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A genecological investigation of the annual rhythm of *Pinus contorta* Dougl. and a comparison with *Pinus silvestris* L.

En genekologisk undersökning av årsrytmen hos Pinus contorta Dougl. och en jämförelse med Pinus silvestris L.

by

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ABSTRACT

In a material of 27 provenances of two-year-old *Pinus contorta* it was found that the annual rhythm, illustrated by degree of lignification, colour of the bark on the terminal shoot, dry/fresh weight of needles, shoot extension, budsetting and electrical resistance, was related to the geographic and climatic parameters of seed source. Regression analyses showed that the rhythm was most closely correlated with the mean January daily temperature and latitude. The analyses also showed how latitude and altitude interact. Budsetting was found to have a pattern of geographic variation that was different from the other expressions of rhythm. A comparison between *P. contorta* and *P. silvestris* with reference to lignification, laboratory frost resistance and field hardiness, indicated that the Canadian pine, which withstands a Scandinavian climate far north of its seed source, presumably manages to do so in spite of a relatively low degree of winter adjustment in late September.

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CONTENTS

1 Introduction 5
2 Material 6
3 Methods 6
4 Results and discussion 8
4.1 Assessment of annual rhythm 8
4.2 Variation due to seed source 11
4.3 Comparison of rhythm and frost hardiness in provenances of *Pinus contorta* and *Pinus silvestris* 16
5 Conclusions 22
Acknowledgements 22
Literature 23
Sammanfattning 24

1. Introduction

Lodgepole pine, *Pinus contorta* Dougl. ex Loudon, has been paid great attention in northern and central Europe during the twentieth century. In test plantations it has proved to be hardy with growth potential in many different environments, from the maritime climate of the British Isles and Norway to continental parts of central Europe, Scandinavia and Finland. Tested provenances have largely come from those areas of the distribution range in western North America that are more heavily populated and where this pine is used commercially. Thus the areas most frequently represented in tests of greater age are in Washington, Oregon, Idaho, Montana, the Frazer valley in British Columbia and the Banff area of Alberta, whereas the vast areas of northern British Columbia, Alberta and the Yukon territory are rarely represented.

Tests of the geographical variation in *Pinus contorta* have been carried out on the morphology of field-sampled material (Critchfield, 1957; Jeffers & Black, 1963; Roche, 1966) and on germinants (Critchfield, 1957), but studies of the annual growth rhythm of a large number of provenances grown in a uniform environment have not been reported. The above-mentioned authors have found great geographic variation within the species, the most significant differences being between coastal and inland provenances.

In Scandinavia and Finland some provenances of Lodgepole pine have proved to be hardy compared to the native Scots pine (*Pinus silvestris* L.) even in a severe climate (Stefansson, 1957; Feilberg, 1964), and a need has arisen to test provenances from the northern part of the distribution range. This is why a cone collection was made in central B.C. and along the Alaska highway in northern B.C. and the Yukon.

The study of the annual growth rhythm and laboratory frost hardiness on two-year-old seedlings that is presented below shows that the variation is large enough to warrant a detailed genecological investigation of the species before its introduction into afforestation.

2. Material

The seed from *Pinus contorta* originated from cone collections made in 27 stands throughout western Canada (Fig. 1). Cones were collected from squirrel caches and the seed can therefore be assumed to represent a large number of trees within each stand. The same person made all the collections.

The seed from *Pinus silvestris* was collected from 30 scattered stands representing all parts of Sweden. The seed from each stand was a mixture obtained from at least ten trees.

Seedlings from the two species were grown without replications in a Swedish nursery at latitude 63°30′N, longitude 16°30′E and altitude 250 m. The study was carried out in 1965 during the second growing season and the seedlings were never transplanted. Some variation occurred because of overcrowding in the nursery beds.

3. Methods

The methods used to study the annual growth rhythm were identical to those mentioned by Hagner (1970) They are briefly presented below.

Bark colour: A subjective, ocular description of the bark colour of the new terminal shoot, which changes from green to brown in August. Numbers 1—5 were given for gradations from green to brown respectively.

Lignification: An anatomical investigation of the peripheral woodcells was made in late September. The percentage of fully lignified cells was estimated.

Dry matter: Needles collected in the middle of October were dried in an oven to find the percentage of dry-weight/fresh-weight.

Shoot length and shoot elongation: The shoot development was registered four times during the growing season; before, after and twice during elongation, 14/6 and 8/7. "Shoot length" inicates the length of the shoot on 14 June as a percentage of the fully developed shoot measured in the late fall. "Shoot elongation" represents the shoot extension from 14 June to 8 July expressed as a percentage of the length of the fully developed shoot.

Fig. 1. Western Canada and the origin of 27 provenances of *Pinus contorta*.

Budsetting: The percentage of seedlings with terminal buds. A weighted sum of estimates made 12/7, 20/7 and 29/7.

Electric resistance measured in October by means of two steel electrodes 5 mm apart inserted into the stem immediately below the cotyledons.

4. Results and discussion

4.1 Assessment of annual rhythm

The measurement of annual rhythm gave the results shown in Tab. 1. Analyses of variance were carried out to compare the efficiency of the various methods. Variance components for variation within and between the provenances are presented in Tab. 2.

Tab. 1. Data on the seed sources and the annual rhythm of 27 provenances of *Pinus contorta*.

Prov no.	Lat °N	Alt ft	Alt m	Drym[a]	Shoot length[b]	Shoot elong[c]	Ligni[d]	Bark[e]	El[f]	Bud[g]
581	50.65	4700	1430	25.74	12.7	23.0	16.6	1.85	23.71	73
582	51.58	3800	1160	25.17	14.3	26.3	20.2	1.74	23.04	56
583	53.07	2200	670	24.43	13.0	24.7	12.7	1.48	22.29	63
584	54.07	2300	700	26.39	13.3	23.0	18.9	1.72	22.79	31
585	54.32	3000	910	24.74	11.0	22.7	19.5	1.43	22.35	24
586	54.50	2400	730	25.31	9.3	24.7	28.1	1.42	22.15	30
587	55.40	2850	870	27.36	10.3	24.7	25.7	1.90	23.76	55
588	56.73	3000	910	26.39	10.0	24.3	34.5	1.97	24.28	70
589	56.77	3000	910	27.45	11.7	28.0	34.7	1.80	—	72
590	57.52	4100	1250	27.35	19.3	24.3	37.5	1.83	—	95
591	58.83	1500	460	26.37	12.7	28.7	39.7	2.15	24.59	43
592	58.87	2500	760	27.22	11.0	25.7	40.9	1.68	—	73
593	59.72	2000	610	27.37	13.7	27.7	41.4	2.37	23.43	70
594	60.05	3000	910	27.03	15.0	22.7	35.7	1.97	23.63	54
595	60.20	3000	910	28.28	18.3	25.7	37.1	1.62	21.98	53
596	60.38	2500	760	27.01	21.7	24.3	34.5	1.89	21.56	55
597	60.87	2200	670	26.44	17.7	24.0	34.9	1.67	—	63
598	60.70	2800	850	26.51	17.0	27.0	36.7	1.71	—	72
599	60.33	2400	730	28.75	18.3	25.7	34.6	1.90	—	43
600	58.41	100	30	28.74	18.3	28.7	30.7	1.76	—	14
601	54.53	300	90	26.21	13.7	26.3	13.5	1.31	—	5
602	55.18	1000	300	29.01	15.0	28.7	26.9	1.66	—	16
603	48.77	1150	350	26.18	14.3	27.3	5.8	1.56	—	6
604	60.82	2500	760	29.37	22.7	22.0	21.7	2.76	21.49	29
605	63.37	1600	490	33.31	28.0	22.7	26.4	2.04	22.66	29
606	51.03	4600	1400	28.21	29.0	29.0	25.7	2.74	24.09	100
607	49.37	100	30	26.53	17.7	29.7	1.8	1.74	—	3

[a] Dry-/fresh weight of needles, per cent, 10 October.
[b] Length of shoot 14 June in per cent of total length in fall.
[c] Shoot extension 14 June—8 July in per cent of total length in fall.
Fully lignified cells along xylem periphery, $\% \times 1/2$, 30 September.
[e] Colour of bark on terminal shoot in middle of August; arbitrary scale 1 = green, 5 = brown.
[f] Electric resistance, arbitrary scale, October.
[g] Seedlings with terminal buds, percentage, a mean from 12, 20, 29 August.

It is obvious that the *electrical method* is not very accurate since the variation between repeated measurements on the same seedling is the source of 34 per cent of the total variance. Nevertheless this method showed highly significant differences between the provenances, because as many as 40 seedlings per provenance were measured. If differences between individual trees or similar provenances are to be measured using this method a better apparatus (Brach & Mason, 1965) than the one used here will have to be designed.

The *bark colour* method resulted in a fairly high variation between repeated measurements on the same provenance. This method was also used on *P. silvestris*, where the result was much more reliable as this species shows more distinct colours. If this method is to be used on *P. contorta* it may be necessary to develop an objective assessment of the colour.

Budsetting is a fairly accurate method as it is not too difficult to assess the presence or absence of a bud. The values also reveal that the main source of variation is between provenances.

The assessment of the degree of *lignification* requires much laboratory work (Hagner, 1970). On this material the method has proved to be fairly accurate since the error variance plus the variance due to differences between seedlings does not amount to more than 26 per

Tab. 2. Components of variance for the variation within and between provenances as a percentage of the total variance.

	Variance in per cent of total variance
Electric resistance:	
Between repeated measurements of the same seedling	34
Between seedlings within provenances	47
Between provenances	19
Bark colour:	
Between mean values from repeated observations of the same provenance	63
Between provenances	37
Budsetting:	
Between mean values from repeated observations of the same provenance	15
Between provenances	85
Lignification:	
Between seedlings within provenance	26
Between provenances	74

Analyses of variance give F-values showing highly significant differences ($p<0.001$) between provenances for all four methods.

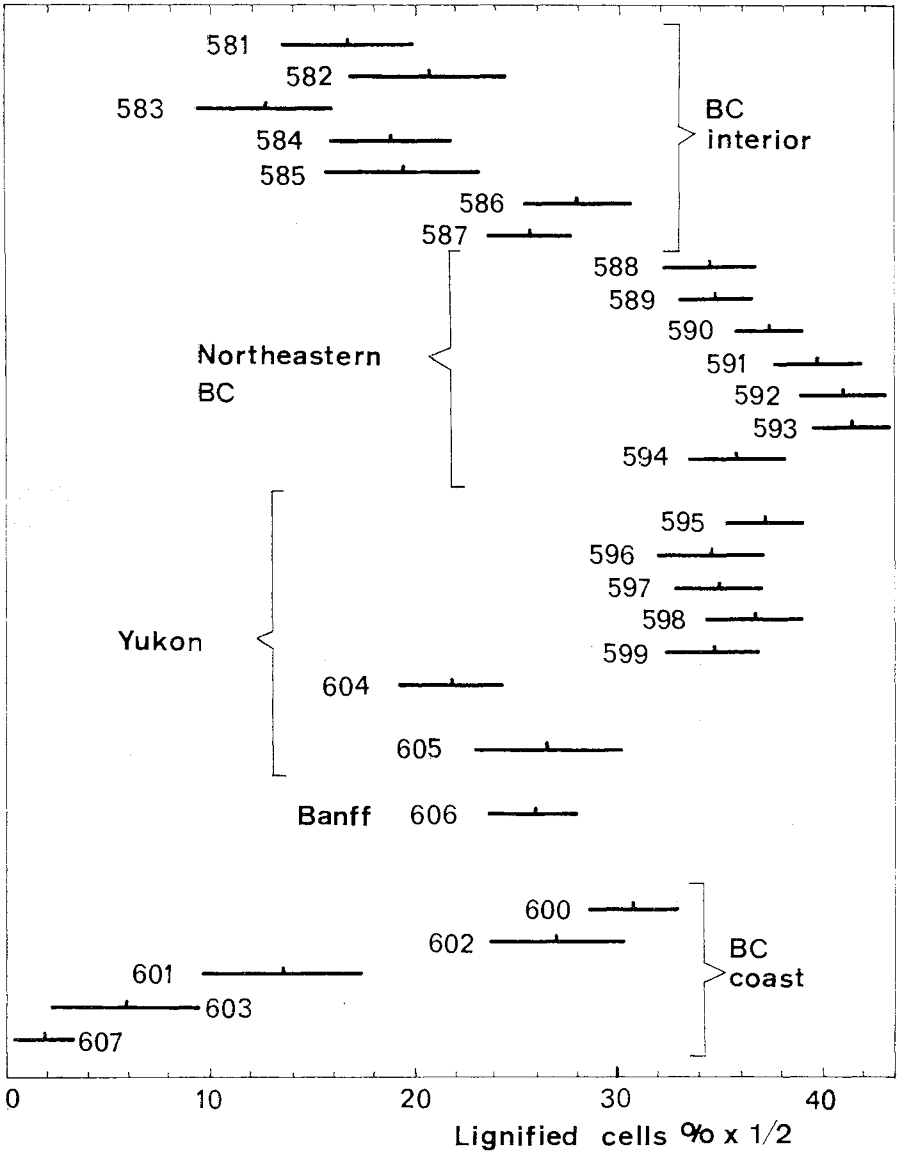

Fig. 2. The degree of lignification on 30 September. On each side of the mean the extension of two standard errors is drawn.

cent of the total variance. Differences between the provenances, and the clinal trend within this material, are shown by the provenance mean values (Fig. 2).

The *dry matter* is not shown in Tab. 2 since it was obtained from unrepeated bulk samples and the variation due to inefficiency of the method cannot be extracted from the total. This is also the case for *shoot measurements* because individual seedlings were not recorded separately.

4.2 Variation due to seed source

In the analyses of variance (Tab. 2) it was found that the provenances are easily distinguishable by means of the values for electric resistance, bark colour, budsetting and lignification. As it is of interest to discover what the expressions of annual rhythm describe in terms of hardiness or climatic resistance, one has to consider the results in connection with the climatic and geographic parameters of the seed sources (Fig. 3). Facial expressions have been chosen because of the human ability to recognize several features at once if they are presented as parts of a face.

From Fig. 3 one can easily make an ocular multi-dimensional identification of groups and trends. The coastal provenances are typical and different from the inland provenances (except the most norther coastal one no. 600). Among the southern provenances no. 606 from Banff in Alberta, situated on the dry eastern side of the Rocky Mountains, is very different from the provenances from the interior of British Columbia (581—586) even though it originates from a relatively similar latitude. The Banff provenance is more like those from the western Yukon than those from the interior of British Columbia. Taking all the provenances from the interior of B.C. and northward it can easily be seen that the rhythm changes in a clinal manner.

An unexpected trend among the northern provenances is shown by the lignification which decreases from provenance 593 towards west and north, and which is as low in 605 from the most northerly seed source as it is in 606 from Banff on latitude 51°N. The reason could be the falling altitude, but this is not very likely since it has been shown for *Pinus silvestris* (Hagner, 1970), and will be shown in this paper, that the lignification is more closely related to latitude than to altitude. The budsetting, however, exhibits the same trend, but this characteristic is closely related to altitude (see below). Conversely, shoot length, bark colour and dry matter values show a trend which is logical in respect to latitude and opposite to that of lignification. The reason for the discrepancy between the methods might be that very northern provenances with fast rhythm were influenced by the

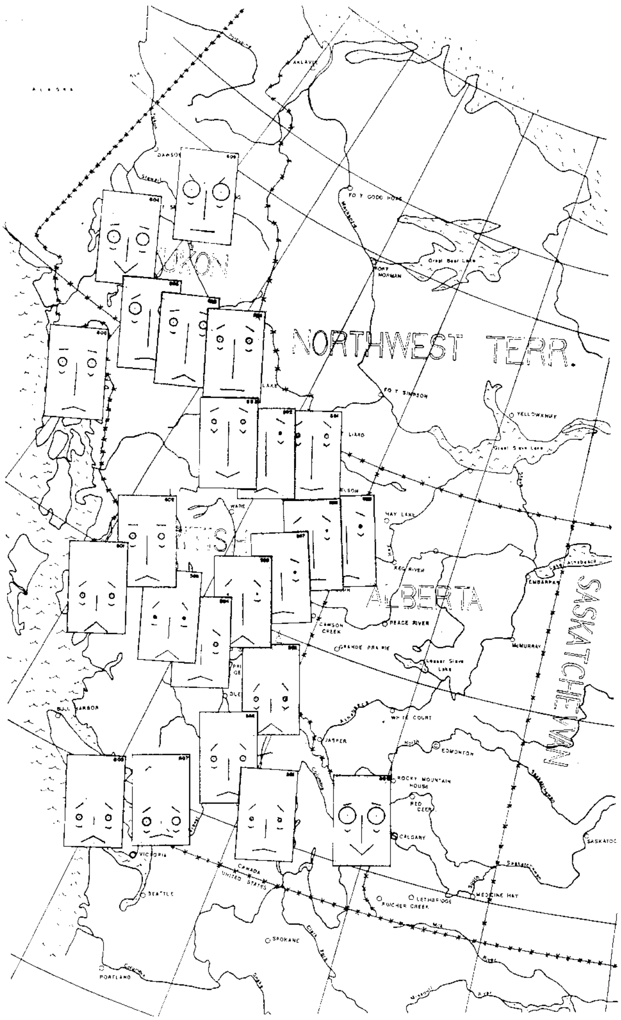

Fig. 3. The annual growth rhythm of 23 provenances of *Pinus contorta*. Nose = Lignified cells percentage, ǀ = low, | = high. Eyebrows = Dry matter percentage, ∕∖ = low, ∖∕ = high. Eye diameter = Shoot length percentage, · = low. ⊙ = high. Mouth = Bark colour, ⌃ = green, ⌄ = brown. Eye wrinkle = Seedlings with terminal bud, percentage, ⌄ = low, V = high.

long warm fall in the testing environment, so that the cambium started a renewed activity.

This kind of ocular analysis can indicate trends and groups but cannot replace a multivariate analysis designed to define the probability and significance of the facial differences. As the assemblage of this material was not designed for a multivariate analysis, only correlation and regression analyses have been carried out to study the clinal trends.

Because of the diversity of topography and climate in the area from which this material was sampled, the main climatic or geographic factor of importance for the variation in annual rhythm is probably different in different parts of the area. Therefore a regression analysis, with the aim of finding correlations between geographic and climatic parameters and rhythm traits, was limited to a central group of 12 provenances, the most southern being at Salmon Arm (581, lat. 50°N) and the most northern at Liard River (593, lat. 59°N). Of course a subjective choice of this kind will ensure in advance a maximum influence of latitude, but the altitudinal range within this group is also large enough (1500′—4700′; 460—1430 m) to enable a study of this variable.

Several climatic parameters have been chosen from the Atlas of Canada and from tables published by the Canadian Dept. of Transport. With these, plus latitude and altitude, correlation analyses have been made (Tab. 3).

From the number of asterisks (significance levels) it can be seen that lignification is the trait with the largest covariance with the environmental parameters. Dry matter content and shoot elongation are the next best while shoot length does not correlate at all. A very interesting result is that budsetting correlates with only one factor, altitude, and that no other rhythm trait is significantly correlated with this parameter. This is in close agreement with results published earlier concerning *Pinus silvestris* (Hagner, 1970), where budsetting proved to correlate with altitude to much higher degree than any other rhythm trait.

The correlation coefficients indicate that the following environmental parameters are most closely correlated with the agent causing adaptation to a certain rhythm in the natural populations within this district: Latitude, Mean January daily temp., Difference between July and January mean daily temp., Mean January daily minimum temp., Normal heating degree days with a temperature below +18°C in January.

These factors correlate with rhythm traits which, according to earlier investigations on *Pinus silvestris* (Dietrichson, 1961, 1964;

Tab. 3. Correlations between rhythm variables and climatic and geographic parameters of the seed source. The asterisks indicate the significance level for the probabilities of 0.1 % (***), 1 % (**), 5 % (*). "Not significant" is indicated as (—). The number of observations is 12.

	Lignified cells %	Bark colour	Shoot elongation	Shoot length	Dry matter	Budsetting
Mean Jan. daily temp. (atlas)	***	*	*	—	**	—
Diff July and Jan. mean daily temp.	***	*	*	—	**	—
Mean April daily temp. (atlas)	***	—	*	—	**	—
Mean Oct. daily temp. (atlas)	***	—	*	—	**	—
Sum April and Oct. mean daily temp. (atlas)	***	—	*	—	**	—
Extreme highest recorded (atlas)	***	—	—	—	***	—
Extreme lowest recorded (atlas)	***	—	*	—	**	—
Annual mean daily diff. between max. and min. temp. (atlas)	—	—	—	—	—	—
Growing season, no. days with temp. above ÷6 °C (atlas)	***	—	*	—	**	—
Mean annual no. of degree days with temp. above +6 °C (atlas)	***	—	—	—	**	—
Extreme lowest recorded	*	—	—	—	—	—
Extreme highest recorded	**	—	—	—	*	—
Mean Jan. daily min. temp.	***	*	*	—	**	—
Diff. mean July daily max. and mean. Jan. daily min. temp.	***	*	*	—	**	—
Normal heating degree days with temp. below ÷18 °C July	—	—	—	—	—	—
Normal heating degree days with temp. below +18 °C May+Sept.	**	—	—	—	**	—
Normal heating degree days with temp. below +18 °C Jan.	***	*	*	—	**	—
Normal heating degree days with temp. below +18 °C April ÷ Oct.	***	—	—	—	**	—
Latitude	***	*	*	—	**	—
Altitude	—	—	—	—	—	*

Hagner, 1970), reflect the hardiness expressed for instance by survival after ten years in the field. Conversely, altitude of seed source is a factor related to the agent that causes adaptation to a certain time of budsetting, which has a pattern of variation that is different from the other growth rhythm traits.

Based on the results from the correlation analysis a stepwise regression analysis was performed with each one of the rhythm variables as dependent and the four best (in relation to the specific growth rhythm trait) environmental parameters as independent. As a curvilinear relationship could be expected the independent variables were also included in squared form (Tab. 4).

Tab. 4. Regressions of rhythm traits on climatic and geographic parameters of the seed source. N = number of observations. $t_{b_1(2)}$ = "t" value of the first (second) regression coefficient. R^2 = coefficient of determination. F = "F" value of the regression. Levels of significance are indicated as: * = probability 0.1 %, * = 5 %.**

Regression	N	t_{b_1}	t_{b_2}	R^2	F
Lignification = $11.426 + 0.01326\ X_1$	11	9.75***		0.913	95.0***
Dry matter = $23.82 + 0.008126\ X_2$	11	4.84***		0.722	23.4***
Elongation = $15.00 + 0.1335\ X_3$	11	2.60*		0.430	6.79*
Bark colour = $0.3382 + 0.01885\ X_3$	11	2.68*		0.444	7.18*
Bud setting = $13.04 + 0.01281\ X_4 + 0.06857\ X_5$	11	2.71*	2.34*	0.580	5.52*

X_1 = Mean January daily temperature, squared.
X_2 = Normal heating degree days, April + October, squared
X_3 = Diff. mean July daily max. and mean January daily min. temperature
X_4 = Altitude in feet
X_5 = Mean January daily min. temperature.

The measurement of the lignification was obviously very good because 91 per cent of the variation could be accounted for by the regression with mean January daily temperature. None of the other variables was so closely related to any environmental parameter. Budsetting, which was very accurately ascertained in the nursery, was most closely related to altitude and mean January daily min. temp. However, the unexplained remaining variance was high (42 per cent), but no other evironmental agent of great importance for the adaptation in this trait could be found from this analysis.

With regard to practical forestry, estimates of rhythm or hardiness of seed and planting stock for comparisons of different lots are necessary, and it is reasonable to present the variation as a function of the geographical parameters, latitude and altitude that are always available, rather than as functions of climatic data that are seldom accessible. For this reason a series of regressions with rhythm variables as dependent was made. As independent latitude (L) and altitude (A) were used in simple form and in the following transformations: L^2, A^2, LA, L/A, A/L, 1/A, 1/L. The results are presented in Tab. 5 and Fig. 4, 5, 6 and 7.

The result may be influenced by the fact that the altitude and latitude are negatively correlated in this material, because the land in this part of western Canada descends from south to north. This interaction could be the cause of the negative partial correlation which exists between shoot elongation and altitude (Tab. 5).

Practical forestry has an interest in comparisons between seed lots from various latitudes and altitudes as mentioned earlier, when seed

Tab. 5. Regressions of rhythm traits on latitude and altitude of seed source.

	N[a]	tb_1	tb_2	R^2	F
Budsetting = $17.55+23.50 \cdot 10^{-4} \cdot$ Alt (Lat-50.0)+ $+74.85 \cdot 10^{-4} \cdot$ Alt/(Lat-50.0)	12	4.53***	3.30**	0.703	10.6**
Lignification = $17.29+0.3005$ (Lat-50.0)^2	12	8.19***		0.870	66.7***
Lignification = $14.57+0.2357$ (Lat-50.0)^2+ $+35.61 \cdot 10^{-5} \cdot$ Alt (Lat-50.0)	12	5.01***	1.93NS	0.908	44.2***
Dry matter = $28.88+10.17 \cdot 10^{-5} \cdot$ Alt (Lat-50.0)	12	4.00**		0.616	16.0**
Bark colour = $0.8306+180$ (Lat-50.0)/Alt+ $+2.000 \cdot 10^{-4} \cdot$ Alt	12	3.68**	2.28*	0.603	6.84*
Elongation = $3.554+798$ (Lat-50.0)/Alt	12	3.15**		0.498	9.92*

[a] For explanation of symbols, see table 4.

from the local seed source cannot be obtained and substitutes have to be found. This is why the degree of lignification, apparently the trait with the closest covariance with the potential survival, is also represented in Tab. 5 by a regression in which the coefficient of regression for the term AltLat does not significantly deviate from zero. This regression is illustrated in Fig. 4. If a numerical evaluation of the relative influence of latitude and altitude of seed source upon the lignification is made, one degree of latitude is found to correspond to 400—600 m (latitudinal range 57°—59° and 51°—53° resp.). This figure differs markedly from the one that has earlier been used (1°latitude=100 m) (Schotte, 1923; Eneroth, 1926; Langlet, 1936; Ruden, 1960; Wiersma, 1963) but corresponds to what has been found in an investigation of *Pinus silvestris* (Hagner, 1970).

As to the regression with bark colour, dry matter and budsetting, the first shows a complicated interaction with latitude and altitude (Fig. 5), while the last two towards the north are increasingly influenced by altitude (Fig. 6 and 7). This increase can logically be expected because the climatic tree-line decreases in altitude northwards and the severity of an additional 1000 feet (300 m), would therefore be greater towards the north.

Comparing the relative influence of latitude and altitude, it may be concluded that budsetting (Fig. 6) is dependent on altitude to a greater extent than any other trait (Fig. 4, 5 and 6).

4. 3 Comparison of rhythm and frost hardiness in provenances of *Pinus contorta* and *Pinus silvestris*.

Through a series of freezing experiments with two provenances of *P. contorta* (nr. 603 lat. 49°N, no. 589 lat. 56°N) and three of *P. sil-*

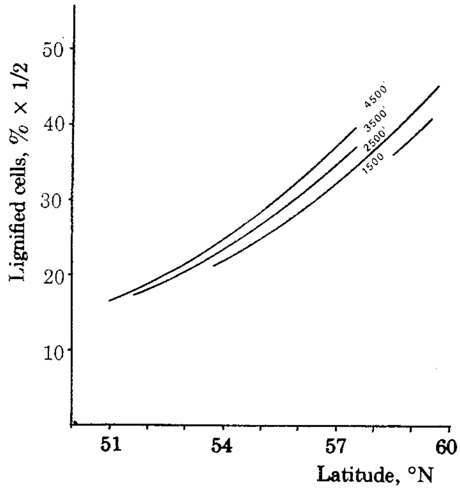

Fig. 4. Regression equation:
$$\mathrm{Lign}=14.57+0.2357\ (\mathrm{Lat}-50)^2+35.61\cdot 10^{-5}\cdot \mathrm{Alt}\ (\mathrm{Lat}-50)$$

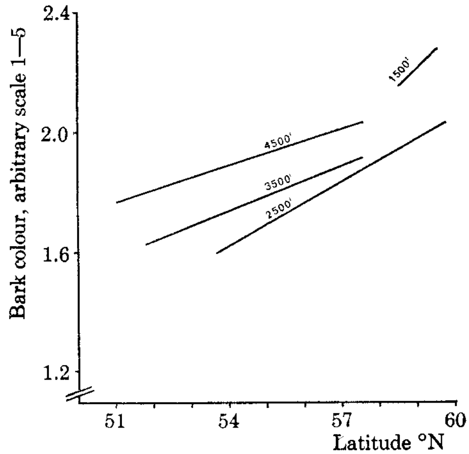

Fig. 5. Regression equation:
$$\mathrm{Bark}=0.8306+180\ (\mathrm{Lat}-50)/\mathrm{Alt}+2.000\cdot 10^{-4}\cdot \mathrm{Alt}$$

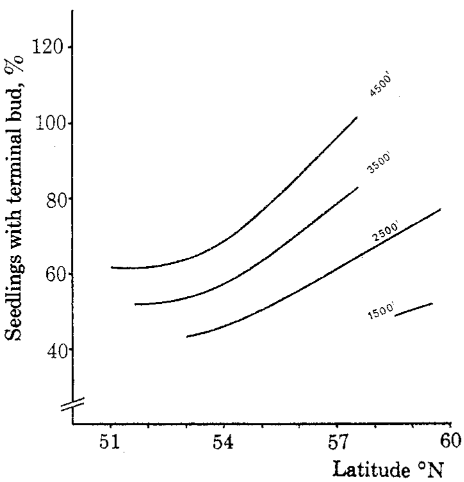

Fig. 6. Regression equation:
$$\mathrm{Bud}=17.55+23.50\cdot 10^{-4}\cdot \mathrm{Alt}(\mathrm{Lat}-50)+74.85\cdot 10^{-4}\cdot \mathrm{Alt}/(\mathrm{Lat}-50)$$

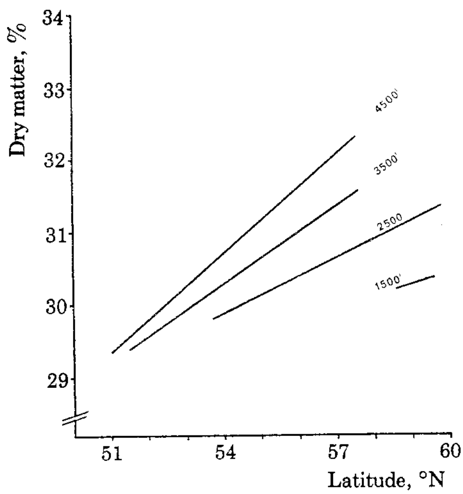

Fig. 7. Regression equation:
$$\mathrm{Drym}=28.88+10.17\cdot 10^{-5}\cdot \mathrm{Alt}\ (\mathrm{Lat}-50)$$

Fig. 4—7. Regressions of the degree of lignification, bark colour, time of bud setting and dry matter content on latitude and altitude of the seed source.

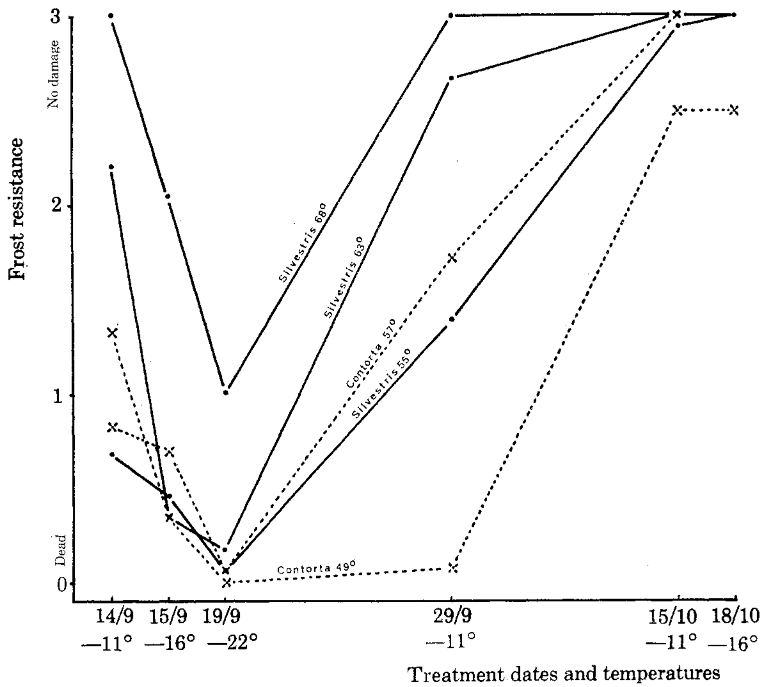

Fig. 8. Frost resistance according to laboratory studies on different dates for three provenances of *Pinus silvestris* and two of *Pinus contorta.*

vestris (latitudes 55°, 63°, 68°N) a comparison of frost hardiness and the degree of lignification could be made between and within the two species. The tested seedlings were potted in single pots in June, grown in the open during the summer and frozen in late September and early October. During the freezing experiment the pots were enclosed in a cardboard box insulated with 5 cm of plastic foam and lowered into a freezer registering —30°C. When the air close to the needles reached a predetermined minimum temperature the box was placed in +8°C, where it slowly returned to outside temperature. The seedlings were then observed for one month in the greenhouse and injuries visible to the naked eye were noted. The results of the freezing experiments are shown in Fig. 8 and 9. Each point in Fig. 8 represents the average frost resistance of nine seedlings.

An anatomical investigation of the degree of lignification was made on approx. 30 provenances from each of the two species on 30 September (Fig. 10). The regression analysis for *Pinus silvestris* is

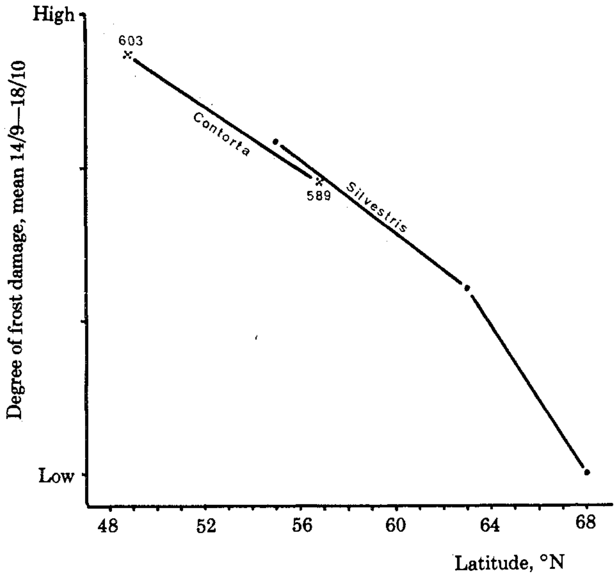

Fig. 9. The relationship between the degree of frost damage and the latitude of seed source for three provenances of *Pinus silvestris* and two of *Pinus contorta*.

presented earlier (Hagner, 1970). For reasons that have been discussed above, only 12 of the provenances from *Pinus contorta* were chosen for the regression analysis.

Fig. 9 shows that the two species have been affected by frost to a degree that is almost identical in provenances that come from corresponding latitudes. This indicates that frost resistance, as measured by the freezing method, is greatly dependent on the photoperiod of the seed source which is directly proportional to the latitude, and to a lesser extent on the temperature. For example, the annual mean temperature at the seed source of 589, at latitude 56°N, corresponds to that of an area of Sweden as far north as latitude 62—65°N, while the winter temperature at the seed source of 589 is much lower than that of the same area in Sweden.

Contrary to the results of the freezing test, the degree of lignification is not the same among Swedish and Canadian pine provenances that originate from the same latitude. The curves (Fig. 10) are approximately parallel and 3 to 5 degrees of latitude apart. That is to say, a provenance of *P. contorta* from latitude 55°N has reached the same lignification as a provenance of *P. silvestris* from latitude 58°N by a

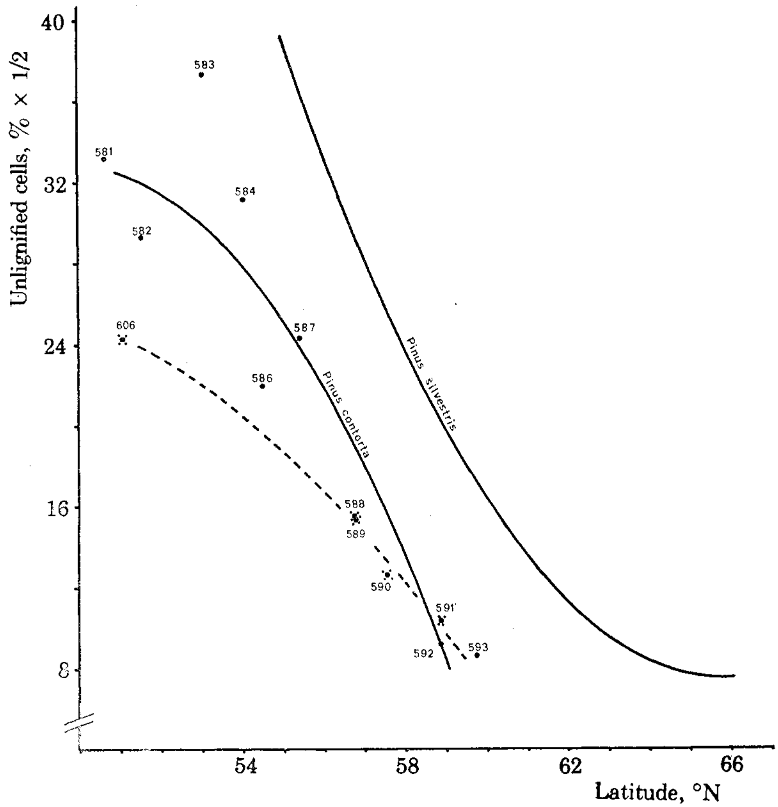

Fig. 10. Regressions of lignification on latitude of seed source. The dotted curve connects the provenances that originate from the eastern side of the Rocky Mountains. Regression equations: *Pinus silvestris* Lign = 76.11–8.794 (Lat–50) + 0.2819 $(\text{Lat}-50)^2$ and *Pinus contorta* Lign = 32.71–0.3005 $(\text{Lat}-50)^2$. The regression equations are presented in Tab. 5 (*Pinus contorta*) and by Hagner (1970) (*Pinus silvestris*).

certain date. Unfortunately the date of harvesting, 30 September, was too late to allow for discrimination among the *P. silvestris* provenances from higher latitudes than 62°N.

The *P. contorta* series does not contain more than one provenance (606, Banff) from the "inland" side of the Rocky Mountains south of latitude 56°N.

If this Banff provenance, which was not included in the regression analysis, is registered on the graph (Fig. 10), it can be seen that the dotted curve for a series of provenances from the eastern side of the Rocky Mountains (606, 588, 589, 590, 591) may have fallen more to the left and given a discrepancy of 4—7 degrees of latitude between the two species.

It was thougt that the two test series show the relative difference in hardiness between the two species, but neither the results from the freezing experiment nor those from the investigation on lignification correspond very well with the results from field tests in Scandinavia and Finland. In these tests the *P. contorta* has shown a very high level of survival considering the low latitude of the seed sources. Many field tests were planted; the following are two of the oldest:

In Finland at 60°N (Mustila arboretum), *P. contorta* from Banff, Alberta, 51°N, produced an impressive result with good growth and survival over a period of approx. 50 years (Tigerstedt, 1960).

In Sweden, at latitude 64°N, 400 m above sea level in a severe mountain climate, *P. contorta* from Banff in Alberta, lat. 51°N, and from Kamloops in British Columbia lat. 50°N, has survived better than Swedish *P. silvestris* from latitude 63°N, over the test period of 36 years. (Stefansson, 1957; Ingerstedt, 1966)). This can hardly be explained by the altitudinal difference of the Swedish (100—300 m) and Canadian (900—1300 m) seed sources alone.

Until recently, there has not been any series of tests with a large number of *P. contorta* provenances in Scandinavia. It is therefore impossible to make any complete comparisons between the experimental results obtained here and the field results. Nevertheless, it may be concluded that the hardiness of *P. contorta,* measured by field survival up to 30 years of age, seems to be higher in the Scandinavian climate than the discrepancy between the regression curve shows. The position in the diagram of the provenances from the eastern side of the Rocky Mountains indicates that the annual rhythm of these provenances should be even faster than that of provenances from the interior of British Columbia.

Thus it is rather surprising that the freezing test did not show any diversity at all between latitudinally corresponding provenances.

Probably one of the reasons why *P. contorta* survives so well is that many of its natural pathogens are lacking in the Scandinavian environment. The vigour, however, in the field tests is often so great that it may be concluded that the primary climatic injuries that usually afford the pathogens entry are probably also lacking. Possibly the Canadian pine withstands the northern European winter climate in spite of a relatively low degree of winter adjustment. Whatever the explanations of the observed discrepancy between field results and growth rhythm, it is obviously important that further studies in this field should be carried out.

5. Conclusions

This investigation has shown that there are several methods available which describe the annual rhythm of *Pinus contorta.* The rhythm was found to have a clinal relation to the climatic and geographic character of the seed source and consequently the annual rhythm may be used for estimations of climatic adaptation and relative hardiness.

It was demonstrated that the mutual relationship between latitude of seed source and rhythm was not the same for *Pinus contorta* and *Pinus silvestris* and that the degree of lignification cannot be used for direct comparisons of long-term hardiness between the two species.

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Sammanfattning

En genekologisk undersökning av årsrytmen hos *Pinus contorta* Dougl. och en jämförelse med *Pinus silvestris* L.

Inledning

Avsikten med undersökningen har varit att studera årsrytmens variation hos *P. contorta* och samtidigt på detta trädslag pröva de metoder, som visat sig effektiva på *P. silvestris* (Hagner, 1970.) Avsikten har även varit att utröna huruvida det inbördes förhållandet mellan årsrytm och härdighet är detsamma hos båda trädslagen.

Material

Materialet hämtades från västra Kanada i 27 autoktona bestånd (figur 1), i vilka kottarna samlades från ekorrbon på marken. All kott insamlades av samma person. Plantorna, som odlades i Sverige på friland utan upprepning i en plantskola på lat. 63°30′N, long. 16°30′Ö, 260 möh, studerades under sin andra vegetationsperiod. Som jämförelse till plantorna med kanadensiskt ursprung studerades också analogt behandlade plantor av *P. silvestris*. Dessa var uppdragna ur frö från 30 bestånd spridda över hela Sverige.

Metoder

De metoder som prövats är desamma som använts av Hagner (1970) för studium av årsrytmen hos svensk tall och som utförligt beskrivits i ett tidigare arbete. Dessa var: den procentuella längden av skottet i juni i förhållande till längden i september, knoppsättningen i juli, terminalskottets barkfärg i augusti, den yttersta vedmantelns lignifieringsgrad i september, kambiets elektriska ledningsmotstånd i oktober och barrens torrsubstanshalt mätt i oktober.

Resultat

Metodval

Resultaten visar att val av metod starkt påverkar variation inom och bland provenienser (tabell 1, 2). Vid de tillämpade sampelstorlekarna erhölls det noggrannaste proveniensmedelvärdet genom uppskattning av knoppsättningen. Mindre noggranna värden gav mätningar av lignifiering och barkfärg. Sämst resultat gav den elektriska metoden (tabell 2). Skottlängden och torrsubstanshalten kunde inte analyseras på motsvarande sätt. Om hänsyn tas till differenser mellan proveniensmedelvärden och variationen bland plantor inom provenienser, uppvisar värdena för lignifieringsgraden mycket distinkta provenienskaraktärer (figur 2).

Variation inom arten

Variationen i årsrytm bland provenienser är mycket stor (figur 3) och har en klinal prägel. Tendensen till en minskad lignifieringsgrad bland de allra nordligaste provenienserna från västra Yukon, motsägs av andra rytmkaraktärer och kan möjligen förklaras av att dessa plantor kommit i ett tillstånd av förnyad kambial aktivitet genom testmiljöns för dem exceptionellt långa och varma höst.

I en serie av korrelations- och regressionsanalyser jämfördes årsrytmen hos provenienserna med ursprungsortens klimatiska och geografiska parametrar (tabell 3, 4, 5, figur 4, 5, 6, 7). Med hänsyn till variationerna i klimat och topografi inom de olika delarna av det område från vilket de 27 provenienserna hämtats, har analysen inskränkts till att omfatta endast en central grupp av 12 provenienser (581—593). Det framgick att följande karakteristika hos ursprungsorten har den största samvariationen med årsrytmen: latitud, medeltemperatur i januari, medeltalet av minimumtemperaturer i januari, skillnaden mellan medeltemperaturen i juli och januari, »normal heating degree days» vid temperaturer under 18°C i januari. Denna samvariation gäller samtliga rytmvariabler med ett undantag, nämligen knoppsättningen. Denna har ett avvikande variationsmönster och synes vara starkt beroende av ursprungsortens höjd över havet, medan övriga variabler visar svag eller ingen samvariation med denna parameter.

I multipla regressionsanalyser studerades samspelet mellan höjd över havet och latitud (figur 4, 5, 6, 7) och resultaten kan sägas visa, att latituden har ett långt starkare inflytande på variationen i rytm än höjden över havet. Undantag gäller för knoppsättningen. Det framgår vidare av regressionerna, att en given förändring i höh och latitud ger en ökande effekt mot norr. Detta är logiskt eftersom man kan förvänta, att härdigheten ökar asymptotiskt när man närmar sig trädgränsen vid förflyttning mot norr på en viss nivå. I jämförelse med en breddgradsförändring synes, i detta material såväl som i tidigare redovisat material av *P. silvestris* (Hagner, 1970), 100 meters altitudförändring ha mindre inflytande än man tidigare räknat med (Schotte, 1923; Eneroth, 1926; Langlet, 1936; Ruden, 1960; Wiersma, 1963).

Jämförelse mellan P. contorta och P. silvestris

I en frysbox hållande —30°C, nedsänktes en skumplastisolerad pappkartong innehållande 9 st. plantor av vardera 3 provenienser *P. silvestris* och 2 provenienser *P. contorta*. Kartongen hölls kvar tills dess en förutbestämd minimumtemperatur hade uppnåtts i kronskiktet. Upptiningen skedde i +8°C med kartongen stängd. Uppskattning av frostskadorna gjordes under en följande månad i växthus. Frysningen upprepades vid 6 tillfällen på dagar och till temperaturer som framgår av figur 8. Frostskadorna (figur 9) stod i direkt relation till ursprungsortens latitud och hade samma omfattning i de båda trädslagen i plantmaterial som hämtats från samma latitud.

Lignifieringsgraden i yttersta vedmanteln uppskattades samtidigt i de två arterna. Regressionsfunktionerna för sambandet mellan lignifieringen och ursprungsortens latitud (figur 10) löper i stort sett parallellt men på ett avstånd av c:a 3—5 breddgrader från varandra.

Vid en jämförelse av dessa resultat med dem som uppnåtts i de många, men ur provenienssynpunkt svagt uppbyggda fältförsöken i Skandinavien och Finland, i vilka *P. contorta* visat en stor överlevelseförmåga upp till 13 breddgrader norr om sin ursprungsort, finner man det anmärkningsvärt att lignifieringen inte visar någon större skillnad mellan arterna och än mer förbryllande att frostskadorna i laboratorieförsöket inte visade några skillnader alls mellan arterna.

Detta kan knappast förklaras enbart som en följd av att många av de naturliga patogenerna, som *P. contorta* har i sitt hemland, saknas i Europa. Möjligen kan den kanadensiska tallen uthärda det nordeuropeiska vinterklimatet trots en låg avmognadsgrad. Detta spörsmål borde klarläggas genom ytterligare forskning.

6.5 Slutsatser

Sammanfattningsvis kan sägas att undersökningen visat att det finns flera metoder med vilka man kan beskriva årsrytm hos *P. contorta* och att rytmen kontinuerligt förändras med ursprungsortens geografiska och klimatiska karaktär. Detta innebär att årsrytmen kan anses skildra klimatanpassningen och därmed den relativa härdigheten.

Undersökningen har även visat att det absoluta mått på årsrytmen, som man erhåller med lignifieringsmetoden, icke utan vidare kan användas för jämförelse av härdigheten hos skilda arter.