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RELATIVE RESISTANCE OF TREE SEEDLINGS TO EXCESSIVE HEAT

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THE PROBLEM.

The studies of forest types and of the limiting factors in the distribution of the Rocky Mountain forest trees, which have been carried on at the Fremont Forest Experiment Station near Manitou, Colo., and elsewhere in the central Rocky Mountain region since 1910, indicate that excessive temperatures due to direct insolation may often be a deciding factor as between one species and another.

In nature, however, and under the usual experimental conditions, it is almost impossible to attain an intense heat or an injurious temperature without rapid and usually thorough drying of the surface soil. For this reason it has been very difficult to draw safe conclusions as to whether seedlings which succumb under direct insolation and extreme heating of the surface soil were in fact first injured by the temperature or by this dry condition.

With a moist condition, the first injury under intense heat may be to the leaves. But in direct sunlight the surface of the soil, unless it is very moist, reaches a higher temperature than the leaves of the seedlings. If, therefore, the high temperature is approached gradually with opportunity for soil drying and heating, the first injury may be to the stem of the seedling, which wilts at the ground line and causes the seedling to collapse. This constitutes a "borderline" case between heat injury and moisture shortage. More prolonged heating and drying will cause a general wilting, plainly due

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to the inability of the seedling to supply moisture equal to the transpiration. Of course, this loss of water may be accompanied by direct heat injury as well; but, in general, if the soil drying has advanced very far, the result should be thought of as due primarily to lack of water.

In the present study the effort has been made to devise tests which would show the ability of seedlings to withstand high temperatures, as distinguished from a lack of water in the stems or leaves. The general assumption has been that if the protoplasm is heated to a temperature of 140° F. or 60° C., direct injury, from which recovery is not probable, will ensue almost immediately. It seems improbable that the qualities of protoplasm differ appreciably in this respect as between the several species. On the other hand, the extent to which the cells of the plant remain below the air temperature, or fail to be heated by radiation penetrating to their interior, must vary considerably according to the absorptive nature of the cell walls and plastids, and the rate at which the heat is being dissipated by vaporization and transpiration. Information has been particularly sought to answer the questions: Are the seedlings of different species protected in different degrees by their varying transpiration rates? Is this the basis for their apparently different heat requirements, heat tolerances, and light tolerances?

LITERATURE AVAILABLE.

There is little information in the scientific literature on direct heat injury to plants growing under natural conditions. That excessive temperatures from direct insolation may be a deciding factor between one species and another was claimed by Bates in a recent article (*2*)[1], and is brought out again in his more elaborate discussion (*3*) of the physiological requirements of the Rocky Mountain trees and in his extensive data on climatic and soil conditions just published (*3A*). In the second citation it is clearly shown that the common belief that spruce requires more water than pine is not well founded, and is, in fact, definitely controverted by transpiration measurements. Engelmann spruce (*Picea engelmannii*), Douglas fir (*Pseudotsuga taxifolia*), lodgepole pine (*Pinus contorta*), and western yellow pine (*P. ponderosa*), require increasing amounts of water in the order named, either on a basis of the increments or the leaf-exposure area.[2]

The concept is therefore reached that since spruce transpires less water than pine it may be more sensitive to heat, primarily because the incident energy is not so largely utilized in the evaporation process. It is, however, admitted by Bates (*3*) that since spruce has long been accustomed to seek cool places, where alone its seedlings may survive, it has acquired the habit of slow, shallow rooting, because these cool places are rarely subjected to rapid drying or to extreme drying of the surface soil. Conversely, western yellow pine, since it needs much heat for its proper functioning and development, has become accustomed to soils which are directly exposed to

[1] The numbers in italics in parentheses refer to "Literature Cited" at the end of this bulletin.

[2] Reference to citation (*2*) will show that this arrangement depends on several conditions. The arrangement given is the first deduction from transpiration tests in 1917.

the sun and which are quickly and frequently dried out, at least in the superficial layer. The pine, therefore, has the quick, deep-rooting habit and the large seeds which make such rooting possible even before the cotyledons have unfolded. Piñon pine (*P. edulis*), which grows in even warmer situations than yellow pine, has this habit developed to a high degree, opening its cotyledons and shedding the seed coat with the greatest deliberation while a strong tap-root is being formed.

It is, therefore, easily seen that in investigating the present reactions of seedlings of the different species, not only the fundamental physiological requirements must be taken into account, but adaptations of form and habit which fit the trees for certain combinations of conditions commonly occurring in nature. Western yellow pine and Douglas fir, as shown by the large size of their seeds and the deep rooting of the seedlings, are clearly adapted to sites whose moisture supply changes rapidly, whatever their total requirements for moisture may be. Lodgepole pine and Engelmann spruce seedlings come from much smaller seed, and are about equally frail, shallow rooting, and unadapted to quick drying of the surface.

The fact that the few references on heat resistance that have been found are taken from observations in the more arid portions of the United States, seems to indicate the close dependence of excessive temperatures upon a dry condition of the atmosphere, and a consequent aridity of the soil surface. The problem, as understood in this discussion, arises from the great intensity and heating power of sunlight, due both to the aridity and high altitude of much of the Rocky Mountain region. In moister regions the problem is no doubt less serious.

The first specific evidence of direct heat injury to tree seedlings appears to have been noted by Hartley (*5*) and Bates (*1*) in 1909, in the conduct of planting experiments in the Nebraska sandhills, where the occurrence in a single day's observation of a soil surface temperature of about 60° C. led Bates to the belief that the losses in plantations on south exposures, where much higher temperatures doubtless occur at times, might be primarily due to this factor. This appeared especially probable in cases where the small trees had been partly or completely buried by moving sand; but it was also noted at this time that many trees, which had not been covered and did not die, had considerable enlargements of their stems at the ground line.

Hartley (*5*) in 1918 published his observations of heat injury noted at about the same time in Nebraska and elsewhere. He concluded that lesions which were common on the stems of very young seedlings in the nursery were undoubtedly due to excessive heating of the surface soil, while similar lesions on the stems of trees as much as 4 years old were probably due to the same factor. Experiments were conducted in the laboratory which showed that stem injury very similar to that noted in nursery beds could be produced by heat applied in several ways, but more readily above than below the surface of the soil.

Elsewhere it has been frequently noted in the handling of nursery stock that trees growing close together had normal stems, while those spaced widely enough to permit much sunlight to reach the ground showed lesions on the stems. Korstian and Fetherolf (*6*), for example, found that by inclining spruce seedlings slightly to the south when transplanting them the ground was sufficiently shaded by the foliage to practically eliminate the injury which they termed "stem-girdle."[3]

That the optimum temperature for assimiliation and other chemical activities within the plant may be considerably below the maximum temperatures experienced, has of course long been recognized. Cieslar (*4*), for example, discussing the experiments of Lubimenko to determine the effect of light and temperature upon assimilation of *Abies*, *Picea*, *Pinus*, *Larix*, *Taxus*, *Tilia*, *Robinia*, and *Betula*, states that "with medium light intensity, the assimilation rises to a temperature optimum, varying with species, then sinks (with higher temperatures), excepting with the larch, which continues to increase its assimiliation to the highest temperature used. Similar results were secured under the strongest light." Cieslar concluded that "a close relation between light and temperature influence exists and that the (shade) tolerant species behave differently from the intolerant. The former decrease in (assimilative) energy very rapidly after the maximum; the latter very little, or not at all. So it may be said that the foliage of intolerant species is less sensitive to heat than that of tolerant." The results of the experiments reported here substantiate this last statement.

MacDougal and Working (*8*), experimenting with *Opuntia* at the Desert Laboratory, found that "joints of this plant maintained a fair rate of enlargement at a temperature of 56.5° C., the air surrounding them being 58° C. (136° F.), and the growth of young joints of the same plant stopped and shrinkage ensued when the temperature rose to 144° F. in an air temperature of 146° F., but growth was resumed when their temperature fell below 122° F." Of special significance was the finding that "data from observations in which temperatures were taken from the air have but little value in any estimation of the working temperature of active protoplasm, by reason of the abnormal hydration and transpiration conditions introduced. These conditions as well as the proportions and state of the main colloidal components must determine the temperature effects." It is very likely that the transpiration conditions involved in the above study were considerably more severe than those involved in the present consideration of the central Rocky Mountain conifers. In a comparative study of species, however, we are not more concerned with absolute plant temperatures than with the recording of air temperatures and the different reactions to specific external conditions.

The usually close connection between heat injury and excessive transpiration is likewise illustrated in a discussion by Munns (*7*) of the effect of the Santa Ana wind on various eucalypts. This wind is a hot current which occurs in southern California in the vicinity of the mountains. While the effect of the wind on the foliage of eucalypts is described as a "burning," the conclusion is that this

[3] One of the factors that has no doubt retarded the study of possible injuries from excessive heat has been the lack of suitable thermometers for recording the plant temperatures closely enough to establish the connection between them and the injury. While the apparatus has not been used in the present study, some of the difficulties of temperature measurements have been solved by E. Shreve (9). The apparatus described consists of a comparatively simple and small thermocouple outfit, the sensitive junction of which may be pressed against the surface of a leaf, obtaining a quick response to its temperature and therefore not seriously interfering with the conditions which most directly influence that temperature.

was in the nature of a rapid drying, and that the various degrees of injury were controlled more by soil differences than by any other variable in the habitat or in the species. Trees on sandy soils of relatively small water-holding capacity were most injured, and those on loamy soils of relatively high capacity were best able to withstand the unusual demand for water at the leaves. Therefore, the conclusion seems justified that this instance does not give an illustration of heat injury, in the strict sense of the term, and it is difficult to conceive of any temperature recorded in naturally heated moving air being high enough to produce heat injury, at least so long as the foliage retained any moisture whose evaporation might have a cooling influence.

DESCRIPTION OF EXPERIMENTS.

PRELIMINARY TESTS.

The first actual experiments in heat resistance made by the present writers, in 1919, appear to have given what have been described above as "border-line" cases, involving drying injury quite as much as or more than direct heat injury. These tests have been described and reported by Bates (*3*) and, therefore, need be only briefly mentioned to give the reader a full understanding of the problem. Seedlings of the four Rocky Mountain species which have been mentioned, as well as the eastern white pine, were grown in a number of pans, which after germination had taken place were kept at different moisture contents, varying from 3 to 14 per cent. The pans were heated by sunlight in a greenhouse, where the air temperatures were sometimes raised by artificial heat. Maximum temperatures of about 130° F. were recorded by blackened thermometers resting on the surface of the soil. The pans were watered early each day so that, by the time the maximum temperature was attained, they had had considerable opportunity to dry. The most heavily watered pans were never in a dry condition, however, and the moistest soil did not permit any loss that could possibly be ascribed to heat injury. The losses increased quite definitely with decreasing moisture, so that the influence of this factor is evident. Most of the injury took the form of stem wilting, similar to that described by Hartley (*5*). Douglas fir and yellow pine showed the lowest percentages of injury, followed by white pine, Engelmann spruce, and lodgepole pine. The severe injury to lodgepole was ascribed in part to its slow germination, so that the seedlings were younger and more frail than those of other species when the first severe exposures were given. It seems quite certain that the poor showing of both the lodgepole and spruce seedlings was due to their frailty, small mass to resist drying, and relatively small root systems to supply moisture.

PLAN OF TESTS IN 1922.

The second series of experiments was planned to test the resistance to heat injury exclusively of the various species at the ages of 30, 45, 60, and 90 days. It was conducted in the greenhouse and laboratory at the Fremont Forest Experiment Station.

On June 30, 1922, enough seed[4] of lodgepole pine, Engelmann spruce, Douglas fir, and western yellow pine was sown in four of the seed-testing tills, to secure approximately 100 seedlings of each species in each till. The contents of one till were used for each periodic test. The soil was coarse and derived by sifting from the granitic soil of the region. In order to secure the best germination the tills were kept under the regular seed-testing conditions, which include a daily maximum temperature of about 85° F. at the soil surface. They were watered daily. Germination was prompt, all species starting in from 7 to 15 days, and all seeds but those of lodgepole pine germinated fully within about 30 days.

The first test was made July 30, when the seedlings were heated in the electric oven, the temperature of which is readily regulated and controlled by a thermostat. The atmosphere within was kept saturated by means of a pan of water placed over the heating coil, the object being to reduce the drying of the seedlings to the lowest possible point. The procedure was as follows:

For each subtest, five seedlings of each species, selected at random, were so placed between wet blotters that the root portion of each was protected and well supplied with water, while the aerial portion was exposed. The blotters were held together with clips, and the whole was placed in the oven in a horizontal position, with the leaves of the seedlings not in contact with any solid object. A maximum-registering thermometer was placed with its bulb in the same plane with the leaves of the seedlings. At the expiration of the allotted time, the packet was promptly removed from the oven, the thermometer was read, the time noted, and the blotters again moistened and placed so that the seedlings projected over the edge of a table. As the seedlings wilted, they were removed and the time at which wilting took place was noted. After the immediate observation each set was removed to the side, kept moist, and observations made for wilting at intervals of a few minutes for seven hours.

For the three later tests, made on August 15, September 2, and September 28 and 30, an entirely different plan was followed. The purpose was to produce a heating and drying effect similar to that produced by sunlight. A commercial electric heater was used as the source of heat. The heating coil, which uses about 550 amperes, is 2¾ inches long, and 1⅛ inches in diameter, and the reflector 8¾ inches in diameter.

For the second test the seedlings from one of the tills were transplanted about August 5, after being hardened by continuous exposure to the sun for several days. Ten deep 6-inch galvanized pots were prepared, each containing six seedlings of each species placed in rows. These pots were exposed to the sun five days prior to the time of the test and given water each day until the day before the test. The soil was decidedly moist at the time of testing.

One pot was used for each subtest. To attain various temperature effects, the electric coil was placed at distances varying from 1 to 2.5 feet from the center of the top of the pots at angles of 45° to 75° with the surface of the soil. Two thermometers were used, one with the

[4] The source and quality of the seed employed is a matter of record, and for present purposes need not be described.

bulb partly covered by the soil, the other suspended in the air with the bulb in the same plane as the "crowns" of the seedlings. Exposures were for five minutes or more, but in all cases so short as to cause little drying of the soil. In consequence, the thermometer exposed in the air and nearer to the heating coil than the soil thermometer always recorded the higher maximum temperature. Since the injury was almost wholly to the leaves of the seedlings, it is this temperature of the air thermometer, receiving the same direct radiation as the seedlings, which will be referred to. The temperatures were observed throughout the period of test, and the maxima, which ordinarily were obtained near the end of each test, were recorded. In the tables all temperatures noted are the maxima, in degrees Fahrenheit.

After each subtest the pot was watered and kept shaded for a half day or so to note any immediate results, after which it was transferred to the seed-testing table in the greenhouse, where it attained a daily maximum temperature of approximately 77° F. at a depth of 1 inch in the soil, or about 85° F. at a depth of one-fourth inch. Daily observations were made to note wilting.

The third test, made 64 days after sowing, employed four pots which had been used in the second test and had lost no seedlings in the exposures of that test. The seedlings were subjected to the direct radiation for periods of 6, 8, 10, and 12 minutes, at such distance from the coil as to produce in all cases maximum temperatures of about 150° F.

For the fourth and final test, 90 to 92 days after sowing, the same procedure was employed as for the second test; except that, instead of placing the seedlings in rows, the four species were scattered promiscuously, using as before six seedlings of each species in each pot. The pots were exposed several days before testing to make certain that the seedlings were well established, and the final tests used the electric coil in conjunction with solar heat. The period of time varied from 12 to 128 minutes, and the thermometer recorded air temperatures from 110.84° to 161.06° F.

After the completion of the fourth test on September 30, the pots were placed under observation until November 17, since the seedlings by this time had become hardened to the extent that many of them survived for several days. The immediate results in each test were noted for each species; such as, two killed, four badly cooked, one slightly injured. The judgment formed at this time as to the extent of injury, however, had no bearing on the final results. The seedlings were not removed from the pots until obviously dead, and none were removed until the second day. At the expiration of the periods of observation in each of the three tests, the seedlings were classified as dead; injured, will eventually die; injured, will recover; and uninjured.

RESULTS IN MOIST AIR 30 DAYS AFTER SOWING.

In test 1, the seedlings were subjected to hot-air temperatures in a saturated atmosphere, ranging from 101° F. for two minutes, which caused no loss, to 150.5° F. for four minutes, which caused the death of all seedlings. The results are shown in Table 1, where the subtests are arranged in the order of increasing temperatures.

TABLE 1.—*First test of heat resistance in moist, hot air, 30 days after sowing, July 30, 1922.*

[Five seedlings of each species used in each test.]

Subtest No.	Oven temperature.	Exposure time.	Number of seedlings wilting after exposure, classified by species and by elapsed time.[1]			
			Western yellow pine.	Lodgepole pine.	Douglas fir.	Engelmann spruce.
	°F.	*Min.*				
4 [2]	111.0	6	2-0-0-1-0-0-0	1-0-1-1-0-1-1	0-0-0-1-0-2-0	0-0-2-1-0-0-0
5	122.0	10	3-0-0-0-0-0-1	2-0-1-0-0-0-0	4-0-0-0-0-0-0	2-0-0-1-0-0-0
6	124.0	2	0-0-0-0-1-2-0	0-1-0-0-3-0-1	0-0-0-0-1-0-1	0-0-0-0-0-2-1
1	125.5	5	0-2-1-0-0-0-0	3-0-1-0-0-0-0	0-0-1-1-0-0-0	1-1-0-1-0-0-0
3	128.0	5	3-0-0-0-0-0-1	3-1-0-0-0-0-0	3-0-0-0-0-0-0	2-2-0-0-0-0-0
9	132.5	4	3-0-0-0-0-0-0	1-0-1-0-1-0-0	1-0-0-0-1-1-0	1-0-0-0-1-1-0
8	134.5	3	1-0-0-1-1-0-0	2-0-0-2-0-1-0	0-0-0-2-0-1-0	0-1-0-1-0-1-0
11	135.0	2	0-0-0-1-1-0-3	0-0-0-0-2-1-2	0-0-1-0-1-0-3	0-0-0-1-0-2-2
12	137.0	3	3-0-2-0-0-0-0	2-0-3-0-0-0-0	4-0-1-0-0-0-0	2-0-0-0-0-1-2
10	138.0	5	5-0-0-0-0-0-0	3-0-0-0-2-0-0	2-0-0-0-3-0-0	1-0-0-1-3-0-0
7	139.0	2	0-0-0-2-1-0-0	0-0-0-2-0-1-0	0-0-0-2-0-0-0	0-0-0-1-0-1-1
15	143.3	2.5	4-0-0-1-0-0-0	3-0-0-1-1-0-0	1-0-0-1-2-0-1	1-0-0-1-0-0-3
16	148.0	1	0-0-0-0-5-0-0	0-0-0-0-3-0-2	0-0-0-0-4-0-1	0-0-0-0-1-0-4
14	149.7	3	5-0-0-0-0-0-0	4-0-1-0-0-0-0	2-0-2-0-1-0-0	2-0-1-0-0-0-2
13	150.5	4	5-0-0-0-0-0-0	5-0-0-0-0-0-0	5-0-0-0-0-0-0	5-0-0-0-0-0-0
Total			34-2-3-6-9-2-5	29-2-8-6-12-4-6	22-0-5-7-13-4-6	17-4-3-8-5-8-15
Grand total			61	67	57	60
Per cent			76.2	83.8	71.2	75.0

[1] The seven divisions under each species correspond to minutes of elapsed time after removal from oven, in the following order: 0–4–10–20–60–180– over 180.
[2] Subtest No. 2 was made at 101°, with a 2-minute exposure, no seedlings wilting.

The reactions of all species were much alike; in fact, no species can be said to be decidedly more resistant than any of the others under conditions which tend to eliminate all transpiration, and therefore to put the species on a basis of equality. Lodgepole pine suffered most, losing 100 per cent by wilting at a temperature of 124° F. for 2 minutes; 40 per cent, however, survived 139° F. in a different subtest for the same period. In a third instance all species withstood 139° F. for 2 minutes, while in another group all lost 100 per cent when submitted to 135° F. for 2 minutes. The explanation of these variations is not readily discernible. It does not seem probable that the seedlings of all species should have been stronger in one instance than in another. The variations are more likely to have been due to differences in humidity, which near the critical temperature is probably the decisive factor. All trees were destroyed at 148° F. with a 1-minute exposure, and from study of Table 1 it seems that approximately 141° F. for a period of 1 minute may be considered critical for all species. A total of 80 seedlings of each species was used. The totals lost in all tests, which may be indicative of relative resistance, were as follows: Douglas fir, 57; Engelmann spruce, 60; western yellow pine, 61; and lodgepole pine, 67.

The pines exhibited the disastrous effect of too much heat by wilting more promptly than spruce or fir, but suffered no more severely after longer periods. The pines are more succulent at this early age, and their morphological structure is not so strong in relation to their size as that of spruce and fir. Sixty-nine per cent of the yellow pine, 66 per cent of the lodgepole, 56 per cent of the fir, and

50 per cent of the spruce wilted within the first 15 minutes. In practically all instances the injurious effect of high temperatures was shown first by the needle tips, which, because of their small masses, would naturally become heated more quickly.

It is believed that this test of the 30-day seedlings more nearly furnishes an expression of the effect of injurious temperatures upon the protoplasm itself than do the tests upon the older seedlings, because of the fact that transpiration was of minor consequence. In the saturated atmosphere maintained throughout, the pines could not take advantage of their power of transpiring more readily than the others and thereby keep down internal temperatures. The great difficulty in any tests of this nature lies in the inability to separate the transpiration factor from the heating factor which might more immediately cause the coagulation of the protoplasm. Therefore, by eliminating transpiration it was to be expected that all species would react alike to high temperatures, assuming all protoplasms to be subject to coagulation at the same temperatures. It should be noted, however, that while test 1 comes nearest to eliminating transpiration, it is conversely farthest from simulating actual field conditions.

RESULTS IN DRY AIR 46, 64, AND 90 TO 92 DAYS AFTER SOWING.

Since these three tests were performed in a similar manner, and the results obtained were much alike, they will be considered together. The results at the ages of 46, 64, and 90 to 92 days, respectively, are shown in Tables 2, 3, and 4. The subtests are arranged in each table in the order of maximum temperatures recorded.

TABLE 2.—*Second test of heat resistance. Exposure to radiation from electric coil 46 days after sowing, seedlings transplanted in sand.*

[Six seedlings of each species used in each test.]

Pot No.	Maximum temperature in air.	Maximum soil temperature.	Exposure.	Number of seedlings dead, mortally injured, slightly injured, and uninjured, by species.[1] Western yellow pine.	Lodgepole pine.	Douglas fir.	Engelmann spruce.
	° *F.*	° *F.*	*Min.*				
1	90.5	78.7	10	0-0-0-6	0-0-0-6	0-0-0-6	0-0-0-6
2	106.7	88.7	10	0-0-0-6	[2] 0-0-0-5	0-0-0-6	0-0-0-6
3	116.6	98.2	14	0-0-0-6	0-0-0-6	1-0-1-4	0-0-0-6
4	137.8	112.3	13	0-0-0-6	0-0-0-6	[3] 0-0-0-6	0-0-0-6
5	154.8	118.3	10	1-0-0-5	0-0-0-6	[3] 5-1-0-0	[3] 1-1-1-3
10	165.2	134.2	10	[4] 3-0-2-1	2-0-1-3	[5] 6-0-0-0	[5] 6-0-0-0
9	172.4	121.2	8	[6] 2-1-2-1	[6] 2-0-1-3	[5] 6-0-0-0	[6] 4-0-2-0
6	176.4	117.6	5	0-0-1-5	1-0-0-5	[3] 6-0-0-0	[3] 6-0-0-0
7	176.4	118.3	6	3-0-1-2	0-0-0-6	[3] 6-0-0-0	[3] 6-0-0-0
8	181.8	122.4	7	[6] 2-1-1-2	[6] 1-0-0-5	[5] 6-0-0-0	[5] 5-0-1-0
Average	147.9	111.0	9.3				
Total				11-2-7-40	6-0-2-51	36-1-1-22	28-1-4-27
Grand total				81-4-14-140			

[1] The four divisions under each species refer, respectively, to the following degrees of injury: Dead seedlings; injured seedlings that will die; injured seedlings that will live; uninjured seedlings.
[2] Only five lodgepoles transplanted into this pot.
[3] All seedlings in pot slightly cooked.
[4] Three of the seedlings cooked during exposure.
[5] All seedlings cooked.
[6] One seedling cooked.

Reactions in these tests were dissimilar to those in the first, because a dry atmosphere introduced the factor of transpiration. In all cases the soil was moist enough so that wilting could not be ascribed to lack of soil moisture. There was no constant relation between air and soil temperatures, the ratio of soil to air temperature increasing with the period of exposure. For the critical air temperatures above approximately 140° F., the soil temperatures were from 15° to 50° less. In only one instance did the soil temperature exceed 140°; 144.8° was secured with an exposure of 30 minutes, which produced an air temperature of 161° F. Under ordinary field conditions, where the soil is not commonly so moist as under these experimental conditions, a higher temperature is likely to be recorded by a thermometer at the surface of the ground than in the air above the ground; and the seedlings are subject to wilting, not only in the leaves but also in the stem where it comes in contact with the surface of the ground.

TABLE 3.—*Third test of heat resistance: Exposure of seedlings that survived second test to radiation from electric coil 64 days after sowing.*

[Six seedlings of each species used in each pot.]

Pot No.	Maximum temperature in air.	Maximum soil temperature.	Exposure.	Number of seedlings dead, mortally injured, slightly injured, and uninjured, by species.[1]			
				Western yellow pine.	Lodgepole pine.	Douglas fir.	Engelmann spruce.
	° *F.*	° *F.*	*Min.*				
1	147.2	102.0	6	0-2-3-1	0-0-0-6	A (6) 4-2-0-0	A (6) 1-0-3-2
2	150.8	110.0	8	B (1) 1-0-2-3	[2] 0-0-0-5	B (6) 3-2-1-0	2-0-1-3
3	152.6	107.0	10	B (2) 1-1-3-1	0-1-1-4	B (5) 3-2-1-0	B (4) 2-0-2-2
4	150.8	106.3	12	B (3) 3-0-2-1	B (1) 0-1-2-3	B (6) [3] 4-0-0-1	1-1-0-4
Average	150.4	106.3	9				
Total				5-3-10-6	0-2-3-18	14-6-2-1	6-1-6-11
Grand total				25-12-21-36			

[1] Capital letters indicate immediate condition of seedlings following exposure; figures in parentheses indicate seedlings so affected, as follows: A=slightly cooked; B=seriously cooked. The four numbers under each species indicate the final condition, in the following order: Dead seedlings; injured seedlings that will die; injured seedlings that will live; uninjured seedlings.
[2] Only five lodgepoles transplanted in this pot.
[3] Of five firs in pot 4, the one escaping injury was very short stemmed.

Throughout the tests at high temperatures, the fir was most visibly affected. The needles appeared to be both shriveled and blistered, for which superficial effect the word "cooked" has been used. The spruce was affected in a similar manner, but less markedly. The pines apparently took care of themselves by excessive transpiration up to the limit of their ability to supply water to the leaves. In view of the fact that the yellow pine seedlings were considerably taller than the others, and thus more exposed, they resisted well. When the danger point was reached their needle tips shriveled first. Lodgepole may have received some protection from the taller seedlings; but its general high resistance in all the tests discounts this factor, especially since the spruce seedlings of approximately the same height suffered much more severely.

TABLE 4.—*Fourth test of heat resistance: Exposure to radiation from electric coil 90 to 92 days after sowing, seedlings potted in sand.*

[Six seedlings used in each pot, except where noted.]

Pot No.	Maximum temperature in air.	Maximum soil temperature.	Exposure.	Number of seedlings dead, mortally injured, slightly injured, and uninjured, by species.[1] Western yellow pine.	Lodgepole pine.	Douglas fir.	Engelmann spruce.
	° *F.*	° *F.*	*Min.*				
5	110.8	107.0	128	0-0-0-6	0-0-0-6	0-0-0-6	0-0-0-6
10	111.4	102.0	78	0-0-0-6	0-0-0-6	0-0-0-6	0-0-0-6
2	111.4	105.5	30	0-0-0-6	0-0-0-6	0-0-2-4	0-0-0-6
9	115.7	105.5	87	0-0-0-6	0-0-0-6	0-0-0-6	0-0-0-6
1	118.0	112.1	30	0-0-0-6	0-0-0-6	0-0-1-5	0-0-0-6
3	133.3	119.5	30	0-0-0-6	0-0-0-6	0-0-2-4	0-0-0-6
9 [2]	135.0	130.2	35	A 0-0-3-3	C (1) 1-0-0-5	E (2) 1-0-3-2	F (1) 2-0-1-3
10 [2]	142.7	119.0	15	0-0-1-5	0-0-1-5	0-0-5-1	1-0-1-4
5 [2]	142.6	141.8	50	F(2) C(2) 3-0-2-1	B (1) 3-0-0-3	F(2) C(2) 3-1-2-0	B (1) 2-1-1-2
8	146.8	123.0	12	[3] 0-0-2-2	[3] 0-0-0-2	E (4) [3] 2-0-2-1	E (1) [3] 0-0-0-3
7	152.2	121.5	15	A 1-1-2-2	0-0-2-4	E(2) C(3) 3-1-1-1	B (1) 2-2-0-2
4	154.4	126.8	12	A 0-1-4-1	0-0-1-5	E (4) 2-2-2-0	B (2) 2-0-3-1
6	161.1	144.8	30	E (5) 4-0-1-1	D (1) 3-0-1-2	E(5) [4] C(1) 6-0-0-0	C (2) 2-3-0-1
Average	133.5	119.9	42.5				
Total				8-2-15-51	7-0-5-62	17-4-20-36	11-6-6-52
Grand total				43-12-46-201			
Average [5]	149.0	122.6	13.5				
Total [5]				1-2-9-10	0-0-4-16	7-3-10-3	5-2-4-10
Grand total[5]				13-7-27-39			

[1] Capital letters indicate immediate condition of seedlings following exposure; figures in parenthesis indicate number of seedlings so affected, as follows:
A=Young needles cooked; B=Slightly injured; C=Seriously injured; D=Badly burned; E=Cooked; F=Killed.
The four numbers under each species indicate the final condition, in the following order: Dead seedlings; injured seedlings that will die; injured seedlings that will live; uninjured seedlings.
[2] Second exposures given these pots, after two days' observation showed no apparent injury from first exposure.
[3] Owing to mishap after the exposure, only 4 yellow pine, 2 lodgepoles, 5 firs, and 3 spruce were left in pot 8 for final observation.
[4] This injured seedling plainly was protected by the leaves of a taller seedling, but died eventually.
[5] These averages and totals are for pots 10, 8, 7, and 4 apart, whose period of exposure makes possible a comparison with earlier tests.

Of 156 lodgepole seedlings used in the three tests, 15, or 10 per cent, died or were injured so severely that death was only a matter of time; 31, or 19 per cent, of the 160 western yellow-pine seedlings; 53, or 33 per cent, of the Engelmann spruce seedlings; and 78, or 49 per cent, of the Douglas fir suffered likewise.

The point clearly brought out by these tests was the great resistance of lodgepole pine, which surpassed even yellow pine. Although it is a well-known fact that lodgepole reproduction is most easily secured and thrives best on open burned areas, where extremes of temperature are likely to occur, its natural range at high elevations greatly reduces the probability of its having to resist temperatures as high as those experienced by yellow pine, and its total heat requirements are apparently less. Its preference for bare mineral soils as a germinating bed is an expression of its need to secure readily available soil moisture. In the light of results given here, a failure of lodgepole seedlings under excessive temperatures must be construed as being due to relatively short root length and corresponding inability to secure necessary moisture.

Douglas-fir seedlings suffered most severely under the high temperatures, considerably more so than the spruce seedlings of frailer structure, and far more than the yellow pines. This reaction corresponds to some extent with common occurrences noted in the open. Douglas-fir seedlings require, to a decided degree, some form of protection during the first two or three years of their existence, or until safely established. It has been observed where the two species occur together and the soil is reasonably moist that spruce seedlings are more often found without protection than those of fir.

Very few fir seedlings recovered when visibly injured. It appeared on even casual observation that lodgepole and spruce seedlings recovered from slight injury much more rapidly than the fir. Western yellow pine was intermediate in this respect. Where no visible "cooking" was observed immediately, but later observation showed that the seedling was injured, a portion of the stem or the bases of the needles, rather than the tips, were likely to be affected; and where such injury existed, the seedling usually succumbed.

INFLUENCE OF AGE OF SEEDLINGS.

A portion of the data in Table 4 is summarized in the last three lines so that the results of this test may be compared in part with the earlier tests on a basis of similar time and temperatures. Thirty-five and six-tenths per cent of the seedlings were killed or severely injured at 46 days of age, 39.4 per cent at 64 days of age, and 23.3 per cent at 92 days of age. The mean temperatures recorded in the subtests, which are thus compared, were 147.9° F. for 9.3 minutes, 150.4° F. for 9 minutes, and 149° F. for 13.5 minutes. The higher loss in the second period is fully accounted for by the 2.5° additional temperature; and there may, of course, have been variations in atmospheric conditions or in the arrangement of the apparatus which made the recorded temperature more effective at one time than at another. However, the average result for the third period shows clearly that the seedlings become more resistant with age. This seems to be true of all the species considered, but is possibly true in a slightly greater degree for the spruce and lodgepole seedlings, which at the outset are extremely small and frail.

TEMPERATURE SCALE FOR EACH SPECIES.

It is evident that some individual seedlings offer much greater resistance to heat injury than do others of the same species, age, and general origin. Such variations are to be expected with all organisms. Owing to the comparatively small number of seedlings tested for each age, period, and temperature, these variations make it very difficult to determine with any precision either the effects of different periods of exposure under the same temperature conditions or of different temperatures for similar exposures.

Regarding the effects of different periods of exposure, as many comparable data as are available have been examined, and it is found that beyond a period of five or six minutes, which was the shortest employed in the radiation tests, there is not so much additional injury with added time as might be expected. This confirms the idea, which has been previously emphasized, that in nature it is probably the momentary maximum temperature which determines the degree of injury. It is also in agreement with results obtained in 1919, which showed that seedlings surviving one severe exposure were in no danger from a repetition of the same thing. However, it is entirely conceivable that transpiration which affords protection may temporarily attain a rate which can not be maintained indefinitely, and that the protection will therefore break down.

To arrive at an approximate measure of the effects of different temperatures, it has been necessary to counteract the large number of variable factors by averaging the results in three temperature groups without regard to the time factor. The temperature groups cover respectively all the tests below 140° F. which caused any injury, those between 140 and 160° F., and those above 160° F. In order to obtain for each test a summation of all the degrees of injury, the classes of injury shown in Tables 2, 3, and 4 have been rated as follows: One seedling killed, $16\frac{2}{3}$ per cent injury; one seedling injured, will die, $12\frac{1}{2}$ per cent injury; one seedling injured, will live, $4\frac{1}{6}$ per cent injury. This rating is based on six seedlings in a group, and is increased proportionately for smaller numbers, so that the possible sum for a group is 100 per cent.

By averaging the temperature and degrees of injury for all of the tests in each temperature group, three ratings have been established for each species. The lower temperature groups show greater average age of seedlings, but also longer exposures; and it is believed that these two factors will be just about compensating, so that the effects of different temperatures are brought out well enough for comparative purposes.

The curves drawn through the three points for each species are shown in Figure 1. The marked differences between the four species are clearly brought out. While too much significance should not be attached to the shapes of the several curves, it is apparent that Douglas fir is much more sensitive than the other species at comparatively low temperatures. At about 150° F. the spruce shows a more marked sensitivity. The shapes of their curves suggest that the pines might resist a very high temperature before all individuals would be killed; but there is every reason to believe that at a slightly higher temperature than any recorded in these tests, first the yellow pine, and soon thereafter the lodgepole, would show complete breakdowns.

CONCLUSIONS.

In considering the general application of these experiments with possible forms of heat injury to seedlings of the four most important trees of the central Rocky Mountains, the following observations are of value:

1. Under laboratory conditions approaching natural field conditions, the wilting of seedlings of all species was mainly in the nature of a collapse of the stem at the ground line. In this particular, the small, frail, shallow-rooted seedlings of Engelmann spruce and lodgepole pine were much more susceptible to injury than the larger, deeper-rooted and firmer-stemmed seedlings of western yellow pine and Douglas fir.

2. Seedlings removed from the soil at the age of about 30 days, and subjected to heating in air practically saturated with water vapor, showed considerable injury after a 6-minute exposure at 111° F., and increasing injury with higher temperatures, so that it may be estimated that an exposure of one minute at approximately 141° F. would cause critical injury to all seedlings of the four species. The injury at the higher temperatures took the form of almost immediate drooping or wilting of the entire aerial portion, and little

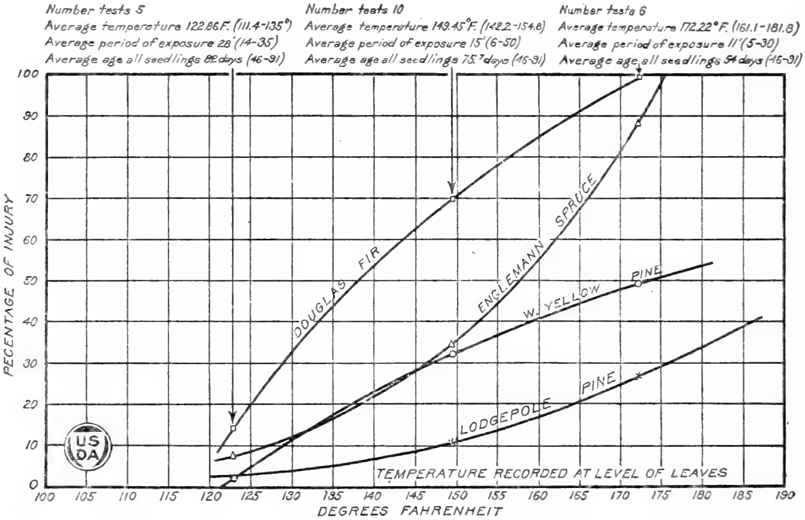

FIG. 1.—Average extent of injury at various temperatures under direct radiation.

or no difference between the species was brought out. It thus appears that conditions designed to heat the entire plant to a temperature of about 140° F., without time or opportunity for appreciable water loss from the leaves, are immediately fatal.

3. Direct radiation from an electric heating coil with reflector supplying greater heating power and less luminous intensity than sunlight, applied to the seedlings at the ages of 46, 64, 90, and 92 days, served to create a condition of internal heating of the leaves similar to that produced by sunlight, but in greater degree and acting more promptly, so that the factors of water loss and water supply would not materially affect the results. The greater sensitiveness of Douglas fir under these conditions, followed closely by spruce seedlings, at least at the higher temperatures, was very apparent. The seedlings of lodgepole pine showed the least injury at all temperatures.

While some injury was noted when the recorded temperatures were as low as 120° to 130° F., this was only after long exposures, and the fact that many seedlings lived through exposures of 170° to 180° F. for from 6 to 8 minutes shows clearly, by comparison with the results in moist air, that under ordinary atmospheric conditions the internal temperatures of the leaves must be markedly kept down by evaporation, as has been suggested by Bates (*2*, *3*), in considering the relation of transpiration rates to heat requirements. Since the order of susceptibility of the species closely approximates that assumed by Bates, it becomes fairly certain that a free rate of transpiration, as compared with a more restricted rate, offers a measure of protection from the direct effects of very intense insolation.

Under natural conditions, on exposed southerly slopes in the central Rocky Mountains, maximum temperatures at the surface of the soil as high as 154° F. have been recorded, and this as late in the season as September 21. Temperatures as high as 160° F. may not be uncommon. In contrast, the maximum temperatures at the soil surface on north exposures are little higher than the maximum air temperatures, or from 100° to 110° F. From the mere fact of the occurrence of temperatures as high as 150° F., it is evident that extreme heat, though of short duration and rare occurrence, may be an important factor in preventing reproduction generally and in drawing a line between the natural habitats of the different species. Where soil drying accompanies high temperatures, as it almost invariably does in nature, temperatures of only 130° F. may do considerable injury. With a moist soil there is some injury to the leaves of all species at 130° F., but many individuals will escape injury until the temperature reaches 150° F. or more.

While lodgepole pine seedlings show great sensitivity at an early age, their superior protection against direct heat injury to the needles counterbalances in part any weakness which they may show in rooting, etc., if drying of the surface soil is involved. This is not sufficient, however, to permit this species to occupy so warm and dry a zone as that chosen by yellow pine. Spruce is quite sensitive from either standpoint. Yellow pine is most capable of supplying itself with water and is fairly immune to heat injury. Douglas fir is well equipped to obtain its water, but its leaves are most easily superheated.

As between yellow pine and Douglas fir, whose habitats merge in the central Rocky Mountain region, the ability of the latter to replace the former depends almost entirely upon the critical temperature conditions which the germinating seedlings must withstand at the surface of the soil. It is known that Douglas fir and yellow pine seedlings have almost equal root vigor, and the distinction between the two is clearly due to greater tolerance of heat on the part of yellow pine. On south slopes, where the surface soil temperatures during the dry periods of September and October often reach a maximum of 140° to 150° F., any survival of fir must be confined to spots which are shaded at least a part of the day.

The relatively great ability of lodgepole pine as compared with spruce to withstand high temperatures is undoubtedly the deciding factor in their relations on open, denuded areas. Lodgepole pine reproduces splendidly on intensely heated sites within its range, provided only that its moisture needs are guaranteed by a lack of competing vegetation and reasonable rainfall. However, spruce seedlings often come in under stands of pine, where pine seedlings will not grow at all, and thus ultimately supplant the pine.

4. The resistance of all seedlings becomes slightly greater with aging and accompanying hardening of tissues and with increase in the number of needles, some of which no doubt protect others. Older trees are also much less liable to heat injury than young seedlings, because of the stem protection furnished by bark and the greater distance of the foliage from the ground surface.

5. While in nature high temperatures are seldom entirely dissociated from a more or less arid condition, it is evident that extreme heat must often kill seedlings which would be able to cope with the existing drought conditions. The scale of heat tolerance for the four species suggested in conclusion 3 (lodgepole pine, yellow pine, spruce, and Douglas fir) is the same as the inverted scale of resistance to transpiration, given on page 127 of Bates' (*3*) discussion, as an average for two sets of results obtained under slightly different conditions. The relative heat tolerance of the species is somewhat at variance with their relative heat requirements for optimum growth as this may be judged from the prevailing temperatures of their habitats. All of these factors, as well as light requirements, are important for the forester to have in mind.

The observations presented above bring out the fact that under certain conditions, perhaps seldom occurring in nature, maximum temperatures may be the critical factor preventing natural reproduction. Where this is the case, planting may be necessary or the establishment of a given species may not be possible until the heating action of direct sunlight on the site has been somewhat modified.

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