Effects of Light and Soil Moisture on Forest Tree Seedling Establishment

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CONTENTS

SUMMARY

The present studies were designed to aid in the solution of forest tree seedling establishment problems common to stand conversion practices in Iowa. The primary objectives were: (1) to determine the minimum treatment needed to insure successful survival and growth; (2) to study the relationships of light and soil moisture in plant competition resulting from stand conversion; and (3) to evaluate five species of conifers — European larch, Scotch pine, eastern white pine, Norway spruce and red pine — for adaptability to region, site and underplanting.

Field studies were made at the Brayton Forest in northeastern Iowa and consisted of (1) practical understory treatments to increase survival and growth of five underplanted conifers and (2) controlled experiments to evaluate overstory and understory competition in such plantings. Studies at the State Forest Nursery near Ames were planned to determine the relative growth and photosynthetic characteristics of three of the underplanted conifers (European larch, eastern white pine and Norway spruce) and two shrubby hardwood species (dogwood and hazel) which offer serious understory competition in the forest.

The results of these studies led to the following conclusions: (1) An intensive cutting of the understory and overstory canopies is needed for maximum survival and growth of underplanted forest tree seedlings on the more fertile Iowa soils. (2) A gradual 2-year release of understory-overstory canopies, or the use of heribicides during the critical May-July growth period, or both, probably will be necessary to prevent extreme competition from a released shrubby and herbaceous cover. (3) Light saturation values ranged from 2,500 to 3,500 footcandles for all species, and near-maximum growth rates occurred at approximately 3,500 footcandles for all species except European larch. (4) Drouth survival of forest tree seedlings was increased with an increase in light intensity up to 3,000 footcandles. (5) European larch and eastern white pine are the only species that can be recommended at this time for underplanting; larch, because of its rapid rate of growth under intensive release cuttings; white pine, because of its adaptability to shade and root competition under less intensive cuttings. (6) Growth and photosynthetic efficiency of hazel and dogwood are sufficiently high to cause serious competition for all the conifers studied. (7) The photosynthetic compensation point can be used as an indicator of the tolerance and efficiency of some species. (8) Tolerance is a result of the adaptability of a species to competition for light, soil moisture and nutrients.

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by G. E. Gatherum,[2] A. L. McComb[3] and W. E. Loomis[4]

More than 18 percent (472,000 acres) of the commercial forest area in Iowa is in nonstocked stands (Morgan and Compton 1956). These stands contain so little timber that they are not grouped in any acceptable saw timber, pole timber or seedling and sapling classification. The high density of undesirable shrubs and noncommercial tree species that invade these understocked areas precludes their use in timber production until a new stand is established. The inferior shrubs and tree species must be replaced through a combination of overstory-understory canopy removal and underplanting practices.

A thorough understanding of forest tree seedling establishment is the primary requisite for a successful stand conversion program. These studies were designed to aid in the analysis of seedling establishment problems when stand composition is being changed by underplanting. The primary objectives were: (1) to determine the minimum treatment needed to assure successful survival and growth of underplanted conifers; (2) to study the relationships of light and soil moisture in plant competition through (a) field tests of survival and growth and (b) controlled tests of growth and photosynthesis; and (3) to evaluate five species of conifers to determine their adaptability to region, site and underplanting.

Field studies were made at the Brayton Forest in northeastern Iowa and consisted of (1) practical understory treatments to increase survival and growth of five underplanted conifers and (2) an evaluation of overstory and understory competition with such plantings. Studies at the State Forest Nursery near Ames were planned to determine the relative growth and photosynthetic characteristics of three of the underplanted conifers and of two shrubby, hardwood species that offer serious understory competition in the forest.

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REVIEW OF LITERATURE

Since the first writings of Heyer (1852) on the relative importance of light and soil moisture on establishment of forest reproduction, investigations related to this problem have been both numerous and controversial. Most of the early methods of securing adequate reproduction and high growth rates were based on the work of Heyer. The presence or absence of reproduction usually was attributed to light. Many foresters thought that the high survival of some tree species under the shade of others was principally a matter of plant efficiency under low light intensities. Others attributed the differences among species to variation in responses related to light quality as modified by transmission through the canopy.

In the early 1900's, several research foresters suggested that too much emphasis had been placed on light at the expense of other environmental factors. Some of the conclusions from the early investigations were questioned because of the inadequacy of the photometers used and of the methods used to determine the minimum light requirement. The objections were best described by Grasovsky (1929, p. 23).

"1. The amount of light to which a plant is exposed is not an index to the amount it uses.

2. There are many factors other than light which affect the survival of plants in a given habitat and which must be considered.

3. Light is not the only factor causing the death of the lower limbs of trees in stands where measurements of the minimum light requirements were taken."

The trenching experiments by Fricke (1904) and Toumey (1929) gave impetus to studies of soil moisture. In such experiments, a trench approximately 3 feet deep was dug around the perimeter of one plot, while a paired plot was not treated. Competition from vegetation adjacent to the trenched plot was eliminated when all roots were severed. The increase in soil moisture under conifers through trenching was associated with changes in the vegetation of the forest floor, changes previously associated with increased illumination. Similar results were obtained in other experiments (Aaltonen 1926, Biswell 1935, Coile 1940, Craib 1929, Daubenmire 1930, Grasovsky 1929, Korstian and Coile 1938, Toumey and Kienholz 1931, Toumey and Korstian 1946). However, the inference that light intensity usually is subordinate to soil moisture in the establishment and growth of reproduction was challenged by several investigators (Gordon and Buell 1945, Lutz 1945, Olmstead 1941, Pearson 1930, Shirley 1945). Some early, and many contemporary, studies concerning the effect of light and moisture on photosynthesis, survival and growth of tree seedlings emphasize the importance of both light intensity and soil moisture (Baker 1934 and 1951, Bates 1925, Bates and Roeser 1928, Bourdeau 1954, Burns 1923, Chapman 1945, Decker 1954, Fabricius 1927, Kozlowski 1949, Kramer 1957, Kramer and Clark 1947, Kramer and Decker 1944, Oosting and Kramer 1946).

METHODS OF INVESTIGATION

Field Investigations

Practical Understory Treatments

A study designed to test several understory treatments of possible value in stand conversion practices was established in March 1956 as one approach to artificial regeneration under low-grade forest canopies. The primary objective was to test several methods of potential practical value in understory treatment and to obtain information on materials, equipment and effects on competing understory plants and on planted seedlings.

The experimental area was located in the northeast corner of the Brayton Forest in Delaware County, Iowa. The soil of the experimental area is Fayette silt loam (Eschner 1952), a gray-brown podzolic soil widely distributed in northeastern and eastern Iowa. The parent material is loess. The Fayette soils are moderately fertile, naturally well-drained and readily subject to erosion when disturbed. They occupy the rounded crests of ridges and cover the lower slopes except in hilly uplands. Eschner (1952) found Fayette silt loam to be the most productive of the upland hardwood soils in the Brayton Forest. The experimental plots were located in a cove position on a small drainage with a southwest aspect. Specifically, the aspect averaged 50°W, and the slope, 25 percent. Erosion was slight to none.

The forest in which this study was conducted is typed as partially cut-over, white oak-northern red oak-northern pin oak, good site (Eschner 1952). High-grading practices over the past 50 years have resulted

Fig. 1. Hilly topography and inferior overstory representative of the better section of the area in which the studies were conducted at the Brayton Forest, Iowa.

Fig. 2. Dense understory of dogwood and hazel, characteristic of much of the experimental area, Brayton Forest, Iowa.

in a stand of inferior species and of poor quality stems of desirable species. The overstory consisted primarily of the following species in order of abundance: northern red oak (*Quercus rubra* L.),[5] white oak (*Quercus alba* L.), white elm (*Ulmus americana* L.), northern pin oak (*Quercus ellipsoidalis* E. J. Hill) and shagbark hickory (*Carya ovata* (Mill.) K. Koch.). The major components of the understory in order of abundance were: dogwood (*Cornus spp.* L.), hazel (*Corylus americana* Walt.), ironwood (*Ostrya virginiana* (Mill.) K. Koch.), raspberry and blackberry (*Rubus spp.* L.) and smooth sumac (*Rhus glabra* L.). In much of the area, the density of dogwood and hazel had increased appreciably because of the poor management practices. The typical topography and stand composition are shown in figs. 1 and 2.

The study was established as a split-split-plot ex-

[5] All scientific names are taken from Little (1953).

periment in a randomized complete block design (Cochran and Cox 1957). Each of the three replicates was divided into four plots. These plots received the following basic treatments intended to control understory growth and so favor development of the planted species: check, burning, treatment with a rotary brush beater or basal application of a brush-killer mixture. The basic treatments were made late in March 1956. The brush killer was applied to the understory as a basal spray in a solution consisting of 0.5 pound of 2,4-D + 2,4,5-T in 3 gallons of kerosene. Subplots were established by treatment of half of each plot with a foliage spray on Aug. 16, 1956, to test the need for follow-up control of competing vegetation. This spray contained 0.25 pound of the 2,4-D + 2,4,5-T mixture in 2.5 gallons of water plus 0.5 gallon of kerosene with a wetting agent. The mixture was applied at the rate of 8 gallons per acre.

Sub-subplots of 30 plants of each of five species of conifers, representing a wide range of tolerance, were established in each subplot the first week in April. The following species were used:

1. European larch (*Larix decidua* Mill.), very intolerant.[6]
2. Red pine (*Pinus resinosa* Ait.), intolerant.
3. Scotch pine (*Pinus sylvestris* L.), intolerant.
4. Eastern white pine (*Pinus strobus* L.), intermediate.
5. Norway spruce (*Picea abies* L.), very tolerant.

A 100-percent inventory of conifer survival was made 1 month after planting to evaluate the condition of stock and planting efficiency. Survival, height, and diameter and height growth of all conifers were measured in early fall of 1956, 1957 and 1958. Spring survival was checked in 1957 and 1958.

Controlled Understory Cuttings at Different Overstory-Understory Densities

This study was planned to determine the effect of light and soil moisture on establishment and growth of underplanted conifers. Variation in the intensity of competition was obtained through controlled cutting of the understory in stands of different overstory-understory densities. The location, soils, topography and vegetal cover of the experimental area were the same as described in the first study.

This study was established as a split-plot experiment in a randomized complete-block design within unreplicated, fixed main-plot canopies. The unreplicated main plots established in March 1956 were:

1. No overstory and a dense understory of 24,000 stems per acre that averaged 15 feet in height;
2. A moderate overstory of 87 square feet of basal area and a sparse understory of 6,900 stems per acre that averaged 10 feet in height;
3. A moderate overstory of 117 square feet of basal area and a moderately sparse understory of 10,100 stems per acre that averaged 10 feet in height.

Three replications were established within each of the three covers. Each replicate was divided into four plots. One of the following intensities of cut was assigned to each plot: all understory stems clearcut, two-thirds of the stems removed, one-third removed, none removed. Although stumps of all stems were sprayed with brush killer immediately after cutting and although additional stems not removed were frilled and sprayed with chemical to maintain the desired intensities, considerable sprouting occurred over the 3-year period. Light intensity readings at seedling height, used as a check on cutting intensity over the 3-year period for all overstory canopies, averaged 14, 18, 33 and 71 percent of clear-day light for the check, one-third, two-thirds and clearcut treatments. Measurements of clear-day sunlight in the open between 10 a.m. and 2 p.m. averaged 7,600 footcandles for the 3-year period. Subplots of 30 plants each of European larch, red pine, Scotch pine, eastern white pine and Norway spruce were established in each plot during the first week of April.

Soil moisture samples were obtained from all plots to a depth of 3 feet by 1-foot increments during April, June, August and October of 1956, 1957 and 1958 in the manner described by Lull and Reinhart (1955). Soil temperatures were taken periodically during the growing seasons of 1956, 1957 and 1958 at the surface, at 1-inch and at 3-inch depths from four-fifths of the plots. Light intensity measurements were taken with a Weston illumination meter three times during each of the growing seasons of 1956, 1957 and 1958. Sampling was done on cloudless days between 10 a.m. and 2 p.m. The sequence of measurements was changed through the nine periods of sampling to avoid bias which might occur from seasonal changes in the altitude of the sun. The intensity of sampling was limited to 25 readings per plot to insure a complete recording of light intensities for all plots in 1 day. The photoelectric cell was swung rapidly in a short arc at conifer seedling height to obtain an average of the variable light intensities resulting from the partial diffuse and direct light found under leaf canopies. Survival, height, and height and diameter growth of all conifers were measured in the same manner as described for the first study.

Nursery Investigations

As an adjunct to the studies conducted at the Brayton Forest, a series of growth and photosynthesis tests was established at the State Forest Nursery. These experiments, in which better control of light and soil moisture was possible, enabled a more critical evaluation of the relative effects of light intensities

[6] Tolerance classifications are taken from Baker (1951).

and soil moisture levels on forest tree seedling establishment.

The experimental area was located in the northwest corner of the Iowa Conservation Commission State Forest Nursery, 1 mile south of Ames, Iowa. The soil of the experimental nursery area is O'Neill sandy loam, a brunizem. Its parent material is stratified outwash of the Cary or Mankato glacial drift, or both. This soil occupies high terraces that vary from nearly level to somewhat eroded. The soils and subsoils are not calcareous but tend to be drouthy as the solum overlies a substratum of stratified coarse sand and gravel (Brown 1936).

Growth Test

This study was established as a split-split-plot experiment in a randomized complete-block design (Cochran and Cox 1957). Three replications of three light intensity plots of 480 footcandles, 3,490 footcandles and 7,120 footcandles were established by the construction of nine, 9 x 9 x 6-foot temporary greenhouses from lumber, lath, polyethylene sheet and muslin (fig. 3). These light intensities were measured at noon on clear days, at which time the light intensity in the open averaged 8,440 footcandles. Subplots of two available soil moisture ranges were established within each greenhouse, one from 0.6 to 4.3 inches (12 to 22 percent by weight), the other from 2.8 to 4.3 inches (18 to 22 percent by weight) within the 2-foot soil layer above the gravelly subsoil. The higher soil moisture level was close to the field capacity; the lower varied between near wilting and the field capacity. Within each soil moisture and light intensity treatment, sub-subplots of 20 weighed seedlings each of European larch, hazel, eastern white pine and Norway spruce were established in April 1957. Dogwood was seeded at a rate sufficient to insure 20 healthy seedlings per sub-subplot when thinned 1 month later. Dogwood and hazel were lifted at the end of the growing season because of exceptionally

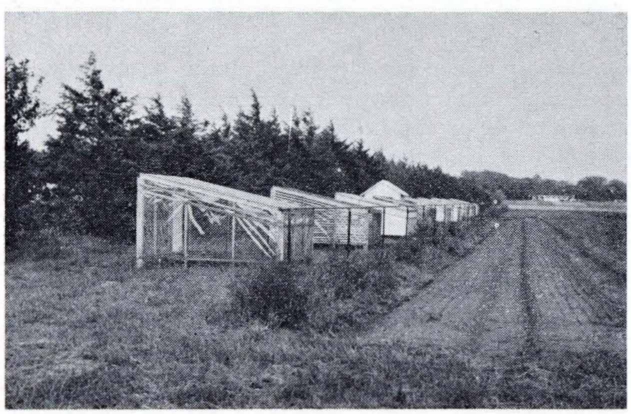

Fig. 3. General view of the greenhouses and mobile photosynthesis unit located at the experimental area, State Forest Nursery, Ames, Iowa.

profuse growth and were seeded again in the spring of 1958. Soil moisture levels and species were separated within each greenhouse by 1 x 12-inch boards.

The soil moisture ranges were maintained throughout the growing seasons of 1957 and 1958 by watering after determining needs with fiberglass-gypsum blocks. Units were placed at 3-, 9- and 15-inch depths in each of the soil moisture treatments in each greenhouse. Weekly measurements of light intensities, soil temperatures and relative humidities were taken within each greenhouse throughout the growing seasons of 1957 and 1958. Light intensities were measured with a Weston illumination meter. Ten readings were taken per greenhouse, and 10 were taken in the open, on cloudless days between 11 a.m. and 1 p.m. The sequence of measurements was changed weekly to avoid bias which could occur from seasonal changes in the altitude of the sun. The photoelectric cell was held at seedling height and swung rapidly in a short arc to average variable light intensities resulting from alternations of diffuse and direct light under the greenhouse covers. Soil temperatures were taken at the surface, at 1-inch and at 3-inch depths within each soil moisture and light intensity treatment. Relative humidities within each greenhouse were measured with a sling psychrometer. Daily fluctuations of soil temperature and relative humidity were determined through measurements at 9 to 10 a.m., 1 to 2 p.m. and 5 to 6 p.m.

A 100-percent inventory of seedling survival was taken 1 month after planting as a check on stock condition and planting efficiency. Hazel and dogwood were lifted in the fall of 1957, and green and oven-dry weights of tops and roots were determined. Survival, height, and diameter and height growth of all seedlings were measured in the fall of 1957 and 1958. Spring survival was checked in 1958. All seedlings were lifted in the early fall of 1958, and green root, shoot and total weights were obtained for all treatments. Samples were taken within each treatment. They were oven dried, and a green-dry weight ratio was determined. Green-weight growth for all species was determined as the difference between initial and final green weight. Shoot-root ratios were calculated for all species.

Photosynthesis Tests

To evaluate the effect of light and soil moisture on the photosynthesis of forest tree seedlings, studies having the following objectives were established:

1. To determine the effect of a range of light intensities on the apparent photosynthetic rates of three conifers and two hardwoods preconditioned at two light intensities and at a soil moisture level close to field capacity;

2. To determine the effect of a range of light intensities on the apparent photosynthetic rates of one conifer and one hardwood preconditioned at two light

intensities and two soil moisture levels; one close to the field capacity, the other varying between near wilting and the field capacity; and

3. To determine the compensation point, defined as the light intensity at which photosynthesis equals respiration, for three conifers and two hardwoods at an average temperature of 79°F.

In the first study, photosynthetic rates of European larch, eastern white pine, Norway spruce, dogwood and hazel seedlings were determined at light intensities ranging from 200 to 10,000 footcandles. The plants were preconditioned (grown) at 10 to 62 percent of clear-day light and within an available soil moisture range of 0.7 to 1.0 inch per foot (18 to 22 percent by weight) from July through August. The observations were replicated four times.

Photosynthesis determinations were made in the nursery with a mobile photosynthesis unit. The rates of photosynthesis were determined by the NaOH tower technique described by Chapman and Loomis (1953). Five absorption towers were used. One was used to measure atmospheric CO_2; the others, to determine CO_2 absorption by four potted seedlings of the same species exposed to different intensities of light.

During a photosynthesis run, the potted seedlings were placed in shade frames covered with various thicknesses of muslin so that light intensities ranging from 200 to 10,000 footcandles were obtained. One potted seedling was exposed to full sunlight, the other three were placed in frames that reduced light intensities to 30, 10 and 4 percent of clear-day light. Because of the variability in light intensities resulting from time changes and cloudiness, average light intensities were obtained with a Weston illumination meter during the hour run. Average temperatures also were obtained at each potted seedling. An additional check on the average light intensity was obtained through the use of the Gunn-Bellani radiation integrator (Shaw and McComb 1959). Seedlings were shifted so that each had been used at a different intensity of light by the time the four replications had been completed.

To express photosynthesis on a per-unit basis, the surface area and the weight of the leaves or needles of each plant were determined at the end of the tests. The surface area of the hardwood leaves was obtained with a planimeter. The surface area of needles was obtained by relating a sample of the needle area of each species to weight and then converting the weight of all of the needles to surface area. The surface area of a single needle of each species was obtained as follows:

1. Eastern white pine
   a. Perimeter $= 2 \text{ x radius} + \frac{2\pi \text{ radius.}}{5}$
   b. Surface area = perimeter x length.
2. European larch
   a. Surface area = length x width x 2.
3. Norway spruce
   a. Surface area = length x width x 4.

In the second study, the photosynthetic rates of eastern white pine and dogwood seedlings preconditioned at 10 or 62 percent of clear-day light and at 0.7 to 1.0 inch per foot (18 to 22 percent by weight) or 0.2 to 1.0 inch per foot (12 to 22 percent by weight) of available soil moisture were determined at light intensities ranging from 200 to 10,000 footcandles. Four replicates were used. Seedling pretreatment, photosynthesis determinations and leaf area and weight measurements were obtained as described for the first study.

In the third study, the photosynthetic rates of European larch, eastern white pine, Norway spruce, dogwood and hazel, preconditioned at 62 percent of clear-day light and within an available soil moisture range of 0.7 to 1.0 inch per foot (18 to 22 percent by weight) were determined at light intensities ranging from 0 to 350 footcandles. Four replications were used. The compensation point of each species at an average temperature of 79°F. was determined at the point where the regression line of CO_2 absorption on light intensity crossed the abscissa—the light intensity at which CO_2 uptake equals CO_2 evolution. Seedling pretreatment, photosynthesis determinations, and leaf area and weight measurements were obtained as described for the first study.

RESULTS

Field Investigations

Practical Understory Treatments

None of the understory treatments appreciably increased seedling survival or growth, although trends were evident (tables 1 and 2). Inadequacy of understory treatments, presence of overstory competition and insufficient experimental precision probably accounted for the lack of significance.

Three-year seedling survival for all treatments ranged from 10 to 21 percent, and differences were not significant (table A-1, Appendix). Survival of all species was reduced significantly during the second growing season (table 1). Some of this mortality presumably was due to insufficient release from understory vegetation, but much of it undoubtedly was due to overstory competition. In areas where understory vegetation had been almost completely suppressed, light intensity readings averaged no higher than 700 footcandles under the overstory canopy on a clear day at noon. Three-year seedling height growth per plant, as an average of all species, under burned, basal spray and brush-beater treatments was approximately 12,

Table 1. Seedling Survival Percentages of Five Conifers Under Four Understory Treatments, Brayton Forest, Iowa.

Growing season	Understory treatment	Red pine	European larch	Scotch pine	Norway spruce	Eastern white pine	Mean
1956	Check	3	30	31	66	73	41
	Burn	6	37	57	67	76	49
	Beater	23	50	56	74	77	56
	Basal spray	38	58	60	71	81	62
	Mean	18	44	51	70	77	52
1957	Check	0	4	12	22	44	16
	Burn	2	0	16	21	48	17
	Beater	12	8	27	27	57	26
	Basal spray	27	10	29	18	62	29
	Mean	10	6	21	22	52	22
1958	Check	0	2	9	11	26	10
	Burn	1	0	9	12	34	11
	Beater	9	3	20	22	46	20
	Basal spray	18	2	22	10	54	21
	Mean	7	2	15	13	40	15

Table 2. Three-Year Seedling Height Growth per Plant in Inches of Five Conifers Under Four Understory Treatments, Brayton Forest, Iowa.

Understory treatment	Red pine	Norway spruce	Eastern white pine	Scotch pine	European larch	Weighted mean
Check		4.7	6.4	8.2	9.6	6.4
Burn	5.0	4.8	7.8	10.0	8.6	7.2
Basal spray	5.3	5.5	7.8	10.5	12.5	7.7
Beater	5.7	6.0	8.5	11.1	8.4	8.1
Weighted mean	5.4	5.5	7.8	9.8	10.2	7.5

20 and 27 percent greater than on the check plots (table 2). The differences, though small, help to emphasize the need for more intense treatment of understory and overstory vegetation.

The 2,4-D + 2,4,5-T foliage spray applied in mid-August to half of each whole plot was ineffective because of the lateness of application. Earlier treatment was not possible because of damage to growing conifers by the brush killer spray. Arend (1955) found a marked susceptibility for all conifers of determinate growth habit before mid-August. These late treatments did not reduce understory competition during the critical May to July period.

Duncan's mean range test (Duncan 1955) showed the survival of eastern white pine to be significantly greater than that of all other species (table 1). Three-year height growth of individual plants of European larch and Scotch pine averaged approximately 10 inches; eastern white pine, 8 inches; and, Norway spruce and red pine, 5 inches (table 2). Subsequent experiments conducted with European larch, eastern white pine and Norway spruce under controlled conditions at the State Forest Nursery indicate that these growth rates were far below the potential of the species. Thus, removal of additional competing vegetation would probably have resulted in greater average height growth by all species.

Differences in diameter growth per plant among species and treatments were not statistically significant. Weighted mean diameter growth ranged from 0.05 to 0.07 of an inch. A comparison of the diameter growth per plant at the Brayton Forest and State Forest Nursery emphasizes again that the growth rates were far below the potential of the species.

Controlled Understory Cuttings at Different Overstory-Understory Densities

Third-year survival of all species grown in a moderate overstory and a moderate-to-sparse understory, or a moderate overstory and a sparse understory canopy was 20 percent higher than with no overstory and a dense understory (table 3). These differences, averages of all cutting treatments, were significant at the 1-percent level (table A-2, Appendix). Height growth per plant, as an average of all species for the 3-year period, was 11.5 inches for moderate overstory-moderate to sparse understory, 10.3 inches for the moderate overstory-sparse understory and 9.6 inches for the no overstory-dense understory canopy (table 4). The rapid sprouting and dense weed growth in the dense understory block reduced the effectiveness of the cutting treatments. Shirley (1945) concluded that conifer seedling development was controlled far more by the competition of a dense understory than by competition of an average overstory.

Survival and growth increased with intensity of understory cutting. Third-year survival in the plots with clearcut understory, where light averaged 71 percent of clear-day light, was 20 to 26 percent greater than in the plots with more understory growth and light intensities of 33 to 14 percent (table 5). These differences usually were significant at the 1-percent level. Height growth under 71, 33, 18 and 14 percent of clear-day light was 14.6, 9.4, 7.8 and 7.9 inches. Height growth increased with increasing light intensity between 18 and 71 percent of clear-day light (table 4).

Survival and growth of all species, except Norway

Table 3. Seedling Survival Percentages of Five Conifers Under Three Overstory-Understory Canopies, Average of All Understory Cutting Treatments, Brayton Forest, Iowa.

Growing season	Overstory-understory canopy	Scotch pine	Red pine	Norway spruce	European larch	Eastern white pine	Mean
1956	No,du[a]	21	43	56	84	75	56
	Mo,msu[b]	20	36	71	71	75	54
	Mo,su[c]	21	44	66	85	69	57
	Mean	21	41	64	80	73	56
1957	No,du	13	16	9	30	44	22
	Mo,msu	12	20	29	50	72	37
	Mo,su	17	30	32	68	64	42
	Mean	14	22	23	49	60	34
1958	No,du	4	9	1	17	29	12
	Mo,msu	10	18	20	42	67	32
	Mo,su	12	20	24	48	55	32
	Mean	9	16	15	36	50	25

[a] No overstory, dense understory.
[b] Moderate overstory, moderately sparse understory.
[c] Moderate overstory, sparse understory.

Table 4. Three-Year Seedling Height Growth per Plant in Inches of Five Conifers Under Three Overstory-Understory Canopies and at Four Light Intensity Levels, Brayton Forest, Iowa.

Overstory-understory canopy	Light-percentage of clear-day light	Species: Norway spruce	Red pine	Eastern white pine	Scotch pine	European larch	Weighted mean
No,du[a]	14	4.7	..	5.6		10.8	5.6
	18	..	..	4.8	5.7	12.6	7.1
	33			8.9		17.9	10.5
	71	9.2	9.3	11.5	14.9	23.6	14.6
	Weighted mean	4.2	3.9	7.6	7.2	18.2	9.6
Mo,su[b]	14	5.5	4.8	8.9	10.0	14.7	9.1
	18	4.1	5.4	7.0	7.6	15.7	8.6
	33	6.6	6.5	5.6	6.9	15.7	9.6
	71	6.4	6.5	12.4	13.0	20.3	13.1
	Weighted mean	5.7	5.8	8.4	9.3	16.5	10.3
Mo,msu[c]	14	4.3	7.6	8.1	6.4	9.1	7.3
	18	5.0		7.9	9.5	13.0	8.4
	33	5.8	7.8	6.5	8.7	13.4	7.8
	71	7.5	10.4	16.4	15.5	20.7	15.5
	Weighted mean	5.6	6.9	9.7	10.3	20.2	11.5

[a] No overstory, dense understory.
[b] Moderate overstory, sparse understory.
[c] Moderate overstory, moderately sparse understory.

Table 5. Seedling Survival Percentages of Five Conifers at Four Light Intensity Levels, All Overstory Plots, Brayton Forest, Iowa.

Growing season	Light—percentage of clear-day light	Species: Scotch pine	Red pine	Norway spruce	European larch	Eastern white pine	Mean
1956	14	15	28	75	68	77	53
	18	20	42	57	81	70	54
	33	23	29	64	80	72	54
	71	23	71	62	91	72	74
	Mean	21	42	64	80	73	56
1957	14	8	9	31	32	65	29
	18	8	11	17	42	52	26
	33	19	11	24	44	62	32
	71	20	57	19	80	68	49
	Mean	14	22	23	49	60	34
1958	14	4	7	23	20	54	22
	18	6	2	10	27	37	16
	33	8	6	15	24	48	20
	71	16	47	13	70	63	42
	Mean	9	16	15	36	50	25

Table 6. Two-Year Seedling Diameter Growth per Plant in Inches of Five Conifers Under Three Overstory-Understory Canopies and at Four Light Intensity Levels, Brayton Forest, Iowa.

Overstory-understory canopy	Light—percentage of clear-day light	Species: Norway spruce	Red pine	Eastern white pine	Scotch pine	European larch	Weighted mean
Mo,su[a]	14	0.06	0.06	0.07	0.08	0.05	0.06
	18		0.04	0.04	0.06	0.12	0.04
	33	0.03	0.05	0.07	0.03	0.09	0.08
	71	0.10	0.11	0.20	0.17	0.20	0.18
	Weighted mean	0.04	0.09	0.09	0.09	0.12	0.10
Mo,msu[b]	14	0.01	0.07	0.06		0.03	0.04
	18	0.04		0.07	0.10	0.08	0.09
	33	0.09	0.13	0.12	0.02	0.03	0.05
	71	0.14	0.14	0.25	0.17	0.18	0.20
	Weighted mean	0.05	0.11	0.15	0.12	0.13	0.12
No,du[c]	14	0.06	...	...	...	0.12	...
	18	...	...	...	0.04	0.05	0.02
	33	...	...	0.06	...	0.17	...
	71	0.14	0.13	0.18	0.19	0.27	0.20
	Weighted mean	0.08	0.11	0.14	0.22	0.23	0.16

[a] Moderate overstory, sparse understory.
[b] Moderate overstory, moderately sparse understory.
[c] No overstory, dense understory.

spruce, increased with light intensity from 33 to 71 percent of clear-day light, but, in general, differences among the plants at the three lower light intensities were not significant (tables 4, 5 and 6). These data corroborate the findings of Kozlowski (1949), Oosting and Kramer (1946) and Shirley (1945). The significant species-light interaction probably is related to the lower response of the more tolerant eastern white pine and Norway spruce to a reduction in competition. The less tolerant species usually give greater response to release from competition (Baker 1951).

The increased survival and growth responses of all species in this study over the practical treatment experiment probably resulted from a more intensive release of the conifers from overstory and understory competition in many of the plots. However, growth still was considerably below the potential shown in the State Nursery experiments.

Soil temperature and available soil moisture levels varied among the cutting treatments. The 3-year average surface soil temperature of the plots receiving 71 percent of clear-day light was 4°F. greater than that of the plots receiving 33, 18 and 14 percent of clear-day light. Average soil temperature differences among the light intensity treatments varied no more than 2°F. at the 3-inch soil depth. Differences in available soil moisture averaged 1 inch per 3 feet of soil depth among the plots for the 3-year period. Obviously, seedling behavior must be considered the net result of all interacting environmental and genetic factors. However, the relatively moderate differences among soil temperatures and moisture lend credence to the emphasis placed on light intensity as one of the controlling environmental factors.

Nursery Investigations

Growth Test

Average green-weight growth per plant increased with an increase in light intensity from 22 grams at 480 footcandles to 58 grams at 3,490 footcandles to 86 grams at 7,120 footcandles (table 7). Growth differences among light intensity levels were significant at the 1-percent probability level (table A-3, Appendix). Green weights of shoot and root growth increased approximately 140 and 155 percent from 480 to 3,490 footcandles and 46 and 32 percent from 3,490 to 7,120 footcandles. Shoot-root ratio differences were small and not significant.

Green-weight growth per plant was 10 percent greater at a soil moisture level close to field capacity than at a level between near-wilting and the field capacity. Shoot growth was 3.7 grams greater, and root growth, 1.5 grams greater under the high soil moisture level. Shoot-root ratios decreased approximately 12 percent with the increase in soil moisture. Growth differences between the two soil moisture levels approached significance at the 5-percent probability level, but the moisture-light interaction was insignificant. Insufficient experimental precision and partial failure of plot irrigation dividers may account for the lack of significance.

Differences among species in green-weight growth were significant at the 1-percent probability level for the 2-year period (fig. 4). European larch was 50, 139, 141 and 190 percent heavier than eastern white pine, Norway spruce, hazel and dogwood. Eastern white pine growth was significantly greater than the growth of Norway spruce, hazel and dogwood. Differences among Norway spruce, hazel and dogwood were not statistically significant. Differences among species-light intensity interactions, significant at the 1-percent probability level, were related generally to the marked increase in response of the very intolerant European larch to complete release from competition. Green weight of European larch increased 470 percent from 480 to 7,120 footcandles; tolerant Norway spruce, 242 percent; and tolerant dogwood, 217 percent. Green weight increases of eastern white pine, intermediate

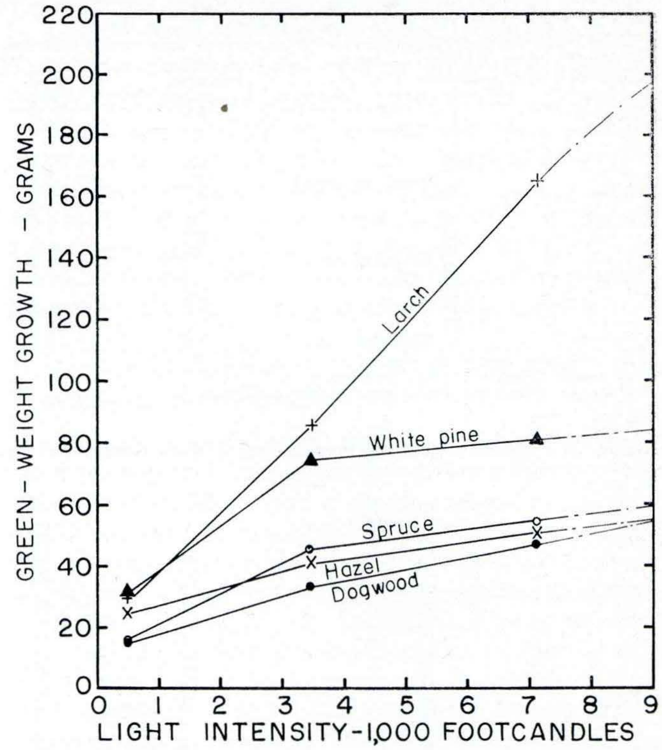

Fig. 4. Two-year seedling green-weight growth per plant of two hardwoods and three conifers at three light intensity levels, State Forest Nursery, Ames, Iowa.

Table 7. Two-Year Seedling Green-Weight Growth per Plant and Shoot-Root Ratios of Two Hardwoods and Three Conifers at Three Light Intensity and Two Soil Moisture Levels, State Forest Nursery, Ames, Iowa.

Light intensity—footcandles	Available soil moisture—inches per 2 feet of depth	Species					
		Dogwood	Hazel	Norway spruce	Eastern white pine	European larch	Mean
Total (grams)							
480	0.55 to 4.29	12.1	29.5	20.2	27.0	30.8	23.9
	2.77 to 4.29	18.0	19.6	11.7	35.1	26.8	22.2
3,490	0.55 to 4.29	27.1	40.0	45.4	69.3	87.5	53.9
	2.77 to 4.29	40.0	42.8	46.6	79.2	84.3	58.6
7,120	0.55 to 4.29	41.3	38.1	58.6	71.6	157.3	73.4
	2.77 to 4.29	54.5	62.2	50.9	90.8	172.2	86.1
Shoot (grams)							
480	0.55 to 4.29	6.2	17.9	15.4	21.0	25.0	17.1
	2.77 to 4.29	10.9	12.8	9.1	26.1	21.8	16.1
3,490	0.55 to 4.29	16.2	17.7	33.3	50.6	68.9	37.4
	2.77 to 4.29	24.8	28.2	33.8	58.0	67.0	42.4
7,120	0.55 to 4.29	25.7	22.5	40.2	56.4	127.5	54.5
	2.77 to 4.29	31.1	33.2	36.4	67.4	140.3	61.7
Root (grams)							
480	0.55 to 4.29	5.9	11.6	4.8	6.0	5.8	6.8
	2.77 to 4.29	7.1	6.8	2.6	9.0	5.0	6.1
3,490	0.55 to 4.29	10.9	22.3	12.1	18.7	18.6	16.5
	2.77 to 4.29	15.2	14.6	12.8	21.2	17.3	16.2
7,120	0.55 to 4.29	15.5	15.6	18.4	15.2	29.8	18.9
	2.77 to 4.29	23.5	29.0	14.5	23.4	31.9	24.4
Shoot-root ratio							
480	0.55 to 4.29	1.05	1.54	3.21	3.50	4.31	2.52
	2.77 to 4.29	1.54	1.83	3.50	2.90	4.36	2.64
3,490	0.55 to 4.29	1.49	0.79	2.75	2.70	3.70	2.26
	2.77 to 4.29	1.63	1.93	2.64	2.73	3.87	2.62
7,120	0.55 to 4.29	1.66	1.44	2.18	3.70	4.27	2.88
	2.77 to 4.29	1.32	1.14	2.51	2.88	4.40	2.53

in tolerance, and intolerant hazel were inconsistent with the tolerance concept; growth of the white pine increased 160 percent, growth of hazel, 105 percent.

Two-year height growth per plant, as an average of all species, increased 45 percent from 480 to 3,490 footcandles but decreased approximately 4 percent from 3,490 to 7,120 footcandles. Mean maximum height growth occurred at about 3,500 footcandles for all species except European larch. Height growth of the larch increased linearly to 7,120 footcandles. Average 2-year height growth for all species increased from 16.8 inches at the lower soil moisture level to 19.0 inches at the higher level. Differences in 2-year height growth between the two soil moisture levels were most pronounced in the two hardwoods. Dogwood increased 21 percent and hazel, 16 percent, from low to high moisture levels (table 8).

One-year seedling diameter growth, as an average of all species, increased from 0.05 to 0.12 to 0.13 of an inch at 480, 3,490 and 7,120 footcandles. Mean maximum diameter growth occurred again at about 3,500 footcandles. One-year diameter growth differences between the two soil moisture levels were not significant. Diameter growth per plant of European larch was 9 percent greater than that of dogwood, 30 percent greater than hazel and 71 percent greater than either eastern white pine or Norway spruce.

Soil temperatures and relative humidities varied among treatments. The average surface soil temperature of the plot receiving 7,120 footcandles exceeded the temperature of the plots under 3,490 and 480 footcandles by 5°F. in the 2-year period. Differences of average soil temperatures among the light intensity treatments varied by 4°F. at the 3-inch soil depth. Two-year average differences in relative humidity varied by 4 percent among the plots.

Photosynthesis Tests

Apparent photosynthesis of all species increased with light intensity up to approximately 2,500 to 3,000 footcandles and then decreased with an increase in light intensity from 3,000 to 10,000 footcandles (figs. 5 and 6). These results substantiate those found for some hardwoods by Bormann (1953), Bourdeau (1954), Decker (1954), Kozlowski (1949) and Polster (1950). In contrast, the rates of photosynthesis of some conifers have increased with light intensity up to full sunlight (Decker, 1954; Kozlowski, 1949; Kramer and Decker, 1944).

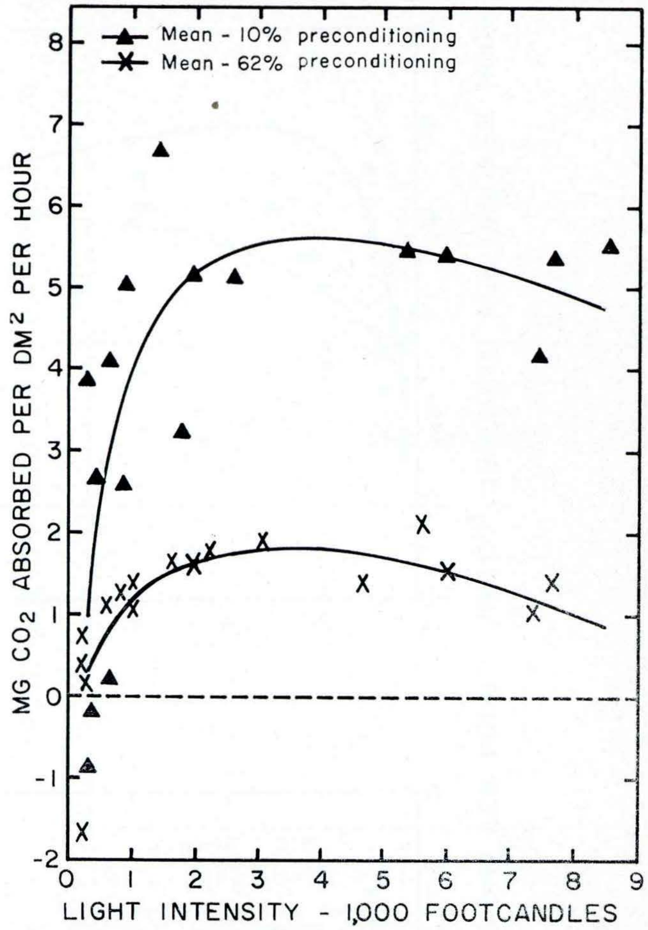

Fig. 5. Effect of light intensity on apparent photosynthesis of European larch preconditioned at 10 and 62 percent of clear-day light. Soil moisture level was near field capacity.

Photosynthesis of all species usually was higher and the variance was greater in the plants preconditioned at low light intensities (fig. 5). The difference in rates between 10 and 62 percent of clear-day light preconditioning was probably related to leaf structure and previous carbohydrate accumulation. All plants were grown under the same light and soil moisture conditions until July to minimize the effect of leaf structure on photosynthesis. However, additional growth during the preconditioning period resulted in the development of a few shade or sun leaves, especially in the hardwoods. The greater variance among seedlings preconditioned at 10 percent light may have resulted from a greater leaf structure difference among

Table 8. Two-Year Seedling Height Growth per Plant in Inches of Two Hardwoods and Three Conifers at Three Light Intensity and Two Soil Moisture Levels, State Forest Nursery, Ames, Iowa.

Light intensity—footcandles	Available soil moisture—inches per 2 feet of depth	Species					
		Norway spruce	Eastern white pine	European larch	Hazel	Dogwood	Mean
480	0.55 to 4.29	5.2	7.8	14.0	19.4	18.9	13.0
	2.77 to 4.29	6.0	7.5	13.2	18.3	24.2	13.8
3,490	0.55 to 4.29	6.3	10.6	21.9	23.2	33.3	19.1
	2.77 to 4.29	7.7	9.9	19.3	22.8	40.7	20.1
7,120	0.55 to 4.29	7.1	9.5	24.3	16.6	33.8	18.3
	2.77 to 4.29	7.1	11.1	29.6	27.4	39.2	22.8
Mean	0.55 to 4.29	6.2	9.3	20.1	19.7	28.6	16.8
	2.77 to 4.29	6.9	9.6	20.7	22.9	34.7	19.0

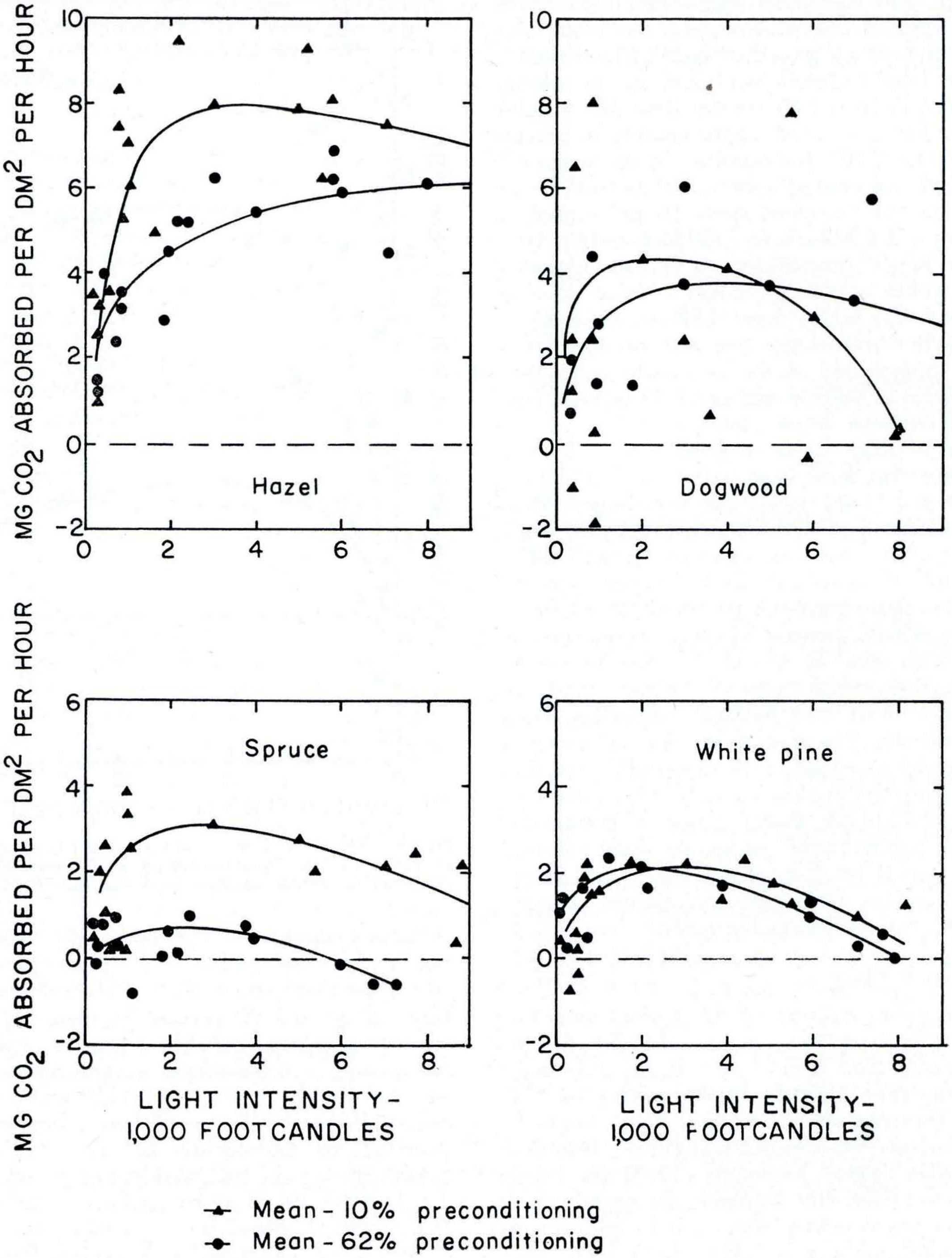

Fig. 6. Effect of light intensity on photosynthesis of hazel, dogwood, Norway spruce and eastern white pine preconditioned at 10 and 62 percent of clear-day light. Soil moisture level was near field capacity.

the individual plants, the difference being caused by a more drastic environmental change when seedlings were transferred from the pre-July initial treatment to the final preconditioning.

The rates of photosynthesis varied with species. The mean maximum rate of hazel was 52, 68, 179 and 318 percent greater than the rates of European larch, dogwood, Norway spruce and eastern white pine (table 9). The effect of light intensity on the rates of photosynthesis of all species preconditioned at two light intensities and one soil moisture level is shown in figs. 5 and 6. The wide variance and intermingling of points around the curves indicate trends but preclude exact statements. Considerable difficulty was encountered in obtaining close correspondence between replicate runs for a given species. The apparent discrepancy in the photosynthesis and growth response of European larch to light (figs. 4 and 5) may be related to the efficiency in the use of manufactured food. Although light saturation for photosynthesis was reached at approximately 3,000 footcandles, highly efficient use of photosynthate may have caused continued growth up to approximately 7,000 footcandles.

The effect of soil moisture level on photosynthesis varied with preconditioning treatment and species. Differences were inconsistent and not significant. Kramer (1959) suggests the measurement of leaf tissue moisture rather than soil moisture to avoid the problems related to differences in leaf and soil moisture tensions.

The compensation point of each species was determined as the point where the linear regression line of CO_2 absorption on light intensity crossed the abscissa. The compensation point of European larch was estimated at 115 footcandles at an average temperature of 78.5°F. (fig. 7). The compensation points of Norway spruce, dogwood, eastern white pine and hazel were progressively greater, up to approximately 350 footcandles. Inasmuch as only European larch and dogwood regressions were significant at the 1- and 5-percent probability levels, the aforementioned sequence merely indicates a trend. With the exception of European larch, the ranking of tree species according to their estimated compensation points conforms to the tolerance classification used by foresters: increased compensation point, decreased tolerance. The greater photosynthetic efficiency at low light intensities in relation to the maximum rates attainable at higher light may account in part for greater tolerance (fig. 8).

Table 9. Mean Maximum Rates of Apparent Photosynthesis in mg. CO_2 Absorbed per dm^2 per Hour for Each Species at Three Light Intensities.

	Light intensity—footcandles			
Species	480	3,490	7,120	Mean
Hazel	5.0	8.2	6.8	6.7
European larch	2.5	5.6	5.2	4.4
Dogwood	3.6	4.8	3.6	4.0
Norway spruce	2.2	3.0	2.1	2.4
Eastern white pine	1.6	2.2	1.0	1.6

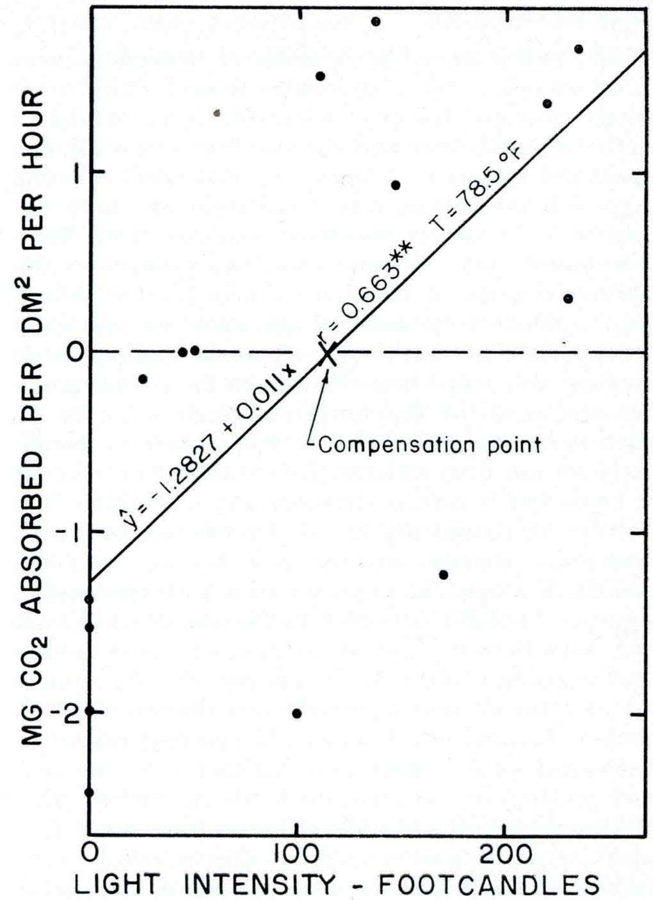

Fig. 7. Compensation point of European larch determined by the light intensity at which the rate of respiration equals the rate of photosynthesis.

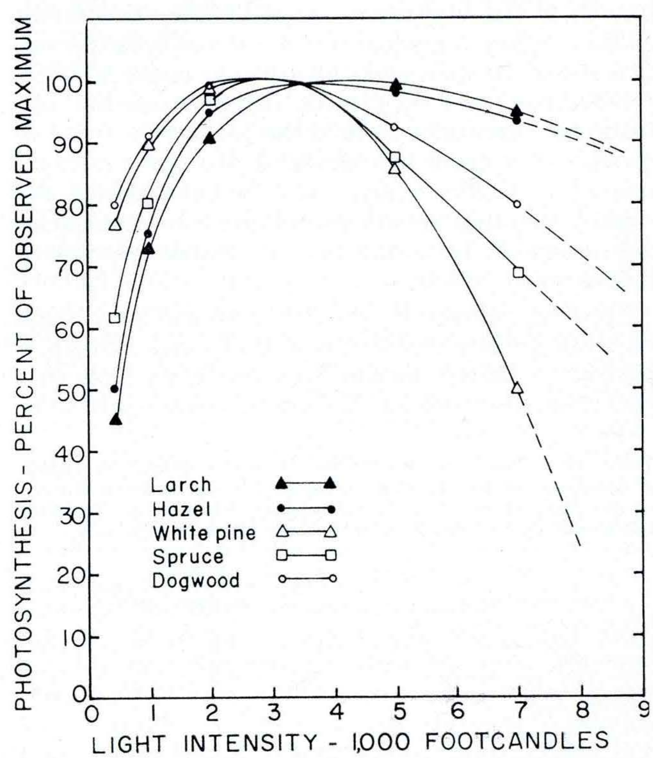

Fig. 8. Photosynthetic efficiency of three conifers and two hardwoods at low light intensities in relation to the maximum rates attainable.

DISCUSSION

All studies related to densities of understory-overstory canopies and to intensities of understory treatment, indicated the need for an intensive cutting of both the understory and the overstory. Survival was increased slightly by burning the understory, beating with a brush beater or by basal spraying (table 1). Height and diameter growth of seedlings at the Brayton Forest was markedly less than growth on the cultivated plots at the State Forest Nursery where near optimum conditions of soil moisture and light were maintained (table 10). A marked reduction in survival was noted from the first to the second growing season at the Brayton Forest (tables 1 and 3). This reduction probably was due in part to insufficient release from understory vegetation, but much of it undoubtedly was due to overstory competition. The average light intensity of 700 footcandles, measured under the overstory canopy on a clear day at noon, was far less than the approximately 3,500 footcandles required for light saturation in the controlled tests at the State Nursery. Complete removal of the overstory and understory at the Brayton Forest effected a marked increase in survival, height and diameter growth (tables 4, 5 and 6). However, the resulting release of herbaceous cover inhibited maximum development and resulted in soil moisture levels on cleared plots that were not significantly different from those subjected to less intense cutting. The relatively high fertility of the Fayette silt loam prevents an immediate cutting of all understory and overstory competition unless some technique is used to prevent the profuse growth of the herbaceous cover. Hawley and Smith (1954) suggest a gradual cutting over a 2-year period, that would be sufficiently intensive to insure seedling establishment and yet provide enough shade and soil moisture competition to hold the herbaceous cover in check. We suggest, in addition, a thorough investigation of herbicides which could be used during the critical May-July growth period, pre-conversion grazing or contour furrowing at 8- to 10-foot intervals to reduce weed growth.

Seedling damage by rabbits, deer and mice must be given primary consideration in all stand conversion programs. Animal damage was severe on plots that had a dense shrub or herbaceous undergrowth, or both. The damage decreased with an increase in the removal of understory shrubs and weeds; thus, the removal of understory shrubs and herbaceous vegetation would be a desirable adjunct to the use of repellents and poisons.

Recommendations regarding the need for control of competition have been based primarily on the results of applied experiments. A more fundamental evaluation of the specific light and soil moisture requirements of underplanted seedlings was attempted in studies at the Brayton Forest and at the State Forest Nursery. Survival of all species except Norway spruce increased with treatments that increased the light intensity from 33 to 71 percent of clear-day light at the Brayton Forest (table 5). Height growth of all species and diameter growth of all species except Norway spruce increased with light intensity from 18 to 71 percent of clear-day light (tables 4 and 6). Maximum height and diameter growth of all species except European larch was attained at approximately 3,500 footcandles at the State Forest Nursery (table 8).

The greater seedling growth response at the State Nursery over that at the Brayton Forest at similar light intensities probably can be attributed to differences in soil moisture and fertility levels. The 71-percent intensity of clear-day light at the Brayton Forest was actually equivalent to 5,381 footcandles, or nearly 2,000 footcandles more than the optimum light intensity in the nursery experiments; yet, lower growth response was obtained at the Brayton Forest. It is assumed that the release cutting necessary to give 71 percent of clear-day light at the forest did not increase water and fertility levels to those found at the State Nursery. The differences in rates of seedling height and diameter growth at the Brayton Forest and at the State Nursery suggest the need for an even more intensive treatment of the competing vegetation than the maximum used in the forest (table 10). The differences, although in part a result of side shade from the overstory of adjacent plots, are primarily a result of competition from sprouting shrubs and herbaceous vegetation. Once again, the necessity of compromising between complete removal of competing vegetation and partial removal to minimize sprouting and weed growth is evident. If no compromise is made, chemicals specific for sprouts and weeds during the critical May-July growth period, pre-grazing or contour furrowing must be used.

The rate of growth in the nursery experiments of all species except European larch was far more rapid with an increase in light from 480 to 3,490 footcandles than from 3,490 to 7,120 footcandles. The increased, but not quite significant, response of all species except Norway spruce to higher moisture levels at all light intensities (table 7) suggests that both moisture and light affect seedling establishment and growth, especially in view of the insufficient experimental precision and partial failure of the irrigation dividers.

Table 10. One-Year Height and Diameter Growth in Inches of Seedlings at the Brayton Forest as Compared With Growth on the Plots at the State Forest Nursery Where Near Optimum Conditions of Soil Moisture and Light Were Maintained.

Experimental area	Species: Norway spruce	Eastern white pine	European larch	Mean
Height growth:				
Brayton Forest, mean of all plots	1.8	2.6	3.4	2.6
Brayton Forest, 71% clear-day light plot mean	2.6	4.5	7.2	4.8
State Nursery	3.6	5.2	13.5	8.8
Diameter growth:				
Brayton Forest, mean of all plots	0.02	0.02	0.03	0.02
Brayton Forest, 71% clear-day light plot mean	0.02	0.06	0.07	0.05
State Nursery	0.10	0.10	0.17	0.12

Even though increased survival, height and diameter growth, and green-weight growth result from increased light intensities, maximum growth responses usually are attained in the forest where competition for both light and soil moisture is reduced. Korstian and Bilan (1957) obtained similar results in studies conducted with loblolly pine in North Carolina. Maximum development of the seedlings used in underplanting at the Brayton Forest should be reached if all understory and overstory competing vegetation is removed as rapidly as is consistent with the problems of excessive herbaceous growth and sprouting. The marked increase in green-weight root growth with an increase of light from 480 to 3,490 footcandles (table 7) is significant in terms of the greater root-absorbing surface of the seedlings grown at the higher light intensity. The greater total weight of seedlings at the lower moisture level under 3,490 and 7,120 footcandles of light, as compared with total weight under 480 footcandles, is closely related to the 197-percent increase in root weight (table 7). The increase in water and nutrient absorption associated with greater root development probably would insure greater survival and plant growth. Kozlowski (1949), Kramer and Decker (1944), and Oosting and Kramer (1946) attributed the reduction in loblolly pine mortality of open-grown seedlings to the increased root ramification resulting from higher light intensities, rather than to more favorable soil moisture conditions. Shirley (1929a, 1929b) obtained increased dry matter in tops, root-shoot ratios, density of growth, stem strength and leaf thickness with increasing light intensity for all species studied. These are characters usually associated with hardiness and drouth resistance (Loomis, 1953).

Light saturation for photosynthesis of the three conifers and two hardwoods was similar. Photosynthesis of all species increased with light intensity until a maximum rate was reached at approximately 2,500 to 3,000 footcandles. This light saturation level for photosynthesis would have been met in the Brayton Forest plots by cutting to obtain approximately 35 percent of clear-day light. The fact that light at 71 percent resulted in significantly greater growth of planted conifers than 33 percent in the forest indicates that factors other than light for photosynthesis were involved.

Beyond approximately 3,000 footcandles, the rate of photosynthesis of all species decreased at variable rates with an increase in light intensity up to 10,000 footcandles. Kramer (1957) suggested that two possible causes of the inhibition of photosynthesis were an accumulation of the products of photosynthesis and differences in leaf structure. Photosynthesis of all species, preconditioned at 10 percent of clear-day light, was generally higher than when preconditioned at 62 percent. Differences were thought to be primarily the result of carbohydrate accumulation in the leaves. However, the growth of new leaves during preconditioning resulted in the formation of some sun or shade leaves and, thus, confounded structure with carbohydrate accumulation.

Subsequent studies should be made which would separate the factors of leaf structure and carbohydrate accumulation. Bormann (1956) has suggested that fundamental variations in the anatomy of sun and shade leaves account for the difference in photosynthetic behavior. Tranquillini (1954) found the compensation point of several shade-grown seedlings to be much lower than that for sun-grown plants of the same species. In view of the results of the present investigation and those of Bormann and Tranquillini, the use of shade-grown nursery stock should be considered in underplanting procedures. A compromise would be necessary to prevent sacrifice of vigor, stockiness and potential winterhardiness, however.

The marked increase in the photosynthetic rate of all species with increase in light intensity up to approximately 3,000 footcandles suggests possibilities of increasing the drouth survival of seedlings. Increased photosynthesis at the higher light level leads to an accumulation of sugars during a dry period when growth is reduced. A shift to root growth under these conditions results in a relatively greater root system than in plants growing at lower light intensities (Loomis 1953).

In terms of survival, height and diameter growth, green-weight growth and photosynthesis, our recommendation concerning the five species of conifers for underplanting would be in the following order:

1. European larch
2. Eastern white pine
3. Scotch pine
4. Red pine
5. Norway spruce

Of these, European larch and eastern white pine are the only species that can be recommended without major qualification.

The survival of European larch was poor on plots where light intensity was low (table 1). However, the extremely rapid growth with decreased competition insured growth dominance of European larch over herbaceous and shrubby species in all areas studied. Height and diameter growth of European larch was essentially matched by Scotch pine only. The low survival of Scotch pine in all areas, however, makes its use questionable in a stand conversion program without further experimentation. Green-weight growth of European larch increased linearly with an increase in light up to 7,120 footcandles (table 7). This was in distinct contrast to the curvilinearity of the growth curves for all other species that reached near maximum growth at approximately 3,500 footcandles. Perhaps higher photosynthetic rates and more efficient use of photosynthate resulted in continued growth up to approximately 7,000 footcandles. Increase in height and diameter growth was also linear up to 7,120 footcandles. The rate of photosynthesis of European larch surpassed that of all other conifers at all light intensities. If European larch were used in a stand conversion program, a very intensive release cutting would be necessary to insure maximum photosynthesis, survival and growth.

If a less intensive release program were desired, eastern white pine should be well adapted. Total yield in a short period under the less intensive release would not compare with European larch grown in a completely released area. However, the variability in photosynthesis and growth response with changes in competition is far less for white pine than for larch (tables 7, 8, 9 and figs. 4, 5 and 6). In general, response to release of the intolerant European larch was considerably greater than that of eastern white pine, intermediate in tolerance.

Growth and photosynthetic rates of hazel and dogwood are sufficiently high to cause serious competition for all coniferous species studied (tables 7, 8, 9 and figs. 4, 5 and 6). The higher potential rate of photosynthesis and rapid growth of hazel indicates an efficient competitor for all underplanted conifers, especially in areas where release is intensive but the elimination of hazel is incomplete. The greater tolerance of dogwood, indicated in part by a low compensation point, enables its survival in an improperly released underplanting of conifers and, thus, increases its potential as a competitor.

The compensation points of the two hardwoods and two of the conifers appeared to fit the tolerance classification: the greater the tolerance, the lower the compensation point. European larch did not fit this concept in that it was the most efficient (lowest compensation point) yet is classed as the most intolerant of the five species. The variability in compensation point with CO_2 content of the air, temperature, moisture and inherent capacity of the species must be recognized before making any general statements regarding species efficiency and tolerance. Tolerant Norway spruce, with the second lowest compensation point, gave the lowest survival, rate of growth and rate of photosynthesis in underplanting tests. Other factors must have been controlling the growth and behavior of spruce. Therefore, the use of the compensation point as a sole predictor of successful seedling establishment, survival and growth is not recommended.

APPENDIX

Table A-1. Analysis of Variance of Seedling Survival of Five Underplanted Conifers in the Practical Understory Treatments.

Growing season	Source	df	Sum of squares	Mean square
1956	Replication (R)	2	189	94
	Understory treatment (T)	3	2,006	669
	Error (a)	6	1,441	240
	Species (S)	4	11,407	2,852°°
	SxT	12	1,229	102°
	Error (b)	32	1,547	48
1957	Replication (R)	2	1,530	765
	Understory treatment (T)	3	3,184	1,061
	Error (a)	6	1,659	276
	Foliage spray (F)	1	13	13
	FxT	3	698	233
	Error (b)	8	1,488	186
	Species (S)	4	20,826	5,206°°
	SxT	12	2,436	203°°
	SxF	4	564	141
	SxFxT	12	434	36
	Error (c)	64	4,486	70
1958	Replication (R)	2	2,446	1,223
	Understory treatment (T)	3	2,474	825
	Error (a)	6	1,874	312
	Foliage spray (F)	1	482	482
	FxT	3	783	261
	Error (b)	8	1,671	209
	Species (S)	4	15,977	3,994°°
	SxT	12	1,826	152°
	SxF	4	352	88
	SxFxT	12	867	72
	Error (c)	64	4,363	68

°° Significant at 1-percent probability level.
° Significant at 5-percent probability level.

Table A-2. Analysis of Variance of Seedling Survival of Five Underplanted Conifers in the Controlled Understory Cuttings at Different Overstory-Understory Densities.

Growing season	Source	df	Sum of squares	Mean square
1956	Overstory-understory (O)	2	145	72
	Replications/Overstory (R/O)	6	965	161
	Light intensity (L)	3	2,063	688°°
	LxO	6	801	134
	LxR/O	18	2,720	151
	Species (S)	4	37,663	9,416°°
	SxO	8	1,458	182°
	SxL	12	5,719	477°°
	SxOxL	24	2,075	86
	Error (c)	96	8,804	92
1957	Overstory-understory (O)	2	8,607	4,304°°
	Replications/Overstory (R/O)	6	2,052	342
	Light intensity (L)	3	7,937	2,646°°
	LxO	6	2,442	407
	LxR/O	18	3,737	208
	Species (S)	4	30,958	7,740°°
	SxO	8	1,998	250°
	SxL	12	7,350	612°°
	SxOxL	24	1,989	83
	Error (c)	96	9,149	95
1958	Overstory-understory (O)	2	13,420	6,710°°
	Replications/Overstory (R/O)	6	1,672	279
	Light intensity (L)	3	11,883	3,961°°
	LxO	6	1,879	313
	LxR/O	18	4,428	246
	Species (S)	4	24,161	6,040°°
	SxO	8	1,940	242°
	SxL	12	7,281	607°°
	SxOxL	24	2,486	104
	Error (c)	96	8,727	91

° Significant at 5-percent probability level.
°° Significant at 1-percent probability level.

Table A-3. Analysis of Variance of 2-Year Seedling Green-Weight Growth per Plant of Two Hardwoods and Three Conifers in the Nursery Investigations.

Source	df	Sum of squares	Mean square
Replication (R)	2	254.0	127.0
Light intensity (L)	2	48,667.2	24,333.6°°
Error (a)	4	393.8	98.4
Soil moisture (M)	1	624.1	624.1
MxL	2	785.0	392.5
Error (b)	6	726.6	121.1
Species (S)	4	45,591.2	11,397.8°°
SxL	8	26,375.9	3,297.0°°
SxM	4	868.1	217.0
SxMxL	8	1,476.8	184.6
Error (c)	48	8,476.2	176.6

°° Significant at 1-percent probability level.

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