VOL. 3 MAY, 1928 NO. 11

HILGARDIA

A Journal of Agricultural Science

PUBLISHED BY THE

California Agricultural Experiment Station

CONTENTS

UNIVERSITY OF CALIFORNIA PRINTING OFFICE
BERKELEY, CALIFORNIA

HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE

PUBLISHED BY THE

CALIFORNIA AGRICULTURAL EXPERIMENT STATION

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LETTUCE SEED AND ITS GERMINATION

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INTRODUCTION

The germination of lettuce seed‡ (*Lactuca sativa*) is inhibited at certain temperatures, above the optimum. These temperatures may not prevent growth, however, of seeds which have already started to germinate. This inhibition seems to be largely a varietal characteristic, for the temperature at which one variety will germinate satisfactorily may completely inhibit the germination of another variety. Furthermore, it usually requires a higher temperature to inhibit the germination of old seed than it does that of freshly harvested seed of the same variety. By freshly harvested seed is meant that which is not more than five weeks old. In the case of most varieties, almost complete failure of the seed to germinate occurs at 30° C, regardless of age, although there are a few varieties that germinate fairly well at this temperature.

In the Imperial Valley of California, and in other sections with similar climate, where lettuce seed is planted in late summer and early fall, unsatisfactory stands are often obtained because of low germination. It is believed that this low germination results from high soil temperatures which prevail at germination time.

These studies have to do principally with the relation of temperatures to lettuce seed germination, but the effect of certain other environmental factors is also considered. They attempt to throw light upon the causes of inhibition of germination at high temperatures; and, they suggest practical methods of overcoming the difficulties of germinating lettuce seed at temperatures somewhat above the optimum.

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‡ By "seed" reference is made to the fruit (akene) of lettuce.

STRUCTURE OF LETTUCE SEED AS RELATED TO GERMINATION

Experiments with lettuce seed, reported later in this paper, showed that it will germinate at higher temperatures with the coats removed than with the coats on. It was found that if seeds are soaked for a half hour the coats can be separated into three distinct coverings. Removal of the outer two has no influence on the germination of seeds at high temperature but when the innermost is removed germination proceeds normally as shown in figure 23. This result suggested the desirability of making a study of the development and structure of these parts of the seed.

Jones[2] describes the general morphology of the lettuce akene, but gives no details as to the development of the pericarp and other coats surrounding the embryo.

Figures 1 and 2 show sections of the ovary and ovule cut through the embryo sac just prior to anthesis. The embryo sac is highly vacuolate and has a single nucleus. The nucellus has almost entirely disappeared, being represented now by a few scattered cells. The single integument consists of from twelve to eighteen tiers of parenchymatous cells, the inner nutritive layer being particularly prominent because of the large size of its cells. There is evidence, at this stage, of disorganization of certain inner cells of the integument (except the epidermis). The pericarp varies in thickness in different parts of the akene. The cells of the pericarp resemble those of the integument, except that on the whole they are smaller; the outer epidermis of the pericarp is distinct but there is no well-defined inner epidermis. Inner pericarp cells have begun disorganization which process progresses with greater speed at certain places than at others, giving rise to large lysigenous spaces adjacent to the integument.

Examination of figures 3 and 4, sections of akenes older than those described above, shows that there has been an enlargement of the akene, which involves in part an increase in the thickness of the integument. There has been further disorganization of inner pericarp and inner integument cells. Figures 5 to 14 show still further disintegration of pericarp and integumentary tissue, enlargement of the embryo sac and embryo, and organization of two endosperm cell layers contiguous to the inner epidermis of the integument.

The inner epidermal cells of the integument finally disorganize (figs. 14, 15, 16); fragments of walls are in evidence, however, as late as ten days after anthesis. Integumentary cells along the sides of the embryo sac disappear sooner than those at the ends. The inner wall of these epidermal cells becomes a prominent structure in the mature seed. This wall closely invests the endosperm, and is with difficulty distinguished from it. That it is of integumentary origin is well shown in figures 15 and 16. This membrane is a continuous one, which in untreated sections, appears translucent in color. It has semi-permeable properties. It stains yellowish red with Sudan III, dissolves in strong hot potassium hydroxide, but is insoluble even in concentrated sulphuric acid. These reactions show it to be fatty in nature. When the pericarp and seed coats of a mature akene are removed, and the embryo, surrounded by the unbroken integumentary membrane and the endosperm, is immersed in concentrated sulphuric acid, the former is thrown into folds and separates from the endosperm. The sulphuric acid apparently dissolves the walls of the endosperm cells and the dissolved substances are obviously highly osmotic for if the seeds are now immersed in distilled water, absorption is rapid, the membrane becomes greatly distended, and finally bursts, the points of rupture usually occurring along the side of the seed. This behavior indicates that the membrane is continuous. When the embryo surrounded by the endosperm and the integumentary membrane is immersed for a short time in hot potassium hydroxide, and then transferred to distilled water, swelling occurs as with the sulphuric acid treatment, but the membrane ruptures much quicker and always near the root tip. The point of rupture corresponds to the position of the micropyle.

The structure of the tissues which surround the embryo of the mature akene may be summarized as follows:

(1) The *pericarp* has rather equally spaced ribs (figs. 1, 3, 8, and 11) which are made up of thick-walled sclerenchymatous pitted cells (figs. 17, 18, 19) which give a strong lignin reaction. In longitudinal sections, these cells appear much like fibers. The pericarp cells between the ribs are somewhat larger, and thinner walled than those of the ribs, but also lignified to some extent. Pericarp cells present in the mature akene represent only a part of those found in the young akene; inner pericarp tissue disorganizes in the course of akene development.

(2) The *integument* is composed of (*a*) a persistent outer epidermis with thick walls (fig. 19), (*b*) remnants of disorganized cells, and (*c*) a conspicuous suberized semi-permeable membrane (fig. 20), which belongs to the wall of the inner epidermis of the integument adjacent to the endosperm. During the development of the seed, most cells of the integument are disorganized.

(3) The *endosperm,* in most parts of the seed consists of a distinct layer two cells thick (fig. 19); at the root end the layer is often three or more cells thick (fig. 20). These cells are thick-walled, with here and there wall projections (fig. 21) into the cell lumen. The projections vary in length, sometimes mere pegs, whereas in other instances they extend from wall to wall, being of the nature of trabeculae. Endosperm cell walls are not lignified, and the lumina are filled with fatty and proteinaceous substances.

During the development of the akene, although there is progressive disorganization and dissolution of the inner part of the pericarp, as well as of the inner part of the integument, the pericarp and the integument are brought very close together by pressure from within, resulting from the enlargement of the embryo.

These morphological studies show that the three parts into which the coats of a mature akene may be separated are (*a*) the remains of the pericarp; (*b*) the outer epidermis of the integument with remnants of disorganized cells of the integument; and (*c*) the membrane from the inner epidermis of the integument together with the endosperm.

PHYSIOLOGICAL STUDIES

Seed Used.—The seed used in these experiments was in most cases the variety known as New York, for it is this which is grown almost exclusively for market in the principal lettuce areas of California. Other varieties were also used. Most of the seed was obtained from C. C. Morse and Company, San Francisco, and was produced by them either near Hollister or Sacramento, California. Seed produced on the University Farm was used in a few experiments, in which freshly harvested seed was needed. The commercially produced seed was used wherever possible, however, because it was graded better than hand-cleaned seed and therefore gave a higher percentage of germination.

Methods.—Experiments were carried out both in the laboratory and in the field. Petri dishes were used as germinating dishes in certain of the laboratory experiments. In each dish was placed a double layer of Canton flannel which was saturated with water and then allowed to drain by inverting the dish for a short time. This made the water content of the different germinators reasonably uniform. The seeds were sprinkled loosely on this moist cloth and the dishes were covered and held at the proper temperatures.

Other experiments were made in the laboratory using flats of garden soil. The flats of soil were placed in a large room, the temperature of which was kept constant within one degree centigrade. An electric fan was installed to keep the air circulating. The seeds were planted about one-fourth inch deep in rows of 100 seeds each. The soil was kept thoroughly moist. Most of these experiments were replicated ten times with controls planted in the same flat with the treated seeds.

Field experiments were conducted both at Davis and at Meloland, Imperial County. The seeds were planted on ridges, imitating commercial practices as closely as possibe.

Influence of Temperature upon Percentage of Germination.—Lettuce seed germinates very well over a considerable range of temperature, but the percentage germination falls off very abruptly at temperatures above 25° C as is shown in table 1.

TABLE 1

PER CENT GERMINATION OF LETTUCE SEED (NEW YORK) AT VARIOUS TEMPERATURES
(Seed 18 months old)

Germination temperature in degrees Centigrade	1°	4°	17°	20°	22°	25°	27°	28°	29°	30°
Per cent germination	99	99	98	98	99	98	76	20	2	0

Seed of the same variety which was only four months old showed a similar behavior but the reduction in germination occurred at a slightly lower temperature (table 2).

TABLE 2

PER CENT GERMINATION OF LETTUCE SEED (NEW YORK) AT VARIOUS TEMPERATURES
(Seed 4 months old)

Germination temperature in degrees Centigrade	1°	17°	20°	22°	25°	26°	29°	30°
Per cent germination	99	98	98	93	83	4	0	0

It is probable that the differences shown in tables 1 and 2 are correlated with the age of the seed. In this connection it should be stated that it is the practice of lettuce growers in sections where lettuce is sown under high temperature conditions to plant seed that is twelve months, or more, old, rather than that produced the current season. It should be mentioned here also, that in cases like those shown in tables 1 and 2, where seeds germinate satisfactorily at low temperatures, but not at high temperatures, the ungerminated seeds are in no way injured by the high temperature. They appear to be as fully imbibed with water as those which germinate. They have been known to remain in this condition for weeks without showing any decay and still germinate well as soon as the temperature is reduced. Data pertaining to this point will be given in another section of this paper.

It will be seen from tables 3 and 4 that varieties differ greatly in the degree of temperature which they can tolerate without any reduction in germination.

TABLE 3

GERMINATION OF DIFFERENT VARIETIES OF LETTUCE SEED ABOUT FOUR MONTHS AFTER HARVEST

(Seed from C. C. Morse and Co.)

Variety	Per cent germination		
	12° C	25° C	29° C
	per cent	*per cent*	*per cent*
All Year Round	99	95	36
All Year Round	97	96	84
Big Boston	97	54	0
Black Seeded Simpson	100	82	29
Deacon	98	67	35
Denver Market	97	58	26
Drumhead	99	96	89
Early Curled Simpson	96	21	0
Grand Rapids	98	95	85
Hanson	92	80	3
Hardy Green Winter	95	89	23
Hicks Hardy White Winter Cos	99	67	8
Hubbard's Market	98	59	0
Iceberg	99	97	92
Mammoth Black Seeded Butter	98	97	48
Mammoth Black Seeded Butter	92	88	31
May King	94	87	7
New York	99	91	1
Prize Head	99	81	1
Salamander	98	96	88
Tom Thumb	97	97	89
Paris White Cos	98	97	63

It will be noticed in table 3 that all varieties gave higher than 90 per cent germination at 12° C, showing that the seed was of high germinating capacity. At 25° C, however, the germination was reduced in twelve varieties to below 90 per cent, while at 29° C only one variety gave over 90 per cent germination. The amount of reduction caused by raising the temperature from 12° C to 29° C varied greatly with different varieties. Six varieties showed less than 15 per cent reduction, as seen from the table, while eight showed a reduction of over 85 per cent germination. New York falls in the group which is the most sensitive to high temperature.

TABLE 4

GERMINATION OF DIFFERENT VARIETIES OF LETTUCE SEED IMMEDIATELY AFTER HARVEST

(Seed grown on University Farm, Davis)

Variety	Per cent germination		
	8° C	12° C	22–25° C
	per cent	*per cent*	*per cent*
Big Boston	44	37	1
Black Seeded Simpson	66	62	22
Black Seeded Simpson	42	41	20
California Cream Butter	14	18	3
Chicken Lettuce	40	34	2
Denver Market	67	71	10
Early Curled Simpson	32	24	1
Grand Rapids	55	57	15
Hanson	28	35	3
Hubbard's Market	15	13	1
Iceberg	52	54	58
Iceberg	61	60	58
Malta	12	14	4
May King	94	95	0
New York	67	69	8
Paris White Cos	91	94	6
Prize Head	49	41	9
Unrivaled	39	46	2
Wayahead	45	51	4

Influence of Dry Storage at Different Temperatures upon Subsequent Germination.—In order to have seed available as quickly as possible after maturity, small quantities of seed from many varieties of lettuce were harvested and cleaned by hand. The percentage at germination was determined immediately for each variety. These results are shown in table 4. In this table it will be seen that there is no significant difference in germination of any of the varieties at 8° and 12° C, from which it would appear that 12° is sufficiently low for satisfactory germination. On the other hand almost every variety that showed any appreciable germination at these low temperatures showed a marked reduction at 22°–25° C, except Iceberg. This shows again the inhibiting influence of high temperature upon the germination of lettuce seed. The seed from each variety was then divided into three parts and placed in open wide-mouthed bottles for storage. Two of these lots were kept at 4° and 12° C, respectively, in constant temperature chambers while the third was kept in the laboratory at about 20° C. At frequent intervals during a storage period of 37 days, seed from each of these lots was germinated at 12° and

TABLE 5

PER CENT GERMINATION OF LETTUCE SEED AT DIFFERENT TEMPERATURES AFTER VARIOUS PERIODS OF STORAGE (DRY)
(Seed grown at University Farm, Davis)

Variety	Germinated at 12° C												
	Stored 0 days	Stored 7 days			Stored 13 days			Stored 20 days			Stored 37 days		
		4° C	12° C	Lab.	4° C	12° C	Lab.	4° C	12° C	Lab.	4° C	12° C	Lab.
	per cent	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*
Big Boston	37	7	26	47	43	28	35	45	24	45	41	31	40
Black Seeded Simpson	62	69	70	68	67	60	66	45	66	67	83	66	66
Black Seeded Simpson	41	36	39	52	51	38	45	45	43	47	42	42	54
California Cream Butter	18	28	8	24	27	25	12	23	20	25	25	29	8
Chicken Lettuce	34	37	47	41	37	50	38	31	44	37	36	45	32
Denver Market	71	74	71	68	70	63	74	67	75	75	70	73	60
Early Curled Simpson	24	16	19	18	23	19	33	28	23	27	22	20	37
Grand Rapids	57	58	63	61	58	61	59	49	59	68	45	56	58
Hanson	35	48	42	32	38	27	33	29	32	37	36	40	41
Hubbard's Market	13	23	30	25	19	26	16	18	25	12	18	24	16
Iceberg	54	50	48	73	58	50	57	51	51	58	49	45	66
Iceberg	60	55	63	71	62	58	82	62	52	72	61	50	65
Malta	14	18	37	7	22	14	5	14	17	7	13	21	16
May King	95	93	95	95	96	96	92	94	94	93	95	94	93
New York	69	45	56	67	58	53	63	62	55	64	57	50	70
Paris White Cos	94	95	95	92	92	93	89	93	91	92	95	93	93
Prize Head	41	45	40	47	45	44	53	39	35	58	44	42	47
Unrivaled	46	64	52	41	66	50	53	63	48	65	61	58	66
Wayahead	51	51	48	55	52	48	47	51	44	57	52	45	52

Variety	Germinated at 25° C												
	Stored 0 days	Stored 7 days			Stored 13 days			Stored 20 days			Stored 37 days		
		4° C	12° C	Lab.	4° C	12° C	Lab.	4° C	12° C	Lab.	4° C	12° C	Lab.
	per cent	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*
Big Boston	3	1	4	6	4	4	5	6	7	20	10	10	7
Black Seeded Simpson	37	37	36	52	26	51	48	39	61	65	54	52	68
Black Seeded Simpson	22	24	23	36	31	38	21	28	28	41	20	25	36
California Cream Butter	5	13	3	13	10	10	7	8	14	15	5	11	5
Chicken Lettuce	3	2	5	5	7	15	4	5	14	17	3	12	25
Denver Market	10	16	15	23	21	22	24	17	30	45	26	30	35
Early Curled Simpson	3	4	4	1	8	4	5	6	6	8	4	11	10
Grand Rapids	16	28	27	42	26	33	26	22	52	56	31	53	52
Hanson	10	7	11	10	10	8	8	10	17	32	11	18	24
Hubbard's Market	1	3	6	5	4	6	7	7	5	8	4	5	12
Iceberg	49	50	44	55	49	48	66	45	47	48	50	52	55
Iceberg	66	66	58	72	52	49	81	57	53	62	51	53	68
Malta	9	11	22	5	12	21	5	10	18	6	10	17	9
May King	2	1	2	3	7	4	7	1	5	19	5	4	8
New York	10	18	15	25	30	21	25	27	32	58	23	36	59
Paris White Cos	6	19	18	42	54	43	47	63	69	84	64	79	75
Prize Head	13	13	14	12	12	24	10	15	20	44	17	31	37
Unrivaled	3	8	8	7	14	15	7	7	24	42	2	19	45
Wayahead	5	10	8	17	12	16	15	13	27	39	11	27	28

25° C. In table 5 are given these germination results obtained on five successive dates. It will be noted that at a germination temperature of 12° C the results obtained at the end of 37 days are not significantly better than those immediately after harvest. At 25° C, however, where the germination immediately after harvest was considerably below that at 12° C, a gradual increase was found in many of the varieties during the period of storage at the temperatures employed.

In no case where seed is germinated at 12° C is there any evidence of improved germination resulting from storage at 4° or 12° C as compared with the storage at laboratory temperature, with the possible exception of Unrivaled and one lot of Black Seeded Simpson stored at 4° C. In other words, the improvement in the germination of the seed after a period of storage (dry) is due to the natural aging of the seed, rather than to the effect of temperature. The results would seem to indicate that dry storage of lettuce seed at low temperatures is no more effective in improving germination than dry storage at ordinary temperatures.

Effect upon Vitality, of Storage (Moist) at Temperatures Which Inhibit Germination.—Moist seeds which are exposed to temperatures of 30° C or slightly above do not germinate even though other conditions are suitable. The seeds are not injured, however, for when transferred to low temperatures, good germination may be secured. Lots of seed were kept under germinating conditions at 30° C from 1 to 13 days after which they were placed at 16°–18° C. The germination each day after they were placed at the lower temperature is recorded in table 6.

TABLE 6

PER CENT GERMINATION OF LETTUCE SEED AT 16–18° C AFTER VARIOUS PERIODS UNDER GERMINATION CONDITIONS AT 30° C

Days stored at 30° C	Per cent germination			
	1 day at 16–18° C	2 days at 16–18° C	3 days at 16–18° C	4 days at 16–18° C
0	....	99	....	....
1	97	....	....	....
2	76	92	99	....
3	62	95	99	....
4	5	76	95	....
6	0	30	88	100
7	0	26	67	98
10	0	68	91	99
13	0	3	64	98

It is to be noted that, although satisfactory germination takes place after the temperature is lowered, recovery is slower the longer the exposure to 30° C. Similar results are reported by Davis[1] who states that lettuce seeds which remained dormant on moist cotton for eight months at 27° to 30° C germinated almost completely in ten days when exposed to fluctuating laboratory temperatures. It appears from the results obtained by the writers that the failure of seeds to germinate at 30° C is not the result of temperatures too high for growth of the embryos, for naked embryos make normal growth at 30° C or at somewhat higher temperatures. At 40° C however, root growth is inhibited, although the hypocotyl and cotyledons make considerable growth even at this latter temperature.

Why Does Lettuce Seed Fail to Germinate at Temperatures which are Favorable to Seedling Growth?—Since 30° C is evidently not too high for growth of lettuce seedlings, experiments were made to determine the reason for the failure of seeds to germinate at this temperature. All the coverings were removed from a number of seeds after a few hours soaking and the naked embryos were placed at 30° C on moist germinators. In 24 hours, in almost every case, growth was apparent as shown in figure 23. When, however, the pericarp and the outer part of the seed coat only were removed leaving the embryo still enclosed by the endosperm and integumentary membrane, no germination occurred, indicating that one or both of these structures prevents germination at high temperatures. Seeds which have been at 30° C for as long as five days without germination will germinate in a few hours at this same temperature after the endosperm and integumentary membrane are removed.

It appears that the first stages in lettuce seed germination are initiated, or at least proceed most satisfactorily, only at low temperatures, providing there is adequate moisture and oxygen. If seed is exposed to the foregoing conditions for varying periods, even though there are no visible signs of germination except swelling of the seed, and then transferred to higher temperatures, germination proceeds normally. The situation just described may also be expressed in another way: at temperatures of approximately 28° C and above, the initial stages of germination are inhibited. As was shown above, the cause of this inhibition may be traced to the tissue which so closely invests the embryo. Absorption of water is not hindered. Davis[1] has shown that in from four to six hours, at temperatures from 20° C to 35° C, the seed absorbs sufficient water for germination. He gives evidence however that the integumentary membrane prohibits the free diffusion of oxygen inward. The oxygen requirements increase rapidly with an increase in temperature, such that an adequate supply fails to diffuse through the membrane at the higher temperatures. Davis[1] states that "when lettuce seed is maintained at a temperature too high to permit of germination, the seed coats gradually become less permeable to gasses as is indicated by a marked falling off in the respiratory intensity." Evidence is also given that this same membrane prevents the free diffusion of carbon dioxide outward. Davis[1] states that carbon dioxide is restricted in its diffusion to a less extent than oxygen. There is also the possibility, as suggested by Sifton,[3] in the case of spinach seed, that there are deleterious products of metabolism in the endosperm or embryo, arising, and possibly accumulating, only at the higher temperatures which inhibit the initial germination stages. The fact remains that the naked lettuce embryo germinates at high temperatures, whereas with the endosperm and integumentary membrane intact, it does not.

Further evidence indicating that the failure of seeds to germinate is caused by insufficient oxygen reaching the embryo, was obtained by germinating seeds in increased pressures of oxygen. The chambers used in the experiments consisted of cylindrical battery jars of 4½ liters capacity inverted in a shallow glass dish about 2 inches in depth. The chamber was large enough so that the respiration of 100 seeds would not greatly alter the composition of the atmosphere within.

The percentages of oxygen indicated in table 7 are the approximate amounts which were placed in the germinating chambers at the beginning of the experiment.

TABLE 7

PER CENT GERMINATION OF LETTUCE SEED AT 30° C IN ATMOSPHERES OF VARIOUS OXYGEN CONCENTRATIONS

Oxygen content of atmosphere (per cent in germinator)	20	29	37	46	50	60	72	80	90
Per cent germination	2	1	3	9	10	1	7	38	33

Figure 22 shows young seedlings (*a, b, c*) which grew at ordinary oxygen pressure and an optimum temperature, and also seedlings (*d, e, f*) which grew at a high oxygen pressure and 30° C. Under the latter conditions, cotyledonary growth is not retarded whereas radicle and hypocotyl growth is inhibited. The growth habit and structure of seedlings at 30° C and ordinary oxygen pressure are normal.

Germination at High Temperatures after Exposure of Moist Seed to Low Temperatures for Varying Lengths of Time.—It has already been mentioned that lettuce germinates well at low temperatures and that growth of seedlings is not retarded by a temperature of 30° C. Experiments were therefore conducted to determine how soon seeds could be transferred from germinating conditions at various low temperatures to 30° C without having the higher temperature cause a reduction in germination.

In table 8 are given some of the results of laboratory experiments using Petri dishes.

TABLE 8

FINAL PER CENT GERMINATION OF NEW YORK LETTUCE SEED AT 30° C AFTER EXPOSURE (MOIST) TO DIFFERENT TEMPERATURES FOR VARYING PERIODS

(Seed harvested the preceding season and germinated in Petri dishes)

Temp., degrees C. at which exposed	Hours exposed						
	0	7	12	16	24	48	72
1°	0	....	....	....	13	20	65
4°	0	....	....	....	....	93	97
16–18° C	0	30	72	71	87	....	....
16–18° C (freshly harvested seed)	0	1	15	48	74	....	....

At the time the above lots of seed were transferred to the germinator at 30° C there was no visible evidence of germination.

The following experiments were carried out using flats of soil in which to germinate the seeds. The germination temperature was 30° C. The treatment consisted of storage at 4° C, moist, for six days. After storage the seeds were dried sufficiently so that they would not stick together, then counted and planted. Ten lots of 100 treated seeds each and a similar number of untreated seeds, as checks, were used in each case (fig. 24). The results are shown in table 9.

TABLE 9

PER CENT GERMINATION IN SOIL FLATS AT 30° C AFTER SIX DAYS STORAGE (MOIST) AT 4° C

Source of seed	per cent germination	
	Treated	Untreated
New York (1927) University Farm, Davis	71	0.2
Prize Head (1926) C. C. Morse and Company	67	0.7
New York (1927) C. C. Morse and Company	67	0.6

Other experiments were carried out in a similar manner except that the seeds were allowed to dry out for longer periods of time after treatment. These also, with the controls, were replicated ten times (table 10).

TABLE 10

PER CENT GERMINATION IN SOIL FLATS AT 30° C AFTER SIX DAYS STORAGE (MOIST) AT 4° C, FOLLOWED BY VARYING PERIODS OF DRYING
(Variety, New York, 1927, C. C. Morse and Co.)

	Per cent germination			
	Dry 2 hours	Dry 2 days	Dry 6 days	Dry 14 days
Treated	67	57	39	32
Controls	0.6	0.7	0.4	0.5

In field tests at Davis twelve lots of 100 seeds each of 1-year-old Prizehead, untreated, and twelve lots which had been kept moist at 4° C for six days were planted in moist soil in ridges so that they could be irrigated. The results are as follows: The average per cent of germination of the twelve lots in warm soil after storage, moist, for six days at 4° C was 65 per cent; whereas, the average of a similar number of lots of untreated seed was 30 per cent. Soil temperatures at the level of the seeds reached 30° C between 9 and 10 o'clock and remained above that point until after 4 P.M. The maximum recorded for this period was 39° C. Seedlings from seeds stored moist at low temperature were appearing in abundance a day before those from the untreated seeds.

In the field tests conducted in the Imperial Valley (1927) near Meloland, seed of the New York variety, 1927 harvest, from C. C. Morse and Company was used. The treatment in each case was as follows: the seeds were placed between the folds of moist cheese cloth, and kept on ice for five days. The temperature range was from about 3° to 5° C. Before planting, the seeds were dried until they would not stick together. The plantings were made on ridges, following the methods employed by commercial growers. The ridges were moist when the seed was planted. The results are shown in table 11.

TABLE 11

PER CENT GERMINATION IN THE FIELD OF SEED STORED MOIST ON ICE FOR FIVE DAYS
(Planted October 10, 1927)

Treatment	Per cent germination			
	After 2 days	3 days	4 days	5 days
Control (untreated) (16 lots)	1	2	7	14
Treated, planted immediately (11 lots)	33	59	....	62
Treated, dry 2 hours (9 lots)	16	56	....	76
Treated, dry 24 hours (5 lots)	24	43	51	....

Reference has been made repeatedly to the storage of seed, *moist*, at low temperatures. These conditions provide for good aeration of the seed. The question arises in this connection whether or not the seed cannot just as well be immersed in water at low temperatures. Tests show that this treatment is followed by very poor germination. This is particularly true if large quantities of seed are employed, such that poor aeration is secured.

DISCUSSION AND SUMMARY

The requirements for the germination of lettuce seed are an adequate supply of moisture, a low temperature (below 25° C), and good aeration. Coats surrounding the embryo do not limit the intake of water. Seeds absorb sufficient water for germination in from four to six hours. High percentages of germination are secured over a wide temperature range, from 1° to 25° C. At temperatures between 25° and 30° C most varieties of lettuce fall off rapidly in percentage germination; at 30° C in most varieties, germination is almost entirely inhibited.

Different varieties of lettuce seed grown under similar conditions and of the same age vary, however, in their response to high temperatures. Some varieties attain fairly high percentage germination at 29° C; others have very low germination at this temperature.

Although there is a varietal difference in the response of lettuce seed to high germination temperatures, these differences disappear when the seed is germinated at low temperatures.

Generally speaking, freshly harvested lettuce seed is inferior in its germinating power to that several months old. With many varieties, the germination at ordinary temperatures improves noticeably in the first few weeks after harvest.

The storage of lettuce seed, dry, at low temperatures for periods of from 7 to 37 days did not improve its germination, as compared with seed stored at laboratory temperatures.

Lettuce seed may be kept at 30° C, either dry or moist, without altering its ability to germinate when placed at a lower temperature. Davis[1] reports that he "kept lettuce seed upon absorbent cotton continuously for a period of eight months at a temperature from 27° to 30° C without perceptible loss of seed."

Within the limits of the experiments here reported the longer the exposure of the seed (moist) at 30° C, the longer the time required for germination when placed at a lower temperature.

The failure of lettuce seed to germinate at temperatures of approximately 30° C and above is ascribed to the inhibiting influence exerted by a structure which closely invests the embryo. This structure includes the endosperm (two layers of cells) and a semi-permeable integumentary membrane. There is evidence that this structure retards gas exchange. The oxygen requirements at high temperatures are greater than at low. Increased oxygen pressure increases the germination percentage. There is also the possibility that there are products of metabolism arising and probably accumulating in the endosperm or embryo at high temperatures, and that these products inhibit initial germination stages.

If the early stages of germination are initiated at low temperatures, growth is uninterrupted by the transference of the seed to high temperatures.

If seed is to be planted in a soil which has a temperature during many hours of the day, of 30° C or above, a treatment as follows is recommended as a practical measure: Store *moist,* with *good aeration* at approximately 4° C for a period of four to six days. Soaking the seed in water at this temperature for any length of time is ineffective, because the seeds do not have sufficient aeration. Practically, this is accomplished by placing the seed between the folds of moist burlap and storing on ice.

Seed that has been treated as recommended above may be thoroughly dried at room temperature with no appreciable loss in viability. One lot of treated seed gave a germination of 32 per cent after fourteen days drying at room temperature, whereas the untreated check gave a germination of 0.5 per cent. These experiments suggest the probability that certain changes initiated at these low temperatures, when moisture and oxygen are adequate, are irreversible.

ACKNOWLEDGMENTS

The writers wish to thank Dr. H. A. Jones for the use of slides from which part of the morphological studies were made and Miss Mabel Wiesendanger who made a number of the drawings.

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1924. The germination of lettuce seed. Proc. 16th Annual Meeting, Assoc. Off. Seed Analysts of North America. 68–69.

[2] Jones, H. A.
1927. Pollination and life history studies of lettuce (Lactuca sativa L.). Hilgardia 2:425–479.

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1927. On the germination of the seed of Spinacia oleracea, L., at low temperatures. Ann. Bot. 41:557–568.

PLATE 1

Fig. 1. Diagrammatic cross-section of lettuce ovary two hours before anthesis.

Fig. 2. Cross-section of portion of lettuce ovary, two hours before anthesis.

Fig. 3. Diagrammatic cross-section of lettuce ovary, twenty-six hours after anthesis.

Fig. 4. Cross-section of ovary wall, and seed coats of lettuce, thirty-four hours after anthesis.

NOTE.—In the plates following three different magnifications were employed. Figs. 1 to 21 underwent the same reduction. Figs 1, 3, 5, 8 and 11 are × 47; Figs. 2, 4, 6, 7, 10, 12, 13, 14, 15, 16, 17, 19 and 20 are × 237; Figs 9 and 18 are × 245.

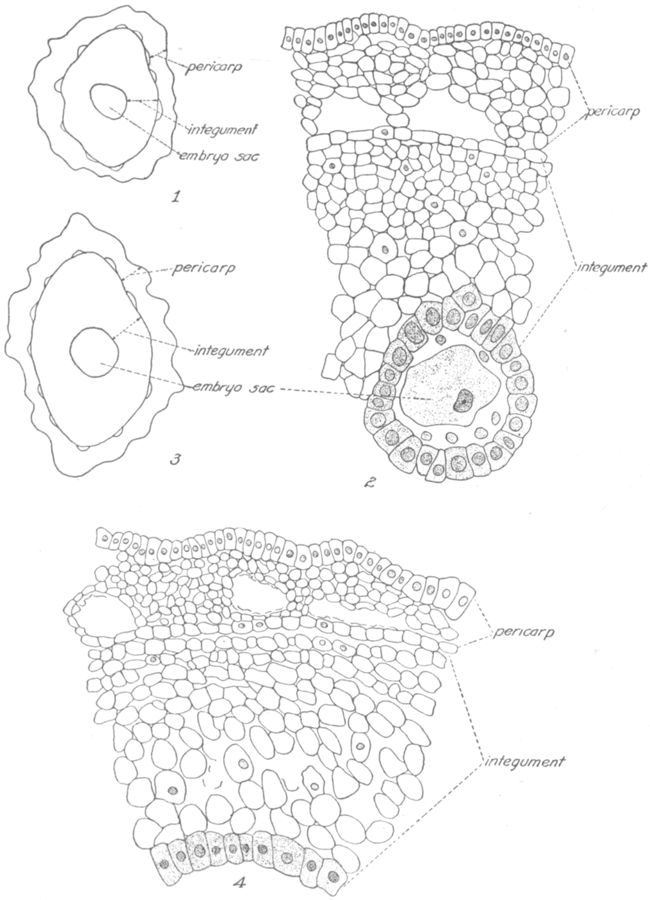
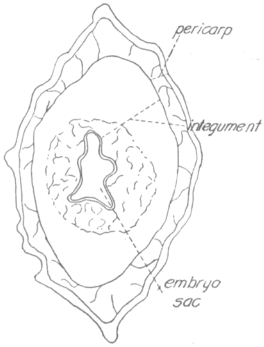

pericarp
integument
embryo sac
1
pericarp
integument
pericarp
integument
embryo sac
3
2
pericarp
integument
4

PLATE 2

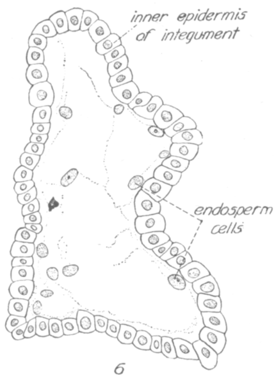
Fig. 5. Cross-section of lettuce ovary, three days after anthesis.

Fig. 6. Section of embryo sac.

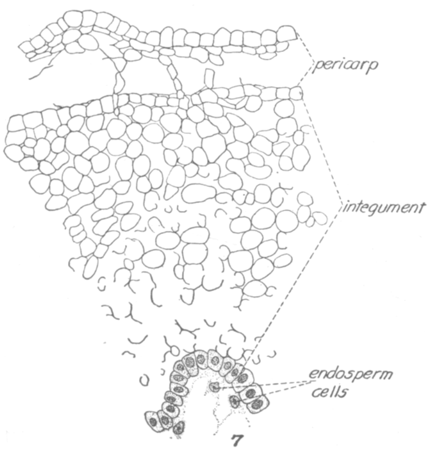
Fig. 7. Cross-section of a portion of lettuce ovary, three days after anthesis.


pericarp
integument
embryo sac

5


inner epidermis of integument
endosperm cells

6


pericarp
integument
endosperm cells

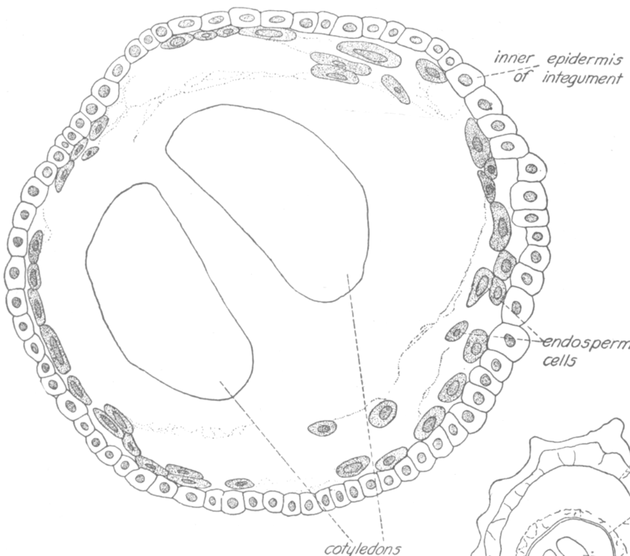
7

PLATE 3

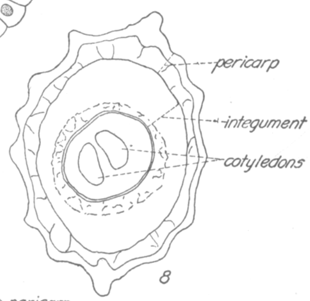
Fig. 8. Cross-section of lettuce ovary, four days after anthesis.

Fig. 9. Same as figure 8, showing details of a portion.

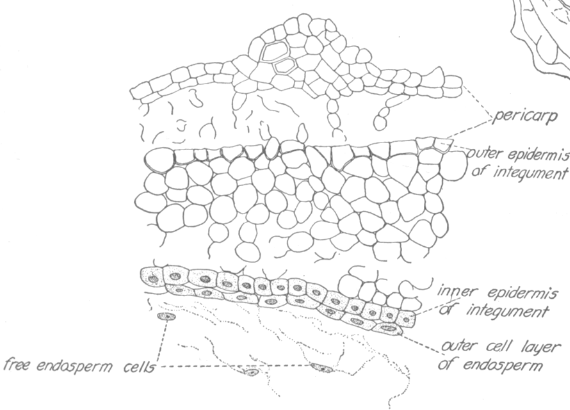
Fig. 10. Cross-section of lettuce ovary, five days after anthesis.


inner epidermis
of integument
endosperm
cells
cotyledons

9


pericarp
integument
cotyledons

8


pericarp
outer epidermis
of integument
inner epidermis
of integument
outer cell layer
of endosperm
free endosperm cells

10

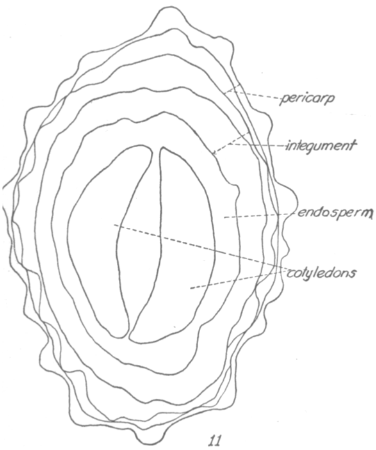
PLATE 4

Fig. 11. Cross-section of lettuce akene, seven days after anthesis.

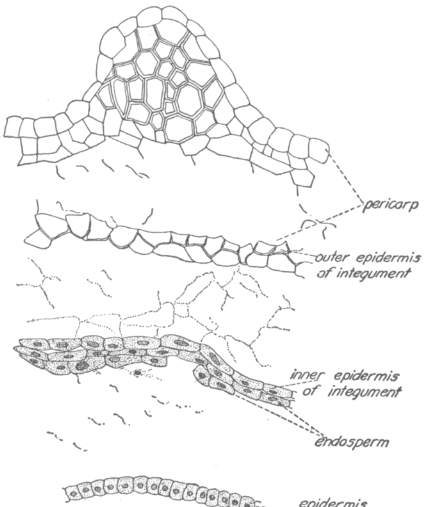
Fig. 12. Same, showing detail of structure through stem growing point.

Fig. 13. Same, through root tip.

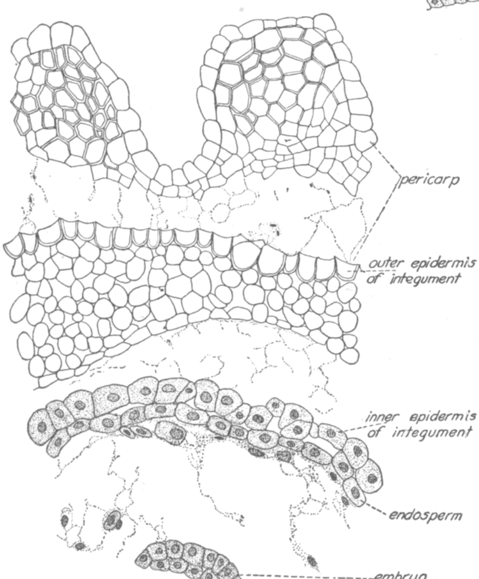
Fig. 14. Portion of endosperm, showing disintegrating epidermis of integument, and suberized membrane, eight days after anthesis. Section taken alongside of embryo.


pericarp
integument
endosperm
cotyledons

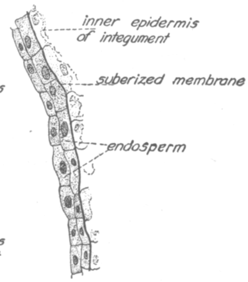
11


pericarp
outer epidermis of integument
inner epidermis of integument
endosperm
epidermis of embryo

12


pericarp
outer epidermis of integument
inner epidermis of integument
endosperm
embryo

13


inner epidermis of integument
suberized membrane
endosperm

14

PLATE 5

Fig. 15. Portion of endosperm and inner epidermis of integument, ten days after anthesis. Section taken near root tip.

Fig. 16. Same as preceding, showing further disintegration of walls.

Fig. 17. Cross-section of a portion of akene, ten days after anthesis, inner epidermis of integument has disappeared. Section taken near middle of seed.

Fig. 18. Lengthwise section of a portion of akene, ten days after anthesis.

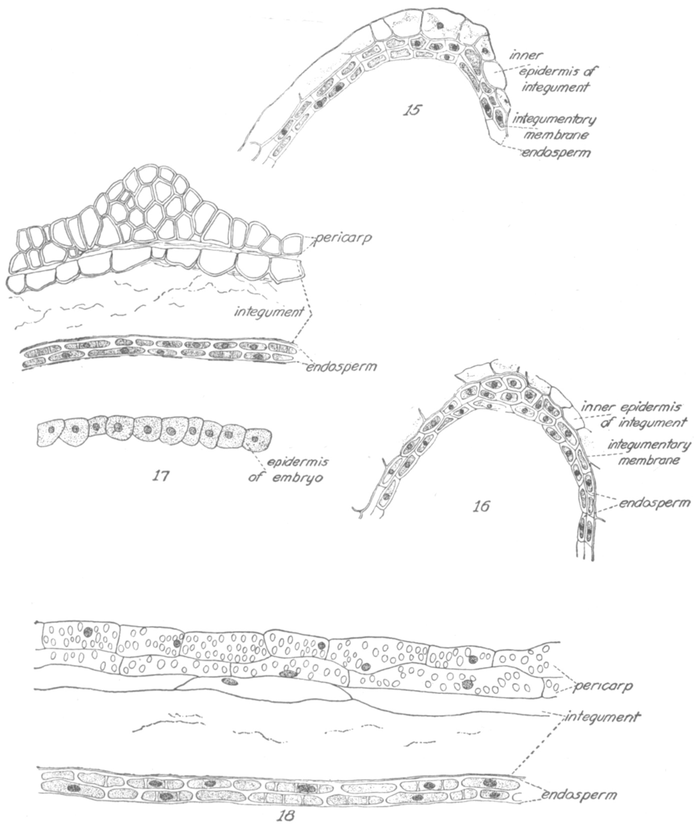
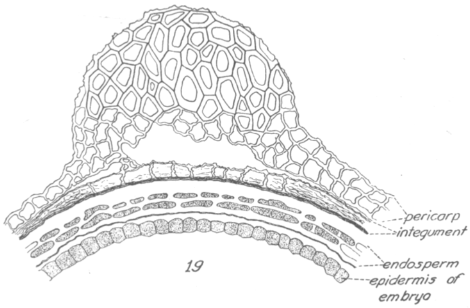

inner
epidermis of
integument
15
integumentary
membrane
endosperm
pericarp
integument
endosperm
17
epidermis
of embryo
inner epidermis
of integument
integumentary
membrane
endosperm
16
pericarp
integument
endosperm
18

PLATE 6

Fig. 19. Cross-section through the coats of mature lettuce akene.

Fig. 20. Cross-section of endosperm of mature lettuce akene, cut through the radicle of the embryo.

Fig. 21. Surface view of endosperm cells. The dotted lines indicate the walls of the lower layer of endosperm cells.


pericarp
integument
endosperm
epidermis of embryo

19


integumentary membrane
endosperm

20

21

PLATE 7

Fig. 22. Early stages in the germination of lettuce seed; *a, b,* and *c,* grown at ordinary oxygen pressure at 30° C, *d, e,* and *f,* grown under high oxygen pressure at 30° C. In the latter, note that radicle and hypocotyl growth is retarded, whereas cotyledonary growth is not retarded.

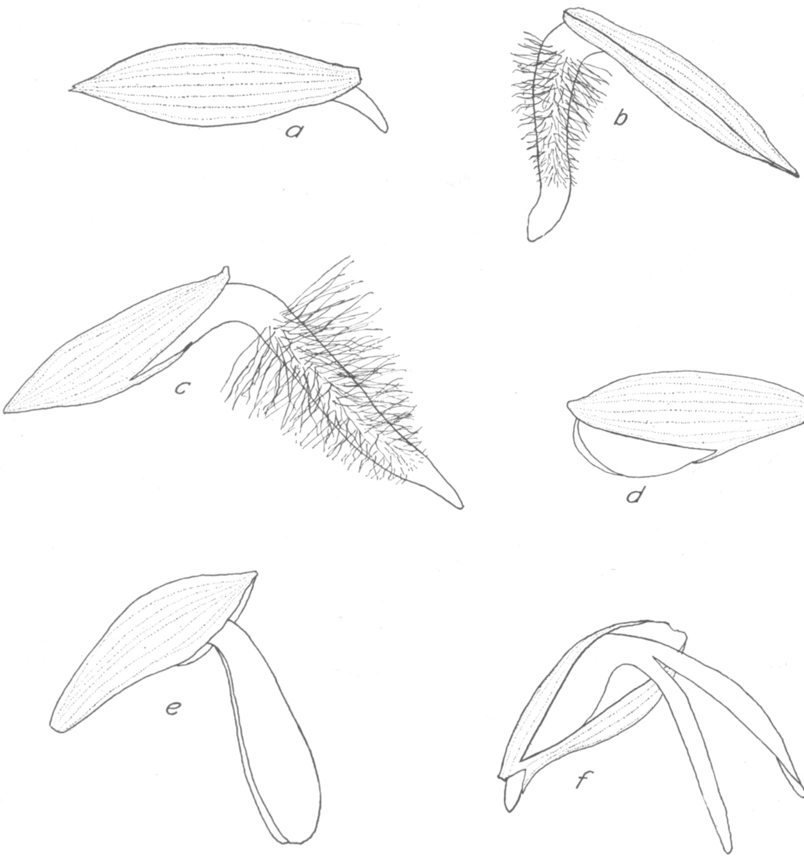

a
b
c
d
e
f

PLATE 8

Fig. 23. Akenes after 36 hours at 30° C, with ample moisture and oxygen. Upper row: endosperm intact, but pericarp and integuments removed; lower row: all coats, including endosperm, removed.

Fig. 24. Influence of the exposure of lettuce seed, moist, to low temperature, upon its subsequent germination at 29° C. Variety, Prize Head, about 1 year old. Left, seeds kept moist at 4° C for 6 days, between folds of cloth, and then planted in garden soil at 29° C; 674 seedlings from 1,000 seeds. Right, seeds kept dry at laboratory temperature and then planted in garden soil at 29° C; 7 seedlings from 1,000 seeds. Seeds planted Sept. 14; count and photograph taken Sept. 17.

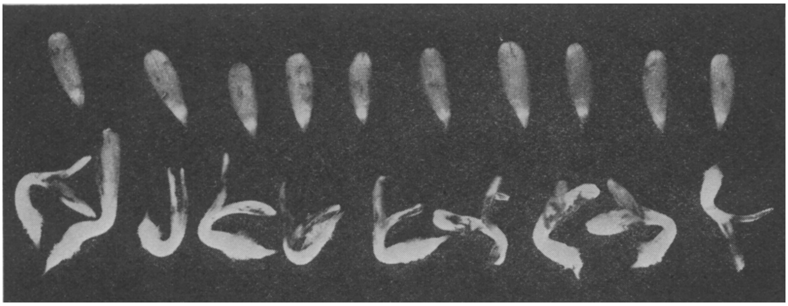


Fig. 23.

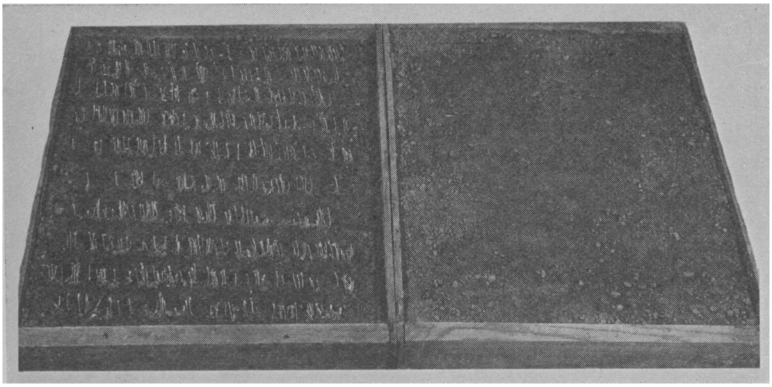


Fig. 24.

The titles of the Technical Papers of the California Agricultural Experiment Station, Nos. 1 to 20, which HILGARDIA replaces, and copies of which may be had on application to the Publication Secretary, Agricultural Experiment Station, Berkeley, are as follows:

1. The Removal of Sodium Carbonate from Soils, by Walter P. Kelley and Edward E. Thomas. January, 1923.
3. The Formation of Sodium Carbonate in Soils, by Arthur B. Cummins and Walter P. Kelley. March, 1923.
4. Effect of Sodium Chlorid and Calcium Chlorid upon the Growth and Composition of Young Orange Trees, by H. S. Reed and A. R. C. Haas. April, 1923.
5. Citrus Blast and Black Pit, by H. S. Fawcett, W. T. Horne, and A. F. Camp. May, 1923.
6. A Study of Deciduous Fruit Tree Rootstocks with Special Reference to Their Identification, by Myer J. Heppner. June, 1923.
7. A Study of the Darkening of Apple Tissue, by E. L. Overholser and W. V. Cruess. June, 1923.
8. Effect of Salts on the Intake of Inorganic Elements and on the Buffer System of the Plant, by D. R. Hoagland and J. C. Martin. July, 1923.
9. Experiments on the Reclamation of Alkali Soils by Leaching with Water and Gypsum, by P. L. Hibbard. August, 1923.
10. The Seasonal Variation of the Soil Moisture in a Walnut Grove in Relation to Hygroscopic Coefficient, by L. D. Batchelor and H. S. Reed. September, 1923.
11. Studies on the Effects of Sodium, Potassium, and Calcium on Young Orange Trees, by H. S. Reed and A. R. C. Haas. October, 1923.
12. The Effect of the Plant on the Reaction of the Culture Solution, by D. R. Hoagland. November, 1923.
13. Some Mutual Effects on Soil and Plant Induced by Added Solutes, by John S. Burd and J. C. Martin. December, 1923.
14. The Respiration of Potato Tubers in Relation to the Occurrence of Blackheart, by J. P. Bennett and E. T. Bartholomew. January, 1924.
15. Replaceable Bases in Soils, by Walter P. Kelley and S. Melvin Brown. February, 1924.
16. The Moisture Equivalent as Influenced by the Amount of Soil Used in its Determination, by F. J. Veihmeyer, O. W. Israelsen and J. P. Conrad. September, 1924.
17. Nutrient and Toxic Effects of Certain Ions on Citrus and Walnut Trees with Especial Reference to the Concentration and Ph of the Medium, by H. S. Reed and A. R. C. Haas. October, 1924.
18. Factors Influencing the Rate of Germination of Seed of Asparagus officinalis, by H. A. Borthwick. March, 1925.
19. The Relation of the Subcutaneous Administration of Living Bacterium abortum to the Immunity and Carrier Problem of Bovine Infectious Abortion, by George H. Hart and Jacob Traum. April, 1925.
20. A Study of the Conductive Tissues in Shoots of the Bartlett Pear and the Relationship of Food Movement to Dominance of the Apical Buds, by Frank E. Gardner. April, 1925.