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PHOTOSYNTHESIS AND GROWTH OF SELECTED SCOTCH PINE POPULATIONS

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LYHENNELMÄ:

TUTKIMUKSIA VALITTUJEN MÄNTYPOPULATIOIDEN FOTOSYNTEESISTÄ JA KASVUSTA

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Eight Scotch pine seed sources, ranging from 42° to 66° north latitude, were grown under a constant, 16-hour photoperiod in the greenhouse for approximately 6 months. Rates of photosynthesis and growth measured at the end of 6 months were strongly related to latitude of seed source. However, the seedlings that grew most had the lowest rate of photosynthesis per gram of needle weight. Therefore, for the eight sources studied, a selection for high photosynthetic efficiency would be a selection for slow growth. A possible explanation for this is offered. Seed source and light intensity had an interacting effect on rates of photosynthesis only in seedlings of the two northernmost seed sources.

INTRODUCTION

The natural range of Scotch pine *(Pinus sylvestris* L.) is perhaps greater than that of any other tree species of commercial importance. Currently, this species is being planted extensively in the United States. The occurrence and magnitude of genetic variation in physiological processes within the species should be known, and the relationship of such variation to within-species growth variation should be determined. The physiological response of Scotch pine to

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different levels of environmental factors is also important, even in the absence of intraspecific variation, if an optimum plant-environment relationship for a given production goal is to be created.

Scotch pine exists over a broad latitudinal range and shows a differential response among seed sources to daylength (Jensen and Gatherum 1965). It is possible that rates of photosynthesis also vary among seed sources grown in a common environment. If variation in rates of photosynthesis can be shown to exist, and the relationship of photosynthesis to growth can be defined, measurements of rates of photosynthesis could be used, with other criteria, to increase productivity through selection.

Since light intensity is an important external factor affecting rate of photosynthesis, the specific effect of this variable on rate of photosynthesis in Scotch pine and the extent of its interaction with seed source should be known. Respiration also is an important yield determining process and may be affected by the same factors that affect rate of photosynthesis. Therefore, when rates of photosynthesis are measured by CO_2 exchange, rates of respiration should also be measured.

The effect of seed source on rate of photosynthesis in Scotch pine has been investigated by Gatherum (1965) in a preliminary study. Differences in rates of photosynthesis per seedling were demonstrated. The effect of seed source on photosynthesis and respiration in conifer seedlings of other species has been studied by McGregor et al. (1961), Krueger and Ferrell (1962), and Bourdeau (1963). McGregor et al., using 1-year-old loblolly pine seedlings, found a difference in net photosynthesis between Georgia and Florida seed sources, with the difference accounted for by a corresponding difference in quantity of photosynthetic tissue. Krueger and Ferrell found differences in photosynthesis and respiration between Douglas fir seedlings from Rocky Mountain and Coastal seed sources. In Bourdeau's study eastern white pine seedlings from southern seed sources were more efficient photosynthetically in weak light and had lower compensation points than those of northern origin, but the southern sources were less efficient at low temperatures. Bourdeau concluded that genetic variability in photosynthetic and respiratory responses exists in white pine, but appears only under certain combinations of treatment and environmental conditions. These studies together with studies of other species (Huber and Polster 1955, Bourdeau 1958, Mooney and Billings 1961, and others) indicate that genotype can affect photosynthesis in two ways: (1) by determining the quantity of photosynthetic tissue produced and (2) by determining the efficiency (CO_2 fixed per unit tissue per unit time) of photosynthetic tissue.

In this investigation, Scotch pine seed was obtained from European seed sources representing a relatively wide latitudinal but narrow longitudinal range. Studies were conducted to (1) test differences in rates of photosynthesis and respiration and in growth and distribution of assimilate among seed sources, and (2) determine the effect of selected light intensities on rates of photosynthesis and respiration. First year seedlings were used.

Growth and distribution of assimilate were measured to provide a basis for comparison among rates of photosynthesis and to allow comparison between photosynthesis and growth for the seedlings included in this study. Wright and Bull (1963) have presented extensive growth data for 120 Scotch pine seed origins grown in Michigan.

MATERIALS AND METHODS

Seed was acquired in 1963 from eight European sources (Table 1). The seed was supplied by governmental agencies and a private seed dealer. For all seed lots, origin was certified by the agency or dealer. Seed sources were chosen to sample the north-south range of Scotch pine in eastern Europe where natural stands are most frequently encountered. Because Scotch pine does not occur naturally at lower elevations in the southern portion of its range, seed origins from identical elevations could not be obtained.

Table 1. Seed origin.
Taulukko 1. Siemenen alkuperä.

North Latitude (degrees) *Pohj. leveys, °*	East Longitude (degrees) *It. pituus, °*	Elevation *Korkeus merenp.* m	Country *Maa*
66	26	150	Finland
62	24	100	Finland
60	23	15	Finland
57	25	100	Latvia
54	20	137	Poland
50	16	780	Czechoslovakia
49	21	690	Czechoslovakia
42	25	1 220	Bulgaria

Seed from the eight sources was sown in 1-gallon pots in the greenhouse in a randomized complete block design on November 24, 1964. The soil in which the seed was sown was a 1: 1: 1 mixture of acid peat, sand and Clarion loam. Seedling heights were measured twice (May 25 and July 8, 1965) during the growth period. At the time of the first height measurement, the seedlings were thinned to one per pot by severing stems at the soil line. The experiment proper consisted of 112 pots with one seedling each.

After all seedlings had set bud, they were divided into three experimental groups of adjacent, eight-seedling blocks. The first group, consisting of two blocks, was used for preliminary testing. The second group, consisting of six blocks, was used to determine the effect of seed source on rates on photosynthesis and respiration at one light intensity (6,000 foot-candles). The third group, also consisting of six blocks, was used to determine the effect of seed source and light intensity on rates of photosynthesis and respiration. In the latter experiment, two light intensities (3,000 and 9,000 foot-candles) were used. A split-plot experimental design was employed, with adjacent, eight-seedling blocks combined to make 16-seedling main units to which the two light intensities were randomly assigned.

Rates of net photosynthesis were measured in the laboratory by enclosing each seedling in a controlled-environment chamber. The pot in which the seedling was growing was enclosed in a polyethylene bag sealed around the base of the stem to isolate CO_2 evolved in soil respiration from the measurement system. CO_2 concentration in the chamber was continuously monitored with an infrared gas analyzer. The output signal from the gas analyzer was recorded on a strip-chart, and a tangent to the curve thus generated was drawn at the point where the curve crossed the chart line indicating a CO_2 concentration of 400 ppm (modified method of DECKER 1959). From this tangent the rate of consumption or evolution of CO_2 in ppm per hour was computed, and these rates were converted to rates in mg CO_2 per hour per seedling and mg CO_2 per gram fresh and dry weight of needles. Rates of dark respiration were measured by darkening the chamber with light-tight cloth immediately after measuring rate of net photosynthesis and proceeding as described. Rates of gross photosynthesis were obtained by adding rates of net photosynthesis and dark respiration. Chamber temperature was maintained at 15 ± 1° C for all measurements.

After rates of photosynthesis and respiration were measured, all seedlings were immediately harvested, and height and fresh and dry weights of the top, stem, juvenile needles, mature needles and roots were recorded. Dry weights were obtained by drying the fresh material for 24 hours at 70° C.

For both experiments, one block (eight seedlings) or main unit (16 seedlings) was moved from the greenhouse to the laboratory during one day, so that greenhouse position was confounded with time of measurement. Thus, variation from both these sources was partitioned into the block sum of squares during analysis of variance. Preliminary testing with the first group of seedlings showed no massive effect of time of day, during daylight, on rates of photosynthesis and respiration. All laboratory measurements for the two experiments were made within 12 days.

RESULTS

Growth varied significantly[1] among the eight seed sources. Most growth variables showed a curvilinear relationship with latitude of seed source, with growth maxima occurring at latitudes between 47° and 51°. Seedling height,

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[1] Analysis of variance tables may be obtained from the senior author upon request.

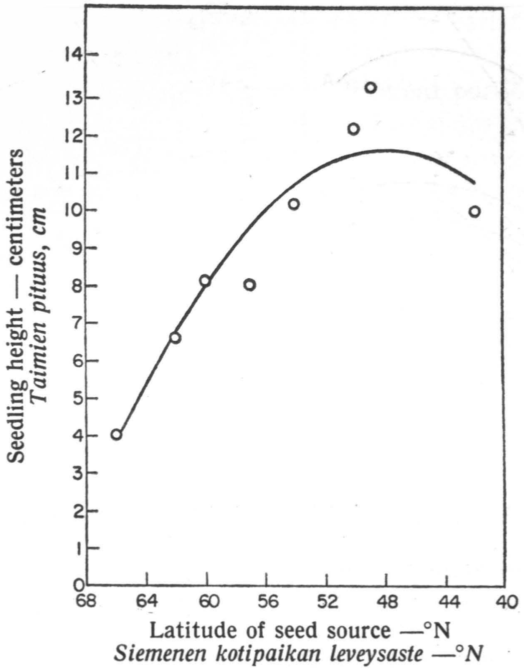
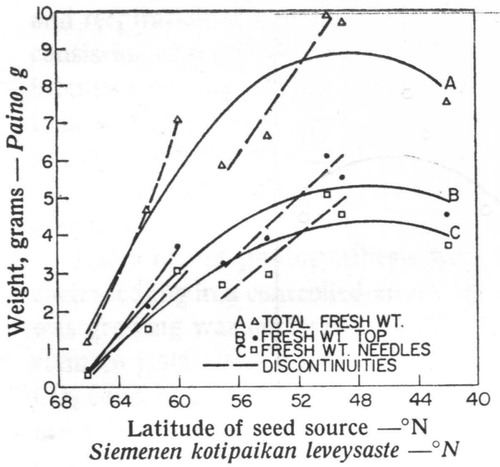


Figure 1. Relationship between seedling height measured at the end of the growth period and latitude of seed source.

Kuva 1. Kasvukauden päättyessä mitatun taimipituuden ja siemenen kotipaikan leveysasteen välinen korrelaatio.

measured during and at the end of the growth period, showed a curvilinear relationship with latitude of seed source (Fig. 1). However, the significance of the quadratic component of variance appeared to be caused entirely by the inclusion of the source from 42° latitude. Fresh and dry weights of seedlings, seedling tops, and total needles also exhibited a curvilinear relationship with latitude of seed source (Fig. 2). Again, the curvilinearity appeared to be caused by the inclusion of the source from 42° latitude. Because fresh and dry weights varied similarly with latitude, only fresh weights are illustrated. Fresh and dry weights of stems and roots were strongly related to latitude of seed source, but the quadratic component of the latitude of seed source sum of squares was not consistently significant. Fresh and dry weight of juvenile needles increased linearly as latitude of seed source decreased (Fig. 3). Fresh and dry weight of mature needles, however, showed pronounced curvilinearity. Again, only fresh weights are illustrated.

Shoot-root ratios, based on mean fresh and dry weights of tops and roots, varied curvilinearly with latitude of seed source (Fig. 4). No estimate of error was possible because shoot-root ratios for individual seedlings were not computed. A second degree polynomial relating shoot-root ratio to latitude of seed



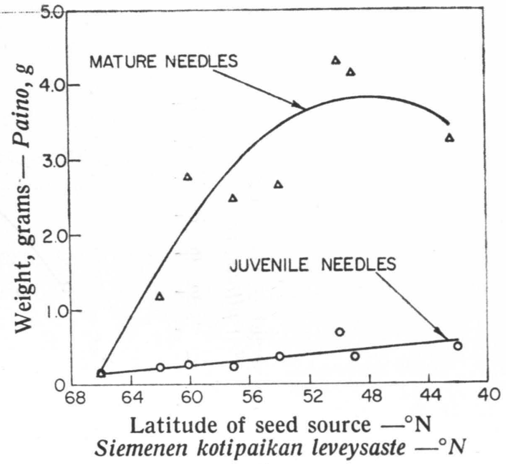
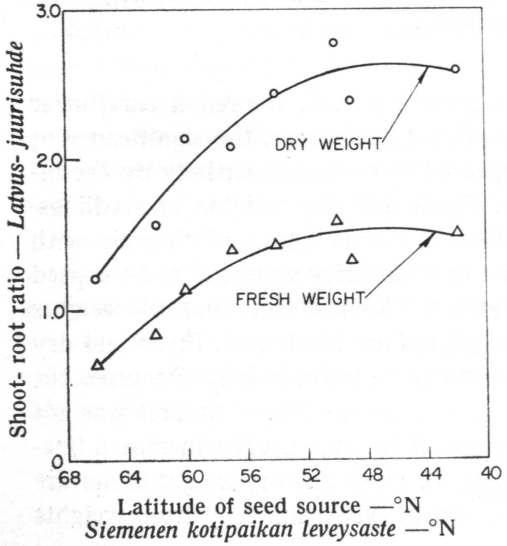


Figure 2. Relationship between fresh weight and latitude of seed source, with latitudinal discontinuities indicated.

Kuva 2. Taimien tuorepainon ja siemenen kotipaikan välinen korrelaatio (A = kokonaistuorepaino, B = latvaosan tuorepaino ja C = neulasten tuorepaino).

Figure 3. Relationship between fresh weight of juvenile and mature needles and latitude of seed source.

Kuva 3. Nuorten sekä valmiiden neulasten tuorepainon ja siemenen kotipaikan korrelaatio.



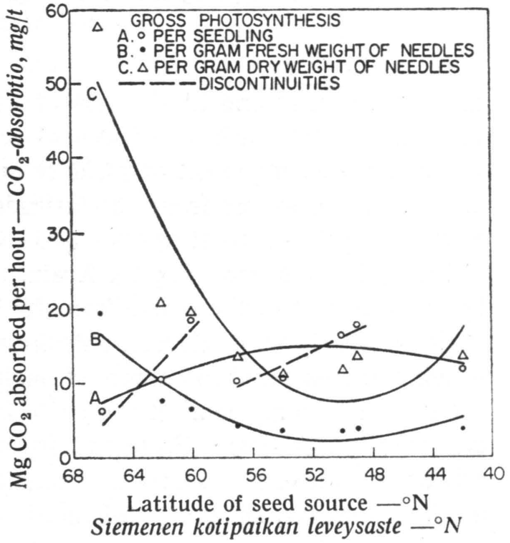


Figure 4. Relationship between shoot-root ratio and latitude of seed source.

Kuva 4. Latvus-juurisuhteen ja siemenen kotipaikan välinen korrelaatio (ylempänä kuivapaino, alempana tuorepaino).

Figure 5. Relationship between rate of gross photosynthesis and latitude of seed source.

Kuva 5. Bruttofotosynteesin intensiteetin ja siemenen kotipaikan korrelaatio (A = tainta kohti, B = neulasten tuorepainon ja C = neulasten kuivapainon grammaa kohti).

source accounted for approximately 90-percent of the variation in mean shoot-root ratios.

Percentages of total dry weight found in different portions of the seedlings are presented in Table 2. In general, percentage of total dry weight in the needles increased with decreasing latitude of seed source, and percentage of total dry weight in the roots decreased with decreasing latitude of seed source.

Table 2. Effect of seed source on percentage distribution of assimilate.

Taulukko 2. Siemenen kotipaikan vaikutus assimilaattien prosentuaaliseen jakaantumiseen.

Latitude of Seed Source (degrees) *Siemenen kotipaikan leveysaste (°N)*	Percentage of Total Dry Weight *% kokonaiskuivapainosta*		
	Needles – *Neulaset*	Stem – *Runko*	Roots – *Juuristo*
66	41	14	45
62	46	15	39
60	55	13	32
57	56	11	33
54	54	17	29
50	60	13	27
49	58	12	30
42	58	14	28

Departures from the curvilinear or linear relationship with latitude of seed source exhibited by growth variables were small but perhaps biologically significant. Two major discontinuities were apparent; the first between the three sources originating north of the Baltic Sea (66°, 62°, 60°) and the Central European sources (57°, 54°, 50°, 49°), and the second between the Central European sources and the single Southern European source (42°), (Fig. 2).

Rates of net and gross photosynthesis, expressed on a per seedling basis, varied curvilinearly with latitude of seed source, and maximum rates occurred at approximately 50°. Rates of net and gross photosynthesis expressed per gram fresh or dry weight of needles also varied curvilinearly with latitude of seed source. However, maximum rates occurred in seedlings of the northernmost seed source, which grew least. Minimum rates occurred at approximately 50°, the latitude at which total needle weights were maximum (Fig. 5).

Discontinuities in the relationship between net and gross photosynthesis per seedling and latitude of seed source occurred at the same latitudes as the discontinuities that occurred in the relationships between growth variables and latitude of seed source (Fig. 5). These discontinuities did not appear, however, when rates of photosynthesis per gram of fresh or needle weight were plotted over latitude.

No significant differences occurred in rates of respiration among seed sources, but addition of rates of respiration to rates of net photosynthesis strengthened the relationship between latitude of seed source and rates of (gross) photo-

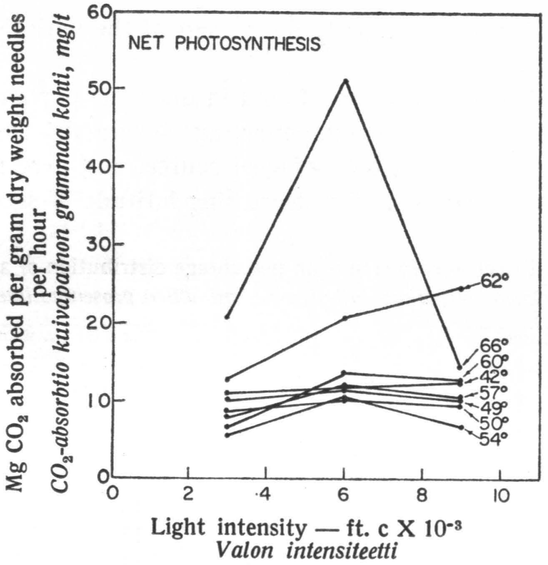


Figure 6. Relationship between rate of net photosynthesis per gram dry weight of needles of each of the eight seed sources and light intensity.
Kuva 6. Kunkin kahdeksan provenienssin nettofotosynteesin intensiteetin (neulasten kuivapainon grammaa kohti) ja valon intensiteetin korrelaatio.

synthesis. Rates of respiration were at or just under threshold values for accurate short-time detection by the measurement system; therefore, instrumental error may be partially responsible for the great variability in observed rates.

Light intensity and latitude of seed source had an interacting effect on rate of net photosynthesis when expressed per gram of needle dry weight. The northernmost seed source (66°) exhibited a decrease in rate of net photosynthesis over the 3,000 to 9,000 foot-candle range, while the next seed source south (62°) exhibited an increase in rate of net photosynthesis over the same light intensity range. When rates of photosynthesis measured at 6,000 foot-candles (group 2 seedlings) were plotted with the rates at 3,000 and 9,000 foot-candles (group 3 seedlings) for all seed sources, the greatest variation in rate of photosynthesis was again exhibited by the two northernmost sources (Fig. 6).

DISCUSSION

Two general relationships of the dependent variables to seed source were evident. (1) Growth in height, fresh and dry weight, and rate of photosynthesis per seedling all showed similar relationships to latitude of seed source. This indicates that rate of photosynthesis per seedling, hereafter referred to as photosynthetic capacity (Campbell and Rediske 1966), is essentially a growth measurement. (2) Rates of photosynthesis per gram of fresh and dry weight of needles (expressions of photosynthetic efficiency) were also strongly related to seed source, but were lowest in the seed sources where growth variables were greatest. Thus, photosynthetic efficiency appeared to be inversely related to photosynthetic capacity and growth. This seems to be either a semantic or a biological contradiction, but it is neither. Rather, it indicates that in the seedlings which grew most rapidly, a smaller fraction of total needle weight was photosynthetically active. There are at least two possible explanations for this. In seedlings with greater total needle weight, more mutual shading of needles may have occurred during measurement of photosynthetic rate. However, since the first year seedlings were small and essentially unbranched, and since the lighting was angled as well as vertical, it is unlikely that mutual shading was great enough to account for the observed differences. More likely, anatomical and biochemical differences in needles among the seed sources were the major cause of apparently reduced photosynthetic efficiency in the more rapidly grown seedlings.

To explain the existence of internal differences in needles among seed sources, it is necessary to first explain the strong relationship of growth and photosynthetic capacity to seed source. Langlet (1942—43), in describing latitudinal variation in Scotch pine, hypothesized that adaptation to photoperiod was a major factor in determining differential response of seed sources subjected to a common environment. Wareing (1950 a) and Karschon (1949) demonstrated that first-year Scotch pine seedlings respond to changes in photoperiod. Jensen and Gatherum (1965) demonstrated a differential response to daylength among Scotch pine seed sources, although no clearcut latitudinal trends were discovered. The seedlings from different seed sources grown under a 16-hour photoperiod in the present study were similar in appearance to the seedlings of a single seed source grown under a range of photoperiods by Wareing (1950 a). Photoperiod varies more regularly with latitude than any other factor known to affect plant growth. Vaartaja (1954) has hypothesized that photoperiodic ecotypes of trees may exist, partially on the basis of growth differences observed in Scotch pine seed sources of different latitudinal origin. It is logical, in view of previous work, to explain the relationship between latitude of seed source and photosynthetic capacity and growth observed in this study on the basis of differential adaptation to photoperiod. Thus, the growth and photosynthetic capacity of a given seed source depended primarily on how closely a constant, 16-hour photoperiod approximated the photoperiod to which the seed source was adapted. The seed sources that grew most did come from latitudes where maximum daylengths are approximately 16 hours. Also, the variation in daylength over the year decreases as one moves from north to south. Thus, the southern sources would be more nearly adapted to a constant daylength than the northern ones.

Wareing (1950 b) established that duration of needle growth in Scotch pine is affected by daylength. It is possible, therefore, that differential needle growth response to photoperiod caused the apparent inverse relationship between photosynthetic capacity and efficiency. It can be seen in Figure 3 that the ratio juvenile needle weight/mature needle weight is greatest in the northernmost seed sources and least in the seed sources that exhibited maximum growth. This ratio thus roughly parallels rate of photosynthesis per unit of needle weight. Bormann (1956) reported that juvenile needles of loblolly pine fixed more CO_2 per unit weight, under certain conditions, than did mature needles. It is possible that production of more mature needles by the seed sources more closely adapted to the 16-hour photoperiod reduced the aggregate photosynthetic efficiency of these sources.

If these results were used as selection guides in tree improvement work, trees with the least photosynthetically efficient foliage would be selected for most rapid growth. This ambiguity can, in this case, be resolved by reexamining photosynthetic efficiency and its relationship to needle development. In this study, the seedlings less adapted to the 16-hour photoperiod probably produced fewer needles immediately following the cotyledon stage and thus produced less photosynthate over any given interval of time. The photosynthate produced was used to a greater degree in the maintenance of existing protoplasm. Thus, the quantity of photosynthate available for new wall construction and carbohydrate storage was reduced in the less-adapted seed sources. Therefore, the rate of photosynthesizing protoplasm to stored carbohydrates, cell wall and non-photosynthetic protoplasm was greater in the less-adapted seedlings. Because of this, the less-adapted seedlings appeared to have a higher photosynthetic efficiency. Loomis and Williams (1963) suggested that the most photosynthetically efficient crop would be one which used minimum photosynthetic surface to store a given amount of dry matter (if dry matter is equated with yield). Similarly, the most photosynthetically efficient needle would be one that used a minimum of photosynthetic protoplasm to produce and store a given amount of carbohydrate. This view of photosynthetic efficiency might prove more useful than the classical one for some tree improvement purposes.

For the dependent variables measured, variation was continuous in so far as relationship to latitude of seed source indicates continuity. If, therefore, a clinal or ecotypic description of genetic variation in Scotch pine must be chosen, these data, for only eight seed sources, support the former. However, as age increases, genetic material selected by regional influences may become increasingly important physiologically. Growth behavior of seedlings from latitudinally disparate origins within the same general climatic region may then become similar, obscuring earlier growth differences due to selection under different day-lengths. Discontinuities in the relationship of growth and photosynthetic capacity to latitude of seed source may indicate such regional differences (Figures 2 and 5).

No explanation is available for the opposite response to light intensities above 3,000 foot-candles exhibited by the two northernmost seed sources. Further research is obviously needed on the specific physiological and anatomical responses of latitudinal series of seed sources to selected controlled environments.

SUMMARY

Eight *Pinus sylvestris* L. seed sources, ranging from 42° to 66° north latitude, were grown under a constant 16-hour photoperiod in the greenhouse for approximately six months. Rates of photosynthesis, as measured by an IRGA, and growth, as measured by increase in height and fresh and dry weight, differed among seed sources at the end of the six month growing period. Photosynthetic capacity and growth were strongly related to latitude of seed source, and were greatest in the seed sources coming from a parent environment in which maximum photoperiods are about 16 hours. Photosynthetic efficiency (rate of photosynthesis per gram needle weight) was also strongly related to latitude of seed source, but was lowest in the seedlings which exhibited the greatest growth and photosynthetic capacity. This may have been due to (1) more mutual shading of needles on the larger seedlings and (2) a lesser proportion of juvenile needles on the larger seedlings or (3) biochemical differences in the use of photosynthate in the needles. Seed source and light intensity had an interacting effect on rates of photosynthesis only in seedlings of the two northernmost seed sources.

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LYHENNELMÄ:

TUTKIMUKSIA VALITTUJEN MÄNTYPOPULATIOIDEN FOTOSYNTEESISTÄ JA KASVUSTA

Tutkimus kohdistui kahdeksaa eri alkuperää olevasta siemenestä perustettuihin mäntyviljelmiin, jotka kasvatettiin kasvihuoneessa noin kuuden kuukauden ajan 16 tunnin vuorokautisessa valaistuksessa. Siemen oli peräisin 42° ja 66° N välillä sijaitsevilta paikkakunnilta. Kuusi kuukautta kestäneen kasvukauden päättyessä voitiin eri alkuperien välillä havaita eroja fotosynteesin intensiteetissä, joka mitattiin IRGA:n avulla sekä kasvussa, joka määritettiin pituuden sekä tuore- ja kuivapainon lisäyksenä. Fotosynteesin kapasiteetti ja kasvu korreloivat voimakkaasti siemenen kotipaikan leveysasteen kanssa, ja ne olivat suurimmat niissä proveniensseissa, joiden luontaisilla kasvupaikoilla suurin fotoperiodi vastaa n. 16 tuntia. Fotosynteesin intensiteetti ilmoitettuna assimilaation määränä neulasgrammaa kohti korreloi myös selvästi siemenen kotipaikkakunnan leveysasteen kanssa, joskin se oli pienin parhaiten kasvaneissa ja suurimman fotosynteesin kapasiteetin omaavilla taimilla. Tämä saattaa johtua (1) suuremmasta neulastenvälisestä varjostuksesta suurimmissa taimissa sekä (2) niiden suhteellisesti pienemmästä nuorten neulasten määrästä tai (3) biokemiallisista eroista neulasten fotosynteesin avulla valmistamien aineiden käytössä. Siemenen alkuperän ja valon intensiteetin yhteisvaikutusta fotosynteesin intensiteettiin havaittiin vain kahta pohjoisinta alkuperää edustavilla taimilla.