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NORSK INSTITUTT FOR SKOGFORSKNING /*Norwegian Forest Research Institute*
INSTITUTT FOR SKOGFAG, NLH /*Department of Forestry, Agricultural University of Norway*

Temperature effects on the growth of mountain birch (*Betula pubescens* Ehrh.), elm (*Ulmus glabra* Huds.) and maple (*Acer platanoides* L.) seedlings in continuous light.

*Verknader av temperatur på veksten hos småplanter av fjellbjørk (*Betula pubescens *Ehrh.), alm (*Ulmus glabra *Huds.) og lønn (*Acer platanoides *L.) dyrka i kontinuerleg lys.*

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Oddvar Skre

Ås 1991

Ås, October 1991.

To our Subscribers and Exchange Partners

By a regrettable mistake some errors are appearing in:

Communications of Skogforsk No. 44(5).

Please make the following corrections in the issue received:

Page 28, line 19 from top:
"LWR (LW/W)" should be written **"LWR (=LAR/SLA)".**

Page 33, line 12 from top:
"did not seem to react at all" should be written **"reacted only slightly".**

Thank you !

Sincerely yours,

Birger Halvorsen

Birger Halvorsen

Abstract

SKRE, O. 1991. Temperature effects on the growth of mountain birch (*Betula pubescens* Ehrh.), elm (*Ulmus glabra* Huds.) and maple (*Acer platanoides* L.) seedlings in continuous light. (Verknader av temperatur på veksten hos småplanter av fjellbjørk (*Betula pubescens* Ehrh.), alm (*Ulmus glabra* Huds.) og lønn (*Acer platanoides* L.) dyrka i kontinuerleg lys.) Medd. Skogforsk. *44*(5): 1-44.

As a case study to investigate the growth/respiration relationships and climatic adaptations in ecotypes of mountain birch (*Betula pubescens* Ehrh.), simple growth experiments were carried out on mountain birch seedlings of three different populations in South and Central Norway from different altitudes and latitudes. The seedlings were grown in continuous light at different constant temperatures. For comparison two other tree species were included, one with a continental distribution (*Acer platanoides* L.) and one with an oceanic distribution (*Ulmus glabra* Huds.).

Large differences were found in survival strategy among species and ecotypes. The maple and elm populations and the two southern birch populations all reacted to high temperatures by rapid leaf expansion as a possible compensation for increased respiration loss, and the maple and birch also by increasing their stem elongation rates and thereby competing more efficiently for available light. In the northern subalpine birch population, however, the seedlings developed leaves with high net assimilation rates instead of increasing their leaf area and stem elongation rates. In this population abiotic climatic factors rather than competition therefore seem to be the most important adaptive force.

Key words: Growth rates, leaf expansion, specific leaf area, shoot/root ratio, stem elongation, net assimilation rates, climatic adaptation, temperature compensation.

Utdrag

SKRE, O. 1991. Temperature effects on the growth of mountain birch (*Betula pubescens* Ehrh.), elm (*Ulmus glabra* Huds.) and maple (*Acer platanoides* L.) seedlings in continuous light. (Verknader av temperatur på veksten hos småplanter av fjellbjørk (*Betula pubescens* Ehrh.), alm (*Ulmus glabra* Huds.) og lønn (*Acer platanoides* L.) dyrka i kontinuerleg lys. Medd. Skogforsk. *44*(5): 1-44.

Som eit første steg mot ei utforskning av samanhengen mellom vekst, respirasjon og klimatilpasningar i økotypar av fjellbjørk (*Betula pubescens* Ehrh.) vart det utført enkle vekstforsøk med småplanter av bjørk frå ulike sør- og mellomnorske populasjoner, og frå ulik høgde over havet og breiddegrad. Småplantene vart dyrka i kontinuerlig lys ved ulik konstant temperatur. For samanlikning var også to andre treslag med i forsøket, eit med eit kontinentalt utbreiingsmønster (*Acer platanoides* L.) og eit med ei meir kystprega utbreiing (*Ulmus glabra* Huds.).

Det vart funne store skilnader i overlevingsstategi mellom treslag og økotypar. Lønn og alm og dei to sørlege fjellbjørkpopulasjonane reagerte alle på høge temperaturar med rask auke i bladarealet, som ein mogeleg kompensasjon for auka respirasjonstap, og lønn og bjørk også ved auka stengelstrekking og dermed konkurrera betre om tilgjengeleg lys. I den nordlege subalpine fjellbjørkpopulasjonen utvikla derimot småplantene blad med høg nettoassimilasjonsevne i staden for å auka bladarealet og stengelveksten. I denne populasjonen ser det derfor ut til at det er ikkje-biotiske klimatiske faktorar snarare enn konkurransefaktoren som er viktigste drivkrafta i tilpasninga.

Nøkkelord: Vekst, bladarealutviding, spesifikt bladareal, topp/rot-forhold, stengelstrekking, nettoassimilasjon, klimatilpasning, temperaturkompensasjon.

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Preface

This paper is the second part of a publication series concerning the significance of dark respiration as a limiting factor for growth in cold climates with special reference to mountain birch (*Betula pubescens* Ehrh.).

I wish to thank Professor John Birks at Botanical Institute, University of Bergen, and Frans-Emil Wielgolaski at Norwegian Forest Research Institute, for their professional and linguistic comments. My appreciation also goes to Vibeke Øksnes and Phyllis Berge who have helped me with transcribing and correcting the manuscript.

Fana, January 1991

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Contents

I. Introduction

In an earlier paper (SKRE 1991) it was shown that the dark respiration or *growth respiration* (e.g. MCCREE 1970, PENNING DE VRIES 1972) is an important limiting factor for growth at low temperatures. The existence of an *alternative respiration,* which is not linked with ATP-production (BEEVERS 1970) is a further evidence for this relationship. At the same time a possible role of this mechanism as a way of preventing undesired growth (LAMBERS 1980) raises the question whether growth is a good measure of plant survival in all kinds of environments.

As a case study to examine the climatic adaptations and acclimation potential (e.g. BILLINGS 1974) mountain birch ecotypes or seed populations could give valuable information about the growth/respiration relationships. As an old immigrant *Betula pubescens* is supposed to have evolved close adaptations to the climate at its habitat. In addition to respiration, measurements of growth and photosynthesis of birch at different light, temperature and daylight conditions are necessary to obtain information about climatic adaptations and the acclimation potential in birch ecotypes. Growth experiments in controlled environments have to be supplemented with measurements on plants grown in the field at high or low nitrogen contents. HÄBJÖRG (1972a) measured growth in birch ecotypes as a function of temperature and photoperiod and KARLSSON & NORDELL (1987) at different nutrient levels in the field. Extensive photosynthetic studies on mountain birch have been carried out by SVEINBJÖRNSSON (1983). MCDONALD et al. (1986a,b,c) studied growth and carbon allocation in mountain birch seedlings at different nutrient levels. In agreement with KARLSSON & NORDELL (1987) they found that reduced nitrogen uptake caused stronger growth reduction in leaves than in roots, and as a result of this growth reduction there was starch accumulation in the leaves. However, none of these studies included simultaneous measurements on growth,respiration and photosynthesis, or biomass studies and chemical analysis of plant tissue to investigate source/sink relationships. Such experiments would provide valuable insights into respiration as a possible limiting factor for growth in cold environments.

As a first step to investigate these relationships, simple growth experiments with mountain birch seedlings at different constant temperatures are needed, that are combined with measurements on respiration and photosynthesis in well- defined plant parts, e.g. mature leaves. The plants should be grown in continuous light to avoid photoperiodic reactions (e.g. termination of shoot growth) as far as possible. In the present study two other common tree species were included for comparison, one with a continental distribution (maple or *Acer platanoides*) and one with a western distribution (elm or *Ulmus glabra*).

II. Materials and methods

1. Principles of growth analysis

Analysis of growth, as defined by dry weight increase and outlined by British scientists (BLACKMAN 1919, BRIGGS et al. 1920, WATSON 1952, PEACE & GRUBB 1982) is the first step toward an eco-physiological analysis of primary plant production. A review of the methods is given by EVANS (1972). An advantage of growth analysis is that the primary values on which it is based are relatively easy to obtain, by destructive sampling at intervals from a large population. These primary values are the dry weight of whole plants or plant parts (stems, leaves, roots etc.) and the size of the assimilatory apparatus in terms of surface area (leaf area or leaf + stem area) or eventually in terms of leaf dry weight, leaf protein or chlorophyll content.

The primary values for growth are measured at selected time intervals, and from these measurements the so-called growth indices that describe growth in various plant parts and the relationships between the assimilating apparatus and dry matter production are found. Shoot/root ratios are of special interest in perennial plants, such as mountain birch and most arctic and alpine deciduous plants (cf. SKRE 1985) where shoot growth in the early season usually takes place at the expense of stored assimilates from the underground organs. The growth of the different plant organs seems to take place according to season and stage of plant development, and associated with changes in the direction of assimilate distribution within the plant (see SKRE 1991).

Most environmental variables influence growth characteristics in different ways. The effects of environmental factors on these growth characteristics tend to compensate each other in order to maintain equilibrium between source and sink and between growth in different plant organs (cf. THORNLEY 1972).

Studies of leaf growth in terms of leaf area and/or leaf dry weight tell us how environmental factors such as temperature, light and photoperiod influence the photosynthetic capacity, i.e. how much the plants are investing into assimilating tissue under different climatic and edaphic conditions, relative to other plant parts (SESTAK et al. 1971).

In growth studies shoot elongation is often used as a measure of growth. Preliminary experiments (SKRE, unpubl.) showed that the correlation between the corresponding stem base diameter and root biomass was too low for this parameter to be used for biomass estimation in mountain birch sudlings. The reason was probably that the sampling errors were too large because of the short duration of the experiment, and competition between plants. RUTTER (1955) found, however, that stem elongation was a better measure of dry-weight increase in young conifers than the stem-base diameter, because of competition for available light. According to KARLSSON & NORDELL (1987) the seedling stage is the most critical time in the life of a plant because the root system is not yet developed and carbon resources are so restricted. Seedlings are therefore expected to be more dependent on climatic factors than mature plants.

In cases where the sample size is small or where a short time interval between samplings is needed, it is often necessary to supplement the destructive samplings with non-destructive measurements of growth parameters. The most commonly used parameters are shoot length, numbers of leaves per shoot, numbers of shoots per plant, stand density (numbers of plants per unit area), size of leaves and stems and phenological observations.

The size of the assimilatory apparatus in terms of leaf area (LA) or leaf dry weight (LW) is usually determined by destructive sampling of a representative subsample (e.g. on excised leaf discs) and related to the subsample dry weight. LA then is estimated with adequate accuracy by means of the resulting specific leaf area SLA = LA/LW and total leaf dry weight. On the other hand when leaf area is known from nondestructive measurements, the SLA values can be used to estimate the leaf biomass.

2. Growth experiments

In September 1969 mature seeds of maple (*Acer platanoides*) and three different populations of mountain birch (*Betula pubescens*) were collected from four different mother trees within each population and species, and the seeds from each mother tree were kept separate during the whole experiment as a means of estimating the genetic variability (see Table 1). The three mountain birch seed populations were taken from one low-altitude stand at Ås 95 metre (BM), from a high-altitude stand at Blefjell 750 metre (BH), both in southern Norway, and from another high-altitude stand at Tynset, Central Norway 800 metre altitude (BT). The seeds were dried at room temperature and then stored dry and cool (+4°C) at darkness. The maple seeds were stratified 4 months at +4°C in moist vermiculite to induce germination (cf. WAREING & PHILLIPS 1970), the treatment started 1 March 1970. Seeds of elm (*Ulmus glabra* var. *scabra*) were collected from their mother trees on 15 June and sown immediately without drying. Preliminary studies (SKRE, unpubl.) had shown that *Ulmus* seeds lost their germinating power if stored in dry conditions for longer periods of time. The birch seeds

Table 1. *Localities and altitudes of seed populations.*

Species	*Betula pubescens*			*Ulmus glabra*	*Acer platan.*
Symbol	BM	BH	BT	AA	LL
Locality	Ås	Blefjell	Tynset	Ås	Ås
Latitude	59°43'N	59°45'N	62°13'N	59°43'N	59°43'N
Longitude	10°40'E	09°28'E	11°08'E	10°40'E	10°40'E
Altitude (m)	95	750	800	95	95
Growth form	Mono-cormic	Poly-cormic	Mono-cormic		
Collection year	1969	1969	1969	1970	1969

Table 2. *Chemical analysis of soil subsamples* (n = 4)

	mg/100 g soil	
P-jord	Before experiment	After experiment
P-AL	51	49
K-AL	50	36
Mg-AL	86	112
Ca-AL	1155	1023
NH_4-N	0.9	
NO_3-N	20	
Tot N	345	
B	2.9	
Mg	0.07	
Zn	30	
Mn	78	
pH	5.7	

were sown at the same time as the elm seeds. The substrate was chosen to be a prefabricated mixture of peat, sand and clay, added nutrients («P-jord»). For details of the chemical composition of soil, see Table 2. The soil was filled into 5 x 5 cm peat pots («Jiffypot») in order to avoid disturbing the root system by transplanting. According to VAARTAJA (1956), birch seeds require light (long days) for germination at low temperatures. After sowing, the birch seeds were therefore covered with a thin layer of sand to allow light penetration. On 15 June the maple seeds had also started to germinate and were transplanted to 10 cm plastic pots filled with the prefabricated soil. The pots were placed at 18°C and continuous light (10000 lux).

The birch seeds started to germinate about 10 days after sowing at 18°C and light intensity of 10000 lux while the elm seeds required some more time (20–25 days). Germination percentages varied from 3–8 % (elm) to 12–20 % (maple) and from 9 % to 60 % (birch) depending on mother tree (see Table 3).

By about 25 August, the birch seedlings had developed 4 fully developed leaves and the maple seedlings had 2 pairs of leaves, in addition to the cotyledons. The birch seedlings were then thinned to one plant per pot and the peat pots with plants were transplanted to 10 cm plastic containers filled with prefabricated soil. After 2 days at low temperature(15°C) to recover from transplantation the plants in their containers were distributed amongst the following eight temperatures and continuous light (24 hrs, 10000 lux):

3–6–9–12–15–18–21–24°C

The light source used was 140W Philips TL33 fluorescent tubes with a spectral distribution as shown in Fig. 1 and an illuminance at plant level of 10000 lux, corresponding to an irradiance of 280 μMm-2 sec-1 (PPFD). A total of 8 plants in containers from each mother tree were selected for each temperature. To maintain temperature control, the plants were placed on nets in 2 x 1 x 1 metre wooden boxes with thermostat-controlled heating

cables in the bottom and with open tops. On top of each box, a glass plate was placed to prevent heating from the light tubes above. The boxes except one, were again placed inside the cold store room of Institute of Horticulture at Norwegian Agricultural University, Ås, where the temperature was maintained at +4°C. The last plant group, to be grown at +3°C, was placed in a cool greenhouse compartment of the Botanical Institute at the University. The plants received daylight with supplementary light (10000 lux) from light tubes.

The elm seedlings were kept in the peat pots until they had got two pairs of leaves and had started to develop a new stem segment with single leaves. At this stage (about 10 September) they were transplanted to 10 cm plastic containers with prefabricated soil and 8 plants per mother trees were distributed at each temperature except 12° and 18°C.

The soil in the containers was watered every day to maintain field capacity and watered every week with nutrient solution (Table 4). A representative subsample of plants from each experiment was harvested prior to transplantation for destructive biomass determination. The following non-de-

Table 3. Percentage germination at 20°C in seeds from four separate mother trees of lowland (BM) and subalpine (BH and BT) *Betula pubescens* populations, and lowland populations of *Acer platanoides* (LL) and *Ulmus glabra* (AA). Sowing date 20.06.1970.

Mother tree	Date 1970							
	29.6	1.7	3.7	5.7	7.7	13.7	21.7	31.7
BM 1	36	51	58	64	64	65	65	65
2	7	28	33	35	36	37	38	38
3	19	29	37	37	38	38	38	38
4	8	12	14	17	18	19	20	20
BH 1	1	5	7	8	9	10	11	12
2	12	27	29	31	34	36	37	38
3	6	11	12	14	14	15	15	15
4	7	16	20	21	22	23	24	24
BT 1	2	6	8	10	12	12	12	12
2	10	19	25	29	35	36	37	37
3	35	48	54	57	60	61	61	61
4	15	22	24	26	28	28	28	28
LL 1	0	2	7	10	11	12	13	13
2	3	8	12	16	18	20	21	22
3	2	5	9	11	11	12	12	12
4	2	6	7	8	8	9	9	9
AA 1					1	5	9	9
2							3	3
3							3	3
4						2	9	9

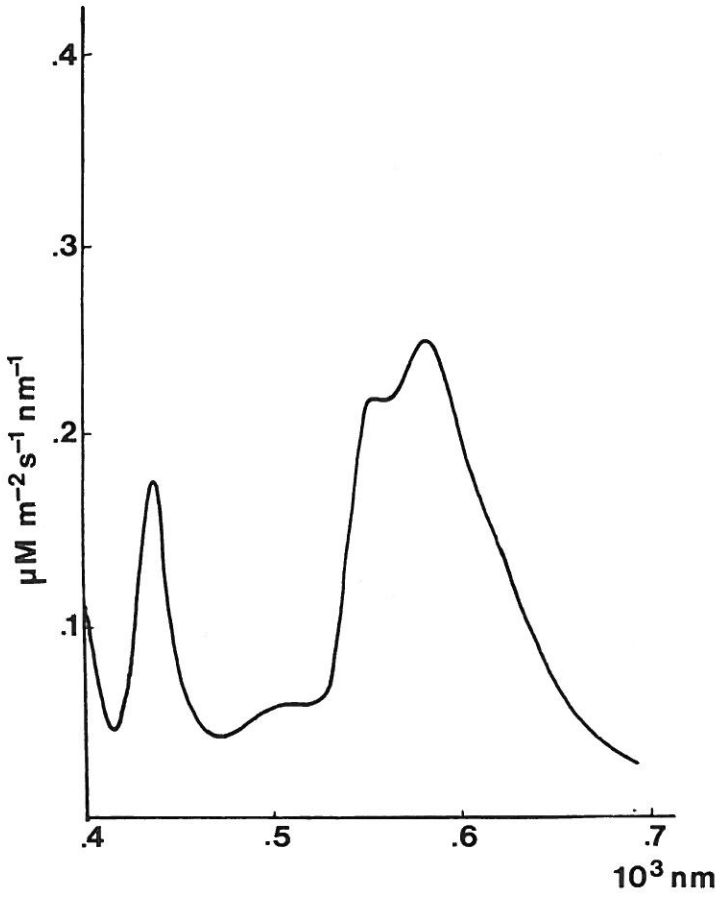

Fig. 1. Spectral distribution of the radiant energy E ($\mu Mm^{-2}s^{-}1$) per wavelength (nm) in the interval 400–700 nm.

structive growth characteristics were then measured every second (24–21–18°C), fourth (15–12–9°C) or eigth (6–3°C) day during the experiment on the remaining plants:

L = stem length from the position of the fourth leaf
l_i = length of leaf number i
b_i = breadth of leaf number i

Each measurement also included estimation of specific leaf area on additional plants, where leaf discs with fixed area were punched out of representative subsamples of leaves. The root and stem biomass was also measured occasionally on these plants, i.e. at transplanting time, after 18 and 36 days at different temperatures, in addition to the destructive sampling time

Table 4. *Nutrient solution* (modified from ARNON 1938)

6 mM KNO_3	2.86 mg H_3BO_3
4 mM $Ca(NO_3)_2$	1.81 mg $MnCl_4 \cdot 4H_2O$
1 mM $NH_4H_2PO_4$	0.08 mg $CuSO_4 \cdot 5H_2O$
4 mM $MgSO_4$	0.22 mg $ZnSO_4 \cdot 7H_2O$
	0.09 mg H_3MoO_4
	per liter

50 ml complete solution per pot was added every week
0.5 ml 0.5% Fe-tartrate was added three times a week.

at the end of the experiment, for rough estimation of net assimilation rates. These plants were not included in the eight plants per mother tree where non-destructive measurements were made.

The temperature and air moisture content within each growth chamber was checked with shielded thermohygrographs and the illuminance with a luxmeter, where the radiant energy was measured by absorption on a selenium sensor. Temperature variations within each chamber were reduced to within ± 1°C by varying the distance, or air space between the glass plate and the upper edge of the growth chamber. Light intensity was kept at constant level by lifting the light tubes as the plants were growing, so as to keep a constant distance.

The growth was followed until the stage when the plants had developed 12 fully grown leaves. The plants growing at the three lowest temperatures (3–6–9°C), however, stopped growing before reaching the 12-leaf stage and started to develop winter buds. All plants were harvested by the end of the experiment, either at the 12-leaf stage or at the stage where visible winter buds were seen but before the leaves started to turn yellow. Some leaves were frozen for measurements of sugar and chlorophyll content, the remaining plants were separated into leaf, stem and root tissue. On four plants per mother tree and temperature the fresh weights of single leaves were measured, then an imprint of the leaves was taken on photographic paper for leaf area determination. The leaves were then oven dried at 80°C and the dry weights of single leaves were measured. Total leaf, stem and root tissue was treated the same way. On these plants no further chemical determinations were carried out.

Leaf area of single leaves was measured manually by means of a planimeter. The dry weights (LW_i) were then compared with leaf area (LA_i) on single leaves of different age within each population and growth temperature, and the corresponding values of l_i and b_i were added in order to estimate the k-values from eq. (1). From these measurements the mean specific leaf area ($SLA = 1/n \, \Sigma LA_i/LW_i$) was also found for leaves of different age and treatment (see Table 5).

(1) $LA_i = k \times l_i \times b_i$

From the growth measurements on single leaves and the SLA values for leaves of different age, the dry matter increase and growth rates of single

leaves and total green tissue per plant was estimated. Similar methods were used by HUGHES (1971) to estimate the production per unit area or per tree in a deciduous woodland plot. The SLA values of total green tissue per plant were calculated from the corresponding values of LW and LA. Also growth curves for single leaves were followed, in order to estimate the turnover time of leaves and how it changed with the age of plant at different temperatures.

3. Statistical treatment of data

The leaf areas and leaf dry weights for single leaves and plants were fitted to sigmoid growth function (BLACKMAN 1919) in order to determine leaf growth as a function of temperature. Similarly, corresponding values of total stem dry weight per plant and shoot length were compared to test the reliability of shoot length as a measure of growth.

Growth data (leaf area and dry weight) on single leaves were computed for plants grown at 9°, 15° and 21°C in 24 hours photoperiod by means of equation (1). For plants grown at 3°, 6°, 12°, 18° and 24°C only the total leaf growth per plant was computed. Based on these data, recorded every second, fourth and eigth day during the stage from 4 to 12 visible leaves, sigmoid growth curves were constructed, based on cubic regressions. The stem and leaf growth rates were based on the linear growth phase, when growth rates are independent on time (BLACKMAN 1919). For this reason the growth curves (Figs. 2 and 4) and significance tests (Table 7) are based on the absolute growth rates rather than relative growth rates.

To test the variation between mother trees and populations, analyses of variance were carried out on corresponding values of stem elongation (cm/day) and growth in leaf biomass (mg/day) per plant during the linear growth phase at each temperature. Another analysis of variance was carried out on the biomass data from the destructive sampling. From these analyses, the total variance was found that could be accounted for by the regression, and the residual variance was tested by F-test. Based on measurements of the estimated size of the fourth leaf and destructive samplings of the same plants at the 12-leaf stage a consistency test was carried out to see to what degree individual differences between plants were exposed and amplified throughout the time period of the experiment.

III. Results

The specific leaf area and the transformation coefficients k (eq. 1) for single leaves of different age at harvesting (Table 5) were calculated for plants of different origin and treatment. The single-leaf values of SLA and k at harvesting, and the measured SLA values during the experiment taken from subsamples were in turn used to estimate the total leaf area and the total dry weight increase of leaf tissue per plant during the experiment from non-destructive measurements of leaf growth (length x width). The ratio l/b between mean maximum length and width of single leaves of different age is

Table 5. Growth parameters of single leaves and numbers of leaves at harvesting in plant individuals from three populations (BM-BH-BT) of mountain birch (*Betula pubescens*) and from one population each of maple (*Acer platanoides*) and elm (*Ulmus glabra*), shown as a function of leaf age after destructive sampling. Confidence limits $\pm 2s_{\bar{x}}$ where $S_{\bar{x}}$ is the standard error, are shown on the mean values. The numbers are not comparable to the nondestructive measurements shown in Figure 7a. In maple the numbers refer to leaf pair.

Numbers of leaves (leaf pairs) at harvesting.

Temp.	Population and species				
	BM	BH	BT	AA	LL
6°C	8	8	9	8	8
9°C	9	9	10	9	8
12°C	12	12	11	10	8
15°C	12	12	12	11	8
18°C	12	12	12	12	8
21°C	12	12	12	12	8
24°C	12	12	12	12	8

SLA = LA/LW = Specific leaf area in cm^2/mg.

Leaf no.	Population and species				
	BM	BH	BT	AA	LL
1	0.37	0.34	0.25	0.23	0.24
2	0.34	0.33	0.28	0.25	0.25
3	0.33	0.31	0.27	0.25	0.27
4	0.33	0.28	0.26	0.25	0.28
5	0.33	0.28	0.28	0.25	
6	0.33	0.29	0.30	0.25	
7	0.33	0.30	0.30	0.24	
8	0.33	0.31	0.30	0.25	
9	0.33	0.32	0.30	0.26	
10	0.33	0.34	0.27	0.27	
11	0.34	0.33	0.25	0.31	
12	0.30	0.26	0.23	0.22	

also shown. The values in Table 5 except SLA are all averaged over temperatures because the temperature effect on the leaf shape was found to be small or insignificant (SKRE, unpubl.). Table 5 is supplemented with Fig. 6a, where SLA is shown as a function of temperature, and with Fig. 3 where some imprints of leaves of different age and from different populations and species are shown as contact prints.

The leaf dry weight (LW) of single leaves is shown in Fig. 2 on a time scale for plants grown at 9°, 15° and 21°C. These data were used to estimate turnover times of leaves, i.e. the time between the corresponding stage of subsequent leaves, at these three temperatures (Table 6). From the single-leaf curves in Fig. 2 and similar data on plants grown at other temperatures the total leaf area and leaf dry weight increase per plant was estimated. The

Table 5 (cont.)

$k = LA(l \times b)^{-1}$ = leaf area transformation ratio.

Leaf no.	Population and species				
	BM	BH	BT	AA	LL
1	0.79	0.77	0.86	0.74	0.70
2	0.74	0.74	0.80	0.72	0.59
3	0.72	0.73	0.81	0.70	0.54
4	0.67	0.71	0.78	0.70	0.57
5	0.68	0.70	0.76	0.71	
6	0.68	0.69	0.74	0.72	
7	0.68	0.70	0.73	0.72	
8	0.68	0.71	0.73	0.72	
9	0.68	0.71	0.73	0.72	
10	0.68	0.71	0.73	0.72	
11	0.69	0.72	0.74	0.70	
12	0.76	0.74	0.77	0.70	

l/b = leaf length/width ratio

Leaf no.	Population and species				
	BM	BH	BT	AA	LL
1	1.09	1.08	1.07	1.75	1.57
2	1.05	1.04	1.06	1.78	1.29
3	1.09	1.03	1.03	2.02	1.13
4	1.11	1.05	1.02	2.04	1.16
5	1.16	1.10	1.04	1.93	
6	1.19	1.13	1.07	1.91	
7	1.21	1.14	1.10	1.93	
8	1.25	1.16	1.12	1.94	
9	1.25	1.17	1.14	1.94	
10	1.28	1.18	1.16	1.95	
11	1.32	1.19	1.17	1.95	
12	1.39	1.24	1.21	1.95	

combined growth curves for each population and species are shown in Fig. 4a. On Fig. 4a the confidence limits $\pm 2s_{\bar{x}}$, where $s_{\bar{x}}$ are the standard errors, are plotted on the observation means of the leaf growth data. The mean growth rates

$$d(LW)/dt$$

were estimated from the slope of the linear part of the fitted growth curves with the standard errors taken from the confidence limits on the means at specific dates after transplantation. The results are presented as a function of temperature in Fig. 4b. The variation in growth rates between mother trees and populations was tested by analysis of variance on the growth in leaf biomass (Table 7) and stem elongation (Table 10) where each temperature was kept separate.

The observed dry weights of leaf, stem and root tissue (LW-SW-RW) from the destructive samplings are listed in Table 8 and shown as functions

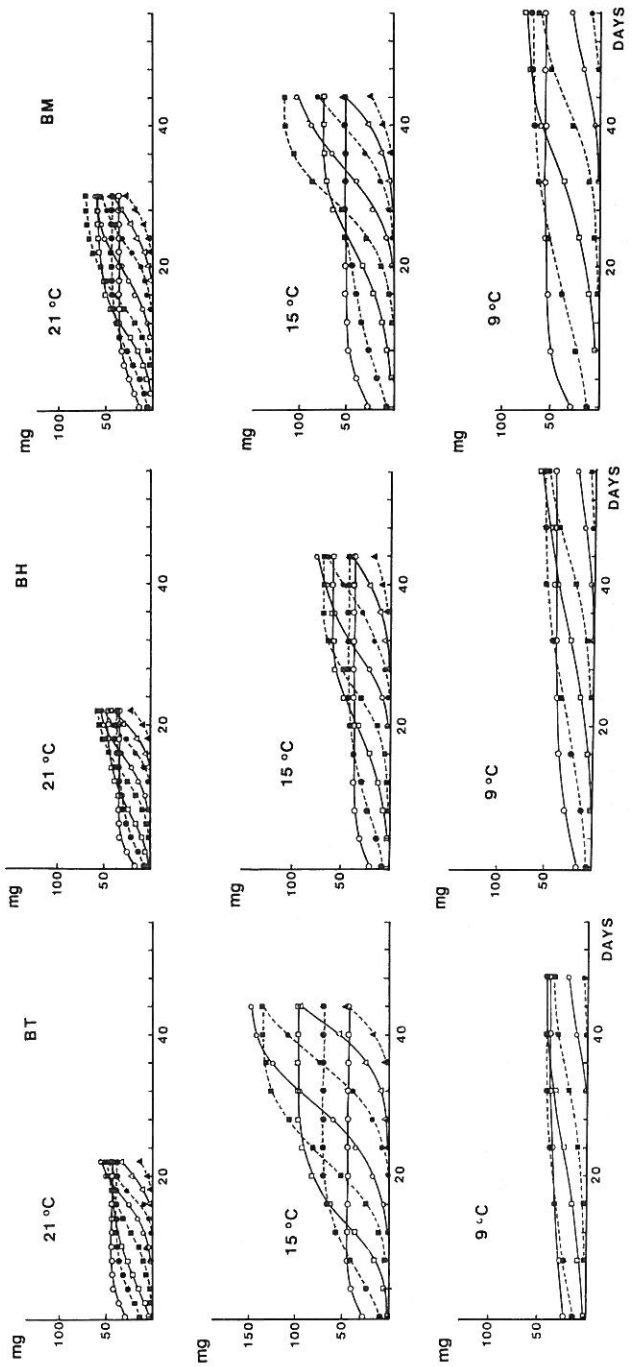

Fig. 2. Growth curves of single leaves, measured as dry matter increase (mg/leaf) throughout the experiment, all four mother trees combined. Time is measured as days from transplantation (4-leaf stage). The symbols are:
BT = *Betula pubescens* (Tynset)
BH = *Betula pubescens* (Blefjell)
BM = *Betula pubescens* (Ås)
AA = *Ulmus glabra* (Ås)
LL = *Acer platanoides* (Ås)

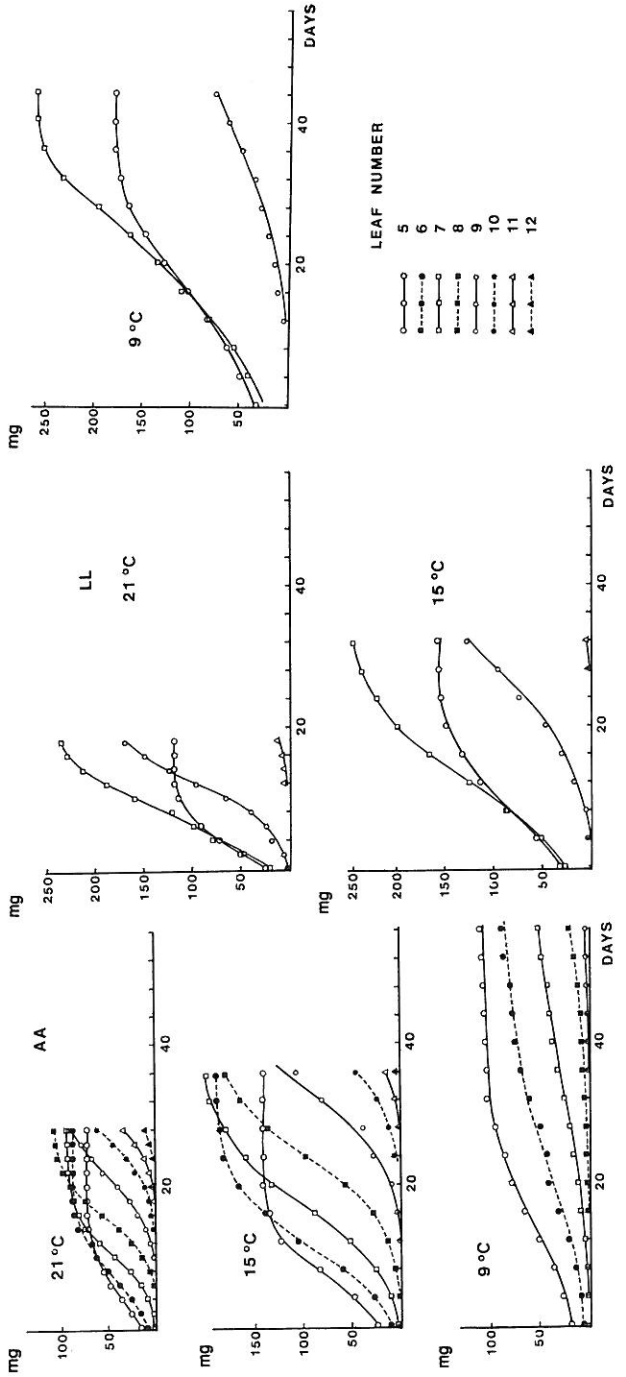

Fig. 2. (Cont.)

Table 6. *Turnover times in days for single leaves at 9°, 15° and 21°C (from* Fig. 2) *with confidence limits* $\pm 2s_{\bar{x}}$ *on the mean values.*

Population	Temperature		
	9°	15°C	21°C
BM	14.8 ± 2.0	7.2 ± 1.2	4.1 ± 0.7
BH	12.4 ± 1.6	7.0 ± 0.8	3.2 ± 0.3
BT	12.4 ±2.7	7.0 ± 1.0	4.4 ± 0.7
AA	17.5 ± 5.8	6.3 ± 1.6	4.1 ± 1.0
LL*	31.0 ± 7.6	15.7 ± 2.4	6.7 ± 1.3

* The turnover times of maple leaves are calculated as the time between the second and third pair of leaves after the four juvenile leaves.

of temperature on Fig. 5. On Fig. 6a the specific leaf area and the leaf area ratios LAR = LA/W from Figs. 5 and 7a, where W is total plant biomass, are shown as functions of temperature for single populations and species. When calculating the total leaf area and leaf dry weight per plant, the mother trees were kept separate to test the variation within seed populations against the total variation within plants grown at each temperature. The result from this analysis of variance on biomass data are shown in Table 8. The result of the consistency test is presented in Table 9. In Table 11 the corresponding values of stem length and stem biomass per plant at harvesting are listed for separate groups of populations and treatments.

Figs. 4b and 5 show that observations are missing on maple growth at 3° and 6°C. The reason is that there were not enough plants for a complete experiment, and the threshold temperature for growth in maple was supposed to be higher than in the other two species. Fig. 4b shows that this was a mistake. Similarly observations on elm growth are missing at 12° and 18°C as a result of too low plant supply. However, observations on specific leaf area were made on a lower number of plants at the missing temperatures (Fig. 6a).

The leaf growth curves in Fig. 4a were basically obtained from measurements of specific leaf area (SKRE, unpubl.) and the leaf area determinations in Fig. 7a. In Fig. 7b two typical net assimilation rate (NAR) curves are shown, where $NAR = (LA)^{-1}\, dw/dt$.

Fig. 3a. Contact prints of leaves and stems of the investigated species, taken at the 12-leaf stage, reduced to one fourth the normal size. The shown birch seedling is from the BH population.

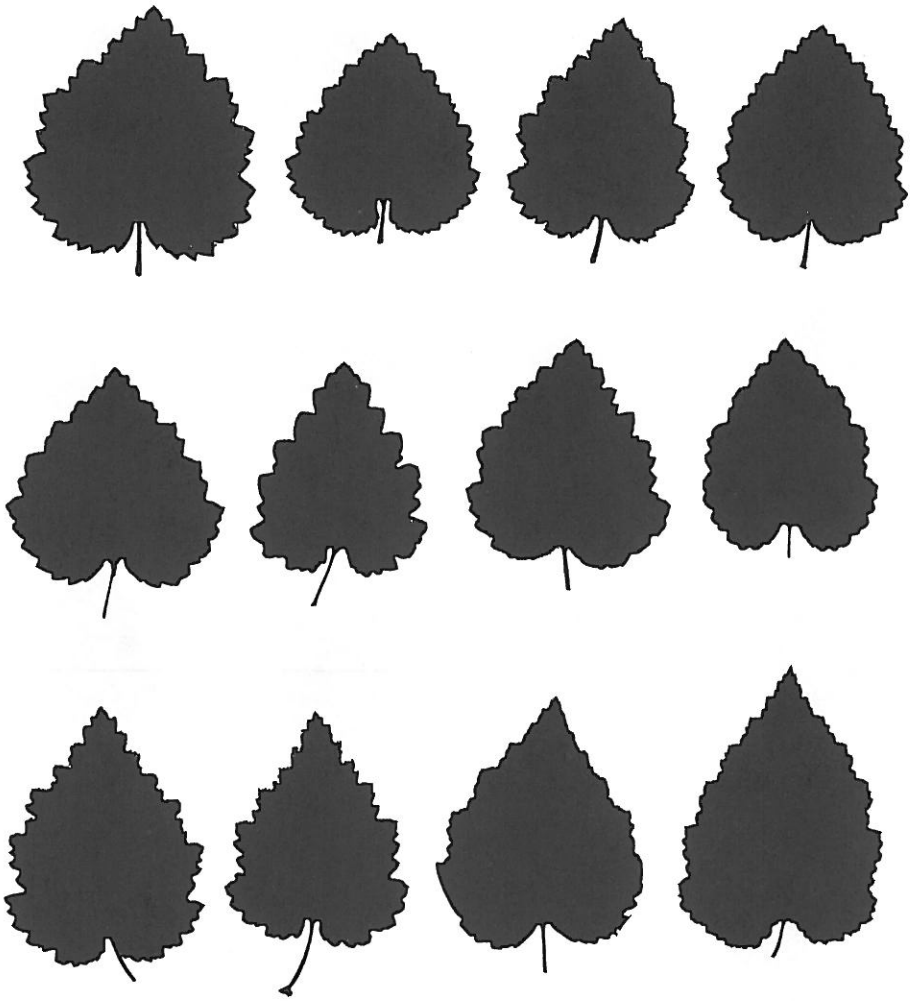

Fig. 3b. Leaf number 8 fully expanded from seedlings raised from four different mother trees, typical shape, reduced to half the normal size. The mountain birch populations are BT (top), BH (center) and BM (bottom line).

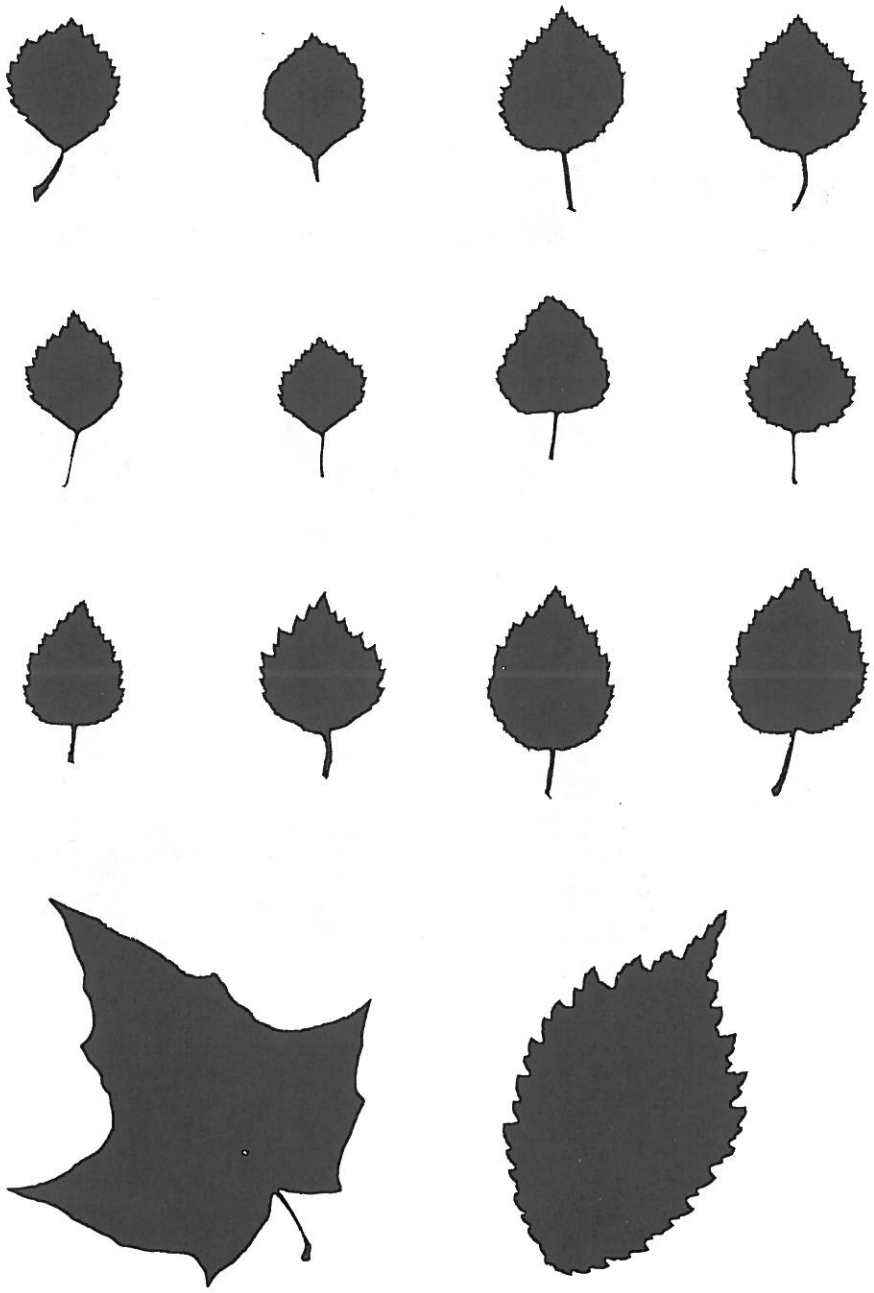

Fig. 3c. Mature short shoot birch leaves from the same mother trees as in Fig. 3b, reduced to half the normal size, and typical mature leaves of maple and elm.

Table 7. Variance ratios (F) and significance levels for daily leaf growth (mg/plant) at different constant temperatures and 24 hours photoperiod during the linear growth phase. Populations and species indicated. The root error mean squares are given in the last column. Significance levels: °P<0.1 ▪P<0.05, *P<0.01. (See Figure 4b for means and confidence limits, shown in the lower part of the table). DF = degrees of freedom.

Species	*Betula pubescens*							
Temperature	3°C	6°C	19°C	12°C	15°C	18°C	21°C	24°C
Source	DF F	DF F	DF F	DF F	DF F	DF F	DF F	DF F
Population	2 5.8*	2 15.0*	2 3.8▪	2 12.9*	2 8.5*	2 8.3*	2 6.1*	2 14.3*
Mother tree	3 0.5	3 0.7	3 0.7	3 9.3*	3 3.8▪	3 0.6	3. 1.7	3 4.7
Interaction	3 1.5	6 3.7*	6 2.4▪	6 8.6*	6 0.4	6 2.0°	6 2.3▪	6 4.1*
Model	8 2.2°	11 4.9*	11 2.2▪	11 9.6*	11 2.8*	11 2.8*	11 2.8*	11 6.1*
Root error ms	30 0.3	44 1.4	42 2.2	45 1.9	48 8.1	51 6.4	48 10.1	45 8.9
BT	0.7±0.3	0.6±0.3	3.3±1.2	7.9±1.8	21.5±4.5	24.3±3.3	17.1±5.0	13.4±2.4
BH	0.3±0.1	2.1±0.5	4.8±1.2	5.1±1.0	12.0±3.0	16.0±2.3	25.9±6.6	27.2±5.8
BM	0.4±0.1	2.9±0.7	5.2±0.9	8.0±1.0	20.7±3.7	20.1±2.9	18.6±2.0	23.4±4.6

Species	*Ulmus glabra*							
Temperature	3°C	6°C	9°C	12°C	15°C	18°C	21°C	24°C
Source	DF F	DF F	DF F		DF F		DF F	DF F
Mother tree	1 0.8	1 0.9	1 0.0		3 1.0		3 2.2	1 0.7
Root error ms	8 0.5	10 0.8	9 5.8		16 9.1		19 5.6	6 4.9
AA	0.5±0.3	1.1±0.4	5.6±3.4		26.7±4.1		20.3±2.5	14.9±3.4

Species	*Acer platanoides*							
Temperature	3°C	6°C	9°C	12°C	15°C	18°C	21°C	24°C
Source			DF F	DF F	DF F	DF F	DF F	DF F
Mother tree			3 1.0	3 1.5	3 0.8	3 2.1	3 0.6	1 1.2
Root error ms			23 3.7	23 5.8	26 8.0	22 6.6	28 10.0	10 3.8
LL			13.6±1.4	15.8±2.3	16.0±2.8	18.0±2.7	15.3±1.7	13.4±2.3

IV. Discussion

1. Growth of single leaves.

According to Table 9 there was a significant correlation between the (estimated) leaf biomass at the 4-leaf stage and the corresponding leaf biomass per plant at harvesting (12 leaf stage). The exception was maple where the correlation at 21°C was hardly significant. In the other species and populations the correlations between initial and final dry weights tended to decrease with increasing growth temperature. The size and source strength of the seedlings before transplantation seem to influence the individual growth rates during the experiment (cf. HUSS 1956). Therefore, care was taken to select plants within each population that were as even-sized as possible at the start of the experiment (see Fig. 4a).

Estimation of leaf biomass by non-destructive measurements generally showed good agreement with destructive samplings. A simple linear correlation of $r_{xy} = 0.95$ between leaf biomass values measured by destructive and nondestructive methods on BH plants grown at 21°C was found (SKRE, unpubl.). Sample size was n = 24. This may also be seen by comparing estimated leaf biomass (Fig. 4a) at harvesting with the measured values (Fig. 5). The non-destructive measurements could therefore be used as a good approximation for estimating leaf growth.

The growth of single leaves followed the general sigmoid growth curve shown in Fig. 2 (cf. BLACKMAN 1919, MORK 1960, BRIGGS et al. 1920). In mountain birch seedlings the final leaf size increased with temperature, but also with the position of the leaf on the stem up to a certain point and then decreased due to growth cessation. Unfortunately the experiment was stopped when the plants had developed 12 leaves or eventually (at 3°, 6° and 9°C) stopped shoot growth. For this reason the maximum leaf size in the northern subalpine BT population from central Norway occurred at leaf number 8 when plants were grown at 9°C but changed to leaf number 11 when the plants were grown at 15°C (Fig. 2). Similar relationships were found in the two other birch populations and in the elm population. In maple, (*Acer platanoides*), however, the second leaf pair always reached the highest final size. The growth rates of single leaves seemed to increase with plant size but also with the final leaf size during the linear growth phase (see Fig. 2). In Table 6 the mean turnover times of single leaves are shown for different populations and species grown at 24 hour photoperiod and constant temperatures of 9°, 15° and 21°C. The decreasing turnover times with increasing age, as seen from Fig. 2, may be partly interpreted as an effect of increased shading. According to THROWER (1964) plants respond to shading by more rapid leaf development. The turnover times were strongly influenced by temperature, especially in the two other broadleaf species *Acer platanoides* (LL) and *Ulmus glabra* (AA). The turnover times in mountain birch varied from 3–4 days at 21°C to 12–13 days at 9°C. Among mountain birch seedlings the southern subalpine population (BH) responded to high temperature (21°C) by increasing the rate of leaf production more than the two other populations (Table 6). This may be an adaptation to different light regimes

Table 8. Variance ratios (F) and significance levels for mg dry weight of leaf (L), stem (S) and root (R) tissue as well as total dry weight (TOT) per plant at the 12-leaf stage, and the corresponding shoot/root ratio (S/R). The effects of separate mother trees and populations are tested against the total variation within each species. All values except the shoot/root ratios are temperature-corrected and referring to 15°C. Significance levels are: ° $P<0.1$, ▪ $P<0.05$, * $P<0.01$. In the lower part of the table are shown the means with confidence limits for single populations and species. DF = degrees of freedom.

Betula pubescens

Source	DF	L	S	R	TOT	S/R DF	S/R F-value
Population	2	31.4*	4.5▪	25.8*	20.2*	2	58.0*
Mother tree ...	3	5.0*	1.7	0.8	1.8	3	3.3▪
Interaction	6	2.8▪	3.6▪	1.4	2.4▪	6	2.8▪
Temperature ..						7	2.9▪
Model	11	8.6*	3.3*	5.7*	5.5*	18	9.0▪
Root error .... ms	429	195.9	153.4	265.9	501.7	422	1.11
	N						
BT	131	628±42	388±26	592±65	1608±110		1.8±0.2
BH	150	442±29	407±26	378±35	1228± 75		3.1±0.9
BM	160	520±28	440±25	413±31	1374± 68		3.1±0.8

Ulmus glabra

Source	DF	L	S	R	TOT	S/R DF	S/R F-value
Mother tree ...	3	0.4	3.3▪	2.2°	1.9	3	4.0▪
Temperature ..						5	9.7*
Model						8	7.6*
Root error .... ms	77	244.1	164.7	219.4	539.2	72	0.81
	N						
AA	80	633±54	459±38	566±50	1658±122		2.5±0.3

Acer platanoides

Source	DF	L	S	R	TOT	S/R DF	S/R F-value
Mother tree ...	3	0.8	4.3*	4.0*	3.4*	3	3.4▪
Temperature ..						5	4.5*
Model						155	4.1*
Root error .... ms	160	147.3	102.3	181.7	305.0	163	1.13
	N						
LL	163	596±23	273±16	314±29	1183±49		3.3±0.8

Table 9. Correlation coefficients between leaf dry weights (mg/plant) at the 4-leaf stage when plants were transplanted at different constant temperatures, and the corresponding leaf dry weights by the time of destructive sampling at the 12-leaf stage Numbers of observations in parenthesis.

Population and species	Temperature					
	9°C		15°C		21°C	
BT	0.39	(16)	0.44	(19)	0.26	(23)
BH	0.69	(18)	0.36	(17)	0.32	(17)
BM	0.60	(20)	0.58	(23)	0.54	(20)
AA	0.87	(11)	0.53	(20)	0.45	(22)
LL	0.38	(27)	0.44	(30)	0.13	(32)

(cf. UHL 1937, GAUSLAA 1984), where southern subalpine mountain birch plants tend to produce smaller leaves with higher heat exchange capacity than northern subalpine and lowland plants, as a response to higher solar radiation. The specific leaf area (SLA) was slightly lower within the subalpine BT population from central Norway than in the two southern birch populations (Table 5). The thick leaves in northern and alpine ecotypes may be a response to temperature and light conditions. According to BILLINGS (1974) arctic plants tend to have a higher chlorophyll content per unit area than southern alpine relatives as a reaction to lower light intensities.

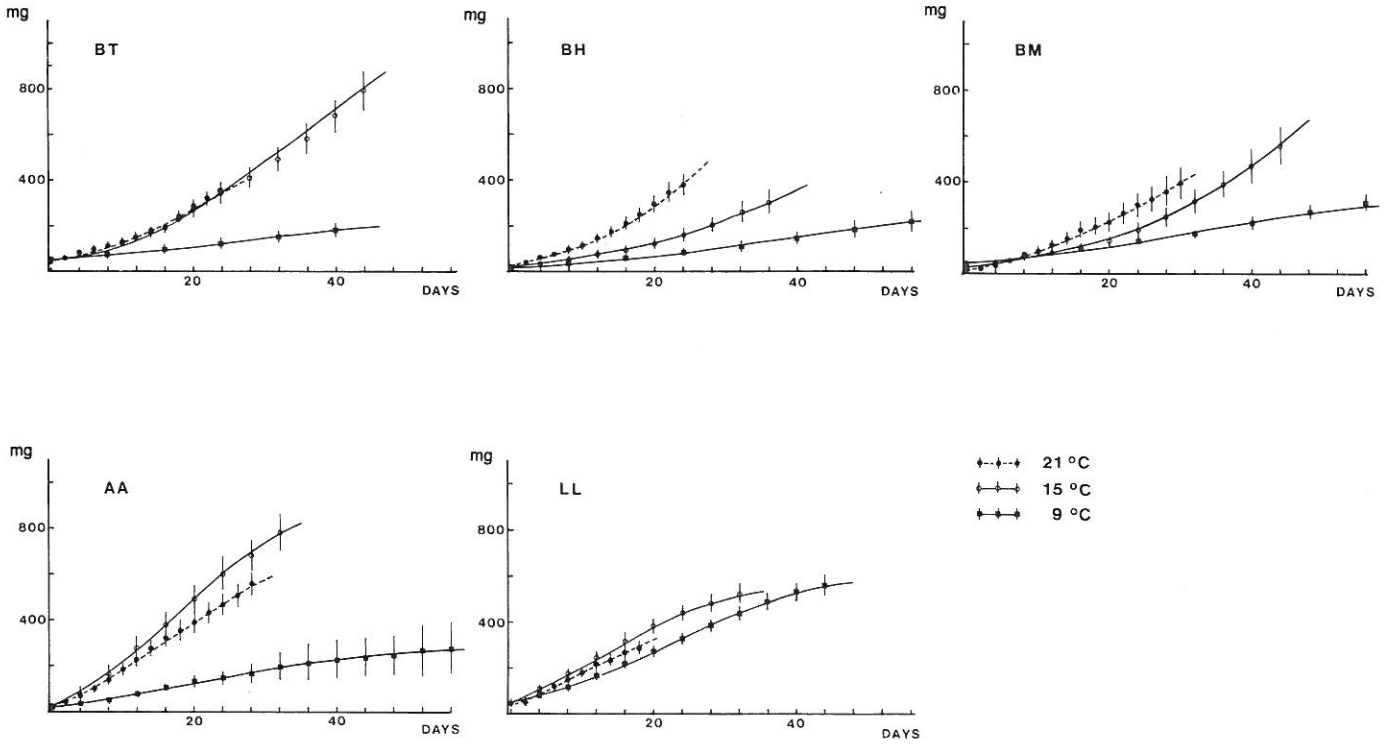

Fig. 4a. Growth in total leaf biomass (mg/plant) throughout the period from the 4-leaf stage to the 12-leaf stage. The growth curves at 9°C, 15°C and 21°C and 24 hours photoperiod for the three mountain birch populations are shown separately. The curves are adjusted to a sigmoid shape with confidence limits $\pm 2s_{\bar{x}}$, where $s_{\bar{x}}$ is the standard error, plotted on the mean observation values. See Fig. 2 for symbols.

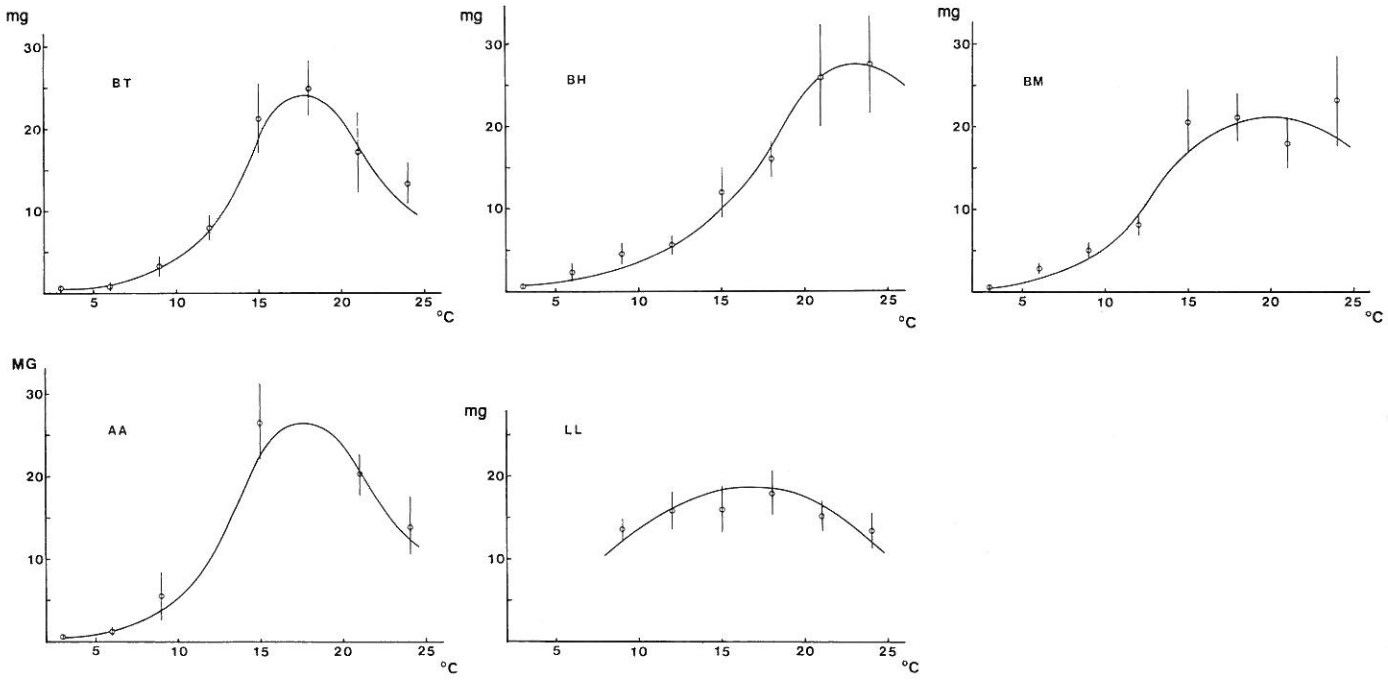

Fig. 4b. Leaf growth d(LW)/dt (mg/day) during the linear growth phase (see Fig. 4a) with confidence limits $\pm 2s_{\bar{x}}$. The values are taken from Figure 4a and similar information for plants grown at other temperatures.

Fig. 5. Destructive sampling at the 12-leaf stage. Mean biomass of leaves, stems, roots and total combined tissue in grams/plant with confidence limits $\pm 2s_{\bar{x}}$ on the total biomass values shown as functions of temperature in seedlings grown at 24 hours photoperiod. The three birch populations are shown separately. See Fig. 2 for symbols. The leaf biomass values are not directly comparable to the estimated values in Fig. 4a.

2. Temperature compensation mechanisms

One major temperature effect on leaf growth is that the size of single leaves (Fig. 2) increased with temperature up to about 15°C and then decreased while the specific leaf area and the leaf area ratio (Fig. 6a) first decreased and then increased above a certain temperature. Because of the strong variations in specific leaf area, with lowest values at 10°–15°C, the leaf biomass (Fig. 2) at the 12-leaf stage was much higher at 15°C than at 21°C, although the total leaf area per plant (Fig. 7a) was lower. The tendency was strongest in leaves of the northern BT population, where the increase in SLA from 15°C to 21°C (Fig. 6a) was particularly strong.

When comparing temperature responses of the specific leaf area in different species and populations, mountain birch from central Norway (BT) and elm (AA) both showed the same pattern with minimum SLA values at 15°C, while in the two mountain birch populations from South Norway (BH and BM) the lowest SLA values were found at 9°C. In maple leaves (LL) the specific leaf area changed very little with temperature. The elm leaves had lower SLA (thicker leaves) then the maple and the three mountain birch populations.

The leaf area ratios LAR (Fig. 6a, dashed line) varied according to the SLA variations, indicating that the leaf weight ratios LWR (= LW/W) change very little with temperature. The LWR values show leaf biomass relative to total biomass, and Fig. 6a indicates that this proportion is highest in elm and lowest in mountain birch from central Norway (BT). Northern birch populations seem to invest more of their resources into root growth than their southern relatives, a conclusion which is confirmed by looking at the shoot/root ratios in Fig. 6b and the biomass distribution in Fig. 5. High shoot/root ratios and high leaf weight ratios show that elm invests most of its above-ground growth into the leaves, in contrast to the southern birch populations and maple where stem growth was more favoured. There was a significant temperature effect on the shoot/root ratio within all three species (Table 8), with minimum values at 10°–15°C (Fig. 6b), but most pronounced in the two southern mountain birch populations and in maple. These plants seemed to compensate for reduced photosynthesis rates at high temperatures by increasing their stem growth (cf. Table 10) rather than by increasing their leaf area, probably in order to compete more efficiently for available light (cf. WARREN WILSON 1972). In southern areas competition for light is more important in the adaptation process than in the Arctic (KALLIO 1984). In mountain birch from central Norway (BT) and elm, however, the shoot/root ratio was approximately constant over the temperature range.

The relatively high root biomass in northern ecotypes was also noted by VAARTAJA (1960) in his study on *Populus,* and he explained it as an adaptation to low soil temperatures. On cold soil the nutrient concentration is low due to slow decomposition rates, and this is compensated by the plants by expanding their root system (cf. CHAPIN 1979). The low leaf area ratios and shoot/root ratios at medium temperatures (10–15°C) may also be explained as a compensation mechanism, i.e. when photosynthetic rates are high,

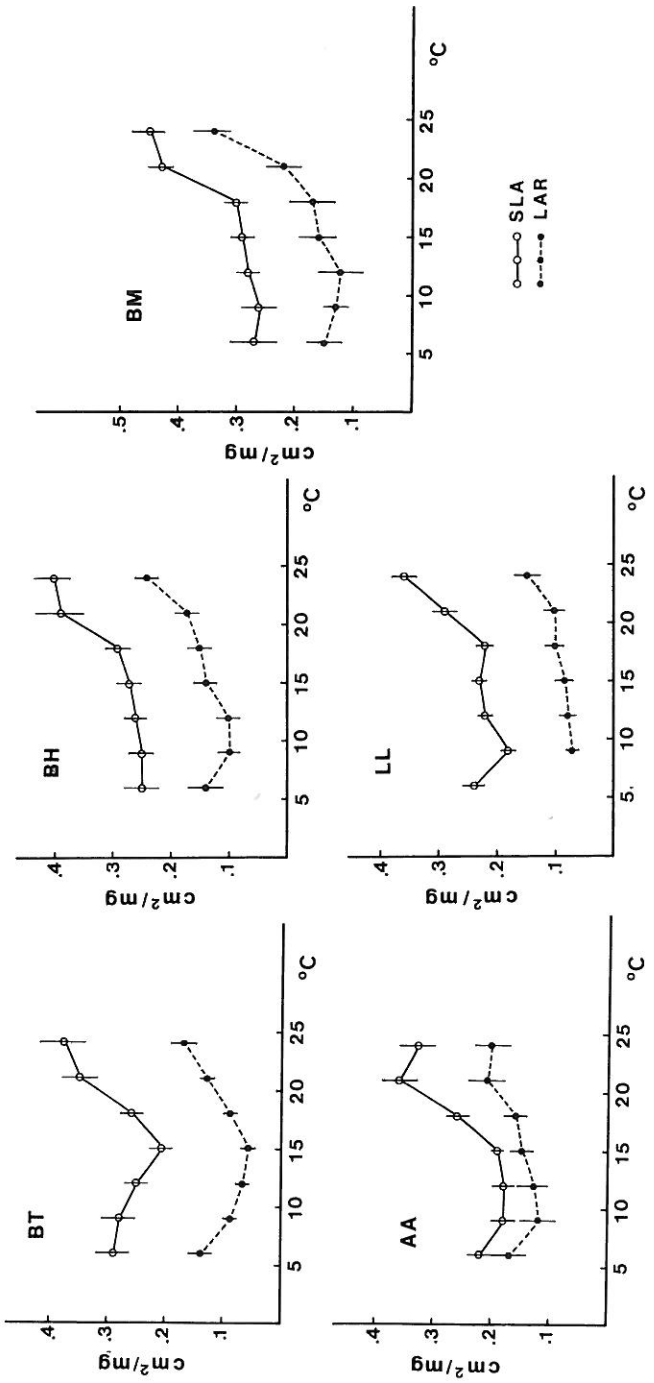

Fig. 6a. Leaf area ratio (LAR) and specific leaf area (SLA) at harvesting (cm^2/mg) taken from Figs. 5 and 7a with confidence limits $\pm 2s_{\bar{x}}$, shown as functions of temperature.

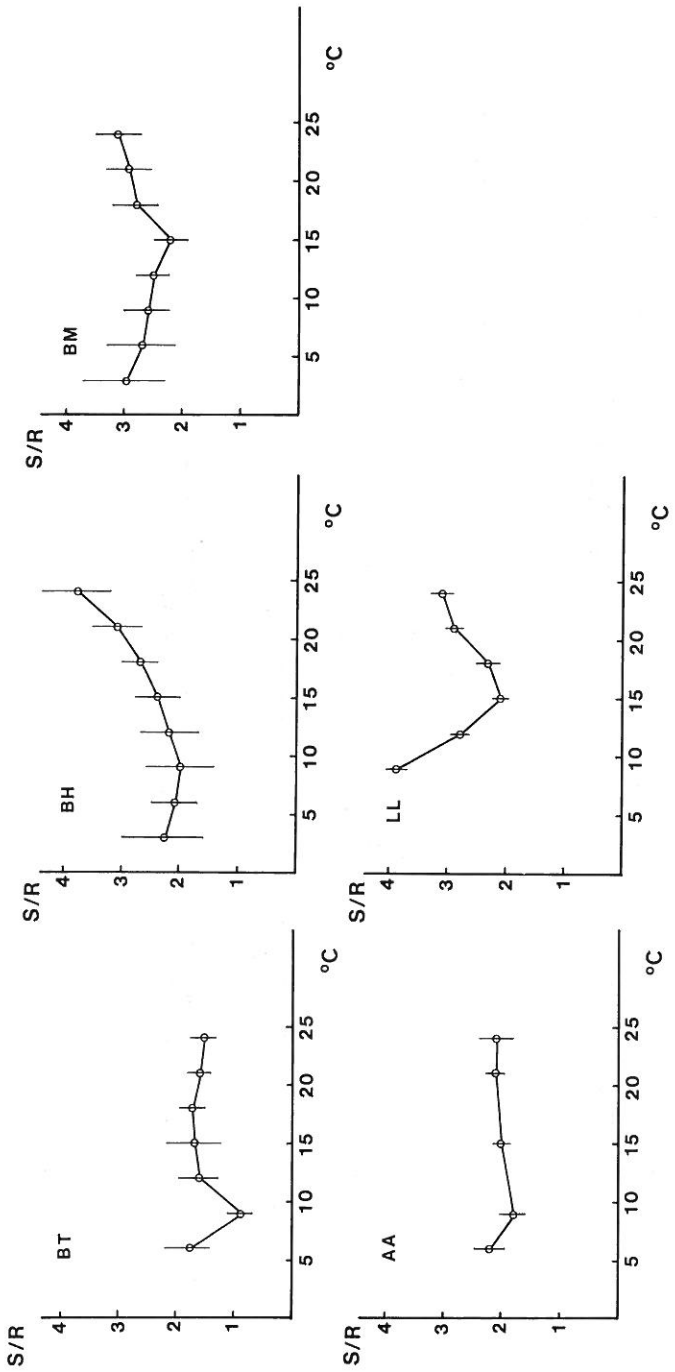

Fig. 6b. Shoot/root ratio based on Fig. 5 as a function of temperature.

plants invest relatively more energy into root growth and structural tissue than when temperatures are more unfavourable for photosynthesis.

In all birch populations investigated there was a small, but gradual transition in leaf size and shape as the seedlings grew older from small, rounded leaves to large ellipsoidal or pointed leaves (Fig. 3). Young, growing leaves were usually more circular in shape and with lower specific area than mature leaves (Table 5). The same relationship also holds for elm leaves (AA).

In maple (LL) the first pair of leaves after the four juvenile leaves (see Fig. 2) was relatively small and circular-shaped relatively to the second pair. The LAR (leaf area ratio) of maple leaves was extremely low as compared with the elm and mountain birch leaves investigated, and with low transformation coefficients k (eq. 1) due to the lobed shape.

As shown in Fig. 3, the size and shape of birch leaves change considerably from the first to the second year. As the plants grow older, the leaves generally become smaller and with lower specific area (SLA). Similar relationships may be found in most deciduous trees. Seedlings have to invest a relatively higher proportion of growth into leaf biomass in order to survive, while older plants also invest in woody, structural tissue (stems, roots and structural leaf tissue). In the same way the increase in specific area and leaf area ratio with temperature above 15°C may be viewed as a compensation for increased respiration loss (i.e. reduced net photosynthesis) at high temperatures. Also the corresponding high LAR and SLA values at low temperatures (Fig. 6a) may be viewed as a compensation for reduced photosynthesis (cf. THORNLEY 1972). It is interesting to note that the investigated populations and species seem to have different ways of compensating for reductions in photosynthetic rates due to unfavourable temperatures (or low light intensity). In *Ulmus glabra* (AA) and all three mountain birch populations studied the leaves compensated for lower photosynthesis by increasing their leaf area ratio (and SLA), but in the two most southerly mountain birch populations (BH and BM) the plants also reacted by increasing their shoot/root ratio, i.e. by increased stem growth (Fig. 6b). In elm and the most northerly birch population (BT) there was no such increase. However, when looking at the stem elongation rates in Table 10 and 11, the tendency to increase stem growth at high temperatures as a compensation for reduced photosynthesis was even more pronounced and was found also in the northern BT population. According to Table 10 the optimum temperatures for stem elongation rates during the linear growth phase were considerably higher than for leaf growth, a tendency that is found in other experiments. HÅBJÖRG (1972a) found that when greenhouse experiments were made in summer (June–July) maximum rates of height growth in mountain birch seedlings occurred at 24°C or about 3°C higher than the optimum for shoot dry weight increase, in good accordance with the present results. When experiments were made in March–April, however, the growth rates were significantly lower, probably due to lower light intensity and shorter day length, and the optimum temperatures for both shoot elongation rates and dry weight increase were also lower, i.e. about 18°C, for the same reason. The illuminance in the present experiment (10,000 lux) was considerably lower than in the daylight rooms used by HÅBJÖRG (1972b), but the effect of lower

Table 10. Variance ratios (F) and significance levels for daily stem elongation (mm/plant) at 9°, 15° and 21°, during the linear growth phase. Population and species indicated. The root mean squares are given in the last column. The confidence levels are: °P<0.1, ▪P<0.05 and *P<0.01. In the lower part of the table are shown the mean values with confidence limits $\pm 2s_x$ for single populations and treatments. DF = degrees of freedom.

Species	*Betula pubescens*						*Ulmus glabra*						*Acer platanoides*					
Temperature	9°C		15°C		21°		9°C		15°C		21°C		9°C		15°C		21°C	
Source	DF		DF		DF		DF		DF		DF		DF		DF		DF	
Population	2	9.6*	2	7.6*	2	3.9▪												
Mother tree	3	0.5	3	1.2	3	0.1	1	0.2	1	0.2	3	0.2	1	0.9	3	0.2	3	0.6
Interaction	5	2.2°	6	3.9*	6	2.9▪												
Model	10	3.2*	11	3.8*	11	2.3▪	1	0.2	3	0.2	3	0.7	1	0.9	3	0.2	3	0.6
Root error ms	39	0.27	54	1.31	48	1.38	9	0.87	16	1.18	19	1.04	23	1.09	26	0.08	28	1.64
BT		0.4±0.1		2.6±0.5		4.6±0.7	AA	1.3±0.5		4.6±0.5		4.3±0.4	LL	1.2±0.4		1.8±0.3		2.3±0.6
BH		0.8±0.2		2.0±0.5		4.9±0.6												
BM		0.7±0.1		3.5±0.8		3.7±0.6												

Table 11. Comparison between stem length L (cm) and stem biomass SW (mg) per plant at the time of harvesting (12-leaf stage). The values at 21°C are not directly comparable to the two lowest temperatures, because the plants were harvested at a fixed stage of development, not at a fixed time.

	L (cm)			SW (mg)		
	9°C	15°C	21°C	9°C	15°C	21°C
BT	3.4	11.2	13.4	90	357	67
BH	5.2	6.4	12.8	108	380	96
BM	4.3	9.2	10.8	160	450	91
AA	8.0	13.6	15.6	205	605	263
LL	3.2	4.0	5.0	248	260	278

light intensity is partly compensated by higher photoperiod (24 hours) as far as the total amount of light is concerned.

According to Table 10 there was no significant mother tree variation in any population or temperature treatment regarding stem elongation rates. There was a very high correlation between total shoot length at harvesting and the corresponding leaf biomass in mountain birch and elm seedlings (SKRE, unpubl.). In maple seedlings this correlation was weaker, but still significant. Table 11 indicates, however, that increased stem elongation at high temperature is not accompanied by increased stem biomass and secondary growth. This seems to be highest at 15°C in all populations except maple.

On the other hand, *Acer platanoides* (LL) leaves did not seem to react at all to temperature changes by changing their LAR and SLA (Fig. 6a). The maple seedlings compensated strongly by increasing both their stem growth and shoot/root ratio at high temperatures. According to WARREN WILSON (1972) reduced light intensities induce stem elongation in order to make the plants more able to compete with other plants for available light. The present study indicates that this strategy is most common in maple and southern birch species, while elm seems to compensate by increasing leaf area in order to catch more light without increasing stem elongation. This strategy was also found in the northern birch population and may be explained by reduced competition from other plants in northern areas (e.g. KALLIO 1984).

Nitrogen fertilization (KARLSSON & NORDELL) (1987) also stimulates leaf growth while long days (HÅBJÖRG 1972a) and high illuminance (HÅBJØRG1972b) tend to increase shoot growth . Leaves that develop in strong light usually have lower specific leaf area, i.e. with the chloroplasts arranged in order to protect themselves against photoinhibition (HOLMGREN 1968). These effects have been investigated in other experiments (SKRE, unpubl.).

3. Variation between and within populations.

There was considerable variation in leaf size and shape within the lowland population (BM) as well as the southern subalpine population (BH), probably because of hybridization, whereas subalpine BT plants from central Norway were more homogenous (SKRE, unpubl.). The growth of single leaves was combined in Table 7 where the offspring of the four mother trees within each population is kept separate to study the genetic variability. Table 7 and Fig. 4b show that the growth rates in leaves of the three mountain birch populations were significantly different, partly because of different optimum temperatures for growth and partly because of higher growth rates at low temperatures (6°C and 9°C) in the two southern populations compared to the most northerly population. The variation between mother trees within populations was relatively small and hardly significant, except at 12°C in mountain birch.

The effect of mother trees on leaf, stem and root biomass per plant at the 12-leaf stage was also tested by an analysis of variance. The results are presented in Table 8. There was a significant variation between mother trees concerning temperature-corrected leaf biomass at the harvesting stage in mountain birch, whereas the effect of different mother trees on the corresponding biomass of stems, roots and total plants was insignificant. On the other hand there was a significant variation in stem and root biomass within the maple population. There was a strong and significant variation between mountain birch populations in leaf and root biomass, the highest values found within the BT population.

The greatest difference, however, was found between shoot/root ratios of different mountain birch populations (Table 8), i.e. the shoot/root ratios were much higher in plants from the two southern birch populations than within the population from central Norway. There was a weaker, but significant mother tree effect and also a significant effect due to temperature (cf. Fig. 6b).

The significant interaction found in Table 8 between mother trees and populations in leaf and stem biomass and shoot/root ratio, is a result of higher variation between mother trees within populations in the two southern populations vs. the population from central Norway (SKRE, unpubl.). The high genetic variability in leaf size within the BM population from Ås may be partly explained by inbreeding from lowland birch (*Betula pendula*) while the variation in the BH population from Blefjell may be explained by inbreeding from *B.nana* (cf. leaf shape in Fig. 3). The mother trees from Blefjell were polycormic in structure, with rounded leaves (cf. Table 5) and some of the trees had upright catkins, like dwarf birch. The BT trees from Tynset, on the other hand, were almost completely monocormic (SKRE, unpubl.). According to KALLIO et al (1983) and NORDERHUS (1952) hybridization may occur in northern areas where the different species occur together, although HAGMAN (1971) claims that such hybridization between *Betula pendula* and *B. pubescens* is inhibited by different cross-incompatibility mechanisms. The different leaf shapes are shown in Fig. 3.

Another interesting result is that the genetic variation in growth rates

within populations seemed to be more significant at 12°C and 24°C than at intermediate temperatures (Table 7). The reason may be that the plants from different mother trees react differently to thermo- and photoperiod. Some plants enter dormancy at a higher temperature (and longer daylength) than others (cf. HÅBJÖRG 1972a).

4. Temperature responses in leaf growth rates.

The growth data from Table 7 were combined into one growth curve for each population with confidence limits $\pm 2s_{\bar{x}}$ plotted around every mean value. In Fig. 4a some of these population curves are shown (e.g. at 9°, 15° and 21°C). The sigmoid shape is still present, although not as obvious as for single leaves (Fig. 2). The growth data were therefore fitted to sigmoid growth curves with some confidence. The leaf growth d(LW)/dt per plant in mg/day was estimated from the slopes of the linear part of the growth curves in Fig. 4a and similar data, and plotted with confidence limits around the mean values in Fig. 4b as a function of temperature. Similar growth curves have also been constructed for leaf area (LA) and shown in Fig. 7a.

One remarkable feature when comparing the temperature response curves of leaf growth in Fig. 4b is the exponential shape of the lower part of the growth curves, indicating a direct connection between dark respiration and leaf growth, According to THORNLEY & HESKETH (1972) there is a direct relationship between ATP-linked growth respiration and the relative growth rates. DAHL & MORK (1959) found a high and significant correlation (r_{xy} = 0.978) between daily apical growth in Norway spruce (*Picea abies* (L.) Karst.) and the corresponding daily respiration.

In Fig. 4b, the lower part of the growth curve is adjusted to an exponential shape. The upper half of the curves are, on the other hand, typical optimum curves, where starvation or lethal effects come into account (cf. DAHL 1951, GAUSLAA 1984). The lowland population (BM) and the southern subalpine BH population, however, include plants with a high leaf area ratio, indicating high photosynthetic capacity and source strength (WAREING & PATRICK 1975). This explains why the temperature optimum for leaf growth was especially high in these two ecotypes, e.g. 23°C in BH leaves and 20°C in BM leaves, respectively. The most northerly BT population had a much lower temperature optimum, about 16°C, and the two broad-leaved species *Ulmus glabra* (AA) and *Acer platanoides* (LL) had still lower optima (15° and 13°C respectively), maybe a result of a higher proportion of non-photosynthetic tissue in their leaves than in *Betula pubescens.* High amounts of respiring but non-photosynthetic tissue in the samples, or high rates of photorespiration generally tend to lower optimum temperatures for photosynthesis in arctic plants (e.g. TIESZEN et al. 1980). For the same reason, photosynthesis rates would be expected to be limiting leaf growth over a wider temperature range, not only at the highest temperatures when respiration rates are high. At the same time the temperature range at low temperatures where the dark respiration is limiting growth would become narrower.
Figs. 4b and 5 seem to indicate that subalpine mountain birch seedlings

from central Norway, as a result of lower photosynthesis/dark respiration ratios in their leaves, are limited by their photosynthesis rates over a wider range of temperatures than more southern populations of the same species. This may be looked on as a compensation for relatively higher respiration loss during nights and during the dark winter season at southern latitudes than further north. According to BILLINGS (1974) the potential for temperature acclimation is also higher in southern alpine than in arctic populations.

Fig. 4b shows that the maximum growth rates during the linear phase vary between 20 and 28 mg/day per plant, with the highest values in the population (BH) with the highest optimum temperatures, as expected. The values agree well with earlier reports by, for example, HÅBJÖRG (1972a, b) on mountain birch ecotypes.

Another result from the growth analysis is that for all three investigated birch populations and the elm population, the threshold temperature for leaf growth seemed to be very close to +3°C, for maple a few degrees higher.

5. Temperature responses in biomass distribution at harvesting.

For stem and root tissue only destructive methods were available, and because of limited amounts of plants only one complete sampling was made, by the 12-leaf stage at the end of the experiment. The results are presented in Fig. 5. Because leaf growth in plants grown at the lowest temperatures (3°, 6° and 9°C) stopped before the end of the experiment, the temperature response curves should be expected to look somewhat different from those in Fig. 4b. This is not the case, however, as the shape and optimum temperatures were surprisingly similar.

In Fig. 5, the biomass of leaves, stems and roots are shown separately as columns together with the total biomass per plant with confidence limits. The root biomass per plant generally seemed to be less influenced by temperature than the leaf biomass.

In maple a stronger decrease in growth rates may be seen from 21°C to 24°C (Fig. 5) than in the other species and populations. This may be partly a result of higher respiration loss due to high amounts of non-photosynthesizing tissue, but may also partly be a result of earlier growth cessation. According to PERRY (1962) temperatures below 10°C as well as above 23°C induce earlier growth cessation in maple, probably caused by the formation of growth inhibitors in the leaves (cf. PHILLIPS & WAREING 1959).

Among the three birch populations the lowest shoot/root ratio at all temperatures was found in the most northerly BT population (Fig. 6b). At 24°C the shoot/root ratio varied from 1.5 in BT to about 4.0 in the southern subalpine population BH while BM and the elm and maple populations were intermediate. The shoot/root ratio as well as the biomass values at the 12-leaf stage were in accordance with the results from later experiments (SKRE, unpubl.) with birch seedlings, taking into account the relatively low light intensity in the present experiments. The shoot/root ratios usually increase with a decreasing light intensity (WARREN WILSON 1972).

The optimum temperatures for leaf biomass per plant at harvesting (Fig. 5) were about 3°C lower than for rates of leaf growth during the linear growth phase (Fig. 4b). The reason is probably that the plants that were grown at the two highest temperatures (21°C and 24°C), reached the 12-leaf stage only shortly after they had entered the linear growth phase (see Fig. 4a). This was most pronounced in BH and BM, the two southern mountain birch populations, where the turnover times for leaves were shortest (Table 6). The rapid leaf turnover rates in the BH population (see also Fig. 2) may be related to the smaller leaf size in this population relative to the BM and BT plants. The difference between birch populations was most significant at 15°C.

On the other hand, the leaf growth rates at low temperatures (6° and 9°C) seemed to be considerably lower within all three mountain birch populations than in elm leaves, because the final size of leaf number 5 and 6 (see Fig. 2) was much smaller than the size of the corresponding elm leaves. It looks like the final leaf size is more or less predetermined, and this will have more significance in plants that develop few and large leaves like elm and particularly maple (LL) than in plants developing many small leaves, like birch in its early stages.

Because the stem/leaf biomass ratios increased with increasing temperature (Fig. 5) optimum temperatures for stem growth were about 2°C higher than for leaf growth in all ecotypes and species except maple (see also Table 10). The optimum temperatures for root growth were slightly lower than for leaf growth.

6. Conclusions.

Finally, some comments are needed about the net assimilation rates $NAR = (LA)^{-1}\, dW/dt$. Because only leaf biomass was estimated regularly, by non-destructive measurements, only rough estimates of NAR can be made. From occasional sampling of stem, root and leaves on small samples (SKRE, unpubl.) the relative biomass of different tissue types was found or estimated, and from these and the leaf expansion curves in Fig. 7a the estimated NAR values were obtained. In Fig. 7b the NAR is shown as a function of time for the two subalpine populations of mountain birch (BT and BH). The results agree well with Figure 4a and show that the net assimilation rates are much more influenced by temperature in seedlings of the population from central Norway (BT) than in corresponding seedlings from the southern population (BH). The highest NAR values in the BT population were found at 15°C, while the corresponding maximum values in the BH population were found at 21°C, in accordance with leaf growth rates (Fig. 4b). In contrast to the growth in leaf biomass (Fig. 4a) the growth in leaf area (Fig. 7a) was always highest at the highest temperatures, even in the northern BT population, but the most rapid leaf expansion seemed to occur in the southern populations (BH and BM).

In a conclusion, the experiment revealed large differences in survival strategy among species and ecotypes. The maple and elm populations and

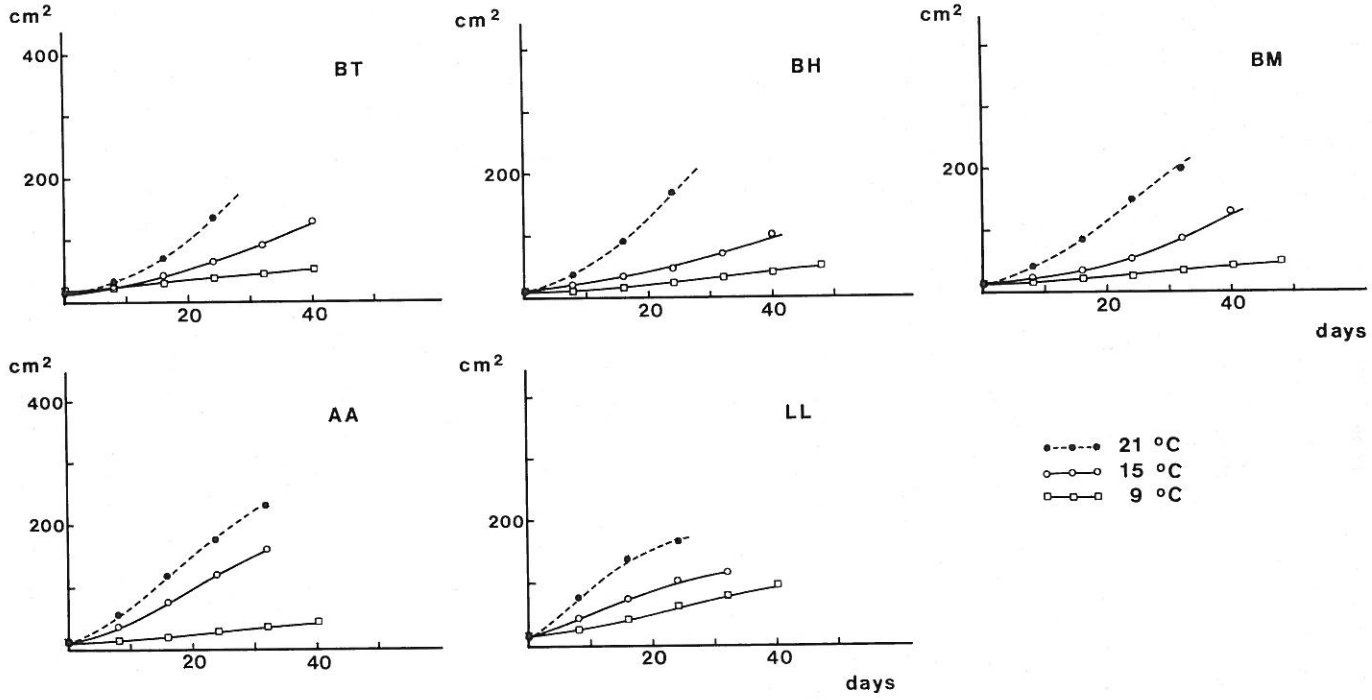

Fig. 7a. Growth in leaf area (cm^2/plant) at 9°, 15° and 21°C and 24 hour photoperiod during the experiment. Only the mean values per population are shown. Time is measured in days from transplantation (4-leaf stage). See Fig. 2 for symbols.

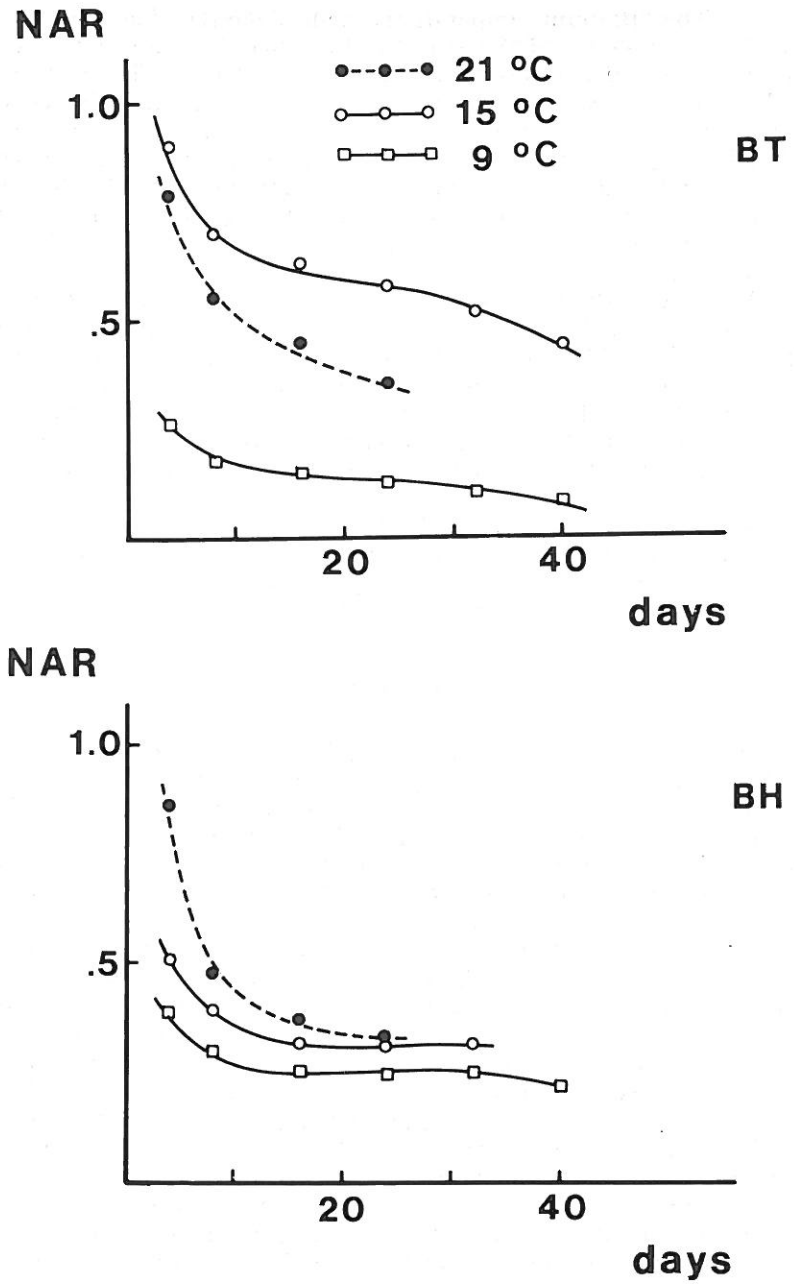

Fig. 7b. Net assimilation rates NAR (mg day^{-1} cm^{-2}) in two mountain birch populations during the experiment, grown at 9°, 15° and 21°C constant temperature and 24 hours photoperiod. Only mean values are shown.

the two southern mountain birch populations investigated all react to high temperatures by rapid leaf expansion as a compensation for increased respiration loss, in order to resume photosynthetic capacity. The birch seedlings develop small leaves with rapid turnover rates, especially the southern subalpine population, while the elm and in particular the maple seedlings develop large, predetermined leaves with high photosynthetic capacity, even at low temperatures. The maple and southern mountain birch populations also react to high temperatures by increasing their stem elongation rates in order to compete more efficiently for available light (cf. WARREN WILSON 1972).

In the most northerly birch population, however, the seedlings seemed to develop leaves with high net assimilation rates, particularly at medium temperatures (15°–20°C) that enable plants to build up large reserves of carbohydrates in the roots to overcome unfavourable periods, while the stem elongation rates (Table 10) and leaf expansion rates were lower than in its southern relatives. In the BT population competition therefore seems to be less important and abiotic climatic factors more important as an adaptive force.

Since all experiments were made at 24 hours photoperiod and the plant material was not analysed for total nitrogen or carbohydrates, the present study needs to be repeated on a similar plant material to investigate other relationships in the temperature responses.

Summary

In order to investigate the relationship between growth and respiration, and climatic adaptations in ecotypes of mountain birch (*Betula pubescens* Ehrh.) growth experiments were carried out in continuous light at different constant temperatures. Seedlings of three different mountain birch ecotypes were included in the study, together with two other tree species, one with a continental distribution (*Acer platanoides* L.) and one with an oceanic distribution pattern (*Ulmus glabra* Huds.).

The study revealed large differences in survival strategy among species and ecotypes. The maple and elm populations and the two southern mountain birch populations investigated all reacted to high temperatures by rapid leaf expansion, probably as a compensation for increased respiration loss, and the maple and birch populations also by rapid stem elongation, that enabled the plants to compete more efficiently for available light. The subalpine birch population from central Norway, however, developed leaves with high net assimilation rates, instead of increasing the leaf area and stem elongation rates. In these plants, abiotic climatic factors rather than competition therefore seemed to be the dominating adaptive force.

The southern subalpine mountain birch population developed small leaves with rapid turnover rates while the elm and particularly the maple seedlings developed large, predetermined leaves, even at low temperatures. The small leaves in the subalpine population might be an adaptation to higher solar radiation. In the two southern mountain birch ecotypes high varia-

tions were found within populations, probably caused by inbreeding with *Betula nana* in the subalpine and *B. pendula* in the lowland population.

During the linear growth phase an exponential relationship was found between leaf growth rates and temperature at low and medium temperatures, indicating a close relationship with dark respiration. At high temperatures, however, a parabolic relationship was found, in accordance with net photosynthesis rates. The optimum temperatures for growth in leaf biomass varied from 15–20°C in elm, maple and subalpine mountain birch from central Norway and to 20–25°C in the southern subalpine birch population. The size of single elm and mountain birch leaves increased with temperature up to 15°C and then decreased, while the shoot/root ratio, the specific leaf area and the leaf area ratio first decreased and then increased above a certain temperature (10–15°C). The optimum temperatures for stem elongation rates were 2–3°C higher than for growth in leaf biomass.

The low shoot/root ratios in the most northerly subalpine mountain birch population, particularly at high temperatures, support the conclusion that these plants are surviving the dark winter season by developing high net assimilation rates and storing assimilates in their roots to overcome unfavourable periods, rather than by rapid shoot growth. Higher root relative to shoot growth may also be an adaptation to low nutrient level in the soil in northern areas.

Verknader av temperatur på veksten hos småplanter av fjellbjørk (*Betula pubescens* Ehrh.), alm (*Ulmus glabra* Huds.) og lønn (*Acer platanoides* L.) dyrka i kontinuerleg lys.

For å kunne utforska samanhengen mellom vekst, respirasjon og klimatilpasningar i økotypar av fjellbjørk (*Betula pubescens* Ehrh.) vart det utført vekstforsøk i kontinuerleg lys ved ulike konstante temperaturar. Småplanter frå tre ulike bjørkepopulasjonar var med i forsøket, saman med to andre treslag, eit kontinentalt (*Acer platanoides* L.) og eit med oseanisk utbreiingsmønster (*Ulmus glabra* Huds.).

Forsøket avslørte store skilnader i overlevingsstrategi mellom arter og økotypar. Lønn og alm og dei to sørlege fjellbjørkpopulasjonane reagerte alle på høge temperaturar med rask vekst i bladareal, truleg som kompensasjon for auka respirasjonstap, og lønne- og bjørkepopulasjonane også ved rask stengelstrekking, som set plantene i stand til å konkurrera meir effektivt om tilgjengelig lys. Subalpin fjellbjørk frå Midt-Norge utvikla derimot blad med høg nettoassimilasjon i staden for å auka bladarealet og stengelveksten. I desse plantene ser det derfor ut til at klimafaktorar, snarare enn konkurranse er den viktigste drivkrafta i tilpasninga.

Den sørlege subalpine fjellbjørkpopulasjonen utvikla små blad med rask omløpstid, medan alm- og spesielt lønnesmåplantene utvikla store, førehandsbestemte blad, også ved låge temperaturar. Dei små blada i subalpin fjellbjørk kan vera ei tilpassing til høg innstråling og varmeveksling. I dei to sørlege fjellbjørk-økotypane var det stor variasjon innan kvar populasjon i

alle vekstparametrar, noko som truleg har samanheng med innblanding av *Betula nana* i den subalpine og *B. pendula* i låglandspopulasjonen.

I den linjære vekstfasen var det ein eksponentiell samanheng mellom temperatur og bladvekst ved låge temperaturar. Dette tyder på ein nær samanheng med mørkerespirasjonen. Ved høge temperaturar, derimot, var samanhengen parabolisk, i samsvar med fotosyntesekurva. Optimumstemperaturen for vekst i bladmasse varierte frå 15–20°C hos alm, lønn og subalpin fjellbjørk frå Midt-Norge til 20–25°C i sørleg subalpin bjørk. Storleiken av enkeltblad hos alm og fjellbjørk auka med temperaturen opp til eit maksimum ved 15°C, medan topp/rot-forholdet, spesifikt bladareal og bladarealforholdet først minka og deretter auka over ein viss temperatur (10–15°C). Optimumstemperaturen for stengelstrekking var 2–3°C høgre enn for vekst i bladmasse.

Det låge topp/rot-forholdet i den nordlegaste subalpine fjellbjørkepopulasjonen, særleg ved høge temperaturar, støttar konklusjonen om at desse plantene overlever mørketida om vinteren ved å utvikla høg nettoassimilasjon og lagra assimilat i røtene for å overvinna kritiske periodar om våren, snarare enn ved rask skotvekst. Meir vekst i røter relativt til i skot kan og vera ei tilpasning til lågt næringsinnhald i jorda i nordlege område.

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