



Forest Research Branch

**SPRUCE SEEDLING MORTALITY
CAUSED BY ADVERSE SUMMER MICROCLIMATE
IN THE ROCKY MOUNTAINS**

by
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Spruce Seedling Mortality Caused by Adverse Summer Microclimate in the Rocky Mountains¹

by

R. J. Day²

INTRODUCTION

Study of the effects of soil surface heating and drying on the survival of hybrid spruce¹ regeneration in the East Slopes Section of the Subalpine Forest Region (Rowe 1959) was stimulated by two earlier regeneration studies undertaken in the Crowsnest Forest.

The initial study in 1958 was to determine the status of regeneration on apparently poorly stocked logged-over land, and to investigate some of the ecological factors which could limit or prevent the satisfactory regeneration of the three native species³: hybrid spruce, alpine fir, and lodgepole pine (Day and Duffy 1963). The results showed that the mean stocking to hybrid spruce, alpine fir and lodgepole pine was 21, 36, and 6 per cent respectively; and that though the mean stocking for the three species in combination was 46 per cent, more than half of the area sampled was less than 40 per cent stocked. Spruce and fir seedlings were better stocked on the cool north and east slopes and in the moister, better protected, and more heavily vegetated microenvironments within each site. In contrast, pine was most abundant in dry, exposed microenvironments with little vegetation. The variation in relative abundance of spruce with the quantity of moist and sheltered microenvironments was more pronounced than that of fir. This suggested that spruce was the most sensitive of the three species to adverse heating and drying of the exposed soil surface.

The broad ecological implications of the regeneration survey were followed up in 1960 and 1961 by a detailed autecological study of the microenvironments occupied by individual spruce and fir seedlings that have established themselves on logged-over land (Day 1962⁴). This study revealed that spruce and fir seedlings occurred mainly in moist or shaded microenvironments. Records of the moisture status of the rooting zone of the 1,400 seedlings showed that only 1 per cent of the spruce and 2 per cent of the fir seedlings were rooted in dry soil during the driest months of the summer. Spruce was found to be three times more abundant than fir in microenvironments with wet soil, equally abundant to fir in microenvironments with moist soil, and less abundant than fir in microenvironments which were drier. This suggested strongly that spruce seedlings are less tolerant of dry conditions or more tolerant of moisture than fir in this region.

The tendency for spruce seedlings to occupy moister and more protected microenvironments than fir was further demonstrated by the fact that more than

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³Nomenclature follows E. H. Moss 1959, *Picea engelmannii* Parry X *P. glauca* (Moench) Voss., *Abies lasiocarpa* (Hook.) Nutt., and *Pinus contorta* Dougl. var. *latifolia* Engelm.

⁴Day, R. J. 1962. The microenvironments occupied by spruce and fir regeneration in the Rocky Mountains. Can. Dept. of For., For. Res. Br., Unpub. M.S.

two thirds of the spruce seedlings sampled on sloping ground were found on the cool northwest, north, northeast, and east facing microslopes. In contrast, fir was distributed equally on microslopes with cool and warm aspects.

Over 70 per cent of the spruce and fir seedlings occupied microenvironments which were either moderately or heavily shaded for most of the day. An analysis of the main objects casting shade on the seedlings discounted the possibility that regeneration was effected in the open and that such shade environments had subsequently developed as a result of the revegetation of the logging sites. Fifty-six per cent of the spruce and 75 per cent of the fir seedlings were shaded by permanent hummocks, stumps, logs, slash, and mature residual trees.

The relative abundance of spruce and fir seedlings per unit area of the various seedbed types sampled is given in Table 1.

TABLE 1. THE ABUNDANCE OF SPRUCE AND FIR SEEDLINGS BY SEEDBEDS RELATIVE TO THEIR ABUNDANCE ON MINERAL SOIL

Seedbed Type	Spruce	Fir
Decayed wood.....	3.5	2.5
Mineral with incorporated humus.....	2.9	2.4
F. and H. humus.....	1.5	2.2
Moss*.....	1.1	0.4
Mineral soil.....	1.0	1.0
L. humus.....	0.04	0.56

* Mainly *Hylocomium splendens* (Hedw.) B. & S. and *Pleurozium schreberi* (Brid.) Mitt.

The best seedbeds for the establishment of spruce and fir seedlings in shaded microenvironments were decayed wood, mineral soil with incorporated humus (A_h horizon), and F. and H. humus. Most decayed wood seedbeds which support spruce and fir regeneration in the Crowsnest Forest are in good contact with the mineral soil. Seedlings, which become established on decayed wood, usually grow into this substratum and develop to normal maturity. The tendency for spruce and fir seedlings to occupy moist patches of soil suggests that the three above-mentioned seedbeds are able to maintain their soil moisture status during summer droughts better than litter, live moss or pure mineral soil. The excellent moisture retention of decayed wood is well known in the region and it seems probable that well-decomposed humus either pure or intermixed with mineral soil is also quite water retentive. Spruce is considerably less able to establish itself on litter than fir. This together with the greater range of relative abundance shown by spruce in Table 1 again demonstrates the poorer tolerance of this species to dry conditions.

During the summers of 1959, 1960 and 1961, soil-moisture records from fibre-glas units on seven site-types showed that most sites were prone to drought in the upper five inches of the soil profile. Surface drought was more acute in open cut-over than beneath partial stand cover and maximum drought periods of three weeks to a month were measured. Because strong insolation is the main cause of surface drought, drought periods tend to be accompanied by high soil-surface temperatures. Thermocouple measurements during a hot dry period in 1960 showed temperatures in excess of 50° C. for periods of several hours on all commonly occurring seedbeds, and that temperatures up to 75°C. occurred for short periods on particularly heat-prone materials.

These initial studies suggested that, after clear cutting in the Subalpine region, heating and drought of the soil surface may cause seedling mortality and regeneration failure. The study outlined in this paper was to test this hypothesis and to determine how important shade and seedbed type are to the survival of spruce seedlings.

REVIEW OF LITERATURE

Excessive heating and drying of the soil surface layers have long been recognized to be main causes of seedling mortality in regions with a dry growing season. The effects of soil surface heating and soil drought on seedlings cannot be discussed independently because a moist surface cannot easily be heated to dangerous levels by strong insolation, and because actively transpiring seedlings may be resistant to high surface temperatures. However, the two types of injury which are caused by excessive heating and drying of the soil may be separated and their causes briefly reviewed.

Drought Injury

Soil drought is a well-known cause of seedling debility and mortality. This is especially so during the first year of growth when seedlings are still in the succulent stage (Boyce 1948). Drought injury is generally caused when the rate at which water is lost to transpiration exceeds the rate of water uptake from the roots. This results in wilting, shrivelling, loss of colour and eventually death by desiccation of the tissues. No mechanical injuries occur.

Stem Girdle

Seedling mortality caused from excessive heating of a dry soil-surface by intense insolation differs considerably from that described above. The seedling is suddenly stricken with bark necrosis in the zone of the root collar causing either part or total collapse of the non-woody stem tissues. If only a part of the stem is affected the injury is referred to as a "heat lesion"; when a complete circle of tissue is affected the injury is termed "stem girdle".

The first diagnosis of excessive insolation as the cause of stem girdle was made in Europe by Mayr (1909). Up to this time several explanations had been given to account for the girdling of seedling stems which had been causing trouble both in the nursery and amongst natural regeneration. The most notable of these explanations were made by Hartig (1883) who suggested that the injury was caused by compression of frozen soil at the root collar. Other nineteenth century workers tried to establish *Pestalozzia hartigii* Tub. as a parasitic cause (Boyce 1948). Fischer (1909) satisfactorily discredited the parasitism theories but could not suggest the true cause of the disease. Munch (1913, 14 and 15) confirmed Mayr's diagnosis and later Hartley (1918) made similar diagnoses in North America.

Reports of stem girdle in North America have come mainly from the Rocky Mountain region of the western United States where a number of workers have demonstrated that the lower zonal limits of conifers is caused by the differential resistance of their regeneration to midsummer drought and heat. Bates (1923) exposed flats of seedlings to strong insolation to demonstrate the susceptibility of four species of Rocky Mountain conifers to high soil-surface temperatures. His work showed that Engelmann spruce and lodgepole pine were more sensitive to

stem girdle mortality than Douglas fir or ponderosa pine¹. Bates and Roeser (1924) later demonstrated that stem girdles at the root collar could not be induced by heating the above species in moist soil owing to the cooling effect of evaporating moisture. They also showed that seedling mortality was caused by needle scorching at considerably higher temperatures than was indicated by Bates' earlier work and was not typical of this type of injury. Roeser (1932), who used the same species with their roots strung through a board into water, induced stem girdle at the root collar by sprinkling on hot sand. Again his results showed that higher temperatures were needed to cause mortality than those recorded by Bates (1932) for similar seedlings growing in sun-dried soil.

The results of these experiments indicate that seedlings growing in moist soil are more resistant to heat than those growing in dry or droughty soil.

The literature indicates that transpiration, thermal emissivity and the condition of the protoplasm are important in determining the heat resistance of plants and plant tissues (Meyer and Anderson 1952, Kramer 1959, Daubenmire 1960, and Hare 1961).

Transpiration can partially combat the effects of excessive heat; it can prevent the leaves from heating to more than 5°C. above the temperature of the surrounding air (Shirley 1936) and it may cool the cortex by as much as 8°C. to 11°C. (Baker 1929 and Renolds 1939). Culm (1926) and Copeland (1932) showed that actively transpiring leaves were from 2°C to 11°C. cooler than leaves which had been prevented from transpiration by a thin coating of petrolatum.

In determining lethal temperatures in relation to rate of transpiration, most workers (Berkley and Berkley 1933 and Shirley 1936) chose to regulate transpiration by regulating artificially the humidity of the air surrounding the seedling rather than by limiting available soil moisture. This method is unsatisfactory because lethal temperatures are not commonly reached in nature during weather with high humidity. Moreover, turgid seedlings in humid air are not likely to be affected by heat as severely as those at similar transpiration rates suffering from drought-induced transpiration stress. Studies of the effects of heat on three species of pine and white spruce in dry air, moist air and water have shown that the thermal death point of these seedlings was highest in *dry* air (Shirley 1936). Even though the cooling effect of transpiration may be small, it may be of considerable importance in determining the heat resistance of seedlings growing in favourable moisture conditions. For example, the ratio of seedling dry weight to water transpired at 51°C. and 18°C. was 13:1 for lodgepole pine and ponderosa pine, 18:1 for Douglas fir and 28:1 for Englemann spruce, respectively (Roeser 1932). Though Roeser thought that the cooling effect of transpiration was the most important factor controlling heat resistance, other factors such as the maintenance of protoplasmic water content by a more efficient water economy could render the pines and Douglas fir more heat resistant during drought than Englemann spruce.

Study of the thermal emissivity of leaves has shown that leaf temperatures may be controlled more closely by heat lost from the leaf by radiation and convection than by heat lost in transpiration (Culm 1926, Watson 1933 and Ansari and Loomis 1959). This suggests that the improved heat resistance of seedlings which are growing in moist conditions may be related more closely to the maintenance of internal moisture status than to the cooling effects of transpiration.

¹ Nomenclature follows E. H. Moss 1959, *Picea engelmannii* Parry, *Pseudotsuga menziesii* (Mirb.) Franco, and *Pinus ponderosa* Laws.

The condition of the protoplasm in the tissues subjected to heating is probably the most important factor in determining the heat resistance of plants; for heat injury is caused by metabolic interruption and by coagulation of the protein content of the protoplasm (Lepeschkin 1935). Generally it is accepted that living tissues which have a low protoplasmic water content, such as the seeds, the tissues of xerophytes and the dormant tissues of mesophytes, are the most resistant to extremes of high (or low) temperature (Meyer and Anderson 1952 and Kramer 1959). Thus young seedlings, which have been subjected to the gradual processes of seasonal hardening, are most likely to be heat resistant owing to the development of protective tissues such as the bark and to the seasonal dehydration of the protoplasm (Evans 1959 and Jutlander 1945).

The rapid desiccation of the tissues of coniferous seedlings that suffer from stem girdle is caused by high soil-surface temperature and drought during the season of normally active growth. Such critical climatic effects are not likely to condition heat resistance in the same manner as the process of hardening. Thus surface temperatures are most acute when lack of soil moisture during the growing season suddenly reduces either the rate of transpiration or the internal moisture economy of the seedling.

Daubenmire (1943) showed that the soil-surface heating is secondary to drought in the determination of the down-slope zonation of Rocky Mountain conifers. He also showed that the two factors can act interdependently to cause severe seedling mortality. His experiments demonstrated that Engelmann spruce and Alpine fir were considerably less resistant to heat and drought than Ponderosa pine and pinon¹. He attributes this to the superior root-system development which reduces their drought susceptibility and to the inherent heat resistance of the last two species. It seems that excessive heat is only a cause of seedling mortality when lack of soil moisture limits transpiration.

A wide range of surface temperatures and exposure times have been given by various workers who have studied stem girdle of coniferous seedlings (Munch 1913, '14 and '15, Bates 1923, Bates and Roeser 1924, Toumey and Neethling 1924, Baker 1929, Issac 1929, Shirley 1936, Lorenz 1939, and Daubenmire 1943). Such a range in temperatures and exposure times must be caused by variation in soil moisture and relative humidity which affect transpiration and protoplasmic moisture content; variations in species, age and vigour of the seedlings under test; and variation in methods of heat application and temperature measurement.

Daubenmire showed that the heat-sensitive seedlings of Engelmann spruce that were grown in *moist* soil began to suffer injuries at temperatures as low as 45°C. when exposed for six hours; whereas the heat-resistant seedlings of pinon could withstand a similar period of heating at 70°C. Generally the work, which was reviewed, indicates that heat injury may become serious for most coniferous species when surface temperatures in the 50°C to 60°C. range are reached for periods of a few minutes up to several hours. However, the severity of the injuries in this temperature range is not only dependent on high temperature but also upon limited moisture supply. The death of seedlings growing in moist soil with a dry surface in the 60°C to 70°C. range may be attributed to the effects of surface heating alone.

METHODS

The experiment was conducted in flats which were placed on the floor of a Subalpine mountain valley in the Crowsnest Forest at an elevation of 5,500 feet.

¹*Pinus cembroides* var. *edulis* (Engelm.) Voss, nomenclature after Harlow and Harrar 1952.

The Soil Types

Four types of soil were selected for the seedbeds. These were chosen for their similarity to the four types of seedbed on which spruce and fir seedlings were most abundant. The seedbed types are described as follows:—

1. *Decayed wood* was taken from entirely rotten spruce and fir logs which were lying on the forest floor. This material was sufficiently decomposed to allow hand granulation to particles ranging down in size from three centimetres. Its color was yellowish red when dry (5 YR 4/6)¹ and dark reddish brown when wet (2.5 YR 3/4).

2. *F. and H. Humus* was composed of intermixed fermentation and humification layers of the local soils. This seedbed contained 75 to 85 per cent F. Humus which is composed of partly decomposed organic matter in which the original structures are hardly discernible. The remaining 15 to 25 per cent was H. humus in which the original organic structures are indefinable. This material was very dark brown (10 YR 2/2) when dry and black when wet (10 YR 2/1).

3. *A_h horizon* was composed of soil with a clay to clay-loam texture (sand 42 to 46 per cent, silt 14 to 15 per cent, and clay 39 to 43 per cent)². This contained incorporated organic matter and 8 to 10 per cent of small stones. The soil was extracted from a nearby clearing in which the soil profile had a well-developed A_h horizon. This material was dark grey (10 YR 4/1) when dry and very dark grey to black when wet (10 YR 3/1 to 10 YR 2/1).

4. *Sandy loam* was a typical local till soil of sandy loam texture (sand 73 to 76 per cent, silt 13 to 15 per cent, and clay 11 to 14 per cent) which contained from 22 to 33 per cent of small stones. This material did not contain organic matter and was pale brown (10 YR 6/3) in colour when dry and brown (10 YR 5/4) when wet.

Preparation of the Flats

Forty wooden flats with internal dimensions of 18 by 18 by 6 inches were prepared with loosely fitting bottom boards to allow drainage. To reduce the loss of soil and to prevent the plugging of the drainage cracks, the flats were filled to a depth of 3/4 to 1 inch with fine stream gravel.

Each of the soil types described above was intermixed carefully and packed manually as tightly as possible into ten flats until level with the sides. Tight manual packing was intended to simulate field conditions. During the phase of watering (page 14), slight shrinkage indicated that the soil types which were used could not be packed as tightly by hand as by the action of infiltrating water and that the flats may not initially have been as tightly packed as in field conditions. Ten equal-seedbeds were prepared from each of the four soil-types. Seedbeds in flats were used in this experiment to eliminate local variations in soil moisture and external soil drainage which might have occurred had the seedbeds been prepared in contact with the soil.

Preparation of the Experiment

Two carefully levelled log platforms each constructed to accommodate twenty flats were arranged in two rows on either side of a gangway near a con-

¹Color values from charts of the Munsell Color Company.

²According to the particle size classification of the International Society of Soil Science.

venient water supply on the valley bottom in Lynx Creek drainage basin. The platforms were orientated north-south and separated by several yards to minimize shading by operators taking measurements in the noonday. The platform that was situated farthest north was fitted with a six-foot-high slat screen with $1\frac{1}{4}$ -inch slats spaced approximately $1\frac{3}{4}$ inches apart. Calculation of the area that was screened by the slats indicated that about forty per cent of the area beneath was shaded. Four polyethylene and wood shelters were prepared to cover each of the four rows of flats. These could be lifted easily on to the platforms to exclude rainfall. The completed experiment is shown in Figure 1.

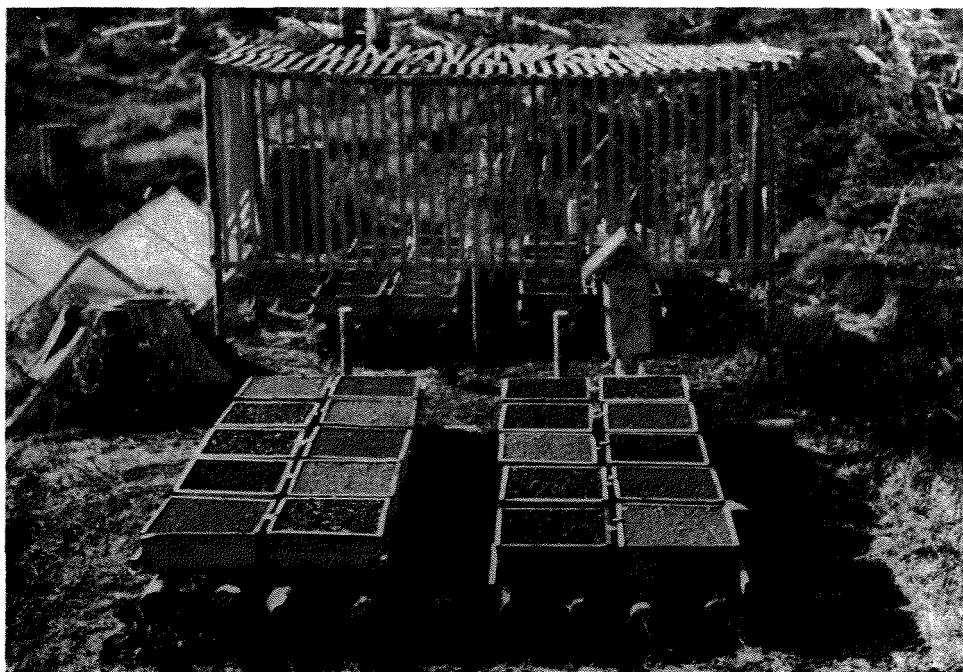


Figure 1. View of the experiment from the south side

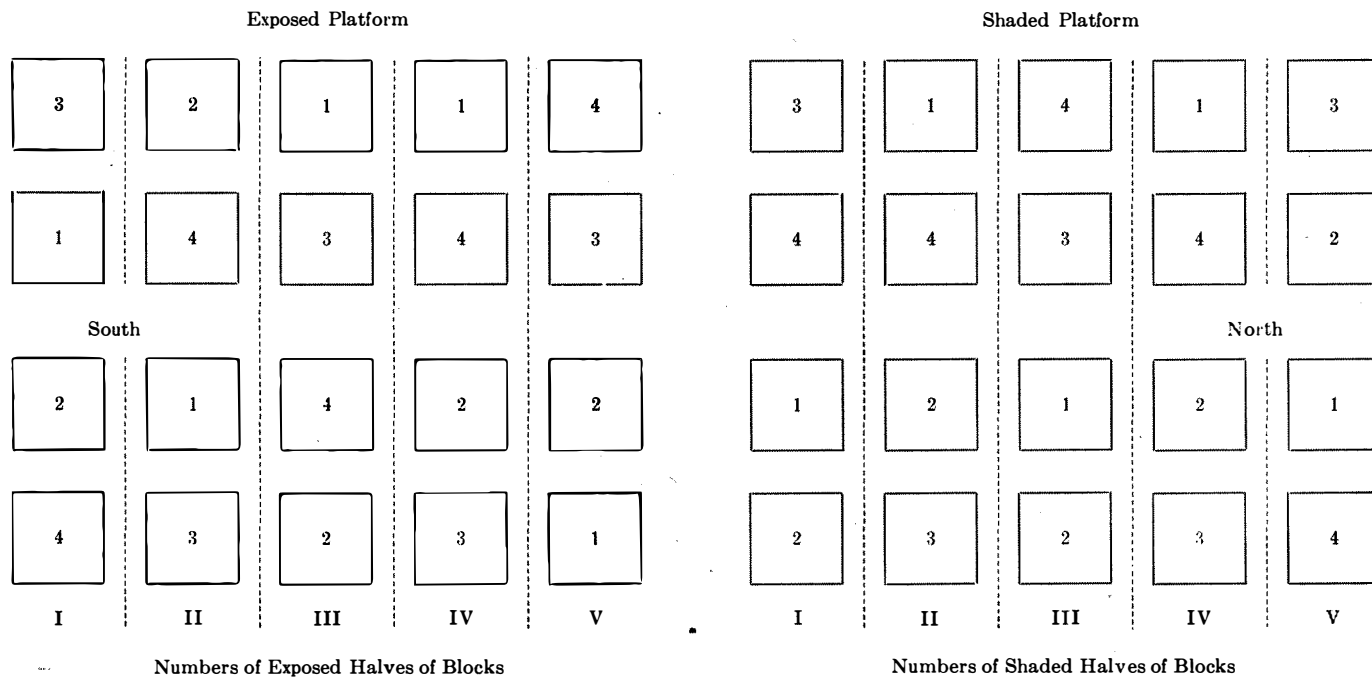
Experimental Design

The flats were arranged in a random block design with five replications of the four seedbeds within each of the two-shade treatments. For convenience in construction and to reduce the time required to record temperature results, the shade treatments were not replicated and the five blocks are separated on the two platforms (Figure 2). The close proximity and uniformity of the flats was considered to be sufficient justification for this departure from usual procedure.

Installation of Instruments

All exposed and shaded flats on blocks I, III and V were equipped with fibre-glass soil-moisture units with internal thermistors¹. Two of these were placed horizontally 1 and 3 inches beneath the soil surface in each of the flats which

¹A Coleman (1946) type ohmmeter was connected for moisture and temperature readings.



Key to Seedbeds

- 1—Decayed Wood
- 2—F. and H. Humus
- 3—A_b Horizon
- 4—Sandy Loam

Figure 2. The Experimental Design

were sampled. This distribution of soil moisture units permitted temperature and moisture measurement at 1 and 3 inch levels on three flats of each seedbed type in each shade condition.

All exposed and shaded flats in blocks IV and V were equipped with fine copper-constantan thermocouples². Two thermocouples were placed in contact with fine-soil particles in an air layer less than 0.03 inches above the seedbed in each flat. To minimize conductivity errors, the thermocouple leads were clipped to the soil surface for at least ten inches (Vaartaja 1949). The northerly blocks IV and V were chosen for thermocouple installation. This reduced the risk of shading by operators who took the readings. This arrangement allowed four-independent measurements of air temperature in close contact with the soil surface to be taken on each seedbed type in each shade condition. These temperatures are referred to as "surface temperatures" throughout this report.

A sensitive propeller-type anemometer that was fixed on a directional vane was set up level with the surface of the flats within a few feet of the experiment. This allowed mean wind velocities to be estimated during periods of temperature measurement. A hygrothermograph and rain gauge, set up at a station at a distance of a quarter of a mile, was used to record summer air temperature, relative humidity and rainfall as in 1959 and 1960.

Seeding and Watering

On June 14 all the flats were watered continuously until they were saturated. A quarter of an inch of the surface soil in each flat was scraped to one side; two hundred hybrid spruce seeds were carefully distributed on the exposed surface. After the seeding had taken place, the soil surface was replaced and tamped down.

The flats were watered at 8:00 a.m., noon., and 4:00 p.m. until July 13. Approximately a third of a gallon of water was applied per flat at each watering. This was equivalent to 0.85 inches of rainfall per day and was sufficient to maintain the soil moisture at 1 and 3 inches at field capacity. On hot clear days, surface drying was sometimes acute between waterings, therefore additional light watering was carried out to prevent loss of germinates. After July 13 the flats were allowed to dry. For the remaining period of the experiment all rainfall was excluded from the seedbeds by covering them with transparent polyethylene and wood shelters. The rain covers were kept on only for the minimum time necessary. Rainfall was excluded so that a drought period could be simulated without interruption from unpredictable summer rainfall.

Germination

Germination began on June 27 and continued until August 4. Ninety per cent of the germination in the shade and in the open had appeared when watering was stopped on July 13. All rooted germinates were marked by coloured tooth-picks and recorded each day. Colour changes were made every four days so that when mortality occurred the period of origin of each dead seedling could be determined. Surface germinates were ignored because they were all so severely affected by drying that they died in two or three days.

²A Rubicon Temperature Calibrated Potentiometer was connected for surface temperature measurement. Copper-constantan thermocouple wire 0.01003 inch diameter (30 A.W.G.) was used.

Mortality

Mortality records were made daily. Types of injury were recorded together with the period of origin of each dead seedling. After cessation of watering, the types of injury that caused mortality were as follows:

(1) *Drought Mortality*

Hybrid spruce seedlings that died without mechanical injury in dry soil may be considered to have been droughted. When the seedlings were suffering from drought, they wilted, shrivelled and dried out, and became buff in colour over a period of two to ten days depending on the severity of the drought and the aridity of the weather. Seedlings killed by drought usually remained upright until they became so brittle that they were snapped off and were blown away by the wind (Figure 3).



Figure 3. Seedlings killed by drought alone. Note shrivelled condition of stems and leaves.

(2) *Stem Girdle Mortality*

Hybrid spruce seedlings affected by this type of injury were usually girdled during periods of peak insolation on clear days. The injury is easily recognized because of an obvious constriction which suddenly appears in the zone of the root collar. The seedling usually falls upon its side whilst still fleshy and apparently healthy. The injury resembles damping-off and might be mistaken for it in moister conditions. However, its occurrence in droughty soil during periods of strong solar radiation rule out this possibility. Within two or three days of the appear-

ance of a stem girdle or severe heat lesion, the seedlings became so shrivelled and brittle that they broke off and were lost in the wind. Though heat mortality was most pronounced in the open flats, it occurred on shaded flats in very hot weather. See Figure 4 for an illustration of heat injury.



Figure 4. Seedling killed by "stem girdle". Note the constriction at the root collar while the stem and leaves are still fleshy.

Soil Moisture and Temperature Measurements

For six weeks, after watering was stopped on July 13, the following daily temperature and moisture measurements were made:

- (1) *Surface Temperatures* were recorded on all flats which were fitted with thermocouples. Measurements were restricted to the hottest part of the day. Series of readings started at 1:00, 1:30, 2:00, 2:30 and 3:00 p.m. were taken on the thirty-two thermocouples which were equally distributed on the four seedbed-types on shaded and exposed flats.
- (2) *Soil Temperatures at 1 and 3 inches* were measured daily between 3:00 and 4:00 p.m. on three flats of each seedbed type in the open and in the shade. Peak soil temperatures of these depths were reached at this time.
- (3) *Soil Moisture at 1 and 3 inches* was measured daily at the same time and on the same fibreglas units as soil temperature. There is no appreciable diurnal fluctuation in soil moisture.

On a number of days chosen for their clear sky conditions, surface temperature and soil temperature measurements at 1 and 3 inches were taken at hourly or half-hourly intervals over periods of twenty-four hours.

RESULTS

Germination

TABLE 2. THE NUMBER AND PER CENT PROPORTION OF SPRUCE SEEDLINGS GERMINATING ON EACH SEEDBED TYPE IN EXPOSED AND SHADED FLATS

Seedbed type	Exposed flats		Shaded flats		Total	
	number	per cent	number	per cent	number	per cent
(1) Decayed wood.....	345	37	298	39	643	38
(2) F. & H. humus.....	194	20	196	26	390	23
(3) A _h horizon.....	204	22	145	19	349	20
(4) Sandy loam.....	197	21	125	16	322	19
Total.....	940	100	764	100	1,704	100
Mean No. per flat.....	47		38		43	

The 200 seeds sown on each flat produced an average of 43 seedlings per flat. Thus only 22 per cent of the spruce seed germinated under the conditions of the experiment even though germination tests indicated that the seed was 76 per cent viable. Germination in the open (averaging 47 seedlings per flat) was better than germination in 40 per cent shade (averaging 38 seedlings per flat). However, both open and shaded flats produced a satisfactory number of seedlings for the experiment. About 50 per flat was considered ideal.

A factorial analysis was made of the variance of the total number of seedlings germinated per flat on the various seedbed types in open and shaded conditions (Appendix I). Decayed wood in the open (averaging 70 seedlings per flat) and in the shade (averaging 60 seedlings per flat) was significantly¹ more productive than all other seedbeds (Table 3).

TABLE 3. AVERAGE NUMBER OF GERMINATES PER FLAT ON EACH SEEDBED TYPE IN THE OPEN AND IN THE SHADE

Seedbed type and shade condition	Average number of germinates per flats
Exposed decayed wood.....	70
Shaded decayed wood.....	60
----- Significant difference -----	
Exposed A _h horizon.....	40
Exposed sandy loam.....	39
Shaded F. & H. humus.....	38
Exposed F. & H. humus.....	38
Shaded A _h horizon.....	29*
----- Significant difference -----	
Shaded sandy loam.....	25*

*There was non-significance between Shaded A_h horizon and Shaded sandy loam.

The super-abundance of spruce germinates on decayed wood suggests that this seedbed is particularly suitable for spruce regeneration. Such superiority cannot be attributed entirely to improved moisture status because 90 per cent of the

¹Significant at the 1% level.

germinates appeared during the phase of watering when all seedbeds were maintained at field capacity. Nor is it related to superior nutrient status, for analyses¹ show that decayed wood was lowest in available nitrogen, phosphorus, and potassium. This indicates that decayed wood may have special physical or chemical properties to stimulate germination. Further research is needed to assess them.

Mortality

The cumulative percentage of mortality of hybrid spruce seedlings per day on each seedbed type in the open and in the shade is given graphically in Figure 5. During the period of the experiment, the results indicate that mortality was much less acute in 40 per cent shade than in the open, with the exception of sandy loam. Spruce seedlings on shaded sandy loam proved to be more mortality prone than those on A_h horizon or decayed wood in the open.

After daily watering was terminated on July 13, factorial analyses of mortality were worked out for drought periods of 7, 14, and 21 days (Appendices II, III, IV). The results of these analyses are given in Table 4. Analyses were not carried out for periods of more than 21 days because the order of seedbed and shade treatments remained in much the same position with respect to seedling mortality for the rest of the experimental period (Figure 5).

Table 4 shows that shade and seedbed had such a varied effect on spruce seedling mortality that the classes of treatment became separated into four significantly different groups after only seven days of drought. Mortality at this time was more pronounced on the exposed seedbeds than on those protected by the slat screen, even though exposed decayed wood suffered less mortality than shaded A_h horizon seedbeds. The surface of the A_h horizon seedbeds tended to dry more rapidly than the other materials during the first seven days due to the formation of quarter-inch deep reticulate fissures which were caused by the high clay content of this soil type. Because of rapid drying, the surface of the A_h horizon seedbed was more easily heated by insolation, and the spruce seedlings on it were more inclined to mortality than those on other seedbed types in equivalent shade conditions. After seven days of drought the most critical seedling mortality (24 per cent) had occurred on exposed A_h horizon seedbeds.

After fourteen days of drought, the various shade and seedbed treatment classes were widely separated into five significantly different groups. Less than 5 per cent mortality had occurred on the shaded organic seedbeds, decayed wood and F. and H. humus and less than 25 per cent had occurred on shaded A_h horizon, shaded sandy loam and exposed decayed wood. However, mortality had become severe on exposed A_h horizon seedbeds with 41 per cent dead, and critical on exposed F. and H. humus and sandy loam with 64 and 80 per cent dead respectively. The change in order of the severity of mortality on these latter seedbed types was caused by accelerated drying of the exposed sandy loam and by very high surface temperatures on the humus. Once the surface cracking had ceased, A_h horizon seedbeds were less severely affected because of good water retention.

After twenty-one days of drought, shade and seedbed treatments were still separated into five significantly different groups (Table 4) arranged in a similar order. Shaded F. and H. humus and decayed wood were still the best seedbeds with less than 15 per cent mortality. Shaded A_h horizon, exposed A_h horizon and exposed decayed wood were in intermediate classes with 26 to 53 per cent mortality occurring. However, shaded sandy loam had dried exceptionally fast since

¹The analyses were carried out by the The Agricultural Soil Testing Laboratory at the University of Alberta, Edmonton (by D. H. Lavery, Chief Analyst).

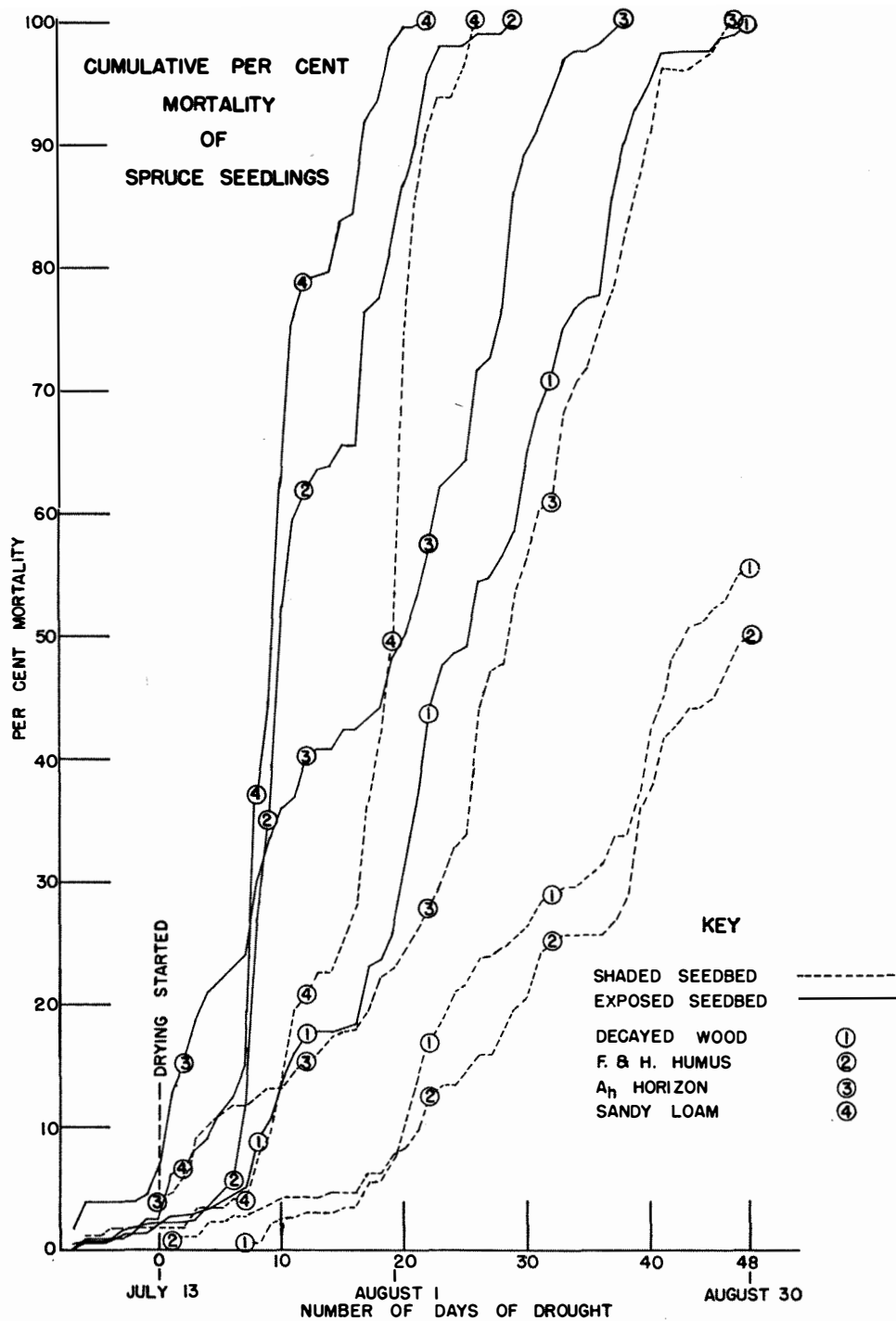


Figure 5.

the fourteenth day which resulted in 86 per cent mortality after twenty-one days of drought. Thus sandy loam proved to be the only shaded seedbed type that was severely subjected to seedling mortality. The critically high level of mortality on this type was only exceeded on exposed F. and H. humus with 90 per cent and exposed sandy loam with 100 per cent mortality.

TABLE 4. PER CENT MORTALITY OF HYBRID SPRUCE AFTER 7, 14 AND 21 DAYS OF DROUGHT

Order	Days of drought after July 13					
	7 days		14 days		21 days	
	Seedbed & shade	Per cent mortality	Seedbed & shade	Per cent mortality	Seedbed & shade	Per cent mortality
Best	(DW)	0.3	(DW)	3.0	(FH)	9.7
			(FH)	4.6	(DW)	14.4
----- significant difference -----						
Second	(FH)	2.6	(A _b)	17.2	(A _b)	26.2
	(SL)	4.0	DW	17.7	DW	36.5
	DW	4.9	(SL)	22.4		
----- significant difference -----						
Third	(A _b)	11.7	A _b	40.7	A _b	52.9
	FH	11.8				
	SL	15.2				
----- significant difference -----						
Fourth	A _b	24.0	FH	63.9	(SL)	85.6
					FH	89.7
----- significant difference -----						
Fifth	—	—	SL	79.7	SL	99.5

Key to exposed seedbeds
Exposed decayed wood DW
F. & H. humus FH
A_b horizon A_b
Sandy loam SL

Key to shaded seedbeds
Shaded decayed wood (DW)
F. & H. humus (FH)
A_b horizon (A_b)
Sandy loam (SL)

The Effects of Soil Drought and Surface Heating on Seedling Mortality

Comparison of the graphs for cumulative mortality (Figure 5) with those for mean soil moisture measured at 1 and 3 inches depth (Figures 6 and 6A) shows that the trends in seedling mortality tended to follow those of soil moisture depletion during the 50-day drought period. Exposed sandy loam, shaded sandy loam and exposed A_b horizon seedbeds dried out most rapidly and their seedlings suffered the most severe mortality. An exception was the exposed F. and H. humus which was subject to equally severe seedling mortality yet did not dry nearly as rapidly at 1 inch and remained moist at 3 inches. Shaded A_b horizon and exposed decayed-wood seedbeds maintained their soil moisture at intermediate levels which resulted in less seedling mortality than occurred on the above-mentioned seedbeds. Shaded decayed wood and F. and H. humus maintained their moisture at both 1 and 3 inches for nearly the whole 50-day drought period. Spruce seedlings on these seedbeds suffered the least from mortality and these seedbeds still supported, after 50 days of drought, from 45 to 50 per cent of the

seedlings which germinated on them. All other seedbeds had suffered 100 per cent seedling mortality by this time.

The fluctuations in seedling mortality which are shown in Figures 7 and 7A are derived by calculations of the per cent mortality of the remaining living seedlings each day. Comparison of these data with the maximum and mean maximum¹ surface temperatures given in Figures 7 and 7A clearly indicates that fluctuations in seedling mortality are more closely related to daily change in surface temperatures than to the slow decline in soil moisture which is shown in Figures 6 and 6A.

The mean maximum surface temperatures in excess of 45°C. are usually accompanied by mortality when soil moisture is limiting (Figure 6). Temperatures above 50°C. are more critical and can cause severe mortality (e.g. F. and H. humus in the open) even when the soil is moist at 1 inch depth. A comparison of shaded and exposed seedbed types in Figures 7 and 7A indicates that shading greatly reduced seedling mortality. This is particularly noticeable in the case of F. and H. humus and to a lesser extent in decayed wood which were subject to higher surface temperatures than A_h horizon or sandy loam seedbeds.

TABLE 5. THE PROPORTION OF SEEDLINGS WHICH DIED FROM DROUGHT AND STEM GIRDLE

Seedbed type	Exposed flats		Shaded flats	
	Stem girdle	Drought	Stem girdle	Drought
	(per cent)		(per cent)	
Decayed wood.....	75	25	21	79
F. and H. humus.....	88	12	27	73
A _h horizon.....	52	48	17	83
Sandy loam.....	68	32	30	70
Total per cent.....	71	29	23	77

Table 5 shows that 71 per cent of the seedlings which were exposed to full insolation died from stem girdle whereas 77 per cent of those which died in the shade were killed by drought. This is in accordance with the surface temperature given in Figures 7 and 7A which shows that maxima and mean maxima temperatures in the open were considerably higher than those measured beneath the slat screen. Twenty-three per cent of the seedlings which died beneath the slat screen were killed by stem girdle. This fact indicates that such injuries can be inflicted while the seedling is briefly exposed to insolation as the bands of sunlight move across the surface of the flats. Since maximum temperatures of 45°C. to 55°C. were the highest recorded beneath the slat screen in hot weather with clear skies and since the motion of the sunlight only permitted heating for quarter- to half-hourly intervals, it appears that stem girdles can be rapidly inflicted when soil moisture is limiting.

The exposed organic materials (F. and H. humus and decayed wood) had the highest proportion of seedlings injured by stem girdle. Generally they were several degrees hotter at the surface than the exposed mineral types (A_h horizon and sandy loam) and the shaded seedbeds. The tendency for sandy loam to have a higher proportion of girdled seedlings than the darker mineral type, A_h horizon, is probably caused by acute early drying which must have severely reduced the heat resistance of seedlings growing on the former seedbed.

¹The mean maxima of four separately placed thermocouples.

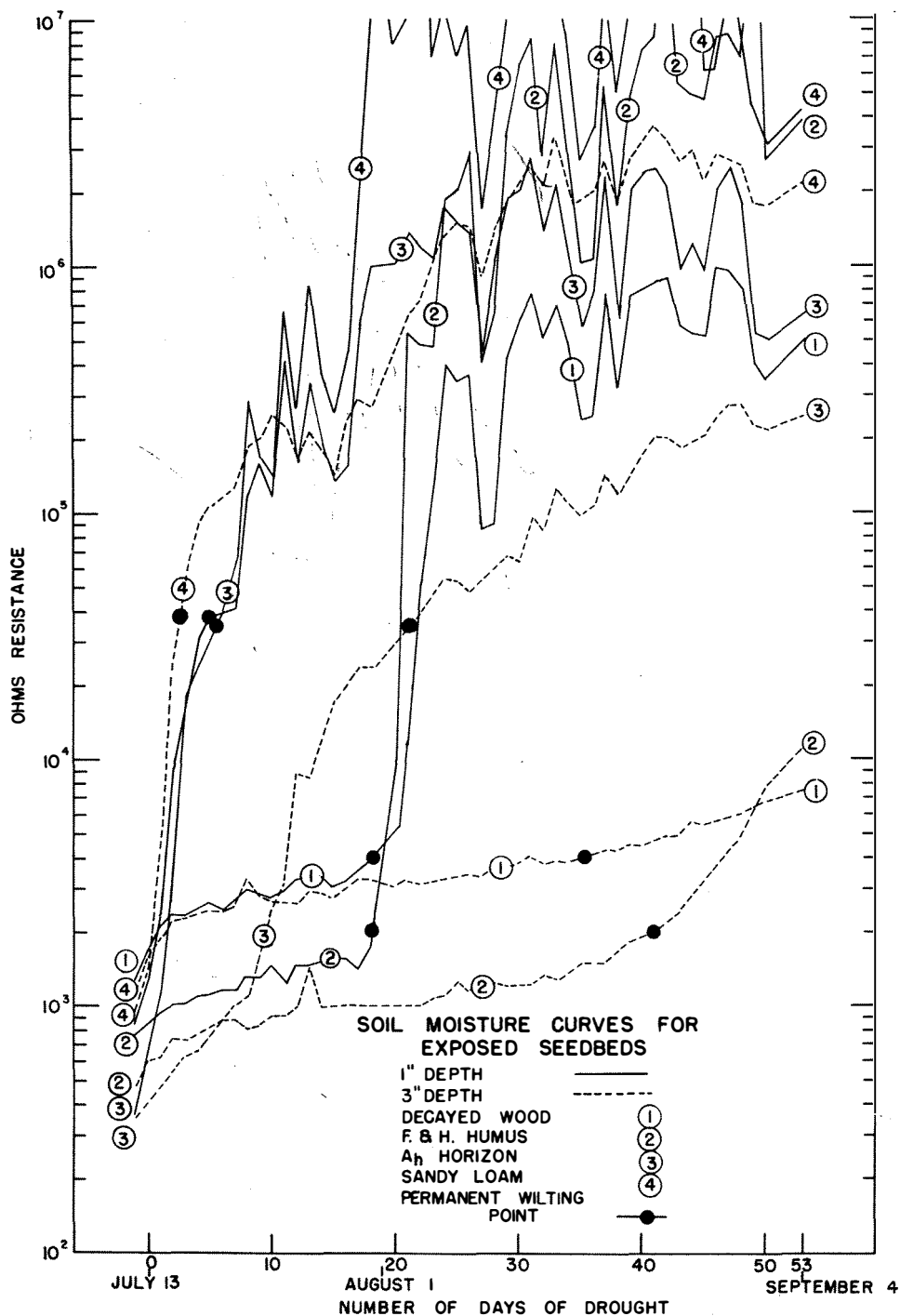


Figure 6.

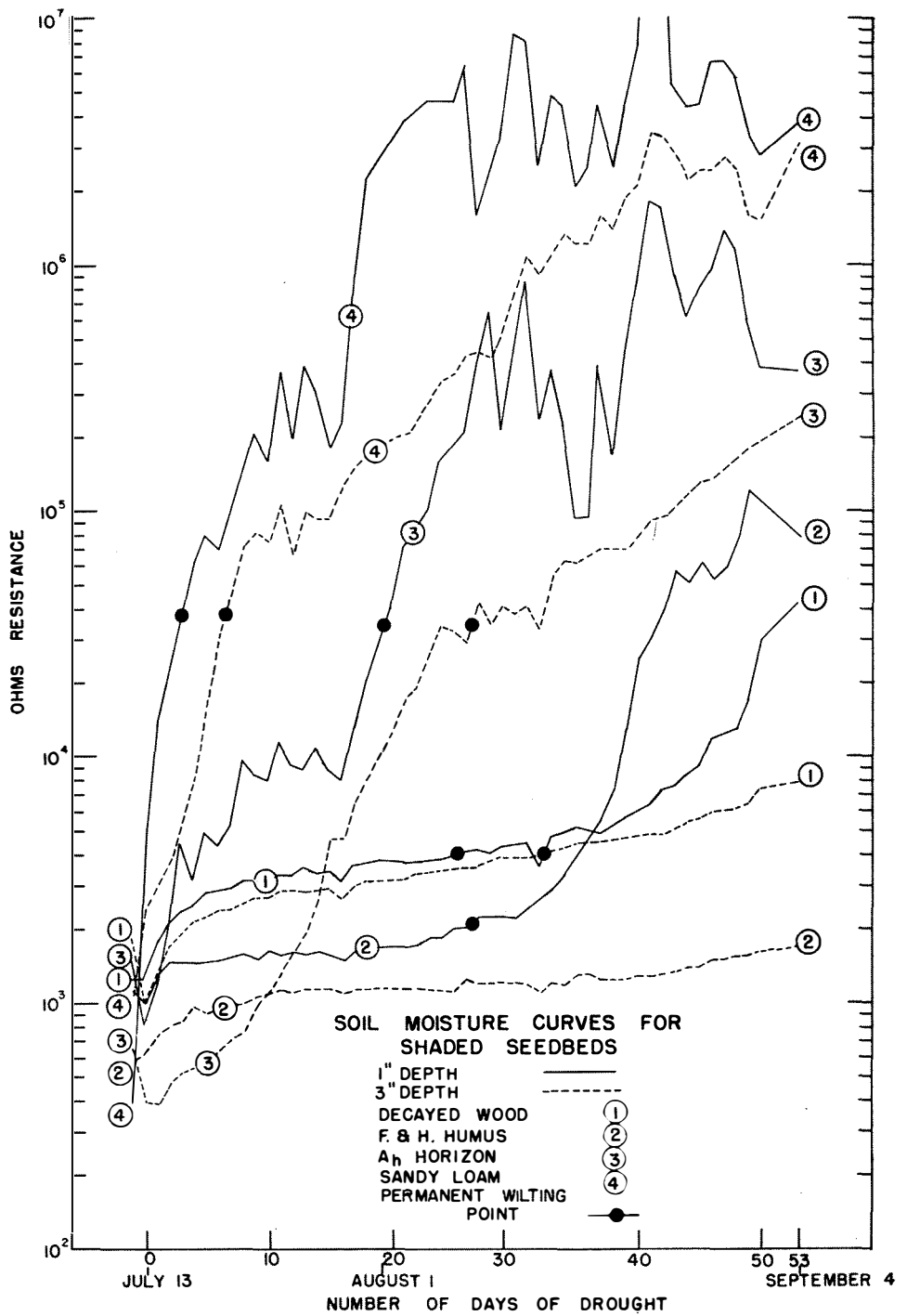


Figure 6A.

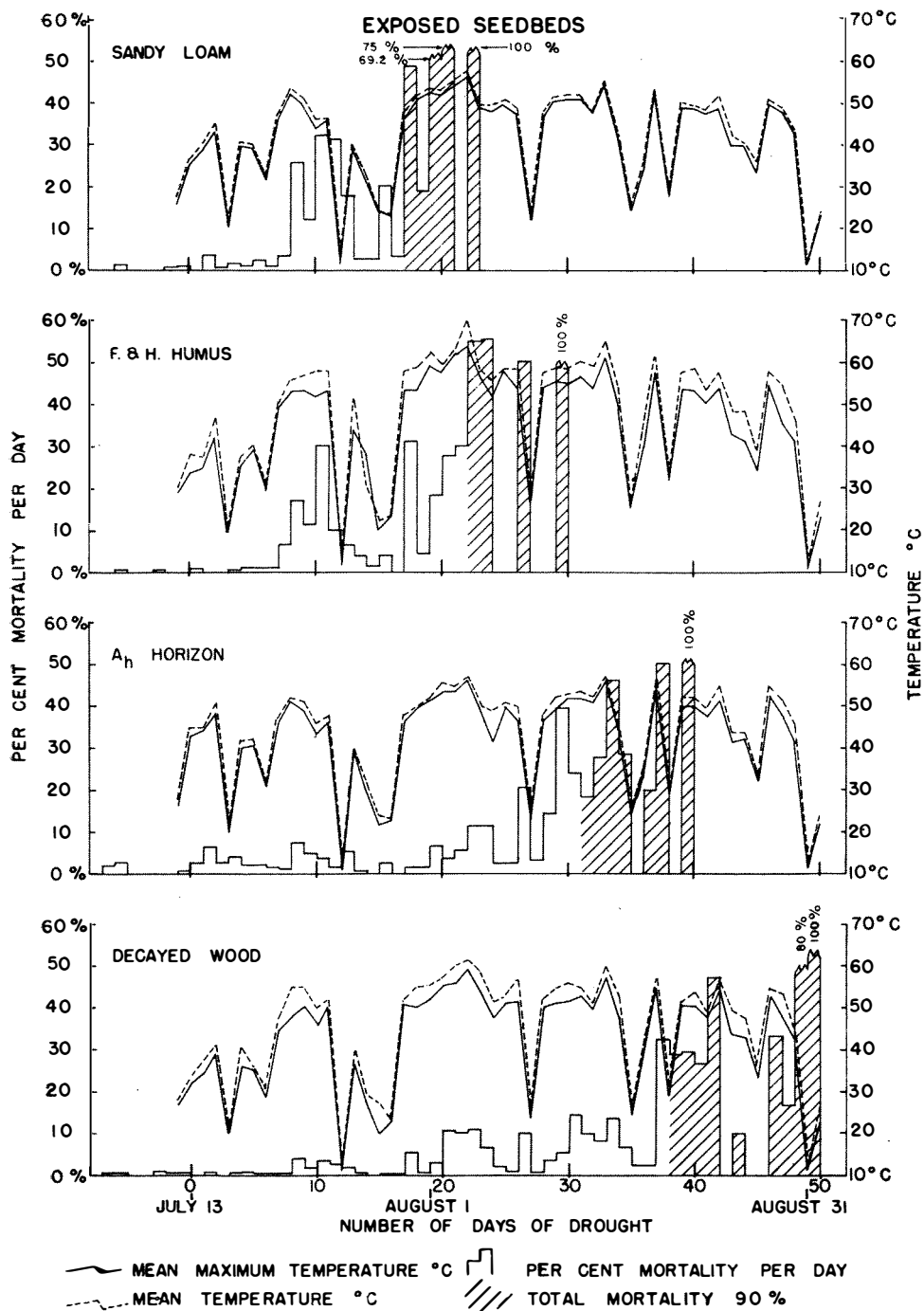


Figure 7.

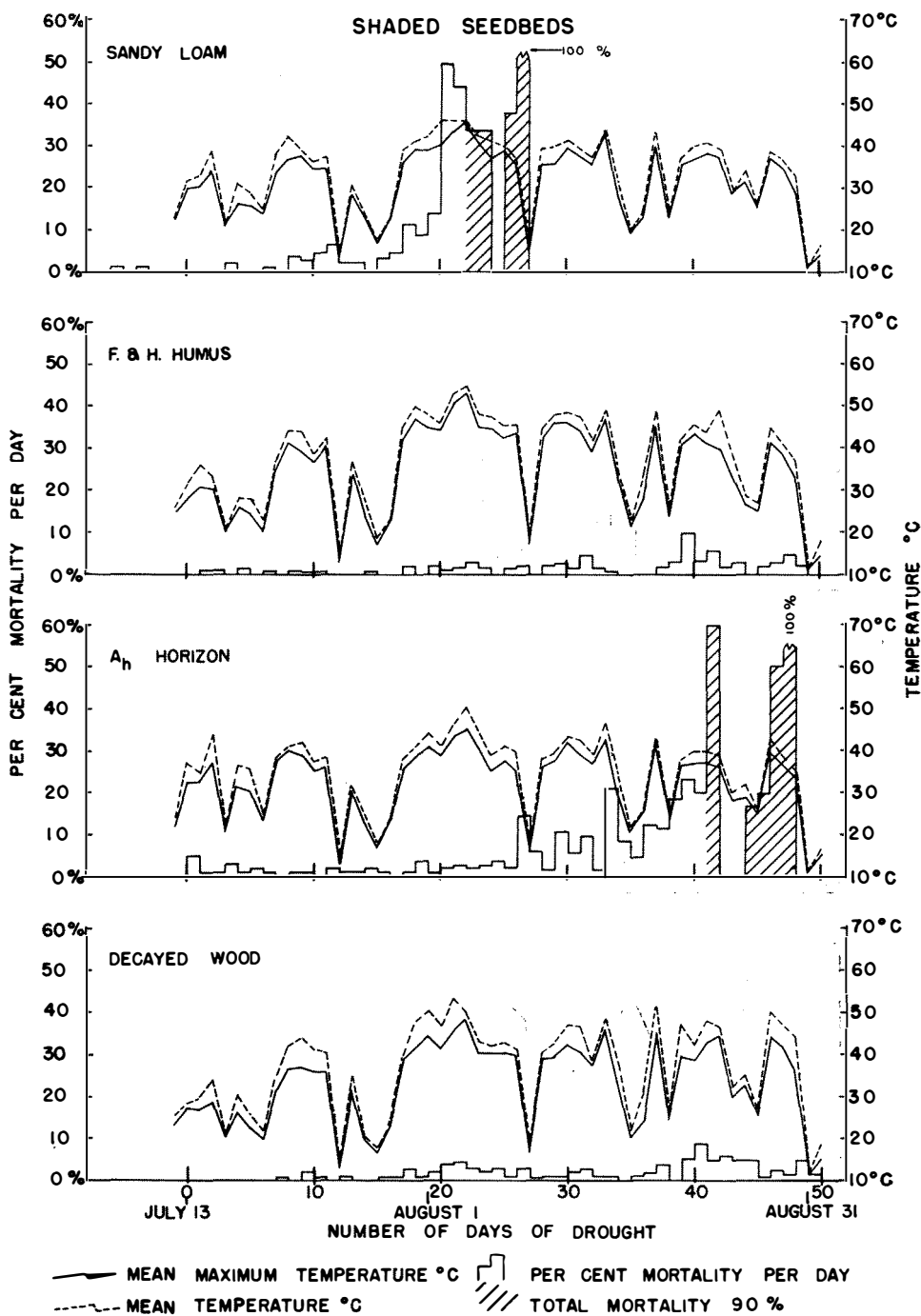


Figure 7A.

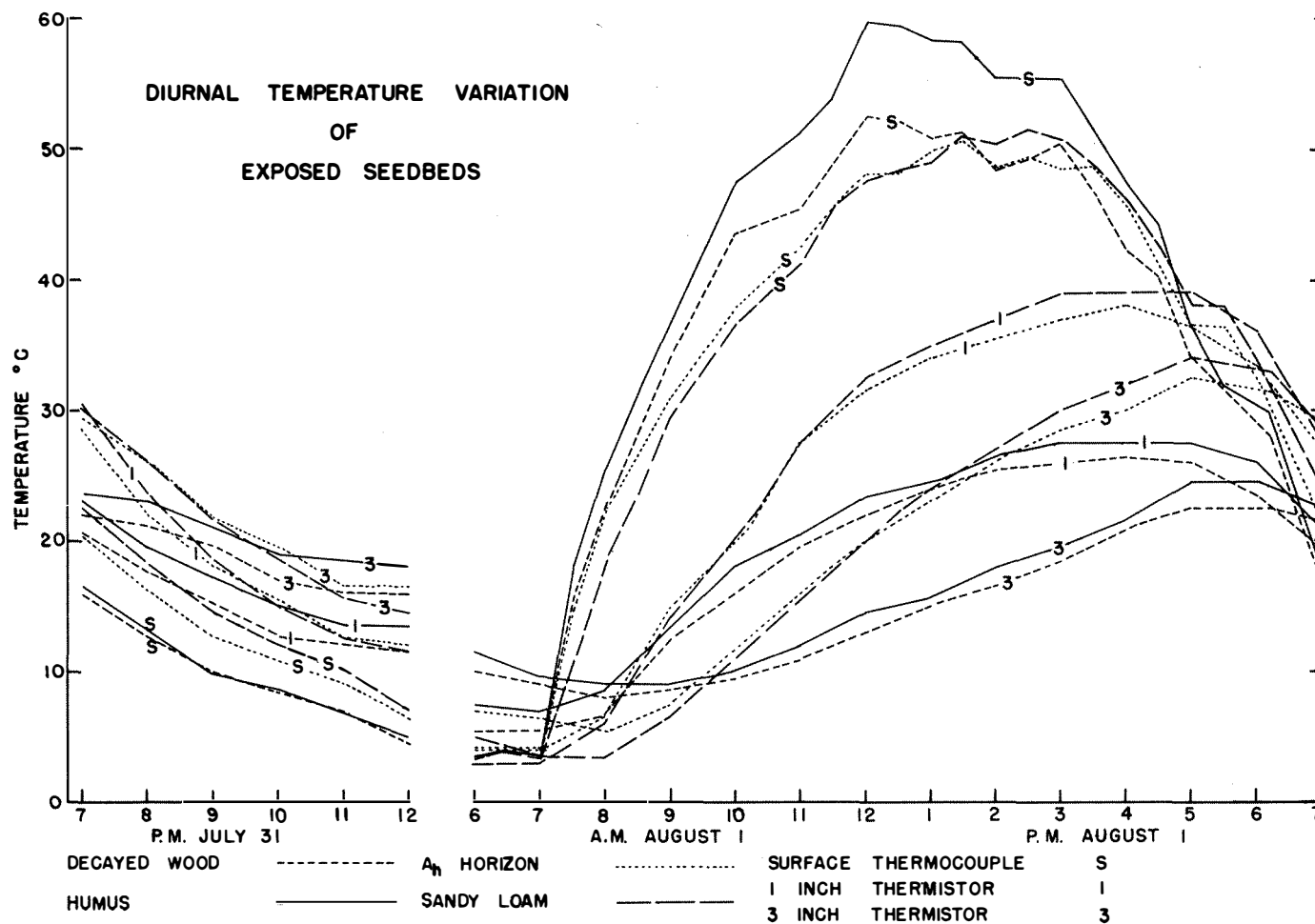


Figure 8.

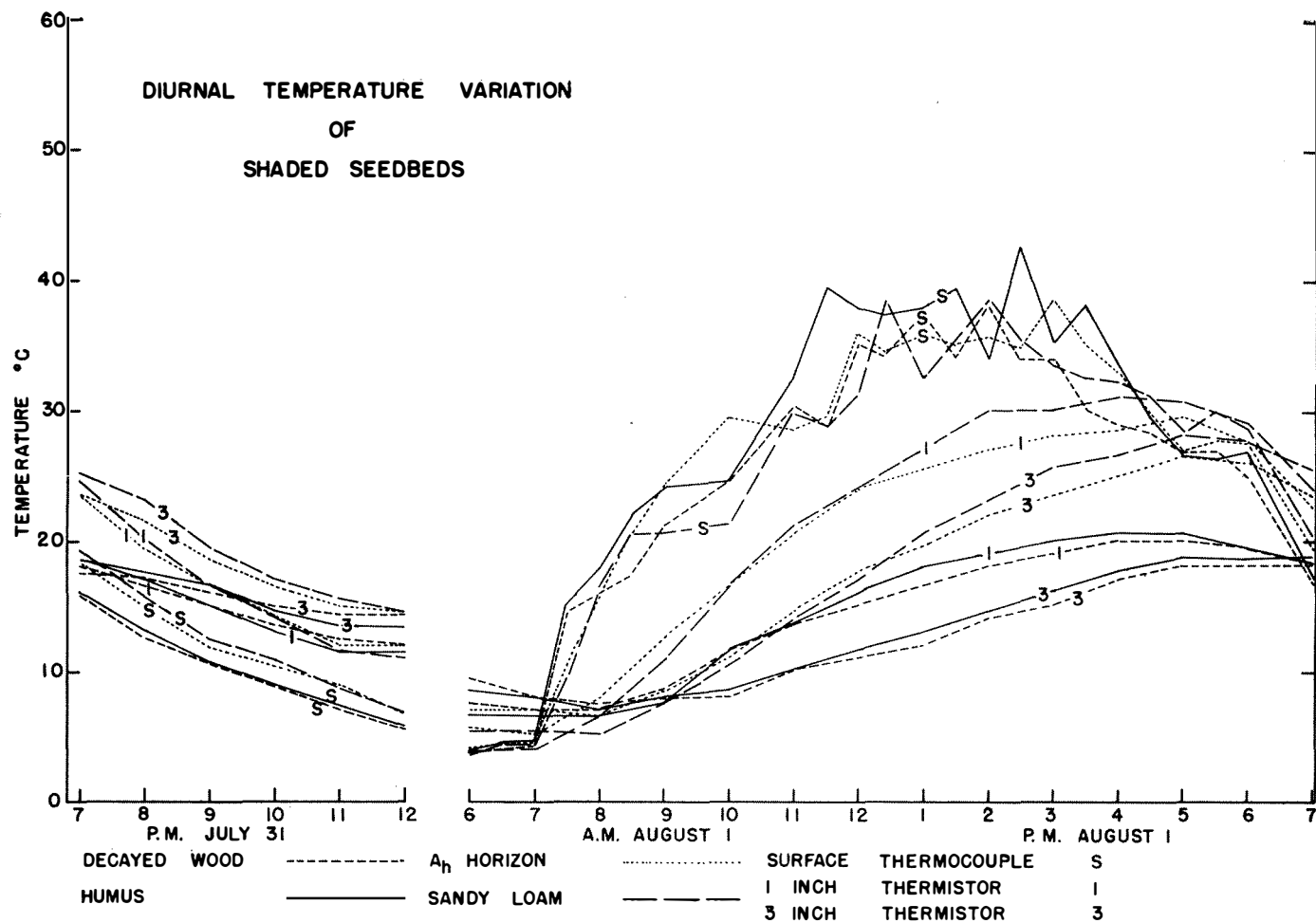


Figure 8A.

Figures 8 and 8A give the diurnal temperature change that occurred at the surface and at 1 and 3 inches depth on the various seedbeds in the shade and in the open on a typical hot summer day (August 1). The order of surface temperatures reached during the day on all seedbeds is reversed at 1 and 3 inches. Though the organic types are hottest at the surface, they are the coolest at 1 and 3 inches, and for much of the day are even cooler at 1 inch than the mineral types are at 3 inches. Such temperature characteristics are in accord with the physical properties of these seedbed types; for the organic materials have a relatively low albedo and thermal conductivity by comparison with the mineral materials. The organic materials are also considerably hotter at the surface (5°C to 10°C. in the open) but are much cooler at 1 and 3 inches (10°C to 15°C. in the open). Because of a hotter surface, the organic materials are more subject to seedling death by stem girdle than are the mineral types which can more readily dissipate surface heat by improved reflection and conduction. However, the conduction of heat from the surface into the soil so raises the temperature of the mineral types at 1 and 3 inches that accelerated drying increases the risk of mortality.

Seedling Growth in Relation to Survival

Table 6 shows that the longer the hybrid spruce seedlings grew during the phase of watering, the greater was their resistance to mortality after watering was stopped on July 13. This suggests that root development for a period of 5 to 16 days before the onset of drought greatly improves the chance of survival.

It is interesting to note that the seedlings which germinated immediately before watering stopped (crop 4) were at first considerably more subject to mortality than the seedlings which germinated during the first four days of drought (crop 5). This indicates that spruce germinates which appear in very moist conditions are less tolerant of a sudden reduction in moisture status than seedlings which are able to germinate in drier soil.

After the experiment was discontinued on September 1 approximately twenty of the largest seedling root systems were carefully extracted from each seedbed type in the open and in the shade. The total length of the taproot of each was measured in centimetres and compared by means of "t" tests (Snedecor 1956). The results are given in Table 7.

TABLE 6. THE PER CENT MORTALITY OF SEEDLING CROPS WHICH GERMINATED DURING WATERING AND DRYING AFTER EQUAL PERIODS OF DROUGHT

Drought period (No. of days after July 13)	Watering periods for the shaded seedlings				
	Crop 1 13-16 days	Crop 2 9-12 days	Crop 3 5-8 days	Crop 4 1-4 days	Crop 5 not watered
	(cumulative per cent mortality)				
4	0	1	2	10	3
8	0	2	2	15	16
12	2	3	5	24	23
16	4	4	8	26	30
20	9	9	14	42	41
24*	25	25	28	49	57

* Note:—These data are only given for twenty-four drought days.

TABLE 6. (Concluded)

Drought period (No. of days after July 13)	Watering periods for the exposed seedlings				
	Crop 1 13-16 days	Crop 2 9-12 days	Crop 3 5-8 days	Crop 4 1-4 days	Crop 5 not watered
	(cumulative per cent mortality)				
4	2	2	4	23	6
8	5	6	7	39	46
12	24	33	47	68	46
16	31	38	53	71	69
20	47	49	60	76	89
24	59	63	73	86	94

TABLE 7. A COMPARISON OF THE TAPROOT LENGTHS OF HYBRID SPRUCE GROWN IN THE EXPERIMENT

Shaded seedbeds		
Seedbed type	Mean taproot length (cms)	Maximum no. of days for growth*
Decayed wood.....	7.9	50
F. & H. humus.....	7.6	50
----- significant difference -----		
A _h horizon.....	4.1	47
----- significant difference -----		
Sandy loam.....	2.7	26
Exposed seedbeds		
Seedbed type	Mean taproot length (cms)	Maximum no. of days for growth*
Decayed wood.....	6.5	50
----- significant difference -----		
A _h horizon.....	4.2	39
----- significant difference -----		
Sandy loam.....	2.8	22
F. & H. humus.....	2.5	30

* Note:—The number of days in the 50-day drought period for which growth was possible before growth was stopped by mortality.

The best taproot development occurred on the seedbeds which were the most water retentive. Differences in taproot length are related to both the rate of growth and to the growth period. For example, seedlings on shaded decayed wood grew three times the average length of taproot as those on shaded sandy loam in twice the time. The order of superiority of mean taproot growth given in Table 7 for the separate exposed and shaded seedbed types is approximately the same

as that for mortality after 14 and 21 days of drought given in Table 4. It is likely that the relative survival of seedlings growing on the various seedbed types was related to their ability to maintain transpiration throughout the drought period by extension of their roots below the droughty zone of soil. When the rate of drying exceeded the rate of root extension the most severe mortality occurred.

DISCUSSION

The results of this study indicate that acute midsummer heating of the upper layers of the soil in clear cut areas is probably as serious a cause of seedling mortality and regeneration failure in the Rocky Mountain forests of southern Alberta as in similar forests in the United States (Bates 1923, Bates and Roeser 1924, Roeser 1932 and Daubenmire 1943).

This study demonstrates the rapidity with which hybrid spruce seedling mortality can occur during a period of midsummer drought in the Subalpine region. At this season, clear skies and low relative humidities permit such rapid drying and heating of the exposed soil surface that immature seedlings that germinate late, after the snow melts in May, are particularly subject to drought or stem girdle.

Shading significantly reduced seedling mortality on all seedbed types which were tested. The severity of seedling mortality in the shade appears to be more closely related to the lack of water retention through the period of drought than to the surface temperature. Thus, the best seedbeds, in order of superiority, were F. and H. humus and decayed wood followed by A_h horizon and sandy loam. Sandy loam dries out so rapidly in the shade that it proved to be more subject to mortality than the more water-retentive materials (A_h horizon and decayed wood) exposed to full insolation. In the shade, drought appears mainly to control seedling mortality. This is supported by the fact that three quarters of the shaded seedlings died from drought injury.

In the open, seedling mortality appears to be related both to water retention and to the degree of surface heating. Seedbeds which are subject to acute surface heating (e.g. F. and H. humus) are liable to severe stem girdle mortality even when moist at an inch depth. As a result, decayed wood and A_h horizon proved to be the best seedbeds in the open. F. and H. humus which suffered from severe surface heating and sandy loam which was the driest followed in order of superiority. All seedbeds in the open were more liable to surface heating than equivalent seedbeds in the shade. This is supported by the fact that three quarters of the exposed seedlings died from stem girdle.

This study helps to explain the tendency for spruce (and probably to a lesser extent, fir) regeneration to be found in greatest abundance on decayed wood, mineral soil with incorporated humus and F. and H. humus seedbeds in shaded microenvironments on clear cut land. The study also helps to explain the reason for the very slow re-establishment for spruce after clear cutting in the Subalpine forests of southern Alberta. The results of this study do not commend the present harvesting practices in the region, nor do they support the theory that the scarification of clear cut areas constitutes a generally applicable regeneration method for hybrid spruce or fir in the Subalpine region. The study indicates that research should be directed to the development of harvesting methods and seedbed treatments that will provide shelter to seedlings so as to minimize the effects of summer drought and excessive surface heating by protection of the soil surface during the regenerative phase.

SUMMARY

In 1961 an experiment was conducted which demonstrated that summer heating and drying of the soil surface can be a severe cause of seedling mortality on logged-over land in the Subalpine forests of southern Alberta. The study followed two earlier field studies in the Crowsnest Forest. These had shown that the hybrid spruce and alpine fir¹ regeneration, which had become established after logging, was mainly restricted to moist and shaded microenvironments. Studies from similar Cordilleran areas in the United States support the theory that this distribution of spruce and fir regeneration is caused by adverse heating and drying of the soil surface after the removal of tree cover.

Spruce seed was sown on four replicated seedbed types. These were contained in deep flats, exposed to full insolation and protected by 40 per cent shade. The seedbeds were maintained at field capacity for a month by watering. After sufficient germination was obtained, the watering was discontinued and drought artificially maintained for a fifty-day period by the exclusion of rainfall. The important findings are as follows:—

(1) It was demonstrated that severe mortality of hybrid spruce seedlings was caused by adverse heating and drying of the surface layers of four seedbed-types which were exposed to full insolation. A slat screen giving 40 per cent shade (or passing 60 per cent full light) significantly reduced mortality on all seedbed types tested.

(2) Seedling mortality increased in severity after watering ceased. Significantly different reactions to the various shade and seedbed treatments occurred after only seven days of drying. After fourteen days, the approximate final order of the treatments was established for the remainder of the drought period. At this time, shaded F. and H. humus (3 per cent mortality) and shaded decayed wood (5 per cent mortality) suffered least. These were followed by shaded A_h horizon (17 per cent mortality), the exposed decayed wood (18 per cent mortality), and the shaded sandy loam (22 per cent mortality). The most severely affected seedbeds were the exposed A_h horizon (41 per cent mortality), F. and H. humus (64 per cent mortality), and the sandy loam (80 per cent mortality). After twenty-one days of drying, seedling mortality had become very severe on the exposed sandy loam (100 per cent mortality), the exposed F. and H. humus (90 per cent mortality), the exposed A_h horizon (53 per cent mortality) and on the shaded sandy loam (86 per cent mortality).

(3) Seedling mortality in the shade was best correlated with the soil moisture retention of the seedbeds. In the open, mortality was correlated with both moisture retention and surface temperature. This was supported by the fact that three-quarters of the shaded seedlings died from drought whereas a similar proportion of the exposed seedlings died from stem girdle.

(4) Surface temperatures of 45° to 50°C. can cause stem girdle. However, severe girdling of seedlings in this temperature range depends on the severity of soil drought. Temperatures above 50°C. cause severe mortality even when the soil is moist at one-inch depth.

(5) The length of growing period before the onset of drought appears to reduce susceptibility to mortality. Taproot measurements indicate that mortality is reduced as long as the rate of root extension exceeds the rate of surface drying. This corroborates the theory that transpiration reduces susceptibility to stem girdle.

¹For nomenclature see footnote page 5.

(6) The results suggest that harvesting methods and seedbed treatments that will provide shelter to the seedlings will result in better regeneration than clear cutting.

SOMMAIRE

Une expérience effectuée en 1961 a démontré que la surchauffe et le dessèchement de la surface du sol en été peuvent être une cause importante de mortalité des semis dans les endroits exploités des forêts subalpines du sud de l'Alberta. Cette étude faisait suite à deux études antérieures effectuées sur place, dans la forêt de Crowsnest, qui avaient démontré que la régénération de l'épinette hybride et du sapin concolore¹, qui s'y était établie après la coupe, se limitait en majeure partie aux micro-milieus humides et ombragés. Des études effectuées aux États-Unis, dans des régions comparables aux Rocheuses, appuient la théorie que cette distribution de régénération d'épinette et de sapin est causée par des conditions défavorables de surchauffe et de dessèchement de la surface du sol après l'enlèvement du couvert forestier.

Pour cette étude, on a semé de la graine d'épinette dans de profondes boîtes de semis contenant quatre répliques de sol; on les a déposées en plein soleil puis on leur a assuré une ombre de 40 p. 100. On en a aussi maintenu, pendant un mois, par arrosage, la capacité de rétention d'eau utile. Après avoir obtenu une germination suffisante on a discontinué l'arrosage et on a maintenu une sécheresse artificielle par l'exclusion de la pluie pendant une période de 50 jours. Les conclusions importantes furent les suivantes:

(1) L'expérience a démontré qu'une mortalité importante des semis d'épinette hybride était due à la surchauffe et au dessèchement adverses de la couche superficielle des quatre types de planches de semis exposées au grand soleil. Un écran de lattes donnant une ombre de 40 p. 100 ou laissant passer 60 p. 100 de la lumière solaire réduisit sensiblement la mortalité dans tous les types de planches de semis mises à l'essai.

(2) La mortalité des semis a augmenté après la cessation de l'arrosage. Il s'est produit de sensibles différences de réaction aux divers degrés d'ombre et aux divers types de planches de semis après seulement sept jours de sécheresse. Après 14 jours, on était déjà fixé sur l'ordre de grandeur des résultats pour le reste de la période de sécheresse. A ce moment-là, les planches d'humus F. et H., à l'ombre (mortalité de 3 p. 100) et celles de bois pourri, à l'ombre (mortalité de 5 p. 100) avaient moins souffert. Venaient ensuite les planches d'horizon A_h, à l'ombre, (mortalité de 17 p. 100), celles de bois pourri exposées à la lumière solaire (mortalité de 18 p. 100) et de terre franche sableuse, à l'ombre (mortalité de 22 p. 100). Les planches de semis les plus durement éprouvées étaient l'horizon exposée A_h (mortalité de 41 p. 100), l'humus F. et H. (mortalité de 64 p. 100) et la terre franche sableuse (mortalité de 80 p. 100). Après 21 jours de sécheresse, la mortalité des semis était devenue très élevée dans les planches de terre franche sableuse, exposées à la lumière solaire (mortalité de 100 p. 100), d'humus F. et H. exposées à la lumière solaire (mortalité de 90 p. 100), d'horizon A_h exposées à la lumière solaire (mortalité de 53 p. 100) et de terre franche sableuse à l'ombre (mortalité de 86 p. 100).

(3) La mortalité des semis à l'ombre était surtout en rapport avec la faculté de rétention de l'humidité du sol des planches à semis. Au soleil, la mortalité était en rapport tant avec la faculté de rétention de l'humidité du sol qu'avec la

¹ Nomenclature: E. H. Moss 1959, *Picea engelmannii* Parry X *P. glauca* (Moench) Voss., *Abies lasiocarpa* (Hook.) Nutt., et *Pinus contorta* var. *Dougl. latifolia* Engelm.

température de surface. Cette constatation s'appuie sur le fait que trois quarts des semis à l'ombre sont morts de sécheresse alors qu'un pourcentage identique des semis exposés au soleil sont morts par suite de la brûlure du collet.

(4) Des températures de surface variant de 45° à 50°C peuvent causer la brûlure du collet, mais une brûlure prononcée des semis dans ces températures-là, dépend du degré de sécheresse du sol. Les températures supérieures à 50°C causent une mortalité élevée même lorsque le sol est humide à une profondeur d'un pouce.

(5) La longueur de la période de croissance antérieure à la sécheresse semble réduire la prédisposition à la mortalité. Les mesurages des racines principales indiquent une diminution de la mortalité aussi longtemps que le taux de croissance des racines excède le taux de dessèchement de la surface, ce qui corrobore la théorie que la transpiration réduit la prédisposition à la brûlure du collet.

(6) Les résultats semblent indiquer que les méthodes de récolte et les traitements des planches à semis qui assureront l'abri des semis, donneront une meilleure régénération que la coupe à blanc.

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APPENDIX I

TABLE 1. ANALYSIS OF VARIANCE OF SPRUCE GERMINATION

Source of Variation	Degrees of freedom	Sum of squares	Variance	F. Ratio
Blocks.....	4	808.4	202.1	2.11 NS†
Shade treatments.....	1	750.2	750.2	7.83**
Seedbed treatments.....	3	6,794.1	2,264.7	23.62**
Interaction.....	3	338.7	112.9	1.18 NS†
Total treatments.....	7	7,883.0	1,126.1	11.75**
Error.....	28	2,684.4	95.9	—
Total.....	39	11,357.8	—	—

**Significant at the 1% level

†Non-significant

TABLE 2. CRITICAL DIFFERENCES BETWEEN THE MEANS

E4~E1 30.8**	E3~E1 29.6**	E1~S1 10.4 NS†	E2~S4 12.8*
E4~E2 0.2 NS†	E3~E2 2.4 NS†	E1~S2 30.8**	S4~S1 34.4**
E4~E3 1.2 NS†	E3~S1 19.2**	E1~S3 41.0**	S4~S2 14.0*
E4~S1 20.4**	E3~S2 1.2 NS†	E1~S4 44.8**	S4~S3 3.8 NS†
E4~S2 0.0 NS†	E3~S3 11.4 NS†	E2~S1 21.6**	S3~S1 30.6**
E4~S3 10.2 NS†	E3~S4 15.2*	E2~S2 1.2 NS†	S3~S2 10.2 NS†
E4~S4 14.0*	E1~E2 32.0**	E2~S3 9.0 NS†	S1~S2 20.4**

*Significant at the 5% level

**Significant at the 1% level

†Non-significant

Key:—E Exposed seedbed S Shaded seedbed 1 Decayed wood 2 F. & H. humus
3 A_b horizon 4 Sandy loam

APPENDIX II

TABLE 1. ANALYSIS OF VARIANCE OF PER CENT MORTALITY OF SPRUCE AFTER 7 DAYS OF DROUGHT

Source of Variation	Degrees of freedom	Sum of squares	Variance	F. Ratio
Blocks.....	4	120.7	30.1	1.31 NS†
Shade treatments.....	1	1,485.4	1,485.4	64.44**
Seedbed treatments.....	3	1,218.4	406.1	17.62**
Interaction.....	3	262.4	87.5	3.80*
Total treatments.....	7	2,966.2	423.7	18.38**
Error.....	28	645.5	23.1	—
Total.....	39	3,741.5	—	—

*Significant at the 5% level.

**Significant at the 1% level.

†Non-significant.

TABLE 2. CRITICAL DIFFERENCES BETWEEN THE MEANS

E4~E1 2.5 NS†	E3~E1 8.2*	E1~S1 19.1**	E2~S4 3.6 NS †
E4~E2 11.3**	E3~E2 16.6**	E1~S2 12.6**	S4~S1 7.2*
E4~E3 5.3 NS†	E3~S1 27.3**	E1~S3 1.4 NS†	S4~S2 0.7 NS†
E4~S1 22.0**	E3~S2 20.8**	E1~S4 11.9**	S4~S3 10.5**
E4~S2 15.5**	E3~S3 9.6**	E2~S1 10.8**	S3~S1 17.7**
E4~S3 4.3 NS†	E3~S4 20.1**	E2~S2 4.2 NS†	S3~S2 11.1**
E4~S4 14.8**	E1~E2 8.3*	E2~S3 7.0*	S1~S2 6.5*

*Significant at the 5% level.

**Significant at the 1% level.

†Non-significant.

Key:—E Exposed seedbed S Shaded seedbed 1 Decayed wood 2 F. & H. humus
3 A_b horizon 4 Sandy loam

Note:—Percentage mortality was converted to $(\text{Arc sin } \sqrt{\text{Percentage}})$ for statistical analysis (Snedecor 1956).

APPENDIX III

TABLE 1. ANALYSIS OF VARIANCE OF PER CENT MORTALITY OF SPRUCE AFTER 14 DAYS OF DROUGHT

Source of Variation	Degrees of freedom	Sum of squares	Variance	F. Ratio
Blocks.....	4	154.0	38.5	0.78 NS†
Shade treatments.....	1	7,717.3	7,717.3	156.57**
Seedbed treatments.....	3	4,855.6	1,618.5	32.82**
Interaction.....	3	1,349.3	449.8	9.13**
Total treatments.....	7	13,922.2	1,998.9	40.55**
Error.....	28	1,380.3	49.3	—
Total.....	39	14,977.9	—	—

**Significant at the 1% level

†Non-significant.

APPENDIX III—Concluded

TABLE 2. CRITICAL DIFFERENCES BETWEEN THE MEANS

E4~E1 41.5**	E3~E1 14.4**	E1~S1 16.6**	E2~S4 24.5**
E4~E2 12.7**	E3~E2 14.3**	E1~S2 12.8**	S4~S1 20.8**
E4~E3 27.0**	E3~S1 31.0**	E1~S3 1.3 NS†	S4~S2 17.0**
E4~S1 58.0**	E3~S2 27.2**	E1~S4 4.2 NS†	S4~S3 5.6 NS†
E4~S2 54.2**	E3~S3 15.8**	E2~S1 45.3**	S3~S1 15.2**
E4~S3 42.8**	E3~S4 10.2*	E2~S2 41.5**	S3~S2 11.4**
E4~S4 37.2**	E1~S2 12.8**	E2~S3 30.1**	S1~S2 3.8 NS†

*Significant at the 5% level.

**Significant at the 1% level.

†Non-significant.

Key:—E Exposed seedbed S Shaded seedbed 1 Decayed wood 2 F. & H. humus
 3 Ah horizon 4 Sandy loam

Note:—Percentage mortality was converted to $(\text{Arc sin } \sqrt{\text{Percentage}})$ for statistical analysis (Snedecor 1956).

APPENDIX IV

TABLE 1. ANALYSIS OF VARIANCE OF PER CENT MORTALITY OF SPRUCE AFTER 21 DAYS OF DROUGHT

Source of Variation	Degrees of freedom	Sum of squares	Variance	F. Ratio
Blocks.....	4	72.9	18.2	0.48 NS†
Shade treatments.....	1	7,898.9	7,898.9	206.35**
Seedbed treatments.....	3	12,975.8	4,325.3	113.00**
Interaction.....	3	2,647.4	822.5	23.05**
Total treatments.....	7	23,522.1	3,360.3	87.78**
Error.....	28	1,071.8	38.3	—
Total.....	39	24,662.8	—	—

**Significant at the 1% level.

†Non-significant.

TABLE 2. CRITICAL DIFFERENCES BETWEEN THE MEANS

E4~E1 52.3**	E3~E1 11.3**	E1~S1 15.1**	E2~S4 7.6 NS†
E4~E2 15.9**	E3~E2 25.1**	E1~S2 19.4**	S4~S1 43.9**
E4~E3 41.0**	E3~S1 26.4**	E1~S3 6.7 NS†	S4~S2 48.2**
E4~S1 67.4**	E3~S2 30.7**	E1~S4 28.8**	S4~S3 35.5**
E4~S2 71.7**	E3~S3 18.1**	E2~S1 51.5**	S3~S1 8.4*
E4~S3 59.0**	E3~S4 17.5**	E2~S2 55.8**	S3~S2 12.7**
E4~S4 23.5**	E1~E2 36.4**	E2~S3 43.1**	S1~S2 4.3 NS†

*Significant at the 5% level.

**Significant at the 1% level.

†Non-significant.

Key:—E Exposed seedbed S Shaded seedbed 1 Decayed wood 2 F. & H. humus
 3 Ah horizon 4 Sandy loam

Note:—Percentage mortality was converted to $(\text{Arc sin } \sqrt{\text{Percentage}})$ for statistical analysis (Snedecor 1956).

APPENDIX V

TABLE 1. THE STATISTICAL RESULTS OF TAPROOT LENGTH COMPARISONS IN THE SHADE

Seedbed Type	Seedbed Type		
	Decayed wood	F. & H. humus	A _h horizon
	(Levels of probability)		
F. and H. humus.....	0.5-0.4 NS †	—	—
A _h horizon.....	-0.001**	-0.001**	—
Sandy loam.....	-0.001**	-0.001**	-0.01**

**Significant at the 1% level or less.

†Non-significant

TABLE 2. THE STATISTICAL RESULTS OF TAPROOT LENGTH COMPARISONS IN THE OPEN

Seedbed Type	Seedbed Type		
	Decayed wood	F. & H. humus	A _h horizon
	(Levels of probability)		
F. and H. humus.....	-0.001**	—	—
A _h horizon.....	-0.001**	-0.001**	—
Sandy loam.....	-0.001**	-0.4-0.2 NS†	-0.01**

**Significant at the 1% level or less.

†Non-significant.