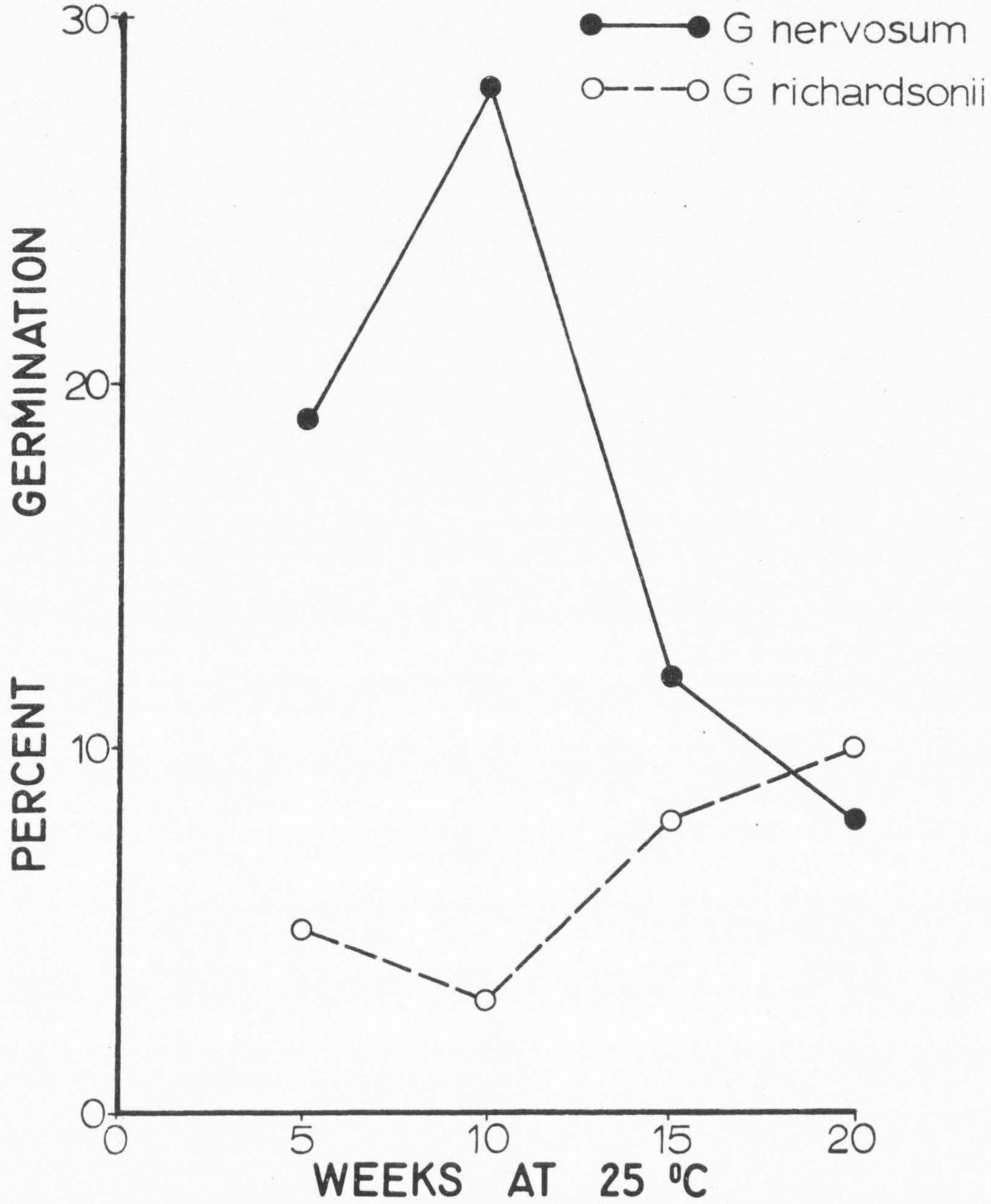

PERCENT GERMINATION
70
60
50
40
30
20
10
0
5
10
15
20
WEEKS AT 1°C
●—● G. nervosum
○---○ G. richardsonii

Figure 13. Percent germination of G. richardsonii and G. nervosum after storage at room temperature.

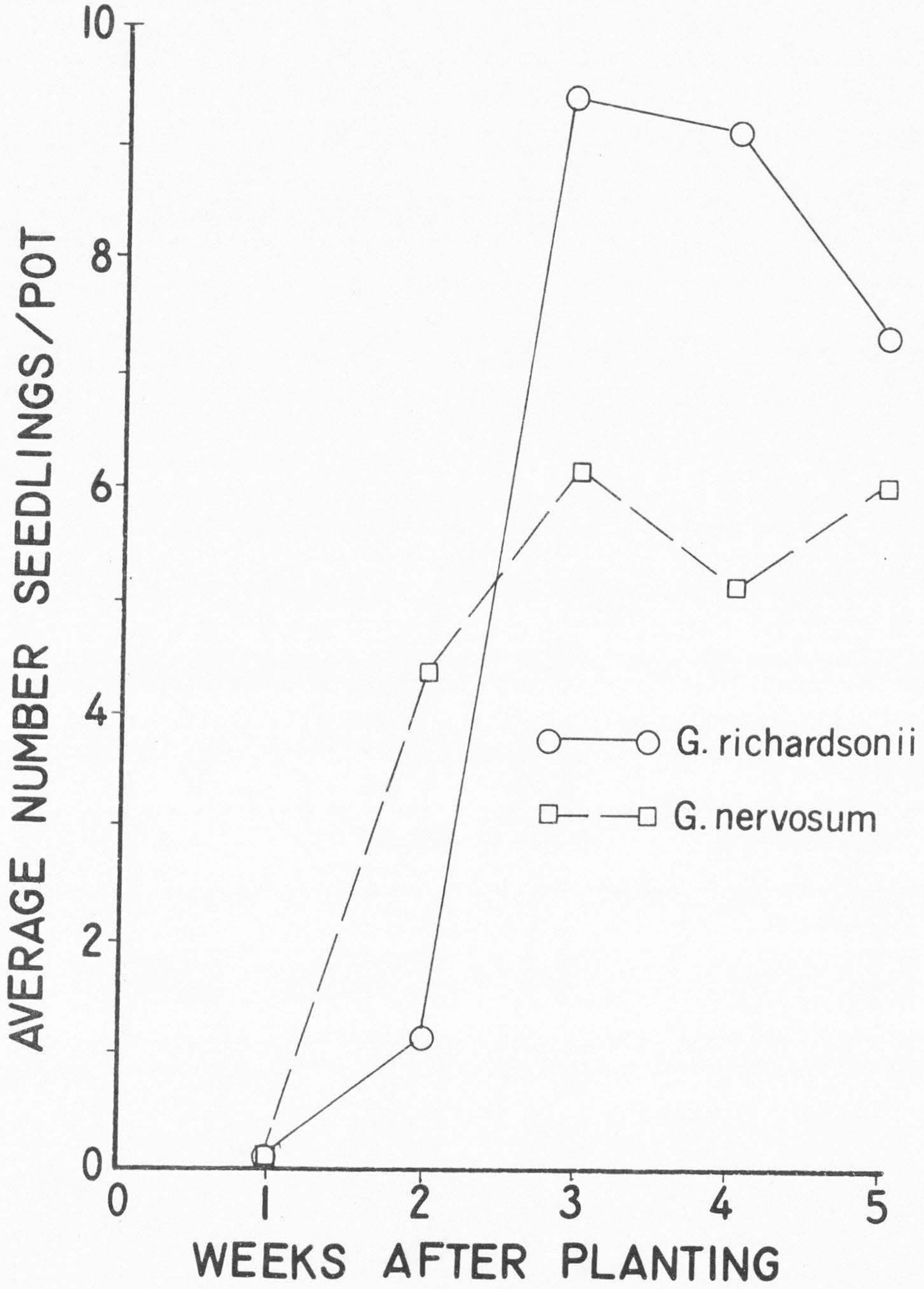

G nervosum
G richardsonii
PERCENT GERMINATION
0
10
20
30
0
5
10
15
20
WEEKS AT 25 °C

necessarily reflect true survival potentials. Individuals are removed from the population as a result of interspecific and intraspecific competition and other mortality factors (e.g. fungi and trampling). To determine the potential seedling survival, it was necessary to use controlled conditions in the greenhouse. Therefore, seedlings which had germinated during the scarification/stratification trials were planted in 25 cm pots in the greenhouse. There were 5 pots with 20 seedlings per pot for each species. The pots were kept moist but not flooded in the greenhouse which had an average temperature of 21°C. The number of seedlings which survived to the first true leaf stage were counted. Mortality after that time was noted and attempts were made to determine the cause. Results were analysed with ANOV at the 95% level of significance.

The precent establishment in G. richardsonii seedlings was significantly greater than in G. nervosum (Fig. 14). The average percent survival over 5 weeks was 38% for G. richardsonii and 30% for G. nervosum. Once the seedlings had reached the first true leaf stage, 97% of them survived. The primary cause of seedling mortality after the first true leaf stage in this experiment was aphid attack.

Another major cause of mortality may be fungi. Rhizopus sp. and Aspergillus sp. are commonly found on the seed coats of both geraniums in the laboratory. They appeared to predominate on G. nervosum. The fungi had 2 methods of attack: they either prevented germination

Figure 14. Average number of seedlings/pot surviving beyond the first true leaf stage for both *G. richardsonii* and *G. nervosum*.


AVERAGE NUMBER SEEDLINGS/POT
WEEKS AFTER PLANTING
0
2
4
6
8
10
0
1
2
3
4
5
G. richardsonii
G. nervosum

by rotting the embryo or they attacked the germinated radicle. The symptoms observed in this experiment were much the same as those observed in the field in the packets under the snow, but the species of fungi were not necessarily the same since *Rhizopus sp.* and *Aspergillus sp.* are more common in the laboratory than in the field (R. Price, personal communication).

Effects of temperature on germination and survival

Soil temperatures varied between sites (Fig. 5) and may have been limiting to germination and seedling survival. For example, the high temperatures in the dry hillside may have prevented *G. richardsonii* from establishing there.

Using a temperature gradient germinator (Barbour and Racine, 1967), a series of experiments were conducted to determine the optimal germination and survival temperatures for both species.

Germination Two replications of 25 scarified seeds each were placed at each of 11 possible positions on the aluminum bar. Using a copper-constantan thermocouple, the temperature of each petri dish on the bar was taken by placing the thermocouple on the moist filter paper in the dish. This gradient, which was the same for each species, appears in Table 3. Each experiment ran for 6 weeks and was repeated twice for each species.

Seedling survival Seedlings which were germinated during the stratification/scarification pretreatment were

Table 3. Temperature gradients along bar and troughs for seed germination and seedling survival in gradient bar germinator (Barbour and Racine, 1967).

	Temperature gradients for seed germination	
Position	A	B
1	15°C	15°C
2	17	17
3	19	19
4	21	21
5	23	23
6	24.8	24.8
7	26.5	26
8	28	28
9	30	30
10	31.5	31
11	33	32.5

	Temperature gradients for seedling survival	
Position	A	B
1	15.5°C	15.5°C
2	18.5	19
3	21	21
4	23	23
5	24.5	24.5
6	25	25
7	26	26
8	27	27
9	28	28
10	29.5	30
11	31	31
12	32.5	32.5

used in this experiment. The two aluminum troughs in the germinator were lined with aluminum foil and filled with sterilized soil. Twelve seedlings at the third true leaf stage were placed in each trough and the temperature at each position was taken with the thermocouple (Table 3). At the end of 4 weeks, plants were judged subjectively on their condition: (1) death - plant brown and completely wilted, (2) chlorosis - plant completely chlorotic (light green in color), (3) poor - evidence of chlorosis; stunted when compared with normal seedlings of the same age, (4) fair - no chlorosis but evidence of stunting, and (5) healthy - new leaves actively being produced, no evidence of stunting.

The optimum temperature range for G. nervosum appeared to be from 20-25°C. Geranium richardsonii was less specific. It indicated a trend of decreasing germination with increasing temperature (Fig. 15).

Seedling survival at different temperatures was similiar for both species (Fig. 16). The optimum temperature for seedling survival seemed to be from 18-25°C for G. richardsonii and 20-25°C for G. nervosum.

Soil moisture response

Depending on field conditions, i.e. relative humidity and radiation load, plant response to water stress will differ (Gates, 1968). It is therefore difficult to isolate a plant's response to water stress from its response to other environmental factors in the field. Therefore,

Figure 15. The effects of temperature on germination of *G. nervosum* and *G. richardsonii* seeds in the laboratory.

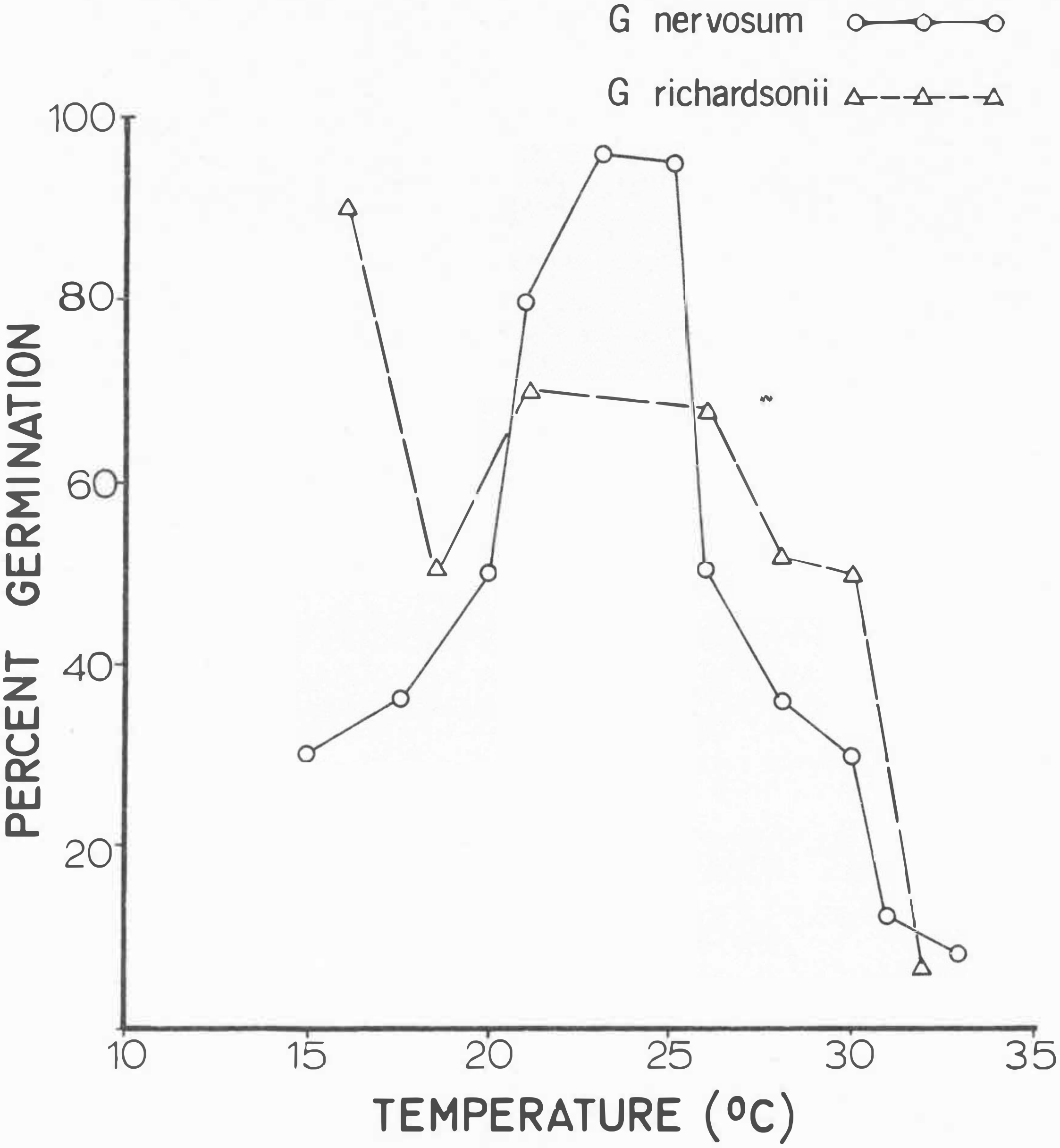
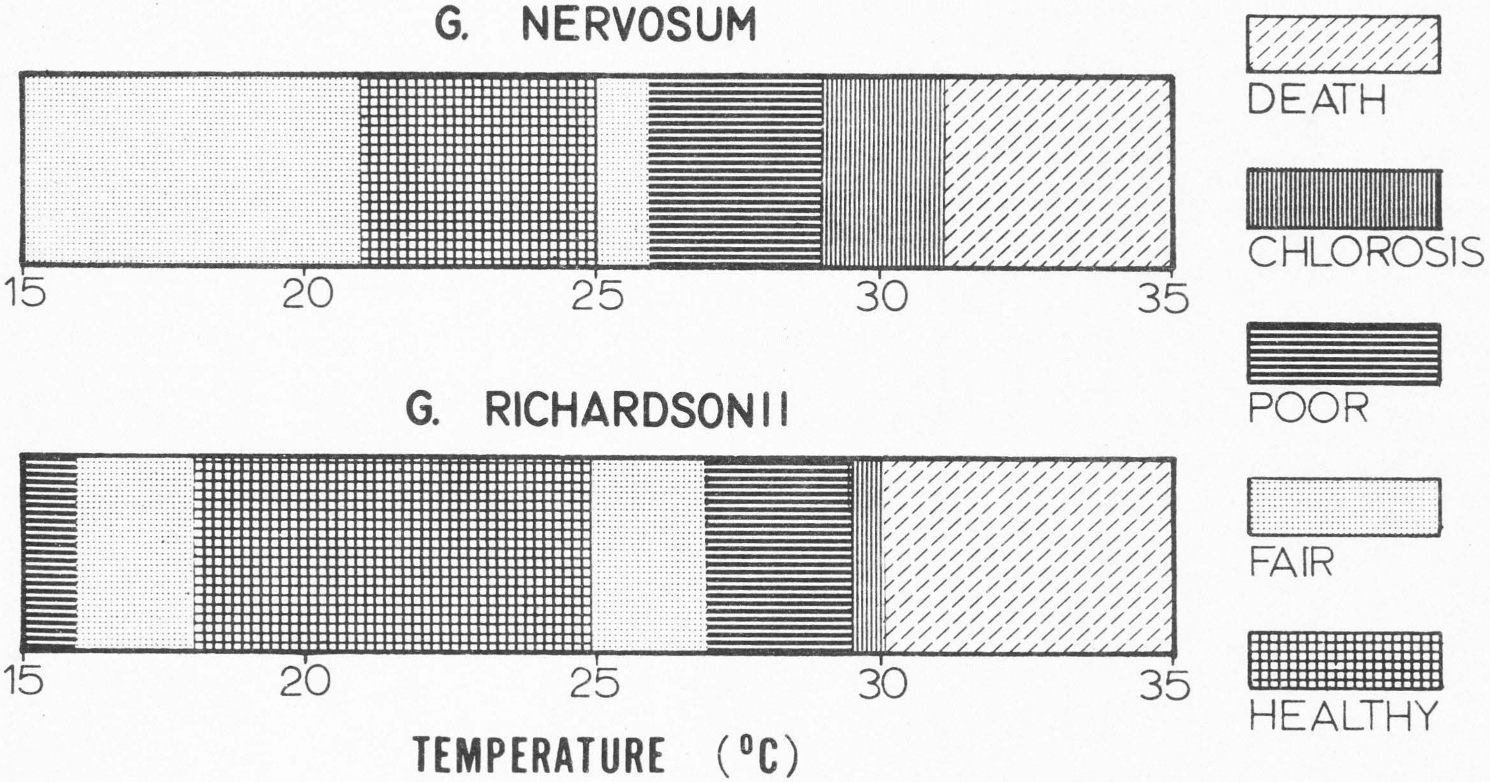

G nervosum
G richardsonii
PERCENT GERMINATION
100
80
60
40
20
10
15
20
25
30
35
TEMPERATURE (°C)

Figure 16. The effects of temperature on survival of *G. richardsonii* and *G. nervosum* seedlings in the laboratory at the third true leaf stage.


G. NERVOSUM
15
20
25
30
35
G. RICHARDSONII
15
20
25
30
35
TEMPERATURE (°C)
DEATH
CHLOROSIS
POOR
FAIR
HEALTHY

experiments to determine the nature of the effects of water stress on *G. richardsonii* and *G. nervosum* were conducted in the laboratory.

Field data indicated that there was a significant difference (ANOV, p .05) in water potential between the *G. richardsonii* habitat (meadow) and the *G. nervosum* habitat (hillside and aspen grove). To determine the effect of this difference on *G. richardsonii* and *G. nervosum* plants, adults and seedlings were grown in the laboratory under uniform conditions and then subjected to different moisture stresses.

Cotter and Platt (1959), when studying the effects of moisture stress on *Portulaca smalii*, set up a watering regime that allowed some plants to be watered every day, some every two days, etc. The difficulty in interpreting the results of an experiment of this type lies in the probability that the soil in all pots of one treatment did not dry out at the same rate and that there could have been variations in soil conditions throughout the pots due to differential water uptake by the roots (Gardner, 1968).

To circumvent this problem, each pot used in experiments on *G. richardsonii* and *G. nervosum* plants contained 3 soil psychrometers described earlier (p. 11). At 2 week intervals, 1 set of pots was saturated so each pot was at 0 bars water potential and then placed on a drying regime. A set consisted of 6 pots of each species: 3 pots contained adult plants, 3 contained 10 seedlings each. As the soil in the pots dried, plants were checked for turgidity, evidence of chlorosis and the production of new leaves. The applicability of these three variables is demonstrated in a discussion of three major effects of moisture stress

> (1) High drought stress often kills plants.
> (2) ρ[net assimilation] of CO_2 can be reduced by low water potentials (sometimes drastically) through partial or complete stomatal closure, through increases in r_m" [mesophyll resistance] to vapor transfer and probably through direct effects on biochemical reactions. . . .
> (3) Higher water loss by leaves often makes less water available to developing flowers and fruits [and probably new leaves]. . . ." (Parkhurst and Loucks, 1972, p. 509).

When plants had completely wilted, turned brown and produced no new leaves for 7 days, they were placed with control plants which were watered every day.

The seedlings of both species reacted in a similiar way to increasing moisture stress. *Geranium nervosum* appeared to be slightly more resistant to moisture stress until soil water potential (Ψ_s) reached about -15 bars (Fig. 17). Both species died if Ψ_s was maintained at -15 bars for longer than 7 days.

Adults of both species appeared more resistant to moisture stress (Fig. 18). *Geranium richardsonii* was able to produce new leaves until Ψ_s reached about -10 bars. *Geranium nervosum*, however, continued to produce new leaves until Ψ_s reached -20 to -25 bars. When adults of *G. nervosum* with flowering stalks were placed under

Figure 17. Effects of increasing soil moisture stress on seedlings of G. richardsonii and G. nervosum. (Healthy = no wilting, new leaves, no loss of color in leaves; Fair = some loss of color, new leaves slightly chlorotic; Poor = no new leaves, some wilting; Wilt = complete wilt with or without chlorosis; Death = no new leaves, all leaves brown.) (Figure also shows range of variation in condition of plants at each point measured.)

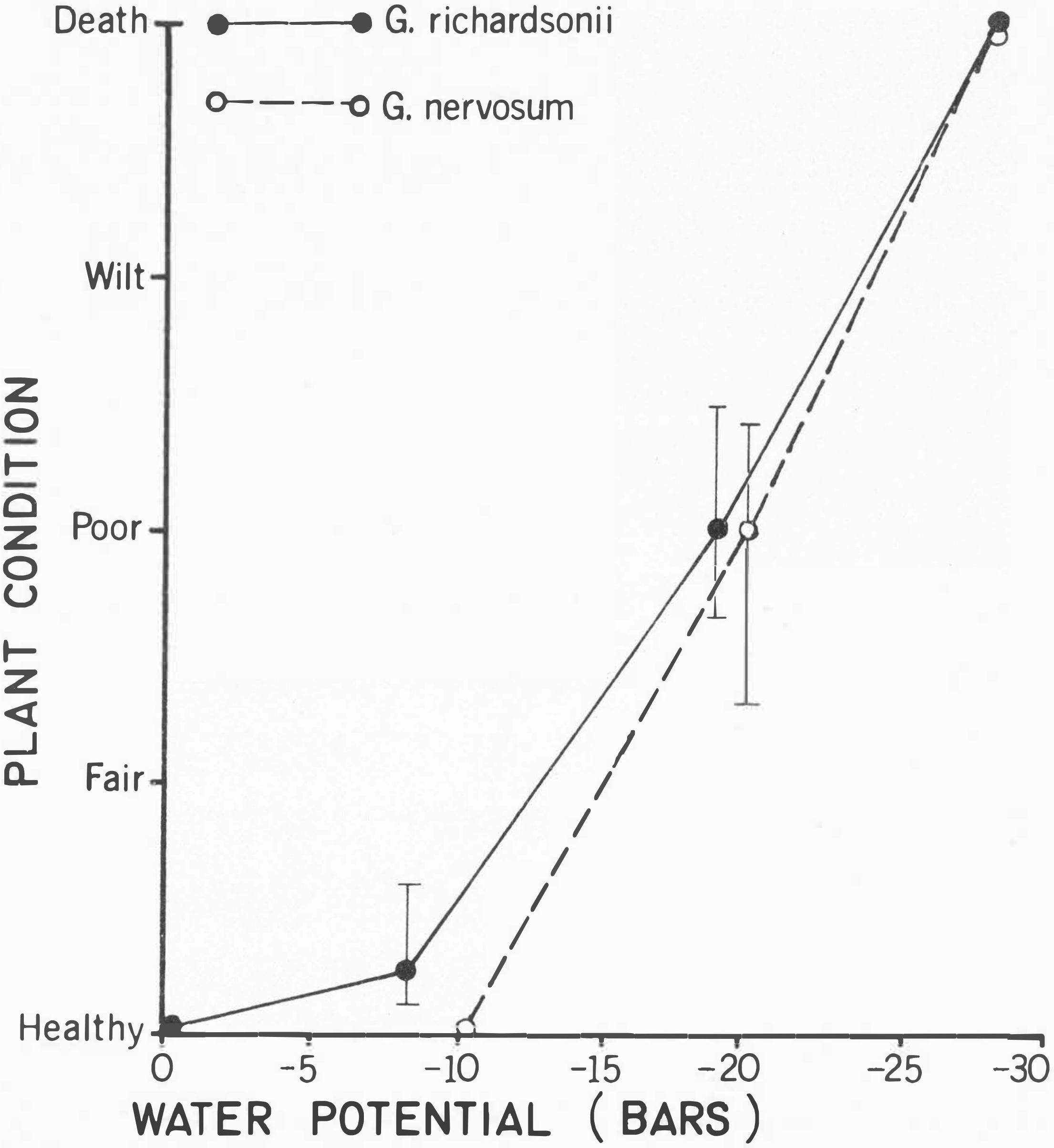
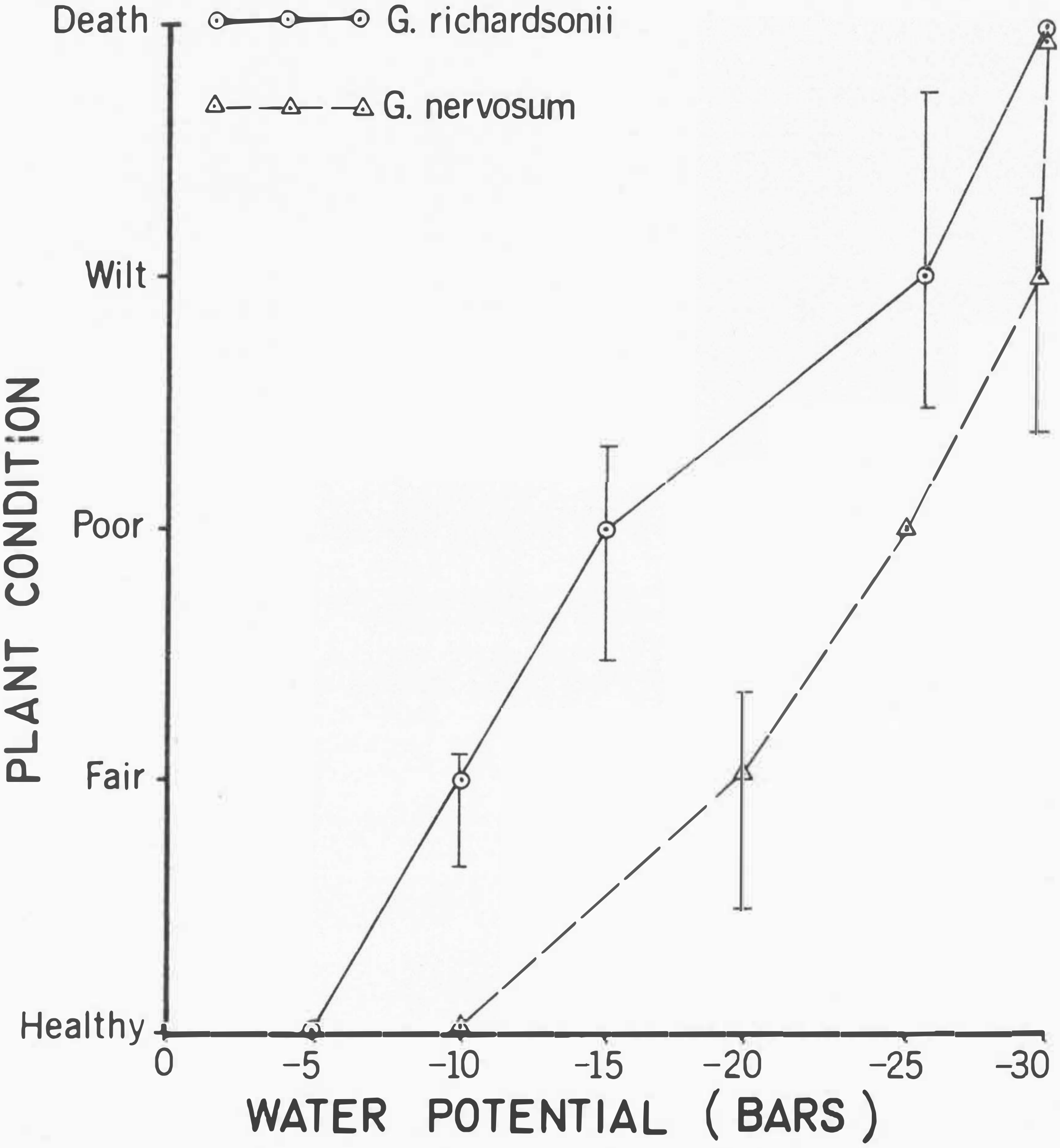

Death
Wilt
Poor
Fair
Healthy
PLANT CONDITION
G. richardsonii
G. nervosum
0
-5
-10
-15
-20
-25
-30
WATER POTENTIAL (BARS)

Figure 18. Effects of increasing moisture stress on adults of *G. richardsonii* and *G. nervosum*. (Figure also shows range of variation in condition of plants at each point tested.)


G. richardsonii
G. nervosum
Death
Wilt
Poor
Fair
Healthy
PLANT CONDITION
0
-5
-10
-15
-20
-25
-30
WATER POTENTIAL (BARS)

moisture stress, the first evidence of stress appeared in the mature leaves and in the initiation of young leaves. Not until Ψ_s reached -30 bars did the flowering stalk begin to wilt. *Lupinus albus* exhibited this same pattern. The apex was less sensitive to water stress while the development of leaf primordia was severely limited; therefore, a senescent decline in growth during wilting was observed (Gates, 1968).

Geranium richardsonii adults demonstrated the ability to recover from severe moisture stress. The development of a physiologically young condition was observed upon rewatering, which is apparently a common phenomenon (Gates, 1968).

Vegetative growth

Leaves The leaves of *G. richardsonii* and *G. nervosum* are both basal and cauline. The petioles of basal leaves on *G. richardsonii* are from 5-30 cm in length; those of *G. nervosum* are from 10 to 48 cm long. For both species, the leaves produced during growth initiation and at the end of the growing season are the shortest. The basal petioles of *G. richardsonii* are almost always glabrous; *G. nervosum* petioles range from completely glabrous to being covered with mostly non-glandular trichomes (Shaw, 1952). However, petioles of *G. nervosum* plants germinated and grown in the laboratory exhibited the glandular trichomes found on *G. viscossissimum*.

The leaves of *G. richardsonii* and *G. nervosum* are 3-22 cm in width (*G. nervosum* usually being the wider), pentagonal in shape and deeply 5-7 parted with the rhombic segments divided several times (Shaw, 1952). Cauline leaves are similiar in both species being as deeply divided, with petioles 0.5 to 1.5 cm in length.

The leaves appeared in small sheaths about 1 cm above the surface from 1-2 weeks after the snow melted. Infrequently, a plant was observed growing through the snow. The plants continued to produce leaves throughout the summer although the majority of new leaves were produced before flowering stalk initiation in mid-June. In *G. nervosum*, after the first week in July, when air temperatures were greater than 30°C (Fig. 5), the foliage produced earlier had matured and the leaves in the center of the clone showed definite evidence of chlorosis and early senescence. By the first week in August, the seeds were maturing; no new leaves were being produced, and all leaves showed signs of advanced chlorosis. *Geranium richardsonii* plants did not begin to show signs of senescence until the second or third week in August. Senescence was not complete until after the first frost in late September.

Lewis (1969) indicated that, if plants of *G. sanguineum* were grown in strong light conditions (heavy radiation load) the leaves were smaller and more highly dissected than leaves of plants grown in less extreme conditions. Parkhurst and Loucks (1972) indicated that shade leaves are more efficient in terms of water vapor, CO_2, and heat transfer when they are large; the sun leaves are more efficient at smaller sizes. As previously discussed, G. nervosum grows in conditions of shade (aspen site) and continuous sunlight (south-facing hillside). Leaf prints were taken on Ozalid blueprint paper to determine whether leaf size was significantly different between the two areas. The prints were cut out and areas of the leaves were determined. There was no significant difference (ANOV, $p > .05$) in leaf area nor was there any apparent difference in margination (degree of dissection) between leaves of deep shade and sun plants although there was an indication that petioles of shaded plants were longer and the leaves slightly larger.

Roots Geranium richardsonii and G. nervosum both arise from a caudex which is branched and sometimes rhizomatous. Martin (1965) indicated that G. maculatum clones grew by means of rhizomes. Geranium richardsonii and G. nervosum, however, did not generally have rhizomes as young (1-3 years) plants; instead, the clone grew by branching. It was possible for older plants to develop rhizomes. The rhizome was usually found in the upper 7-10 cm of soil although, on one occasion, a rhizome originated 15 cm down on the tap root of G. nervosum.

Attempts were made to determine the type of root systems and how deep the roots grew for both species by excavating 3-5 plants in each area. Excavation on the dry hillside was limited to 100 cm due to the rockiness

Figure 19. The filamentous root system of *G. richardsonii.*

of the soil. *Geranium richardsonii* had a filamentous root system with little or no evidence of a tap root (Fig. 19). It usually grew to a depth of 60-70 cm. *Geranium nervosum* had a definite tap root with fewer filamentous roots (Fig. 20). This root penetrated to depths of over 100 cm on the hillside but less than 100 cm in the aspen. There was little variability in the root systems of plants sampled except in the case of rhizomes, as mentioned above.

Flowering

Morphology The flowers of *G. nervosum* first appear from mid-June (hillside) to late June (aspen), while *G. richardsonii* flowers usually appear from late June to early July. Both species continue flowering until well into August. Flowers are cymose and borne on peduncles which arise at the stem node bearing the cauline leaves. The stems are from 30-115 cm tall in *G. nervosum* and 30-90 cm tall in *G. richardsonii* (Shaw, 1952). The flowers in each cyme do not mature at the same time; usually the peduncles lengthen in pairs with one flower maturing while the other is still in bud. Single plants commonly bear buds, flowers, and seeds simultaneously.

Pollination Outcrossing is desirable for most species to allow genetic recombination. There are several mechanisms in plants which insure cross-pollination: (1) pollen tubes of pollen from different plants of the same species grow faster than pollen tubes of the plant's own pollen,

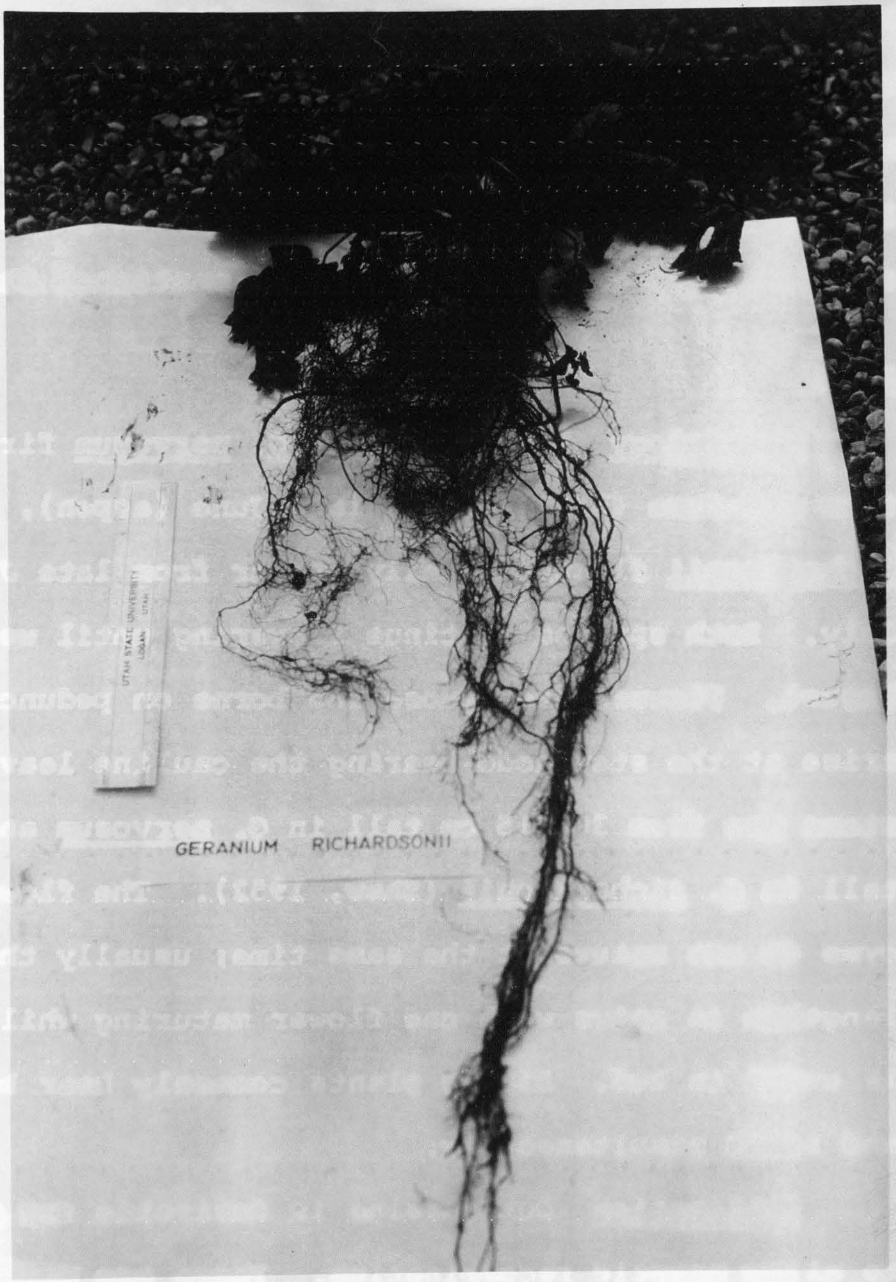

UTAH STATE UNIVERSITY
LOGAN UTAH
GERANIUM RICHARDSONII

Figure 20. The tap root system of _G_. _nervosum_.


GERANIUM NERVOSUM
UTAH STATE UNIVERSITY
LOGAN UTAH

(2) separation of anthers and stigmas in time (either protogyny or protandry), (3) separation of anthers and stigmas in space (actinomorphous flowers) or (4) dioecious flowers (Faegri and van der Pijl, 1971). Since Geranium flowers are bisexual and not actinomorphic, only the first two mechanisms are possible. To determine whether protogyny or protandry were present, the sequence of anthesis was observed and recorded (Fig. 21). As in G. maculatum (Martin, 1965), the flower buds of G. nervosum and G. richardsonii are probably formed the season prior to elongation since, when the flowering stalk begins to grow, the buds appear already formed (Fig. 21A). As the peduncle lengthens, the bud begins to open (Fig. 21B&C). The anthers are dehisced sequentially providing a long period of pollen availability (Fig. 21D). The stigma appears to be ready, i.e. it unfolds, only after all the pollen has been dehisced (Fig. 21E) but there is a possibility that the stigma can become receptive during pollen shedding. Martin (1965) indicated that the probability of this in G. sanguinium was 20%. Protandry is therefore possible and, as pollen tube growth was not measured, differential growth rates of pollen remains a possibility.

Therefore, cross-pollination appears to be a probability and, since wind pollination (anemophily) is not probable in this species (Faegri and van der Pijl, 1971), some mechanism must be used to attract pollinators. Analysis of the pollination mechanism of both species was conducted in four parts: (1) bagging experiments to examine the possibility of parthenogenesis, self-pollination, and successful outcrossing both within and between the species, (2) use of an ether solution saturated with $FeCl_3$ to determine ultra-violet reflectivity, (3) observation and collection of insect visitors to determine behavior and identity of foragers, and (4) analysis of corbicular loads to determine the effectiveness of insect visitors as pollen vectors.

Bagging experiments were conducted at the U.S.U. Forestry Field Station in the summer of 1972. One flowering stalk on 20 plants each of G. nervosum, G. viscossissimum, and G. richardsonii was enclosed in a pollination bag with a polyvinyl chloride plastic window (Forestry Suppliers, Inc.); 5 bags per species were used for each of the following tests. To test the possibility of parthenogenesis, anthers from unopened buds were removed. In testing for self-pollination, all flowers and partially opened buds were removed before covering so unopened buds upon anthesis could receive pollen only from flowers of the same inflorescence. Cross-pollination was accomplished by removing anthers from buds and covering the buds until the stigmas were receptive to pollen. These were then hand-pollinated with pollen either from an individual of the same or another species. Pollinations were repeated several times and the bags were not removed until all flowers had either begun fruit development or had aborted. Seed set occurred in only 2 cases out of 1200 flowers; a G. nervosum x G.

richardsonii cross which yielded 5 seeds and a G. nervosum x G. viscossissimum cross which yielded 2 seeds. Although the bags used were guaranteed to prevent heat buildup, the majority of the flowers inside the bags aborted before the stigmas became receptive, probably due to an unfavorable radiation load. It is suggested that future experiments be performed under greenhouse conditions or using mesh bags.

One of the mechanisms that may attract insects to the center of Geranium flowers is the pattern of lines along the veins of the flower which radiate out from the style column (Eisner, et al., 1969; Faegri and van der Pijl, 1971) (Fig. 21D). In G. nervosum, these lines are easily visable to the human eye; in G. richardsonii, they are not. The possibility that this pattern was reflected in the ultra-violet wave-lengths was examined using a solution of ether saturated with $FeCl_3$ (Kugler, 1963). When applied to the flowers, areas of ultra-violet reflectance turn black while areas of absorption turn light gray. On G. richardsonii flowers which were sprayed with this solution, the veins showed up as black and the background as light gray. Geranium nervosum exhibited a similiar pattern.

Insect visitors to G. nervosum and G. richardsonii were observed from 10 AM to 4 PM once a week from late April to August at the Forestry Field Station. A list of the frequency of visitors (based on the entire sample of insects collected throughout the summer) appears in

Table 4. The most common visitors in June and early July were the flower beetles (*Trichiotinus assimilis*, *Mordella atrata*, *Trichodes ornatus*, and *Epicauta puncticollis*). Pollen and nectar appeared to be the main attractants. *Epicauta puncticollis* was most frequently found on *G. nervosum* and *G. viscossissimum*. This species was observed rubbing its head in the dehiscing pollen, and specimens were often caught with pollen on their bodies. *Trichiotinus assimilis* was found most frequently on *G. richardsonii* while *Trichodes ornatus* and *Mordella atrata* were found with approximately the same frequency on all three species of *Geranium*. All of these species were apparently foraging for pollen and, during late June, appeared to remove the majority of *Geranium* pollen. As more plant species began to flower in early July, the flower beetles were not found as frequently on *Geranium*. They were possible pollinators since *Geranium* pollen was found on collected specimens but, due to their non-fidelity and low pollen loads, they were probably inefficient pollinators. Many species of bees were found visiting *Geranium* flowers, most frequently in July and August. *Bombys rufocinctus*, *Dialictus spp.*, *B. bifarius*, and *Apis melifera* workers were found on both *G. nervosum* and *G. richardsonii*. The other species of bees were caught only on *G. nervosum* and *G. viscossissimum*. *Bombys occidentalis*, *Anthophora terminalis*, and *B. bifarius* were the only species caught with *Geranium* pollen. Of these, *B. bifarius* appeared to be the most frequent visitor.

Table 4. Frequencies of insect visitors to *Geranium nervosum* and *Geranium richardsonii*. (Frequency is based on the number of insects of that species out of the total number of insects caught. Sample size = 560 for *G. nervosum* and 450 for *G. richardsonii*.)

Insect Species	Frequency *G. nervosum*	Frequency *G. richardsonii*
Coleoptera		
Cerambycidae		
Anoplodera chrysocoma (Kby.)	.04	.00
Cleridae		
Trichodes ornatus Say.	.12	.18
Coccinellidae		
Coccinella trifasciata perplexa Muls.	.05	.08
Hippodamia convergans (Guer.)	.05	.08
Meloidae		
Epicauta puncticollis (Mann.)	.12	.18
Mordellidae		
Mordella atrata Mels.	.09	.14

Table 4. Continued

Insect Species	Frequency *G. nervosum*	Frequency *G. richardsonii*
Scarabaeidae		
Trichotinus assimilis (Kby.)	.03	.05
Diptera		
Bombylidae		
Bombylius major L.	.03	.05
Calliphoridae		
Acronesia sp.	.00	.02
Muscidae		
Lasiops sp.	.00	.02
Syrphidae		
Metasyrphus lapponicus (Zett.)	.00	.02
Tachinidae		
Gonia sp.	.00	.02

Table 4. Continued

Insect Species	Frequency *G. nervosum*	Frequency *G. richardsonii*
Hemiptera		
Miridae		
Lygus sp.	.08	.12
Pentatomidae		
Chlorochora uhleri Stal.	.02	.03
Leptocoris trivitattus Say.	.01	.00
Homoptera		
Aphidae		
Acyrthosiphon pisum (Harris)		
Hymenoptera		
Andrenidae		
Panurginus sp.	.01	.00
Apidae		
Anthophora terminalis Cresson	.01	.00
Apis mellifera L.	.06	.09

Table 4. Continued

Insect Species	Frequency *G. nervosum*	Frequency *G. richardsonii*
Bombys bifarius Cresson	.05	.05
B. flavifrons Cresson	.04	.00
B. occidentalis Greene	.02	.00
B. oppositus Cresson	.02	.00
B. rufocinctus Cresson	.04	.06
Cytherus insularis Smith	.03	.00
Colletidae		
Hylaeus sp.	.01	.00
Orthoptera		
Acrididae		
Arphia spp.	.06	.00

The efficiency of bees as pollinators of *Geranium* depends on their constancy to one species throughout one particular trip. Bees which were followed in the field were never observed to go from a *G. nervosum* or *G. viscossissimum* flower to a *G. richardsonii* flower on the same trip; however, they did not appear to distinguish between *G. nervosum* and *G. viscossissimum* flowers and visited them at random during the same trip.

Bud mortality was a common phenomenon, particularly in the aspen grove and dry hillside areas. An attempt was made to quantify the number of buds which failed to mature and to determine the causes of mortality. Twenty-five stalks were marked on each species and the number of potential (buds) and actual flowers was counted. For *G. nervosum*, there was an average of 55 mature flowers on a stalk but no reasonable confidence limits could be placed on this mean due to a standard deviation of 54. The number of flowers per stalk appeared to vary according to the age of the plant and its habitat. An average of 34±9.9% of the buds survived to maturity. *Geranium richardsonii* flowers and buds followed the same pattern although an average of 75±8.5% of the flowers matured. Much of this failure to mature was undoubtedly due to aphids (*Acyrthosiphon pisum*). Aphids were found in all areas, especially on *G. nervosum*, and were most abundant on the buds and developing seeds.

Photoperiodicity and vernalization Growth of a plant may be affected by several factors, the effects of which may vary with age. After a plant has matured to the point that flowering can be initiated, i.e. "ripeness to flower" (Salisbury and Ross, 1969), day length or photoperiod can become the dominant factor in determining when a plant will flower. For example, henbane, *Hyoscyamus niger*, must be 10 to 30 days old before it will respond to the required photoperiod (Salisbury and Ross, 1969). The initial time needed for growth in both *Geranium* species is approximately 3 growing seasons; flowering may begin in the fourth year. The possibility of a photoperiodic response in *G. nervosum* and *G. richardsonii* was examined in August, 1972. Eight plants of each species were placed in growth chambers under each of 3 photoperiod regimes: (1) 8-hr day, (2) 13-hr day, and (3) 15-hr day. The growth chambers had 12-hr alternating temperature regimes of 20° and 4°C, conditions common in the field during the initiation of flowering. All plants used had been grown in the greenhouse from seed collected in the field and had flowered during December, 1971, or March, 1972. They had been kept under an 8-hr-short-day regime since that time.

By the end of October, 1972, none of the test plants had flowered in the growth chambers so they were placed in a greenhouse which had an average temperature of approximately 21°C. At the end of November, some of the plants began to flower again; these plants were the same ones that had flowered the previous December. There is probably a carbohydrate level that has to be reached before the plant becomes sensitive to photoperiod. The time required for *G. fremontii*, for example, to replenish its carbohydrate reserves sufficiently to form new leaves was short (Donart and Cook, 1970) but it may take longer to replenish reserves to the level required for flowering.

Vernalization, defined as "a low temperature promotion of flowering" (Salisbury and Ross, 1969, p. 555), can be an important factor in conjunction with or as a prerequisite to a photoperiodic requirement. For example, *Hydrophyllum appendiculatum*, a biennial forest herb, requires a short period of cold temperatures as well as the correct photoperiod to flower (Morgan, 1971). Neither *G. nervosum* nor *G. richardsonii* appeared to require vernalization for growth or flowering. Plants in the greenhouse grew continually and flowered at approximately 1 year intervals without cold treatment.

Fruiting and dispersal

The first fruits of *G. nervosum* appear in early to mid-July in both the hillside and aspen sites, while fruit production in *G. richardsonii* does not begin until late July. Both species continue to develop fruit until early to mid-August. The *Geranium* fruit consists of a long stylar column at the base of which are arranged five 1-seeded carpels (Fig. 21F). The styloidia are 3-4 cm in *G. nervosum* and are permanently attached to the 5-6 mm long carpel bodies; in *G. richardsonii*, mature styloidia are similiar in size but the carpel bodies are only 2.5 to 4 mm in length (Shaw, 1952). The fruits begin to mature and disperse in late July and early August. Dispersal is generally complete by the end of August.

There are many kinds of dispersal mechanisms used by plants and as many agents available to do the dispersal. Saurochory, dispersal by reptiles; orthinochory, dispersal by birds; and hydrochory, dispersal by water are just a few of the possibilities (van der Pijl, 1969). *Geranium* seeds are dispersed by autochory, i.e. dispersal by the plant itself. Autochory can be accomplished by ballistics, actively or passively throwing the seeds some distance, or by creeping diaspores, as in *Erodium spp.* (van der Pijl, 1969). *Geranium spp.* fall under the category of active ballists which effect dispersal by tension in dead, hygroscopic tissues.

As the carpels of *G. nervosum* and *G. richardsonii* mature, the long flat bands of the style begin to contract. These bands consist entirely of bast fibers (Trelease, 1886) which contract to a greater extent on the surface than along the axis of the style column causing the outer edge of the carpel to bend upward (Fig. 21G). At maturity, the bands break along 5 ventral sutures and recoil elastically (Fig. 21H). The force and suddenness of the recoil causes the seeds to be flung a considerable distance from the parent plant. Martin (1965) indicated that seeds of

G. maculatum could be thrown up to 9 m from the parent while only 6% of the total seed crop fell less than 1 m from the parent.

The seeds, which are black to blackish brown and reticulate, are from 3-4 mm long in G. nervosum and 2-3 mm long in G. richardsonii (Shaw, 1952). They are formed in a 5-loculed ovary which contains 5 coherent carpels, each with one seed. There is a maximum of 5 seeds possible per ovary but the average is 3 for both species.

CHAPTER IV

Growth Rates and Phenology

As has been previously discussed, *G. nervosum* at the Forestry Field Station was subjected to a definite habitat gradient (p. 8). There was an indication, although it was not significant, of a change in plant size or leaf margination from the aspen grove to the hillside in *G. nervosum*. The hillside population began growth from 1 to 2 weeks earlier than other populations, yet, flowering stalk initiation on the hillside began at approximately the same time as other populations along the gradient. Therefore, the questions arose: (1) Is there a difference in growth rates along the gradient? and (2) Is there a difference in the critical environmental factors controlling phenological development at each site?

Growth rates have been correlated with the number and average height (or length) of stems (or leaves) (Laycock, 1970; Wright, 1970). Using the interaction between number of culms and leaf length, Wright (1970) could accurately predict individual plant weights of *Stipa comata* and *Sitanion hystrix*. Laycock (1970) predicted differences in dry weight (correlated with growth rates) by measuring average stem height and number of stems in *Polemonium foliosissimum* and *Mertensia arizonica* var. *leonardi*.

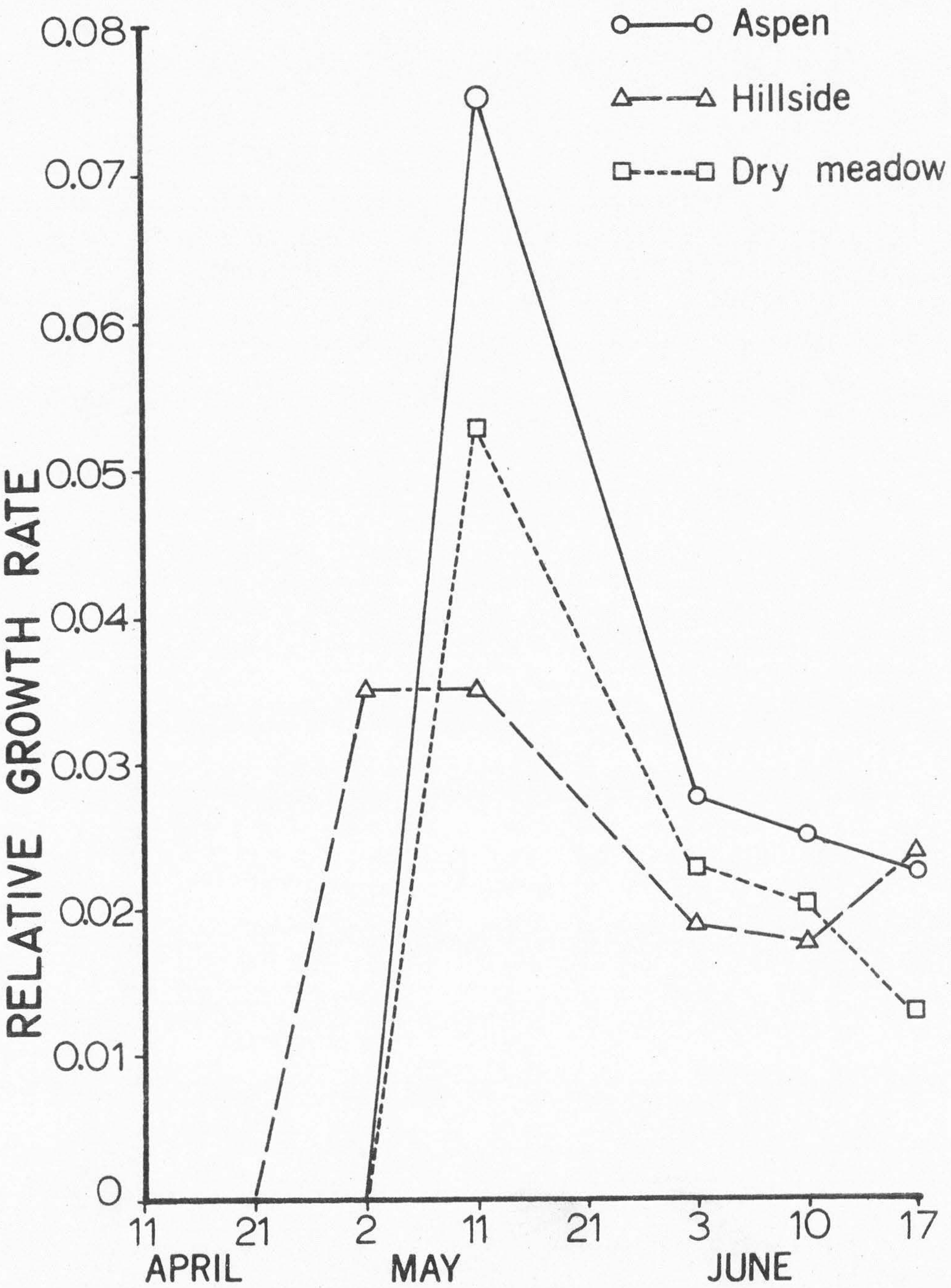
To determine the relative growth rate, i.e. the rate of increase in biomass per unit of biomass present (Kvet, et al., 1971), for *G. nervosum*, the following procedure was used. The hillside and aspen grove sites represented the extremes of the *G. nervosum* gradient, and a third site was selected in the center of the gradient in a dry meadow (Fig. 3). Twenty plants were marked at each site. Average petiole length was obtained by measuring and averaging the length of 4 petioles on each plant once a week for 8 weeks. Relative growth rate was calculated by the formula

$$R = \frac{\ln L_2 - \ln L_1}{t_2 - t_1}$$ (Kvet, et al., 1971)

where R is relative growth rate, L is average petiole length, and t is time. The aspen grove population exhibited a higher growth rate initially (Fig. 22) but there was no significant difference in growth rate between the three areas (ANOV, p .05). Although there was no significant difference in relative growth between the areas, plants of *G. nervosum* growing in the aspen tended to be larger than those on the dry hillside; flowering stalks on the hillside were from 27 to 60 cm long while those in the aspen were from 30 to 106 cm in height.

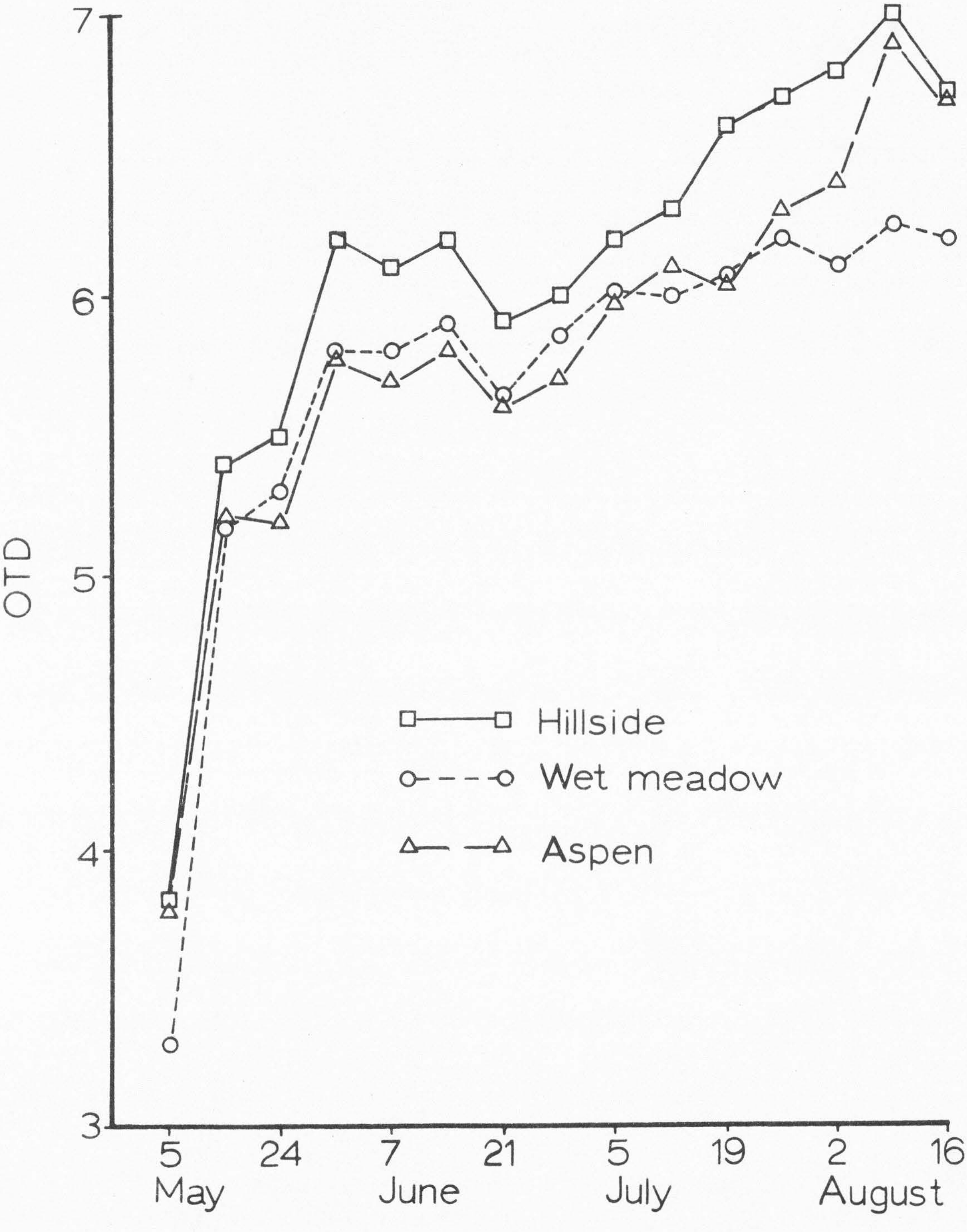
In an attempt to discover which environmental factors were critical in influencing phenological development of *G. nervosum* and *G. richardsonii* in the aspen, hillside, and wet meadow sites, data for each species were analysed by stepwise multiple regression and stepwise multiple regression with subsets using the phenological stage as

Figure 22. Relative growth rates (R) for *G. nervosum* in three sites at the U.S.U. Forestry Field Station in 1971.


RELATIVE GROWTH RATE
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
11
21
2
11
21
3
10
17
APRIL
MAY
JUNE
Aspen
Hillside
Dry meadow

the dependent variable, while the environmental factors were used as independent variables. Environmental factors measured were air temperature at 0, 15, and 60 cm; Ψ_s at 15 and 60 cm; total and weekly precipitation; and total and weekly optimum temperature days (OTD) (Cleary and Waring, 1969). The measurement of the first 4 variables was discussed previously (Chapter II). Values for OTD are based on the optimum growth temperatures for both roots and shoots; for G. nervosum and G. richardsonii these temperatures, for the seedling stage, were 15°C for root growth and 21°C for shoot growth (Fig. 16); no figures were available for the adult stage. To obtain the base value for 1 OTD, the optimum temperatures for root and shoot growth are averaged; for G. nervosum and G. richardsonii, 18°C = 1 OTD. At values lower than 1 OTD, growth of the root and shoot is assumed to be less than optimal. The OTD value for the week at one site is calculated by averaging soil and air temperatures and dividing that by 18°C. For any given growth period, the temperature effect may be calculated by accumulating the weekly fractions of estimated relative growth (Fig. 23) (Cleary and Waring, 1969). This method does not consider the calculation of decreased growth rates when temperatures exceed the optimum. Since maximum air temperatures on the dry hillside only exceeded optimum air temperature in the second to the last week of the summer, growth conditions were still considered to be favorable since the temperatures were still within the optimum

Figure 23. Number of optimum temperature days (OTD) per week in 3 sites at the U.S.U. Forestry Field Station in 1972.


OTD
7
6
5
4
3
5
May
24
7
June
21
5
July
19
2
August
16
Hillside
Wet meadow
Aspen

temperatures indicated by seedling survival (Fig. 16) and 1 OTD was used in calculations for that week as well. Phenological stages were quantified following the example of West and Wein (1970). A tabular sequence of recognizable phenological stages was constructed, and each stage was numerically coded (Table 5). The 20 plants marked at each site for growth studies were visited weekly and phenological stage was recorded. For example, a reading for the hillside in mid-July might be 4.50 where the number to the left of the decimal denotes the phenological stage and the number to the right the percent of the plant that has developed beyond that stage. The phenological progression of _G. nervosum_ and _G. richardsonii_ at the three sites in the summer of 1972 is given in Figures 24, 25, and 26.

Critical factors influencing phenological development differed between sites. Initial evaluation of critical factors was made with stepwise multiple regression. Results for the hillside and wet meadow indicated that OTD was most important in influencing phenological development but total precipitation was indicated as the most influential factor in the aspen grove. The major problem with stepwise multiple regression in ecological experiments where several measurements are taken on correlated variables (e.g. precipitation and moisture availability) appears to be the high degree of correlation between independent variables. One of the assumptions of multiple regression is that these variables act independently. The high degree of correlation

Table 5. Phenological sequences for *G. nervosum* and *G. richardsonii* and their corresponding base scores.

Base Score	Category
1	Dormancy
2	Leaf Initiation
3	Flower Stalk Initiation
4	Flowering
5	Fruit Development
6	Dispersal
7	Senescence

Figure 24. Phenological progression of _G. nervosum_ in the Aspen grove at the U.S.U. Forestry Field Station in 1972. (Figure also shows standard error at each date measured)

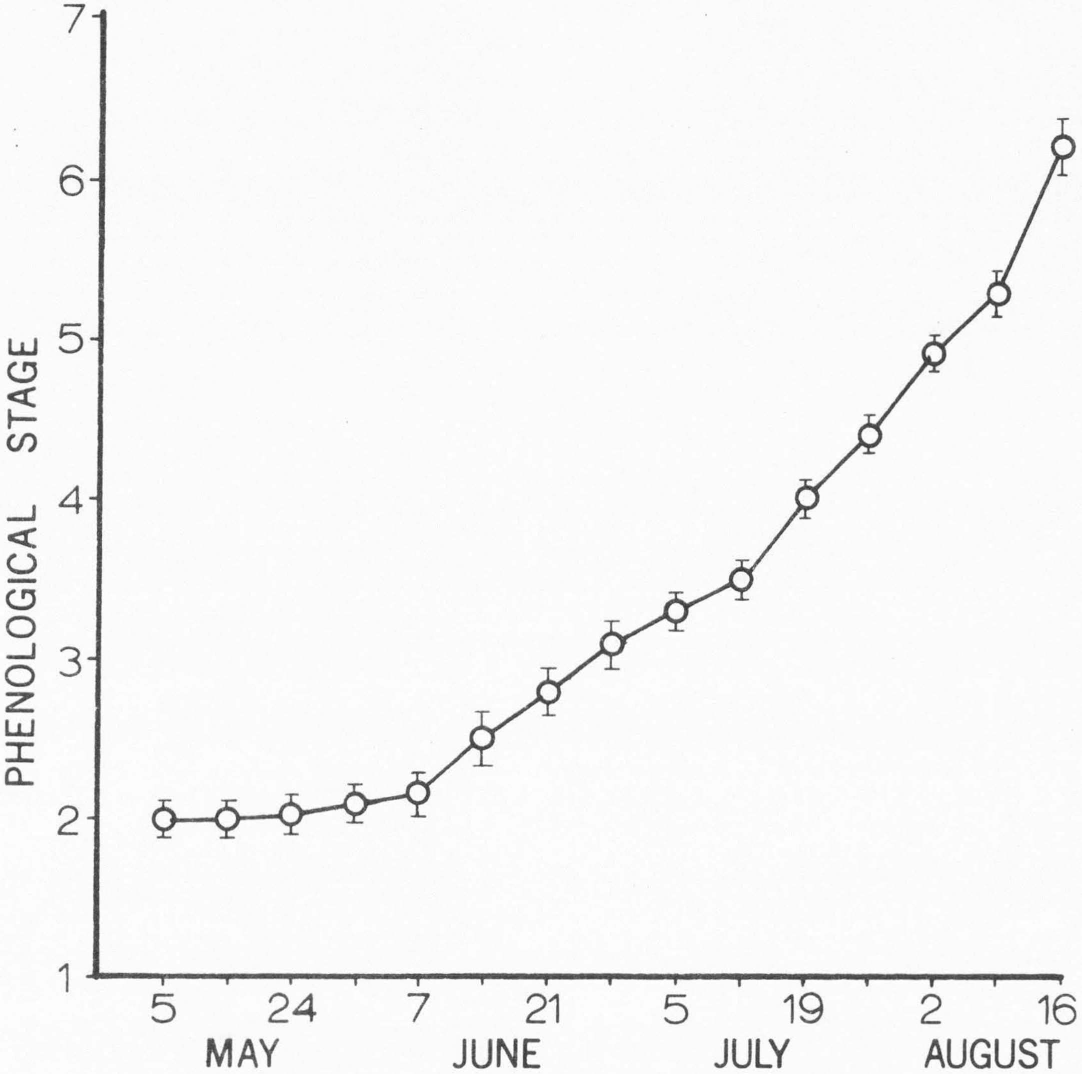

PHENOLOGICAL STAGE
1
2
3
4
5
6
7
5
24
7
21
5
19
2
16
MAY
JUNE
JULY
AUGUST

Figure 25. Phenological progression of G. richardsonii in the Wet Meadow at the U.S.U. Forestry Field Station in 1972. (Figure also shows standard error for each date measured.)

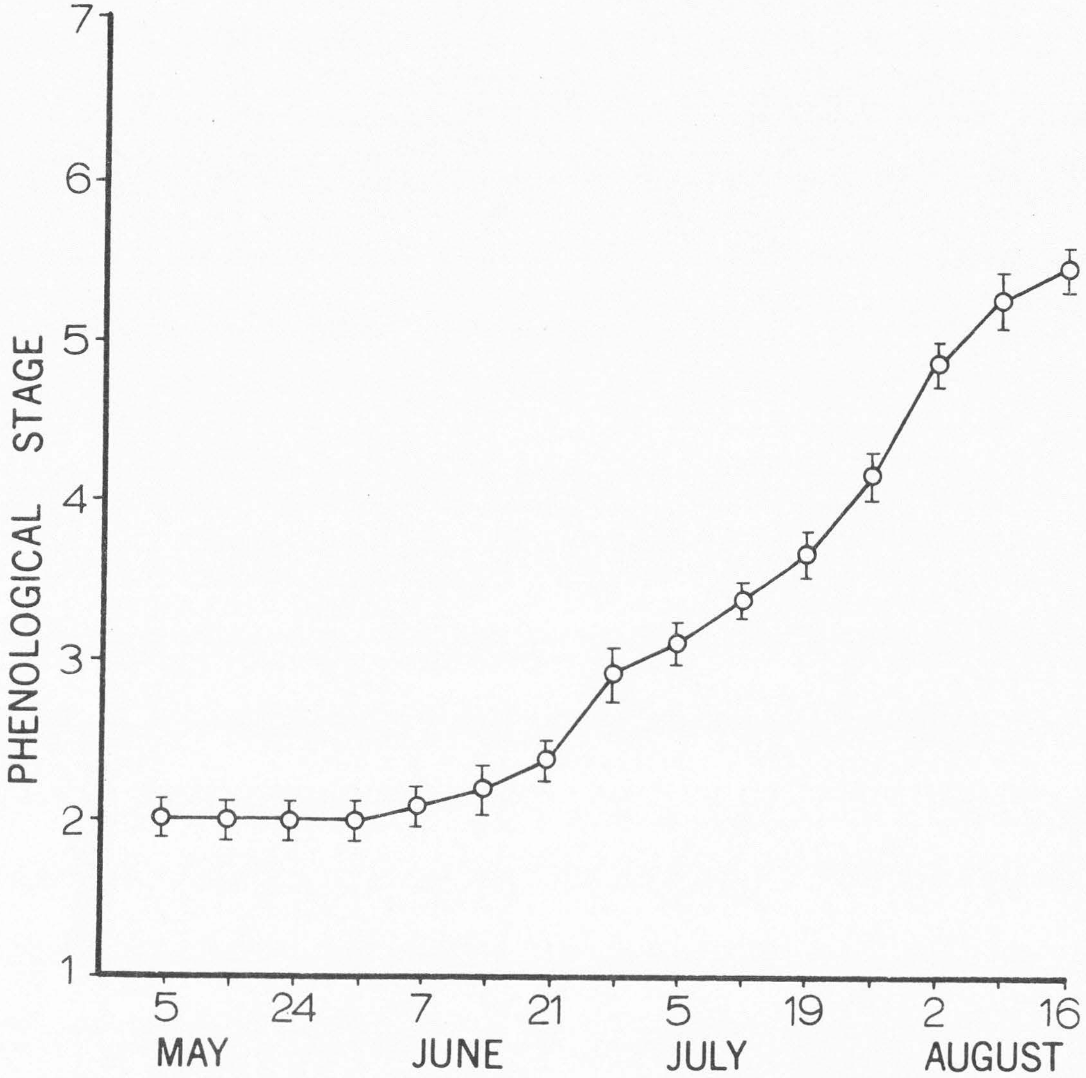
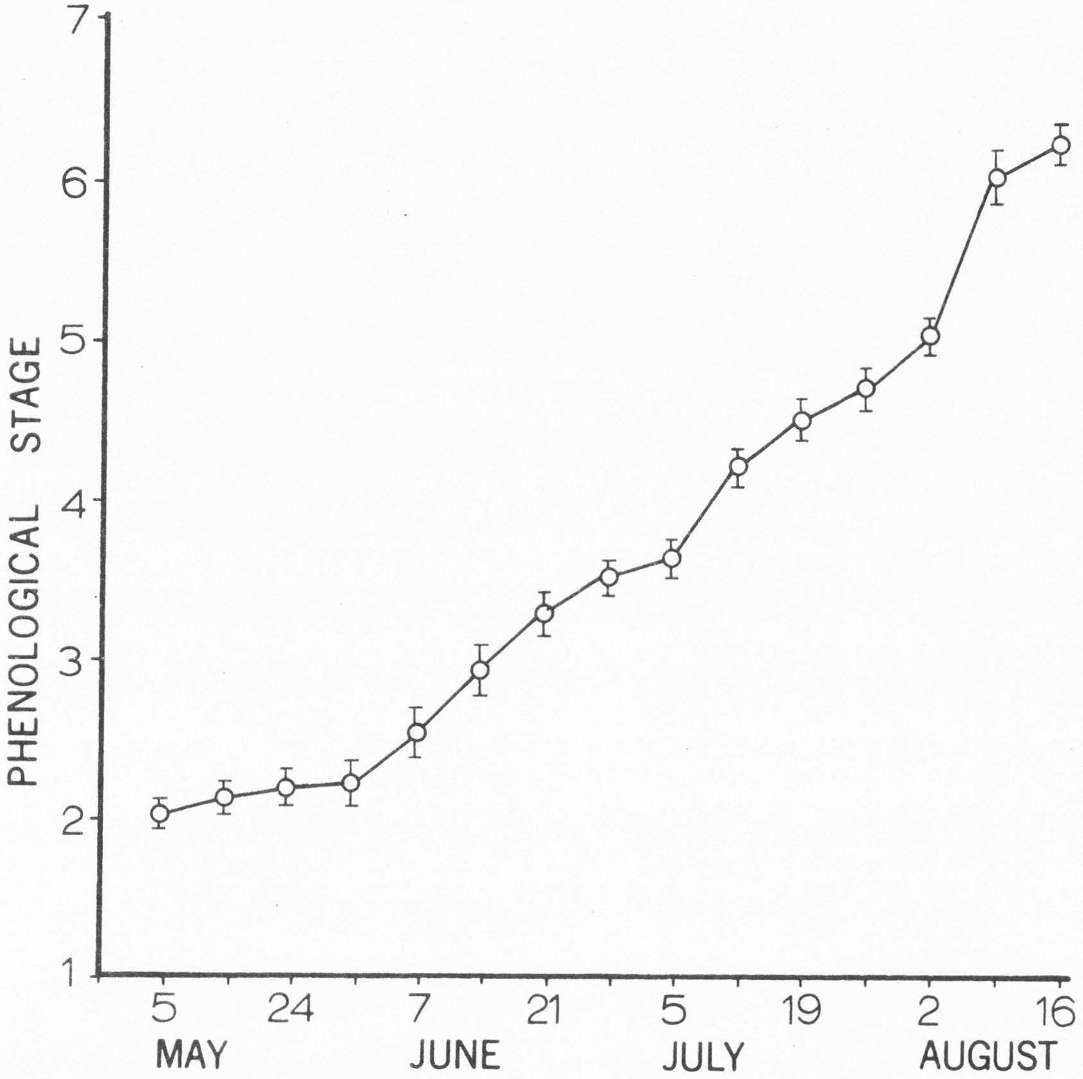

PHENOLOGICAL STAGE
7
6
5
4
3
2
1
5
24
7
21
5
19
2
16
MAY
JUNE
JULY
AUGUST

Figure 26. Phenological progression of G. nervosum on the Dry Hillside at the U.S.U. Forestry Field Station in 1972. (Figure also shows standard error for each date measured.)


PHENOLOGICAL STAGE
7
6
5
4
3
2
1
5
24
7
21
5
19
2
16
MAY
JUNE
JULY
AUGUST

among them as was indicated in the correlation matrix was probably a source of error in the calculations. To avoid this error, similiar variables were grouped into subsets and analyzed by stepwise multiple regression with subsets. Using this procedure, Ψ_s appeared to explain most of the variability in phenology in the aspen grove with a coefficient of determination (r^2) equal to .897. In both the hillside and wet meadow plots, the most influential factor appeared to be OTD (r^2 = .93 in the hillside; r^2 = .94 in the wet meadow).

CHAPTER V

Discussion

Throughout the life cycle of a perennial plant, the environmental factors which influence the development of each stage of growth vary. Factors limiting the establishment of a seedling, for example, may have little or no effect on the growth of the adult. This study has been an attempt to determine what factors influence the development of each stage and how they affect G. nervosum and G. richardsonii.

Dormancy in seeds of G. richardsonii was probably due to requirements for a short period of after-ripening. Geranium nervosum required, in addition, a cold treatment of 4-10 weeks. The seeds of G. richardsonii also indicated a scarification requirement.

Seeds which require scarification usually possess a hard seed coat which is impermeable to water (Pelton, 1961; Baskin and Quarterman, 1969; Baskin and Quarterman, 1970; Rochow, 1970). The seed coats of G. richardsonii and G. nervosum were not impermeable; the seed coats could be broken by the imbibition of water and the subsequent swelling of the embryo. Geranium richardsonii, by virtue of its lower germination rates in non-scarification treatments (Figs. 12 and 13) indicated that its seed coat was less permeable to water than G. nervosum and that scarification could improve germination success. Scarification can be accomplished by weathering (e.g. alternate freezing and thawing) or by the action of microorganisms as in Mertensia ciliata (Pelton, 1961).

In most cases where stratification is needed, the embryo is either immature or dormant (Crocker and Barton, 1957). If the embryo is immature, it requires a period of after-ripening at low temperatures in a moist environment. Geranium nervosum seeds indicated that a period of 5-10 weeks was necessary for maximum germination. The time needed for stratification to be effective varies with each species. Geranium richardsonii appeared to require little or no stratification while G. maculatum, an eastern species, required up to 400 days in the stratification treatment (Martin, 1965).

In some species, for example pokeweed, Phytolacca americana L., stratification also lowers the temperature limits under which germination can occur (Farmer and Hall, 1970). Although G. nervosum seeds indicated that optimum germination occurred from 20°-25°C, a period of stratification may have permitted a greater percent germination at 1°C under the snow than would ordinarily be expected. Geranium richardsonii indicated a lower optimum temperature for germination (15°C) than G. nervosum but it also indicated a greater percentage germination in the field at 1°C than was expected. Neither species germinated as successfully at 1°C as they did in the laboratory between 20° and 25°C

(Fig. 15 and Table 2).

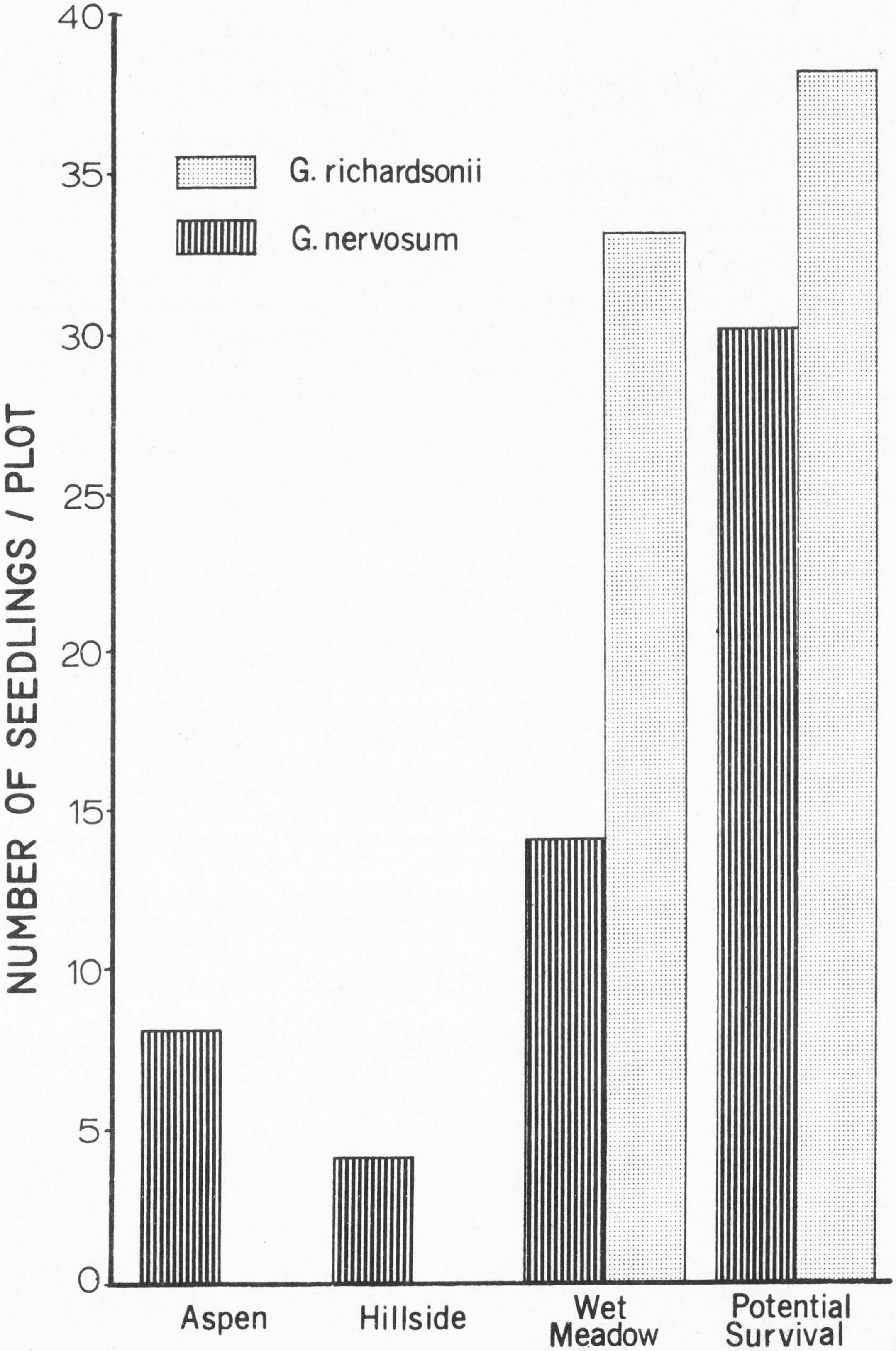
Seeds that have hard seed coats or leaching requirements or both can remain dormant for several years as do seeds of *Mertensia ciliata* (Pelton, 1961), *Psoralea subacaulis* (Baskin and Quarterman, 1970), *Astragalus tennesseensis* (Baskin and Quarterman, 1969), and *Thlaspi alpestre* (Rochow, 1970). Seeds which remain dormant in the soil form a "seed bank" which guarantees that seeds will be available at all times, even in years when the seed crop is poor (Harper and White, 1971). Seeds of *G. richardsonii* and *G. nervosum* probably do not fall into the above category, even though *G. richardsonii* had a scarification requirement. Snow germination studies indicated that there were no viable seeds at the end of the winter; all the ungerminated seeds had rotted. Although the close proximity of the seeds in mesh bags probably helped the spread of the fungus, all seeds were able to imbibe water before they were attacked. The swelling of the embryo indicated that it had probably begun growth before the fungus had attacked it. The permeability of the seed coat and the attack of fungi on the moistened seed probably prevented dormancy for longer than one winter and necessitated dependence on a new seed crop each year.

Perennial species seem to have one of two types of reproduction; they either reproduce only once or they are "repeating producers" (Harper and White, 1971). The species that reproduce only once generally have extreme fluctuations in population size for different age groups since they may grow for several years, reproduce once and die. The "repeating producers" are generally characterized by a long (5-10 years) juvenile period followed by a reproductive period that may last until the plant is 20 years old. The seed crop is generally small and there are few seedlings which become established (Harper and White, 1970). *Geranium nervosum* and *G. richardsonii* fall into the latter category with the exceptions that they have a large seed crop and are probably not that old. There are generally large numbers of seedlings (120 *G. richardsonii* seedlings in a 1 m^2 area at the wet meadow site in 1972) as is found in other perennials, for example, 200 *Mertensia arizonica* var. *leonardi* seedlings were found in a 1.5 m^2 study area but few survived to overwinter and become established (Matthews and Conrad, 1968).

Geranium richardsonii in the wet meadow appears to be in its optimum habitat as far as germination and seedling survival are concerned. The percent of seedlings that overwintered and became established juveniles is very close to the potential establishement, as determined in the laboratory, for that species (Fig. 27). *Geranium nervosum* seedlings do not show this same pattern although the 8% which established in the aspen grove is higher than that found in many perennials, (e.g. 3% in *Mertensia arizonica* var. *leonardi* Matthews and Conrad, 1968).

One of the critical factors limiting the establishment

Figure 27. A comparison of overwinter establishment in the field and potential seedling establishment in the laboratory for *G. richardsonii* and *G. nervosum*.


40
35
30
25
20
15
10
5
0
NUMBER OF SEEDLINGS / PLOT
G. richardsonii
G. nervosum
Aspen
Hillside
Wet Meadow
Potential Survival

of seedlings is soil water potential (ψ_s). Seedlings of both species are susceptable to low (-8 to -10 bars) ψ_s. This susceptability is understandable since seedlings are very sensitive to moisture stress after the extension of the first true leaf (Gates, 1968). As previously discussed, radicles of newly germinated seeds continue to grow slowly in the water-saturated environment beneath the snow to a length of 4 cm. One to 2 weeks after snow melt, the cotyledons emerge and both the root and shoot grow rapidly. The *G. nervosum* habitats (dry hillside and aspen grove) remained at favorable ψ_s until late June or early July (Fig. 6). By this time, *G. nervosum* seedlings had extended their tap roots deep enough (60 cm) to survive until senescence began in mid-July. *Geranium richardsonii* seedlings, with a more fibrous root system, were not able to grow deep enough to reach favorable water potentials. The seedlings were unable to overwinter in those areas. The wet meadow, however, remained at favorable water potentials throughout the summer.

Unlike water potential, the soil temperatures at 15 cm and 60 cm did not appear to be limiting; surface temperatures were the exception. By June 28, 1972, surface temperatures in the dry hillside were in excess of 32°C at 11 AM; the surface temperatures in the aspen grove and wet meadow were rarely in excess of 12-15°C. Although the latter were below the optimum for seedling survival, the dry hillside was well above the optimum range, a fact which probably helped to account for the lower survival rates there. Both species appeared able to adjust to low temperatures (Fig. 15) but only G. nervosum managed to survive at all in temperatures above 30°C.

In addition to the physical limitations placed on plant survival, most species have intraspecific regulators as well. Experiments with agronomic crops (Harper and White, 1971) have indicated that plant population sizes are regulated by a process of self-thinning, which occurs primarily when seedlings are clumped. As a result of the unique dispersal mechanism of Geranium, seedlings rarely occurred in clumps. If dense clumping did occur, as it did in some of the research plots, self-thinning did not appear to begin until the second summer.

Competition between species may also be a regulatory factor in seedling survival, particularly in the wet meadow. Under normal conditions, the grass in the meadow (Agropyron smithii) reached a height of 45 cm by early July forming a dense layer of vegetation above the young seedlings. Geranium richardsonii seedlings became slightly etiolated but continued to grow vigorously. Geranium nervosum seedlings, however, were usually found in open areas between grass clumps or under a loose canopy of grass (Agropyron spp. and Bromus marginatus in the aspen grove and dry hillside). They may have been less able to compete with the heavy grass cover in the wet meadow, a fact which may have accounted for the lower overwinter survival in G.

nervosum in comparison with a good survival in *G. richardsonii*. Further studies should be conducted on the population dynamics and competitive abilities of *G. richardsonii* and *G. nervosum* seedlings.

After seedlings have become established and survived the first winter, a period of vegetative growth, i.e. the juvenile stage, begins. The ability of a perennial or biennial species to become established in an area is reflected in its ability to survive the first dormant period, in this case overwinter, and to initiate growth the following spring. *Geranium richardsonii* was successful in establishing only in the wet meadow. The amount of energy it expended in combating high temperatures on the dry hillside site and limiting ψ_s in the aspen and dry hillside sites apparently prevented the accumulation of sufficient carbohydrate reserves to allow overwinter survival. The high temperatures may also have caused physiological damage, (e.g. to the enzyme systems). Conditions in all three areas are apparently favorable for establishment of *G. nervosum*, with the wet meadow being the most favorable of all the study plots. The large seed size, which indicates greater stored reserves, should give *G. nervosum* a higher chance of survival than *G. richardsonii*. This was demonstrated by Black (1958) in his work with *Trifolium subterraneum* plants with different initial seed sizes and by Harper et al. (1961) in their work with the ecology of species living in the same area. That this is not the case may be due to the fact that G. nervosum apparently has a higher susceptability to soil pathogens.

The juvenile stage probably lasts from 3-5 years depending on environmental conditions. During this period it is virtually impossible to identify to species the three geraniums that grow at the U.S.U. Forestry Field Station. There is great variation in the size of vegetative parts and the pubescence on the petioles making these taxonomic characteristics difficult to use. Flowering parts are necessary for complete identification.

The flowers of G. richardsonii and G. nervosum appear to be distinguishable by bees while those of G. nervosum and G. viscossissimum are not (p. 52). The chromosome number of G. nervosum and G. richardsonii is 2n = 26 (Shaw, 1952). That of G. viscossissimum is not known although Darlington and Wylie (1961) state that perennial geraniums are commonly 2n = 25. Cross-pollination experiments indicate that hybridization between G. nervosum and G. viscossissimum is possible although it is not known if the hybrids are fertile. It is possible that some of the plants on the dry hillside are hybrids which may account for the extreme variability in types of pubescence observed in that area. Hybrids of G. nervosum and G. richardsonii due to the actions of flower beetles must remain a possibility although the random movements of these insects make hybridization between these two species improbable.

Flowering in *G. nervosum* and *G. richardsonii* does not seem to be dependent upon photoperiod or a cold treatment although this is not the case for many other perennials. *Delphinium occidentale*, for example, requires a period at cold temperatures to initiate flowering (J. Holman, personal communication), while Baskin and Quarterman (1970) indicate that *Psoralea subacaulis* requires both warm and cool periods to complete flowering. There is an indication, however, that both geraniums require sufficient carbohydrate reserves to initiate flowering, which may be an adaptation to the requirements of overwinter survival. If the carbohydrate reserves were exhausted in flowering, there would probably not be sufficient time left for photosynthetic activity to store up reserves to survive overwintering and growth initiation the following spring. The plant apparently maintains the requisite carbohydrate supply during flowering by the photosynthetic activities of the leaves. If the leaves were removed, flowering would probably not proceed as usual since it would diminish, without replenishing, the carbohydrate supply. Grazing studies indicate that this may indeed be the case. *Geranium fremontii* plants which had been clipped had fewer flowering stalks than usual, and, apparently, most of the energy was used in replacing the leaves (Donart and Cook, 1970).

According to Gates (1968), the inflorescence, after it is formed, is probably not as sensitive to moisture stress as are the vegetative tissues. This was demonstrated in the moisture stress experiments conducted in the laboratory. In both *G. nervosum* and *G. richardsonii*, the new leaves and vegetative tissue showed evidence of moisture stress before the flowering stalks did. Neither species developed inflorescences when under water stress. Since *G. richardsonii* roots would probably be unable to reach depths in the dry hillside where Ψ_s would not be a critical factor (60 cm), it would be questionable whether adults would flower there even if it were possible for them to become established. Although, in some cases, stressed conditions appear to hasten flowering (Gates, 1968), this does not appear to be the case with either *Geranium* species.

A comparison of the reactions of *G. richardsonii* and *G. nervosum* seedlings and adults to moisture stress clearly demonstrates the notion that seedlings are much more specific in their requirements for survival than are adults of the same species. Both *G. nervosum* and *G. richardsonii* adults can survive wider fluctuations in moisture stress for longer periods of time than can seedlings of those species (Fig. 18). It might be said that the stringent requirements imposed on the survival of seedlings probably insure that the plant will develop in an area that is well within its ability to adapt to the environment.

The duration of the adult or reproductive stage was not determined in this study. Age could not be determined by size due to the fluctuating environmental conditions from study area to study area. In fact, Antonovics (1972) pointed out that individuals of the grass *Anthoxanthum odoratum* of the same age varied greatly in size and diameter and tended to become smaller towards the end of the life span. Of the 60 flowering individuals marked at the beginning of this study in 1971, none died. However, Antonovics (1972) pointed out that, for *A. odoratum*, only a small fraction of the population lived longer than 5 years and that the population half-life was about 2 years. This is probably also the case with *G. nervosum* and *G. richardsonii* although the population structure may change slightly from area to area. More work needs to be done in this area.

Growth of any organism is generally dependent upon the availability of all soil nutrients, carbohydrates, and water to its growing organs. Therefore, a change in the environment which affects the availability of these supplies may be reflected in a change in the size of the various organs. This change in size is reflected along the *G. nervosum* gradient. In the aspen grove, the plants are, on the whole, larger, while on the dry hillside they are smaller as far as flowering stalk height and petiole length are concerned. There is no significant difference in leaf size. This smaller size may reflect a harsher environment on the dry hillside; soil water potential is lower (more negative) there, and temperatures are higher.

Phenology, the cyclic change in the activities of plants and animals (Lieth, 1970), may also reflect changing environmental conditions. The process of quantifying phenological change and applying it to environmental factors, called phenometry, is coming into wider use (Lieth, 1970). Apparently, the most influential factor in phenological development for G. nervosum on the dry hillside is temperature as it is reflected in OTD. There were two assumptions made to use OTD in this experiment: (1) seedling response to temperature can be applied to adults and (2) root and shoot optimum temperatures can be averaged. In the first case, although seedlings are probably much more sensitive to temperatures than are adults, the range of optimum temperatures should be similiar. Cleary and Waring (1969) point out the importance of root growth in response to temperature and emphasize the fact that it cannot be ignored in studies of plant response to temperature. The assumption that root and shoot temperatures can be summed is probably a reflection of the idea that total plant growth is a sum of the response of each of its parts to environmental stimuli. A more valid method, however, would be one which considered root and shoot temperatures seperately rather than taking their average and assuming that figure to be optimal.

The response of the dry hillside environment to OTD was to begin growth 2 weeks earlier than the other areas. Snow melted and the soil warmed earlier here. Although Ψ_s was definitely a limiting factor here (Fig. 6), the depth to which the roots grew (p. 45) probably aided the plants in avoiding much of the water stressed areas. In the aspen grove, temperatures never reached critical levels (Fig. 5) and Ψ_s did. The roots did not appear to grow as deeply in this area (p. 45) and were therefore subject to the influence of Ψ_s. The aspen grove was also more heavily vegetated, a fact that could have magnified the effect of Ψ_s. Soil water potential never reached critical levels in the wet meadow while temperature showed a steady increase throughout the summer and was the factor that had the greatest influence on phenological development.

It is unquestionably true that there is no single factor that can be held responsible for controlling growth in any stage at any particular time. Temperature, Ψ_s, and all other environmental parameters affect the growth and establishment of plants at all stages. There is no doubt, however, that the influence of each changes throughout the plant's life cycle. The goal of this and other environmental studies is to attempt to determine the importance of each factor or combination of factors at each point in the life cycle.

Autecological studies can not only give some insight into the complexities of the environment; they give insight into taxonomic problems as well. Results of this study substantiate the separation of _G_. _nervosum_ and _G_. _richardsonii_ into separate species, but there are several indications that _G_. _nervosum_ and _G_. _viscossissimum_ are not separate species.

Although hybrids are possible between *G. nervosum* and *G. richardsonii* (p. 51), the one seed that germinated has grown into a seedling that is chlorotic to white in color and is dwarfed and grows slowly. The probability that it could be successful when competing with other more vigorous seedlings is slight.

Geranium nervosum and *G. richardsonii*, although they can grow side by side, are separated by a variety of environmental factors. *Geranium richardsonii* is limited by low Ψ_s and high temperatures. *Geranium nervosum* is probably less able to compete in heavy cover or withstand extreme water saturation. There is very little evidence, however, that *G. viscossissimum* and *G. nervosum* are separated by environmental barriers. *Geranium viscossissimum* is apparently able to grow at lower elevations in Logan Canyon and Cache Valley but, when the two species are found together, they are completely intermingled to the point where differentiation between the two is difficult.

One of the key characters delineating *G. nervosum* from *G. viscossissimum* is the erectness of the stems of *G. viscossissimum* and the tendency towards decumbancy of the stems of *G. nervosum* (Jones and Jones, 1943). This difference was not marked at the Forestry Field Station. Both species had erect flowering stalks until about midway through dispersal when senescence began to affect the vegetative parts. The stalks of both species then began to droop and, by the end of the dispersal period, were usually completely decumbent.

The other major difference was the glandular pubescence on the petioles and stems of *G. viscossissimum* and the non-glandular trichomes on stems and petioles of *G. nervosum*. In the field on the dry hillside, there was extreme variation in pubescence. Some plants had half glandular trichomes and half non-glandular trichomes on the same petiole. In the laboratory, seeds taken from *G. nervosum* adults in the field produced plants that had some petioles with glandular trichomes and others that were glabrous (p. 43). This evidence either indicates that this character is so variable it should not be used in a taxonomic key or that some hybridization is occurring.

Hybridization is possible between *G. nervosum* and *G. viscossissimum*. Bees, the chief pollinators, do not appear to be able to distinguish between flowers of the two species (p. 56) and visit them at random. Seeds which were obtained in crosses between these two species (p. 51) germinated and are being grown in the greenhouse. It is not known if the hybrids are fertile.

The above is evidence that *G. viscossissimum* and *G. nervosum* are probably members of the same species. More work needs to be done in cross-pollination and the growth and reproduction of hybrids to assist in making a decision concerning the taxonomy of these plants.

CHAPTER VI

Summary and Conclusions

Both G. richardsonii and G. nervosum appeared to be limited by the same environmental factors although the degree of response was different. Seeds of both species required stratification, and G. richardsonii seeds had a scarification requirement as well. The seedling stage was the most responsive to environmental stress. Both G. richardsonii and G. nervosum seedlings had an optimum temperature range for survival of 20-25°C although they could and did adapt to lower temperatures. Seedlings of neither species could survive Ψ_s of -10 bars or lower. The adult stage of both species was more tolerant of Ψ_s stress and G. nervosum adults could survive Ψ_s of -25 to -30 bars. Geranium richardsonii was less tolerant and appeared to be limited by both Ψ_s and temperature in its distribution at the Forestry Field Station.

The critical factors in controlling the distribution of G. nervosum and G. richardsonii were similiar, i.e. Ψ_s and temperature, but the species reacted to them in different ways. Geranium richardsonii was able to survive in environments that were highly saturated with water and under heavy cover. Geranium nervosum, although limited by temperatures above 32°C was able to live in drier conditions by virtue of a tap root system. Hence, although the distribution of these two species was similiar, they were separated by their response to environmental conditions.

Hybridization is possible between *G. nervosum* and *G. richardsonii*, but the seedlings of these crosses were dwarfed and grew slowly. Crosses between these two species probably do not occur naturally. *Geranium nervosum* and *G. viscossissimum* crosses can occur naturally. Pollinators did not appear to distinguish between species, and seeds which were the result of hand pollination germinated and grew in the laboratory. It is not known whether the hybrids are fertile. *Geranium nervosum* and *G. viscossissimum* were also difficult to distinguish by morphological characteristics where the two species grew together. This indicates that some hybridization may have occurred.

Geranium nervosum and *G. richardsonii* are separated in space by a variety of environmental factors whereas *G. viscossissimum* and *G. nervosum* are not. They appear to have similiar environmental requirements and to be able to hybridize. Both of these factors indicate that *G. nervosum* and *G. viscossissimum* are probably not seperate species.

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VITA

Becky Lee Green

Candidate for the Degree of

Doctor of Philosophy

Dissertation: Autecological Life History Studies of Two Geraniums: Geranium richardsonii and Geranium nervosum

Major Field: Ecology

Biographical Information:

Personal Data: Born in Bakersfield, California, November 14, 1947, daughter of Edward F. and Helen Sharp Brittan; married Thomas W. Green August 31, 1969; no children.

Education: Attended elementary school in Bakersfield, California; graduated from Bakersfield High School in 1965; received the Bachelor of Arts degree from California State University, Humboldt, in biology; completed requirements for the Doctor of Philosophy degree, specializing in ecology, at Utah State University in 1973.

Professional Experience: 1969-1970, teaching assistant, general botany, Utah State University; 1970-1971, university fellowship, Utah State University; 1971-1973, teaching assistant, general ecology and introductory range management, Utah State University.