PHOTOSYNTHESIS AND GROWTH OF SELECTED SCOTCH PINE SEED SOURCES[1]

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A number of problems related to the culture of Scotch pine (*Pinus sylvestris* L.) arose following the increased planting of this species in Iowa. Therefore, a program of controlled-environment experiments to determine the effects of genetic and environmental factors on physiological processes important to the culture of Scotch pine was begun by the Iowa Agricultural Experiment Station. We will report here the results of some of these experiments, done by ourselves and students of the junior author. Some of these results have been published elsewhere, and some have not.

As pointed out by Gatherum (1964), the two principal objectives of the controlled-environment studies are to (1) permit further identification and evaluation of within-species variation of physiological processes in Scotch pine seedlings, and (2) provide a clearer understanding of causes of variation in tree vigor and quality. Because photosynthesis and respiration may be viewed as the basic yield-determining physiological processes in plants, they were selected as dependent factors, measured by the variables CO2 uptake and CO2 evolution, respectively. Growth, as measured by the variables fresh and dry weight and stem and needle elongation, was also considered as a dependent factor in the studies to be reported. In making comparisons among treatments and in relating photosynthesis to growth, we defined the two additional dependent factors, photosynthetic capacity and photosynthetic efficiency. Photosynthetic capacity, as we use the term, is measured by the rate of CO2 uptake of the entire aerial portion of the seedling. Photosynthetic efficiency, on the other hand, is measured by the rate of CO2 uptake per unit of photosynthesizing foliage. Photosynthetic efficiency is, then, photosynthetic capacity divided by foliar quantity.

The independent factors we studied in relation to photosynthesis and growth were seed source, as indicated by the geographic origin of the seed from which the seedlings were grown, and several factors of the environment important in influencing the physiology of trees: photoperiod, temperature, nitrogen, and light intensity. The specific questions about Scotch pine that these studies were intended to answer were:

1. Does seed source affect photosynthesis and respiration?

2. Do seed source and environmental factors interact in their effect on photosynthesis and respiration?

3. How do the effects of these factors on photosynthesis and respiration relate to their effects on growth?

Materials and Methods

Although the Scotch pine seed sources used (table 1) represent a fairly wide range of latitude, they do not, either randomly or systematically, sample the entire native range of the species. Environmental treatments, when applied before measurement of CO2 exchange, were carried out in the greenhouse. Environment was controlled during measurement of CO2 exchange in a chamber described by Broerman *et al.* (1967). Rates of photosynthesis and respiration were measured by monitoring CO2 uptake and evolution in a closed system with an infra-red CO2 analyzer.

Results and Discussion

To bring together the results of the several studies, we discuss seed source in conjunction with each environmental factor studied. This is done for convenience, and is not meant to imply that

Table 1. — Scotch pine seed sources used, ISU studies

ISU no. and seed source	Latitude	Longitude	Elevation
	°N	°E	(Meters)
211; Finland	66	26	150
210; Finland	62	24	100
208; Finland	60	23	15
217; USSR	57	25	100
216; Poland	54	20	140
214; Czechoslovakia	50	16	780
81; Germany	50	9	--
215; Czechoslovakia	49	21	690
82; Austria	48	16	450
218; Bulgaria	42	25	1,220
113; Turkey	40	33	1,500
115; Turkey	40	31	1,400

[1] *Journal Paper No. 5771 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project No. 1582.*

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seed source influences CO2 exchange and growth separately and independently with each of the environmental factors.

Photoperiod

We have not investigated the effect of seed source and photoperiod on photosynthesis directly. However, the effects of seed source and photoperiod on growth and development were studied in first-year seedlings by Jensen and Gatherum (1965). They demonstrated that seed source and photoperiod interact in their effect on height growth and needle elongation. The data indicated that photoperiod could be an environmental factor important in natural selection, since it definitely affected patterns of growth and differentiation in first-year seedlings. The ability of some sources to produce a greater quantity of foliage than others in response to a given photoperiod suggested a relationship between seed source and photosynthetic capacity.

Temperature

Temperature interacted with both photoperiod and seed source in its effect on height growth and needle elongation (Jensen and Gatherum 1965). It did not, however, interact with seed source in its effect on photosynthesis and respiration in second-year seedlings from three sources (208, 216, 214). It is possible that the parent climates of the three sources used in the photosynthesis study are similar enough in growing-season temperatures to preclude differential adaptation of the photosynthetic and respiratory processes to temperature. Additional controlled-environment experiments including more seed sources and more refined physiological measurement are needed before final conclusions about the interacting effects of seed source and temperature on photosynthesis and respiration can be drawn.

Nitrogen

In a study including five seed sources ranging from Bulgaria to Finland (218, 216, 217, 208) and five sand culture nitrogen levels (25 to 500 ppm), nitrogen and seed source had an interacting effect on shoot fresh weight, but not on dry weight, photosynthesis, or respiration (Dykstra and Gatherum 1967). Optimum nitrogen (approximately 400 ppm) increased photosynthetic capacity in all sources, but resulted in a slightly lower photosynthetic efficiency. Probably, part of the reduction in efficiency can be accounted for by mutual shading of needles in the larger-crowned seedlings produced at optimum nitrogen level. However, it is possible that biochemical differences in the distribution of assimilate within the needles also contributed to the reduction.

Light Intensity

Light intensity and seed source interacted in their effect on photosynthetic capacity in an experiment including fourth-year seedlings from four sources (81, 82, 113, 115) (Gatherum *et al.* 1967). Photosynthetic capacity increased with light intensity in the Austrian source up to the highest test intensity, while the German and Turkish sources appeared to reach light saturation (maximum capacity) at lower intensities (fig. 1). No differences in photosynthetic efficiency were observed. This suggests that the differential response to light among the sources was due to differences in quantity and arrangement of foliage, rather than to inherent biochemical differences in the photosynthetic process itself.

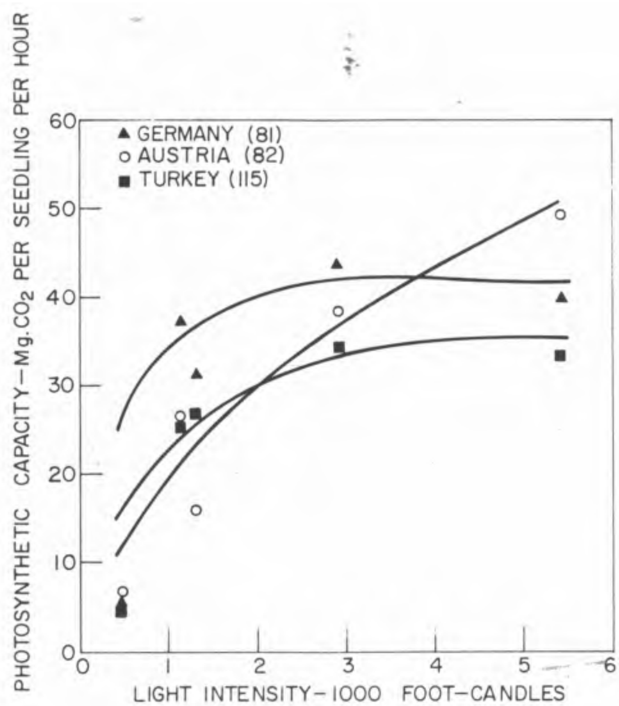

FIGURE 1. — Relationship between photosynthetic capacity and light intensity for fourth-year seedlings of three sources. ISU seed source number is shown in parentheses.

In a subsequent study of first-year seedlings that included eight seed sources (211, 210, 208, 217, 216, 214, 215, 218) and three light intensities (3,000, 6,000 and 9,000 foot-candles), photosynthetic capacity and efficiency both were influenced by the interaction of seed source and light intensity (fig. 2). The interaction appeared to be limited to the two most northerly sources. However, when second-year seedlings of three of the eight sources were tested at the same and at six lower light intensities, no differences in efficiency were

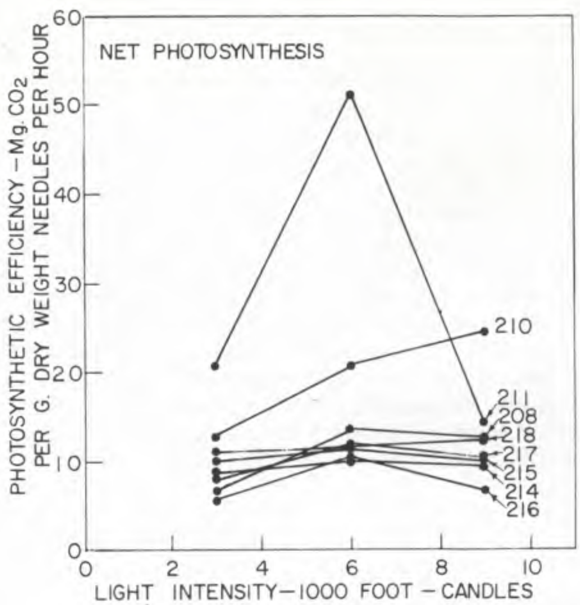

FIGURE 2. — Relationship between photosynthetic efficiency and light intensity for first-year seedlings of eight sources. The trend lines are identified at the right by ISU seed source number.

observed. But again, seed source and light intensity interacted in their effect on photosynthetic capacity.

Taken together, these results imply a basic difference in the photosynthetic properties of the crown between first-year and older Scotch pine seedlings. One probable cause of the difference is the presence of a high proportion of functional juvenile needles on first-year seedlings.

Photosynthesis and Growth

Differences among seed sources in photosynthetic efficiency, photosynthetic capacity, growth, and distribution of assimilate (dry weight) were observed in a study including first-year seedlings from eight sources. Photosynethic capacity and seedling height, fresh and dry weight were positively related. Photosynthetic efficiency, however, was inversely related to height, fresh and dry weight, and photosynthetic capacity (table 2). Seedlings that retained the lowest percentage of their total dry weight in their needles had the highest photosynthetic efficiency, and were from the northernmost sources (table 3). This relationship between high photosynthetic efficiency, low photosynthetic capacity and distribution of assimilate may be accounted for by (1) less mutual shading of needles on small-crowned seedlings or

Table 3. — Effect of seed source on *percentage distribution of assimilate in first-year seedlings*

ISU no. and seed source	Percentage of total dry weight in-- Needles	Stem	Roots
211; Finland	41	14	45
210; Finland	46	15	39
208; Finland	55	13	32
217; USSR	56	11	33
216; Poland	54	17	29
214; Czecho-slovakia	60	13	27
215; Czecho-slovakia	58	12	30
218; Bulgaria	58	14	28

Table 2. — Effect of seed source on fresh and dry weight and photosynthetic capacity and efficiency of first-year seedlings

ISU no. and seed source	Total fresh weight	Total dry weight	Photosynthetic capacity	Photosynthetic efficiency
	g.	g.	mg.CO_2/hr. /seedling	mg.CO_2/hr./g. dry wt. needles
211; Finland	3.1	1.2	5.0	52.5
210; Finland	10.5	4.6	8.3	21.0
208; Finland	17.0	7.1	13.2	13.1
217; USSR	14.2	5.9	9.0	12.2
216; Poland	16.2	6.6	10.5	10.7
214; Czecho-slovakia	24.5	9.9	14.0	9.6
215; Czecho-slovakia	23.0	9.7	14.9	10.8
218; Bulgaria	18.9	7.7	11.2	12.0

(2) less deposition of storage and structural, non-photosynthetic compounds in the needles, or both. Higher photosynthetic efficiency also may be related to the greater contribution of juvenile needles to total needle weight of the seedlings of the northernmost sources. In any case, the higher photosynethic efficiency of these sources obviously does not represent any sort of "photosynthetic superiority" in the sense of more efficient total dry weight production.

Respiration and Growth

Rates of respiration per seedling and, under some treatments, per gram of needles, varied among seed 'sources in second-year and older seedlings. No differences in respiration per gram of needles were observed in first-year seedlings, but, as expected, larger seedlings respired more than small ones. The relationship of respiration to growth, in a sense, is more complex than that of photosynthesis. Presumably, any increase in rate of photosynthesis represents a potential increase in dry weight production. It is not true, however, that an increase in respiration necessarily decreases dry weight production. While substrate is oxidized to H_20 and CO2 during aerobic respiration, and an immediate reduction in dry weight occurs, the chemical bond energy thus generated is necessary for growth processes. Thus, a high respiration rate accompanies the production of new needle tissue. The production of new needle tissue, in turn, can result in greater dry weight production through increased photosynthetic capacity. What should be avoided are seedlings and environmental conditions that result in "excess" respiration. This, however, is extremely difficult to define, let alone identify.

Conclusions

1. Seed source does affect rates of photosynthesis and respiration. However, our work has revealed no differences among sources in photosynthetic efficiency of seedlings older than one year.

2. Seed source and environmental factors can have an interacting effect on photosynthesis and respiration. More controlled-environment experimentation with more seed sources and wider ranges of environmental conditions is needed if the mechanisms of the interactions are to be understood.

3. Photosynthesis, respiration, and growth, as measured in these studies, are not related in a simple manner. A seed source exhibiting rapid growth does not necessarily have a high photosynthetic efficiency, as the term has commonly been used.

4. More physiological and biochemical research is needed if differences among sources in photosynthetic capacity, efficiency, and distribution of assimilate are to be satisfactorily explained. Ideally, such research should precede the use of photosynthesis and respiration characteristics in seed source selection.

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