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REPORT

of

COMMITTEE ON THESIS

The undersigned, acting as a Committee of the Graduate School, have read the accompanying thesis submitted by John Victor Gorm Loftfield for the degree of Master of Arts. They approve it as a thesis meeting the requirements of the Graduate School of the University of Minnesota, and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts.

Frederic E. Clements
Chairman

William S. Cooper

E. C. Stakman

Minneapolis, Minnesota

May 1917

REPORT

of

COMMITTEE ON EXAMINATION

This is to certufy that we the undersigned, as a Committee of the Graduate School, have given John Victor Gorm Loftfield final oral examination for the degree of **Master of A r t s.** We recommend that the degree of **Master of A r t s** be conferred upon the candidate.

Minneapolis, Minnesota

May 1917

Frederic E. Clements
Chairman

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THE EFFECT

OF PHYSICAL FACTORS

UPON PETALOSTEMON PURPUREUS AND

PETALOSTEMON CANDIDUS

A THESIS

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL

OF THE

UNIVERSITY of MINNESOTA

By

John Victor Gorm Loftfield

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER of ARTS

MOM
gL82

THE EFFECT OF PHYSICAL FACTORS
UPON PETALOSTEMON PURPUREUS AND PETALOSTEMON CANDIDUS

I N T R O D U C T I O N

Petalostemon purpureus and *Petalostemon candidus* are two species which show an interesting contrast in leaf structure. *P. purpureus* has five linear leaflets as a rule, in a pinnate leaf with a rhachis so short as to give the appearance of a digitate leaf at times. *P. candidus* has seven or nine leaflets in a pinnate leaf, the leaflets being lanceolate to linear-oblong. In nature these leaf characters are quite constant, so constant that this seemed a good opportunity to study the relative adjustment of the two plants under the influence of changing amounts of the various physical factors. Apparently but slight adaptation would occur, making the response almost purely an adjustment even though the experiment be run for a considerable period of time. This did not altogether hold good.

The significant physical factors as far as plants are concerned are light, temperature, humidity, water content, soil salts, soil texture, and soil salts (2). Other factors such as wind, slope, altitude, chemical composition of soil, dust, pressure (barometric), gravity, etc., are of slight value, or are constant, or act indirectly thru the first mentioned factors. The one of greatest importance, and the one here investigated most is water content.

The plants and fruits of the two species of *Petalostemon* were brought in from the Fort Snelling Military Reservation. The

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plants from this prairie, which is only a few hundred yards across, have been examined year after year by experienced taxonomists, and have been the source of many herbarium specimens, and so they cannot be questioned as belonging to the species assigned. The plants were brought in each with a considerable lump of earth around the roots; nevertheless more or less mutilation occurred, and it was found impossible to bring the plant in wholly intact. The fruits were unusually good the fall of 1915 and these were collected at various times, once before frost and several times after permanent snow had fallen. The soil used in these experiments was the same for all the plants (except in the competition experiment); it contained a rather high percentage of humus, and was a good grade of sandy loam. Its water content at saturation was 39% - 42%, averaging 40%. The work done falls naturally under three general heads, 1st, experiments in germination, 2nd, experiments in growth, and 3rd, experiments in adaptation.

This problem was suggested by Dr. F. E. Clements, to whom the writer is also indebted for suggestions and criticisms.

I. GERMINATION

The Effect of Freezing Upon Germination

One thousand seeds (achenes) of P. purpureus and one thousand of P. candidus were planted in a wooden flat 10 by 16 inches and 8 inches deep, Dec. 18, 1915. Half of each had been gathered before frost and half had been exposed to a freezing temperature several times before gathering (gathered Oct. 18, 1915 and Dec. 2, 1915). The flat was watered once a day with tap water in the ordinary manner. The following table shows the result.

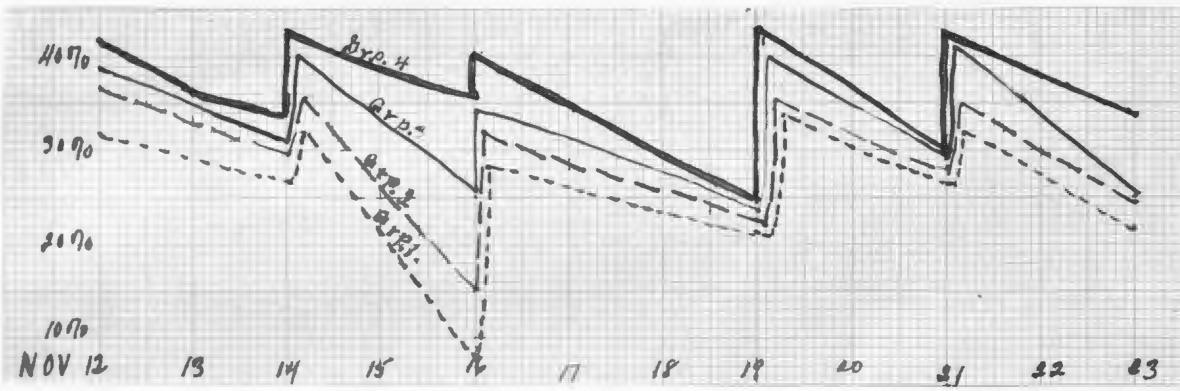
Planted Dec. 18			Jan. 23	Feb. 19	Mar. 18	% Ger.
500 Fruits	P. purpur.	- not frozen	none	3	3	0.6%
500 "	" "	- frozen	3	12	16	3.2%
500 "	P. cand.	- not frozen	1	4	5	1.0%
500 "	" "	- frozen	4	16	17	3.4%

The experiment was discontinued on March 18, 1916. Several seeds which had not germinated were examined from all four lots, and all seemed perfectly sound and able to germinate. From other experiments, it is believed that the seeds would have kept on germinating at irregular intervals for several years. That exposure to a freezing temperature is necessary for germination is improbable; the effect is more likely due to a hastening of changes in the seed, shortening the dormant period.

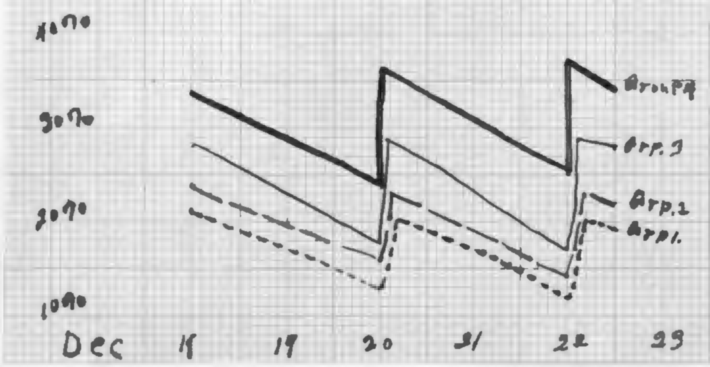
The Effect of Water Content on Germination

Common red four inch pots and their saucers were given three coats of orange shellac inside and out. On Nov. 12, 1915, a similar amount (350 grams) of moist soil was put in each pot and packed firmly. 100 fruits were then placed on the level surface and carefully spaced. Then 20 grams of dry soil was spread evenly over the surface and the surface leveled and firmed without disturbing the fruits. Ten pots of <u>Petalostemon purpureus</u> and ten of <u>P. candidus</u> were planted and treated in the following manner; three pots of each were watered from the top with 20 c.c. of tap water every other day, three of each with 40 c.c. and three of each with 60 c.c. and one of each with 100 c.c. Those planted with <u>P. purpureus</u> were labelled series V and those with <u>P. candidus</u> VI. The groups were labelled respectively 1 to 4 and the pots in the groups a, b, and c. Thus V-1b was planted with P. purpureus, and was the 2nd pot in the group watered with 20 c.c. of water, VI-3c was planted with P. candidus, and the third pot of the group given 60 c.c. of water every other day.

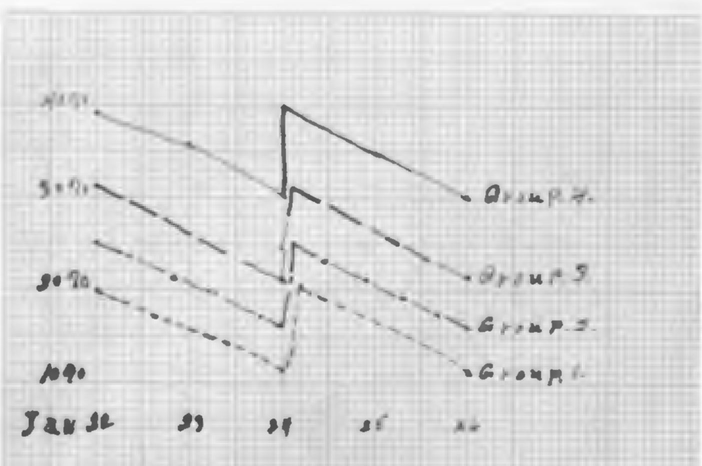
In order to determine the water content of the planted pots, a number of pots were filled with soil in the same manner as the others, and watered in the same manner. As the curves show, there was but little variation in various groups.



As a consequence the method was changed Dec. 18, the same amount of water being used in each group but the water was added from the bottom, i.e., placed in the saucer. In group 3 and 4 too much water was used so a part of the water was still added to the top.



This separated the curves and made them more even, but not as much as could be desired, but the curves were made quite regular by watering according to the rate of evaporation. A Portland jar was filled with water and placed among the plants. Just before watering, the water in the jar was made up to volume from a pipette and the amonnt calculated which would evaporate from the same size surface as the soil surface of a pot. This amount was added to group 1 (average 23 c.c.), twice this amount to group 2, three times this amount to group 3, and five times this amount to group 4, watering every other day as before and mostly from the bottom. This method of watering was used from Jan. 10, 1916 until the experiment ended (April 10, 1916).



The following table shows the results:

Germination to	Dec.10	Dec.18	Jan.23	Mar.10	Plants surviving Mar.10	
V 1a	0	2	2	2	1	
V 1b	0	0	0	0	0	
V 1c	0	1	1	1	1	
V 2a	2	3	3	3	3	
V 2b	2	2	2	2	2	
V 2c	3	4	4	4	4	
V 3a	4	4	6	6	0	(damped off)
V 3b	2	2	5	5	4	
V 3c	1	3	5	5	2	(2 damped off)
V 4a	0	1	1	3	0	(1 damped off) (2 died from other causes)
VI 1a	0	0	0	0	0	
VI 1b	2	3	3	3	0	
VI 1c	1	2	2	2	0	
VI 2a	4	5	5	5	5	
VI 2b	4	7	7	7	7	
VI 2c	1	3	3	3	3	
VI 3a	1	1	4	4	4	
VI 3b	2	2	8	8	8	
VI 3c	0	0	6	6	6	
VI 4a	1	1	2	4	0	(damped off)

It will be seen that no fruits germinated in groups 1 and 2 after Dec. 18th. This is explained by the fact that very thoro wetting is necessary to start the seed (fruits) growing, and that later the seed and soil must dry down to the proper degree of moisture.

The succeeding experiments show this with great clearness. Apparently *P. candidus* can start up under more varied conditions than *P. purpureus*, but this is not so. *P. candidus* starts more quickly than *P. purpureus* and produced more plants before the method watering was changed. After Dec. 18, those seedlings of *P. candidus* which had started up in group 1 promptly died; one plant only of *P. purpureus* in group 1 died but not until a month later. An outbreak in March of *Pythium* in several pots killed a number of plants but did not change results.

Germination in Soils with Constant Water Contents

Four inch shellaced pots were used, as in the previous experiment, and placed in shellaced saucers. Group 1 had the saucers full of water at all times, group 2 were auto irrigated. The experiment started Dec. 18, 1915. 100 seed were planted in each pot.

Group 1-A The pot was filled flush to the top with soil.

Group 1-B Pot filled with fine sand up to 1 inch of top and then soil up to the top.

Group 1-C Pot filled with coarse sand (grains ½-1 mm. in diameter) to 1 inch of the top, soil above as in 1-B.

Group 1-D Pot filled below with coarse sand (grains ½-1 mm.) gravel (½ cm. in diameter), soil above as in 1-B.

Group 1-E Pot filled below with gravel (½ cm. in diameter) soil above as in 1-B.

Group 2-A Soil only -- water reservoir 1 foot below pot.

Group 2-B Soil only -- water reservoir 3½ feet below pot.

The water content analyses showed that group 1-A, -B, and -C, had the same water content (variation 36.0%--38.7%, average 38.2%), group 1-E had a water content of about 14.5% (14.0%--15.2%), group 2-A had a water content of 26.7%, group 2-B had a water content of 25.3%. On this account in working out results, only three groups will be considered, group 1-A, 1-B, and -C, group 1-E, and group 2-A and -B. Six pots of each series were run in the 1st group -A, -B, -C, (hereafter group X), two in each series group 1-E (hereafter group Y), and two in each series of group 2 (hereafter group Z).

The plants were run until March 10th under the above mentioned conditions. After March 10th, they were watered from the top daily with 40 c.c. of water each. Up to this time germination was practically nil.

	Holard	Germination to March 10th		to April 10th	
Group X		V	VI	V	VI
Group A--1	38%	0	0	3	7
Group A--2	38%	0	1	5	7
Group B--1	38%	0	0	2	5
Group B--2	38%	0	0	5	2
Group C--1	38%	1	2	4	5
Group C--2	38%	0	0	6	6
Group Y					
Group E--1	14.5%	0	0	7	5
Group E--2	14.5%	0	0	4	2
Group Z					
Group 2 A	25%	0	0	6	6
Group 2 B	25%	0	0	5	8

Four similar pots with the drainage sealed with corks were next used, two of each were added to Series V and VI of this experiment on January 23, 1916. These were filled with soil and

100 seeds planted in each. These were kept with the water level just about at soil level, so that the soil was supersaturated. No germination had occurred by March 10th; an examination of several of the fruits showed the seed apparently intact but the ovary wall had decayed and in many cases had entirely disappeared. At this date the corks were removed from the drainage of one pot of each series, and treated thereafter like the other pots of the series; in one week two of P. purpureus and ten of P. candidus had sprouted. No germination occurred in the two unchanged pots.

COMPETITION EXPERIMENT

October 16, 1916, I filled four four inch glazed pots with sealed drainage holes, with sifted soil from the Snelling prairie, four pots with shaped pieces of Muhlenbergia racemosa sod, and four with Agrostis alba sod. In two pots of each set, I planted 100 seeds of Petalostemon purpureus in each pot, and 100 seeds of P. candidus in each pot of the remaining two pots of each set. These were run until April 20, 1917, and were watered as infrequently as possible. At the end of the period the germination was as follows:

	Bare soil	Muhlenbergia sod	Agrostis sod
P. candidus			
1st pot	2 (died 1-1-17)	5	0
2nd pot	none	4	0
P. purpureus			
1st pot	2	0	0
2nd pot	3	0	0

The results seem to indicate that P. candidus can start in a bare area, but is much more susceptible to drying out than P. purpureus. P. purpureus is especially fitted to start up in a bare area. *P. candidus* alone is able to start up in *Muhlenbergia* sod and its better germination and growth here was apparently due to the protection against drying out. Neither species seemed able to compete with *Agrostis*. The writer believed from field observations that both species probably started only on denuded areas, often but an inch or so across, such as are common on any prairie. This experiment seems to show that *P. candidus* can start even in the center of a *Muhlenbergia* tuft.

CONCLUSIONS

For germination of the fruits of both species, the fruits need a very thorough wetting and finally a drying down to a more normal holard before growth occurs. The drying down to a moist condition is probably an air reaction; while very wet the seed do not get the oxygen necessary for starting growth. The reason for the long drawn out and varying period of germination can only be guessed at, but the advantage is plain. A few plants start growing every time somewhat favorable conditions occur and if conditions change for the worse, the entire crop of seed is not killed.

Both species can start best in denuded areas, which in many cases is only the space between two tufts of grass left by the death of some annual plant. *P. candidus* can establish itself in some grasses, but *P. purpureus* probably cannot.

II. G R O W T H

The Effect of Temperature, Sunlight, and Water Content Upon Growth

Beginning Monday, Jan. 1, 1917, the temperature was kept quite low for two weeks, the day temperatures about 18° C., night temperatures about 5° C. The following two weeks the day temperatures were brought up to 30° C. and night temperatures to 15° C. During the fifth week, the temperatures were again lowered to those of the first two weeks. At the beginning of the experiment, the height of four P. candidus and four P. purpureus plants were measured. The plants were kept at a water content of 25%. Every Monday thereafter, the height was again measured, showing the result of high and low temperatures on growth in height.

Plant	Height Jan. 1	GROWTH to Jan.8,	to Jan.15,	to Jan.22,	to Jan.29,	to Feb.5
P.purpureus	4.6 cm.	0.0 cm.	0.0 cm.	0.1 cm.	0.3 cm.	0.1 cm.
" "	4.3 cm.	0.1 cm.	0.0 cm.	0.1 cm.	0.3 cm.	0.1 cm.
" "	3.1 cm.	0.0 cm.	0.0 cm.	0.0 cm.	0.1 cm.	0.1 cm.
" "	3.7 cm.	0.0 cm.	0.0 cm.	0.0 cm.	0.2 cm.	0.1 cm.
P. candidus	5.9 cm.	0.1 cm.	0.0 cm.	0.2 cm.	0.6 cm.	0.2 cm.
" "	6.2 cm.	0.1 cm.	0.0 cm.	0.1 cm.	0.5 cm.	0.2 cm.
" "	4.8 cm.	0.0 cm.	0.0 cm.	0.0 cm.	0.3 cm.	0.1 cm.
" "	5.1 cm.	0.0 cm.	0.0 cm.	0.1 cm.	0.4 cm.	0.2 cm.

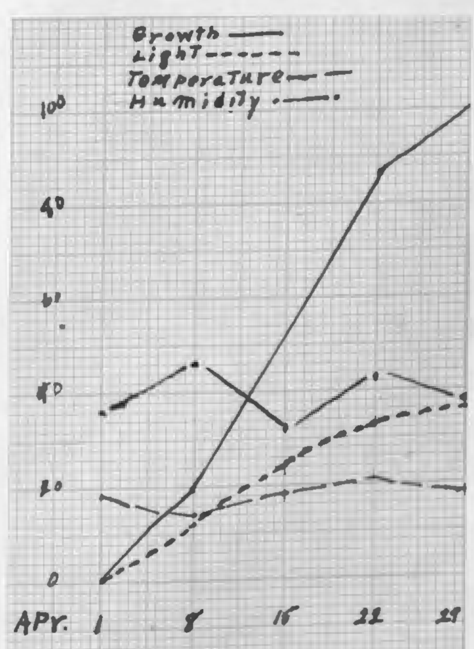
There was little growth the first week of low temperature and none the second week. The first week of warmth started a slight growth but not until the second week was there a good response The next week of cold cut down the growth but did not stop it entirely. The humidity and light were sufficiently uniform to have no appreciable effect on this experiment.

Effect of Light on Growth

During the month of April a careful record of humidity, temperature, and light were kept, and the weekly growth of a number of plants of both species in various water contents. The following table shows the growth record. The numbers represent the height of the stem in centimeters, the tallest stem of each plant being measured.

	April 1		April 8		April 15		April 22		April 29	
	P. purp.	P. cand.	P. purp.	P. cand.	P. purp.	P. cand.	P. purp.	P. cand.	P. purp.	P. cand.
	6.9	8.0	7.0	8.5	7.2	8.8	7.5	9.7	7.5	10.2
water-	9.9	9.7	10.0	10.3	10.5	10.9	11.0	12.0	11.1	12.6
logged	10.9	9.1	11.4	9.5	12.0	10.0	13.0	10.7	13.3	11.0
soil	3.1	11.6	3.7	12.0	4.8	12.7	5.9	13.8	6.5	14.3
	20.6	21.9	22.5	25.2	26.3	30.3	30.1	35.1	32.1	38.4
Holard	24.8	27.1	26.4	30.9	29.5	34.7	32.7	37.5	34.2	40.3
38%	29.3	29.9	31.2	35.0	35.0	40.1	40.2	45.2	40.7	47.9
		26.3		31.3		36.5		41.5		43.8
	31.5	29.1	35.2	33.6	41.0	42.6	45.0	51.8	47.0	56.9
Holard	30.4	21.6	31.5	30.8	33.3	41.0	35.0	49.2	36.1	52.7
25%	28.3		30.0		33.2		36.5		38.3	
	27.4		29.3		33.3		37.2		39.1	
	31.7		33.1		36.0		38.7		40.2	

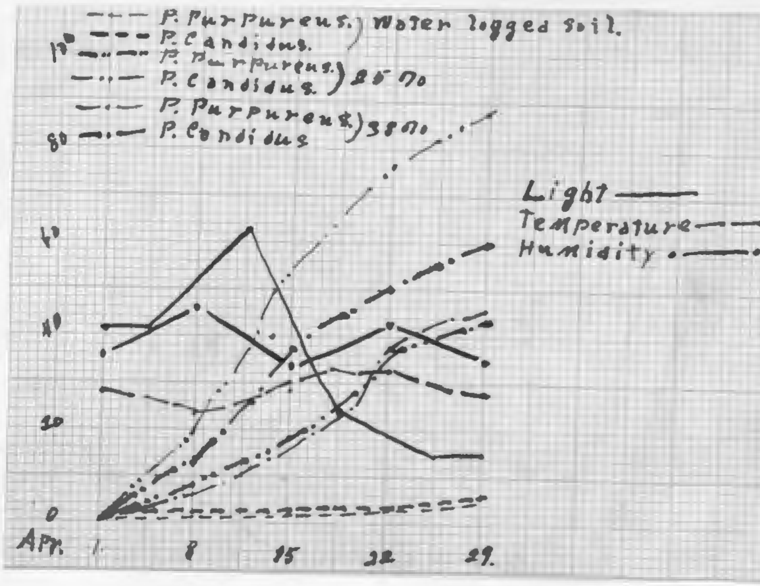
The following curve is the average growth curve. The increases in height of those plants grown at a water content of 25% are plotted as fractions of the total growth for the period. The light curve is formed in much the same manner. The total number of hours of possible sunlight for the period is considered 100% and the amount of actual sunlight each week is plotted as fractions of this, the fraction for each week being added to the fractions of the previous week. Because of this, the light curve represents the growing total of sunlight hours. The humidity and temperature curves could not very well be plotted diagonally, so the curves represent the average temperatures and humidity.



In examining this group of curves, it is readily seen that growth and light do not correlate very well. The first two weeks were weeks of sunshine yet the first week the growth curve shows a slow rise. The third and fourth weeks were weeks of little sunshine yet growth was quite rapid the third week. If there is any relation between the two, it must be due to a decreased amount of food caused by a lowered rate of photosynthesis, and in this case the continued rapid growth the third week can be explained by the fact that the reserve of food had not yet been seriously lowered. Another explanation for the rapid growth the third week might be the high temperatures that occurred that week. Until this experiment has been carried out under conditions of uniform temperature, humidity, water content, etc., no certain correlation can be made.

The Effect of Water Content Upon Growth

This data was taken from the previous experiment. The growth curves represent the average growth in centimeters of each group of plants, six curves in all. The light curve is represented as the percent each week of the total possible hours of sunlight. The humidity and temperature curves are the same as in the previous graph.



These curves resemble the general growth curve. The most unlike is P. candidus grown at 38% water content. P. candidus has a more rapid growth than P. purpureus and seems to respond in growth to a change of conditions more quickly than P. purpureus. The great difference in growth between both species growing in a nearly normal habitat (holard 25%) and growing in a waterlogged soil, is clearly shown by these curves.

The Effect of Subdued Light

One plant of each species and from each of the three sets (holard 25%, 38% and waterlogged soil) was moved into a shade tent covered with very thin, transparent cheesecloth. 70% of the light was cut off by the tent altho there were special openings to allow more light than the cloth would allow. These remained in this tent during the month of April. By the end of the month all the plants had died altho under the same conditions as those plants outside except for the one factor, light. This shows that but little sunlight is not sufficient for growth for either species, and explains why all of the plants either became dormant or made a sickly growth during the mid-winter months.

C O N C L U S I O N S

From the preceding experiments, the effect of the following physical factors upon growth may be summarized as follows. A water content of 20% to 25% is the most favorable for both species, P. candidus favoring the upper water content, and P. purpureus the lower. A high temperature is favorable to growth: this is not surprising when one considers that the time of growth for both species is about mid-summer. Strong sunlight is also a necessary factor, as the experiments with the shade tents show. Insufficient work was done with the effect of humidity to warrant any conclusion.

III. ADAPTATION

In these experiments, four-inch glazed pots were used. The drainage of each was plugged with a cork and then sealed with paraffin - petrolatum mixture, and the pot weighed. A seedling from a series V or VI pot was then transplanted into the pot, using soil of the same composition as before. Then the pot was again weighed, several samples of soil used in the transplanting taken at intervals during the work, and the water content determined. From this data, the weight for any desired water content was determined for each pot. Example.

Water Content of Soil Used	20%
Weight of Soil	120% of weight of dry soil
Weight of Pot and Soil	965 grams (weight of plant negligible)
Weight of Pot	605 grams
Weight of Soil	360 Grams

1.20 : 1.00 :: 360 : x

x == 300, weight of dry soil in grams

Desired water content	25%
Weight of soil at 25% holard	375 grams
Weight of pot and soil at 25% holard	375 + 605 or 980 grams

Each day the pots were brought up to the weights marked on them. The holard would, of course, be higher in certain parts of the soil at first, but the water would be evenly distributed in thirty to ninety minutes (the longer time for the pots at the lowest holard). Then until the next time of watering the holard would slowly decrease 3 to 5%; at no time was the loss greater than 6½%.

The Effect of Waterlogged Soil

Oct. 14, 1916, a seedling of P. purpureus and one of P. candidus was put into glazed pots as described above, except that the pots and the earth were not weighed. The plants were watered normally every day for two weeks. By this time they were well established and the supply of water was increased, a quarter of an inch of water standing above the surface of the soil at all times. By Nov. 11th, P. purpureus had died, and reduction to the former conditions of water content failed to revive it. P. candidus was still alive but roots had developed in the surface layer of water, and hung over the edge of the pot. By the following week, the leaves of P. candidus also shriveled and dropped off. It was also returned to its former water content, but did not show any signs of reviving until Dec. 9th, when several vigorous shoots started up from the base.

A variation of this experiment was tried Mar. 3, 1917. A number of seedlings in the four-inch glazed pots had been dormant all winter, but were beginning to sprout. Three plants of each species were watered in the manner described above, except that once a week, the pot was allowed to dry down to 35% to 38% water content and left there a day. Towards the last, (April 10th) the excessive watering was made continuous with the intention of finding out if the plants had to any extent adapted themselves to live in this habitat. On May 12th they were still growing, and, while much smaller plants, and differing in many respects from those growing in soils of lower water content, they were more or less healthy plants. A dense surface growth of algae (Oscillatoria and Vaucheria) may have added oxygen to the water in great abundance and prevented an excess of CO_2, and in this manner allowed the roots of the plants to respire altho water-logged (See Bergman's Studies on Aeration). However, the plants did adapt themselves to their environment.

The plants grown in this manner were always dwarfed and composed of many shoots arising near the roots. The leaves were curiously three-parted, and especially in the case of P. candidus, the leaflets were very much broadened. There was no noticeable increase in the number of stomata, but thickening of the cuticle was rare. Some of the leaves were very small (Plate II).

The Effect of a Very Moist Soil

Five plants of each species were kept at a halard of about 38% (soil very nearly saturated). During the winter months there was no growth, but along in March 1917, three plants of P. purpureus and four of P. candidus seedling started to grow but died; one P. purpureus started to grow just before the end of the experiment, the other died without starting growth. All four plants of P. candidus produced leaves of the type shown in the plate (Plate IV). Two plants of P. purpureus became startlingly like the corresponding plants of P. candidus; in fact, only a close inspection revealed any difference. Examined alone without comparison with the corresponding plants of P. candidus no botanist would consider them anything but P. candidus. Even in histological details do the leaves of the two species compare; there is no clear difference between the cross-section of the leaves of the two species. But for the fact that these two plants of P. purpureus had produced shoots typical of the species the previous fall, the investigator might have been inclined to believe that two plants P. candidus had been taken by mistake. However, there were a number of little differences which marked them from the P. candidus plants grown under the same conditions. The leaflets were narrower, and had a tendency to form parallel sides, the stipules were distinctly like those of P. purpureus rather than those of P. candidus.

The form of the third plant of P. purpureus was also quite remarkable. Some additional earth added to this pot and not calculated in on the weight for the pot at its proper holard, caused this pot to be kept at a lower holard (32%). This plant was intermediate in form between those grown at 38% water content and the normal plant of this species. The leaflets were just as broad as those grown at a holard of 38% but were longer and had the general shape of a normal leaflet enlarged. The broader form of leaf of the water-logged type of P. purpureus, if very much larger, would to some extent resemble this leaf. The general growth was very much like those grown in the 38% holard, the leaves separated and scattered on the stem in the same manner and with the same type stipules, no short shoots growing out in the axils of the leaves on the main axis as in the normal P. purpureus. Except for the grouping of leaflets in the leaf, and their longer oblong shape, this plant would have been typically P. purpureus grown at a holard of 38%. The plant was smaller than the others in the group, having started at least three weeks later.

There is no doubt but what considerable adaptation will occur in P. purpureus in response to changes of water content. That such adaptations can occur in nature is very improbable, because even with the most careful attention the plants when starting had a tendency to die under these conditions. P. pandidus being largely adapted to such a soil condition already did not change much (Plates IV and V).

The Effect of 25% Water Content.

In these experiments glass Mason jars of two quart capacity were used instead of the four inch pots. Otherwise, conditions were made about the same, the same soil used the same seedlings, etc., the main difference being the increased amount of soil. This undoubtedly made some increase in growth, but a check set showed that the main difference was due to water content. The form and character of the plants was entirely due to water content, and as this is the only part dealt with, the effect of the increased amount of soil need not be considered. The holard of each jar was determined in exactly the same way as for the pots in the previous experiment.

The plants grown at this holard (25%) resembled those grown in the field as closely as greenhouse plants can do so. The difference is first in size, the greenhouse plant being somewhat smaller slightly thinner leaves, due to a lesser amount of sunlight, not quite as much thickening of the cuticle, tho the humidity was kept quite low, so this last difference was very slight. The shape of the leaves (Plate VI) and the general form of the plants (Plate VII) are the same otherwise as the plants grown on the prairie (by comparison with herbarium specimens).

That this the same water content (25%) as the one in which these plants usually find on the prairie, is somewhat doubtful. Conditions are such there that a plant can get moisture at a lower water content and get along because its tap root goes much deeper and because it has many more roots, and also because capillarity keeps up the water supply from below. The water content falls very quickly in a pot, a thing which is not true of prairie or other soil, and the rapid changing from a water content of 30% to 20% for instance, and back again in twenty four hours is probably a violent strain upon the roots of a prairie plant. For this reason, the water content may differ for best growth under greenhouse conditions from that for best growth on the prairie. The type of pot used in this experiment (2 qt. glass jars) caused a very slow loss of water from the soil, for no week was the loss over 5% and generally about 3%, so that these jars were brought up to weight only once a week. This made the fluctuation in the holard more nearly approach that of a prairie and must have had some effect upon the closeness with which these plants approached the normal prairie-grown plants. The check plants (grown in the four inch glazed pots) did not approach normal plants so closely. On the whole, since water content measurements of the soil for prairie plants taken during the growing season are not available, this water content (20% to 25%) must be taken as representing very nearly the best holard for these plants.

The Effect of a Low Water Content.

Five plants of each species that had been kept at a water content of 20%-25% (in the glazed 4 inch pots) and which started to grow during the first week in March 1917, were used in this experiment. Two plants of each species were changed to 14% to 18% water content the third week of March, two more of each species, the first week of April. The first two were only about two inches high or less, when they were changed to the lower holard. No new type of leaf was produced in either species, the effect was the dropping of leaflets, those nearest the base first, the terminal one last. This left each stem a short tuft of leaves and very young leaves at the top, and just below them a number of leaf rhachis and somewhat lower, bare stem. The various zones, of course, were not sharply separated, the leaf zone, for instance would grade into the rhachis zone with a number of leaves with dropping leaflets. There was continued growth in case of <u>P. purpureus</u>, one plant growing three centimeters, the other two and one half centimeters. There was but little growth in case of <u>P. candidus</u>, the only evidence being the production of an occasional new leaf; this ceased very soon, and finally the plants had only three (in one) and four (in the other) leaves at the top, and remained so during the last weeks. The rhachis dropped off very soon after the plants had reached this condition. There was no alteration in leaf structure except that the leaves of <u>P. candidus</u> were slightly narrower and thicker in proportion than in the normal plant. Both leaves and plants were smaller than those grown at a holard of 25%.

Those moved into this lower holard soon resembled the first pair of each species changed to this holard, but none of these continued growth. They reduced the number of their leaves to a tuft at the top and remained in this condition.

After May 1, 1917, the first two plants of each species moved into this lower holard were changed again to a holard of 25%. New shoots arose from the base in both species, but growth was continued in the original shoots of P. purpureus but did not in the plants of P. candidus.

From this experiment it seems that both species, adapt themselves to drought conditions by reducing the leaf surface. If such conditions do not occur for any length of time, both species can resume growth in the same stems, but if such conditions maintain for any length of while, the function of the growing point in P. candidus is lost and it will not again resume growth; it takes evidently a much longer time for this to occur in P. purpureus. In both species, dormant buds at the base are able to start growth upon resumption of favorable conditions. Use of these, however, means waste of the original stem.

S U M M A R Y

The effect of light upon germination is in itself negligible. Some of it is transformed to heat in striking the earth, so there is an indirect effect. The effect upon growth is also somewhat indirect, for it is not in itself as necessary to growth as the food made by its agency. What effect it has upon adaptation is an open question. That it does cause adaptation is not doubted.

but opinions differ as to the manner and degree.

Pick (1882) decided that sunlight affects the internal structure of the leaves chiefly. It makes the cuticle thicker, makes the palisade cells longer and thickens the entire leaf. He decided that palisade cells are ancestral, but that sunlight is necessary for their development. Stahl (1883) decided that sun leaves are smaller, tougher and thicker than shade leaves, have a highly developed palisade, while shade leaves have a poorly developed palisade, or in some cases no palisade, and have less air spaces and sponge than shade leaves. Dufour (1887) decided that light caused leaves to be larger, thicker, and to have better developed cuticle, conductive tissues, and palisade. He decided that the larger thinner leaves ordinarily found in shade forms was due to a higher water content and not to the effect of decreased light. Clements, E. S., (1905) decided that light played a very important part in the internal structure of a leaf. She decided that the amount of sunlight determined whether a cell would stretch out flat (into a sponge cell) to prevent too much light striking that cell.

The present investigations have not covered to any extent the effect of light upon adaptation, but from the above mentioned investigations the following conclusions may be drawn. 1. The leaves of <u>P. purpureus</u> growing at 38% would not have been so broad nor approached <u>P. candidus</u> so nearly in form if the light had been stronger. During the month of March, April, and early May the light is not very intense and 60% of it was cut off in entering the gerrnhouse (this was determined by approximately simultaneous photometer readings with in and without the greenhouse). The differences between normal prairie plants and the plants growing at 25% holard were clearly due to decreased light.

The effect of temperature is chiefly upon germination and growth. There is nothing in any experiment to indicate that that temperature had any direct effect upon adaptation. These investigations show thruout that while the root and basal buds are very hardy, the shoots are easily distroyed by low temperature, lack of sunlight, decreased water supply, etc. Hence, these shoots slowed down or ceased growth upon the advent of cold and started growth again with the coming of warm weather. This tendency to postpone growth until quite warm weather comes along protects this rather delicate shoot by safe-guarding it against spring frosts and cold, and makes it a summer plant. It also explains why the foliage is dead or dying at a time when such plants as goldenrods and wild asters are in full bloom. A high temperature required for germination also insured favorable temperature for the delicate seedling.

The effect of humidity was appreciable upon growth and humidity, but probably nil upon germination directly. Thickness of cuticle upon the leaves grown at a holard of 25% approaching that found on normal leaves was undoubtedly due to the quite low humidity of the greenhouse during the period of growth. Its effect upon growth must be traced to the increased flow of the transpiration stream, and the effect of this upon the food supply. Any effect upon germination is due to the rapid drying of the soil layer and therefore acts indiredtly thru water content.

The effect of water content is very great. This is the most important single factor of the whole group of physical factors and acts directly upon the plant at all times. It controls together with temperature, the germination of the seed. It controlw the growth (together with the other factors) and probably plays the most importnat part in this function. Together with light it plays an all-important role in adaptation.

Haberlandt (1881) tried to show that the arrangement of cells within the leaves and especially the assimilative cells are for the purpose of transportation to and from the veins. Dufour (1887) tried to show that the larger and thinner type of leaf found in the shade, is due to the higher water content found there and not to the decreased light. His plants when grown at the same water contant produced larger, thicker and better leaves in all respects in sunlight than in the shade. His experiments are not convincing, however, since he used only sun plants, and used only extremes of water content, ignoring the fact that the last tends to make only water content the significant factor. His conclusions are moreover, not in agreement with those of the other ingestigators, and so need not be considered further.

From these investigations the following conclusions may be drawn.

1. A very high water content, decreasing over a period of a week or two to a water content of about 25% (for this type soil) is the most favorable to germination.

2. For growth a water content of about 25% to 30% for P. candidus, and 20% to 25% for P. purpureus, and not fluctuation very rapidly, is the best for growth.

3. A very high water content such as occurred in the pots where water stood over the surface of the soil, the plants were dwarfed, the leaves small and resembling seefling leaves with rather broad leaflets. In P. purpureus there also occurred occasional leaves

with very narrow and folded leaflets; they seemed to have failed to expand properly for some reason. Cross sections of the leaves of both show a very loose and spongy structure and with only a thin loose layer of palisade tending to resemble sponge curiously, some cuticular thickening is present.

4. A rather high water content, that is, one approaching saturation, does not dwarf the plants very much but together with decreased light causes profound changes in P. purpureus. These leaves have a decreased palisade with many air spaces, and a very loose sponge. The upper cuticle is quite thick in P. purpureus in places, and not nearly so in P. candidus. Save for this thickening, a broader leaflet, and a slightly different manner of strengthening the edge of the leaf (not using so much palisade packed in the edge), the cross-sections of the two might be identical.

5. A very low water content causes the plants to loose their lower leaves, causes the growing point of P. candidus stems to die in a few weeks and also of P. purpureus stems if continued for a month or more. The leaf cross-section shows quite a thick cuticle, and a few air spaces. P. purpureus showed very much palisade and but a thin layer of sponge. Near the edge of the leaf the palisade occurs on the under surface as well as the upper, and this layer meets the upper layer in the middle of the leaf. It soon gives way to the sponge. Except the few air spaces and the thickened cuticle, the P. candidus leaf is like a mesophytic leaf in arrangement of palisade and cuticle.

6. Since all these plants were grown under the same conditions of light, temperature, and humidity, the difference must be due to water content alone.

7. *P. purpureus* can b made almost identical in form to *P. candidus*.

8. Since *P. purpureus* can approach *P. candidus* so closely, it seems reasonable to suppose that the ancestral form of *P. purpureus* must have been nearly the same as *P. candidus*. This reasoning is based upon the hypothesis that it is easier for a plant to revert to a former form than produce an entirely new form. All attempts to produce a form of *P. candidus* resembling *P. purpureus* have been futile.

9. The ability of *P. purpureus* to start in a bare area and to grow at a lower water content than *P. candidus* explains why *P. purpureus* so often moves in on bare dry areas in the western plain. *P. candidus* moves in next, and then grasses, since the vegetation covering the surface has raised the water content.

10. The role played by the *Petalostemons* in succession is undoubtedly the same as that of clover or alfalfa in crop ratation. They raise the nitrogen content of the soil, and keep it up as they are found at all times in all prairies to a greater or less extent. Root nodules have always been found on the plants brought in, and are even on the seedlings from the time they are a month or so old.

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Plate I. Corner of Greenhouse showing plants and instruments. The recording photometer is to the left and behind Fries hygro-thermograph.

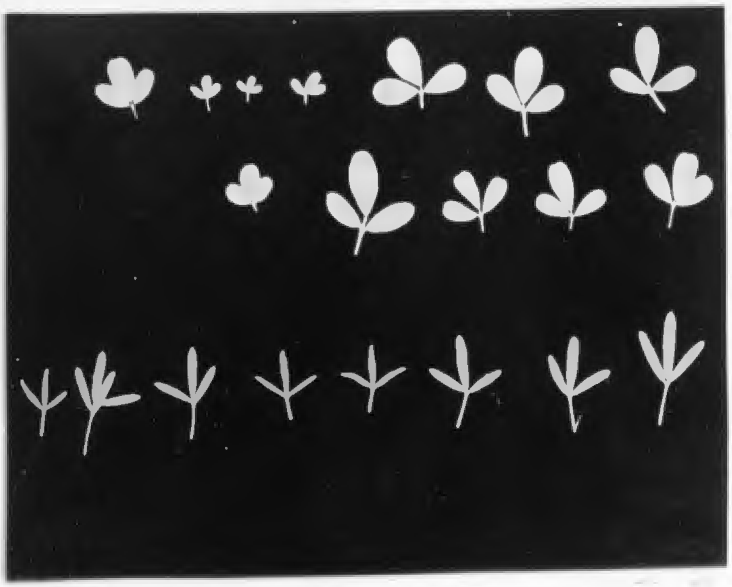

Plate II. Prints of the leaves of waterlogged plants. The leaves of P. candidus are above and the leaves of P. purpureus are below.

Plate III. Prints of the leaves of P. purpureus grown at 38% water content.

Plate IV. Prints of the leaves of P. candidus grown at a water content of 38%.

Plate V. Plants grown at a holard of 38%. P. candidus is on the left (2 plants) and P. purpureus is on the right.

Plate VI. Prints of leaves of plants grown at a water content of 25%. P. candidus is above, and P. purpureus is below.

Plate VII. Plants grown at a water content of 25%. P. candidus is left, and P. purpureus is on the right.