The Accumulation mechanism of the supernumerary (B-) chromosome in Picea sitchensis (Bong.) Carr. and the effect of this chromosome on male and female flowering

By V. M. Kean*[+]), D. P. Fox*) and R. Faulkner**)

Summary

(i) The behaviour and phenotypic effects of a supernumerary chromosome were investigated in grafts of Sitka spruce at Wauchope (Roxboroughshire) and Ledmore (Perthshire).

(ii) In male meiosis the heterochromatic B-chromosomes fail to pair with each other or with members of the A-chromosome set and orientate in a random fashion at metaphase-I.

(iii) Plants reach the same stage of male meiosis on progressively later dates as the B-chromosome number increases. A similar effect is observed with female flower development.

(iv) Controlled crosses were performed between plants of known B-constitution and the frequency of B-chromosomes in the offspring determined.

(v) B-chromosomes are distributed through the male and female germ lines in an approximately random fashion. They do not behave in a Mendelian fashion.

(vi) When only the female parent has 1 or 2 B-chromosomes there is marked accummulation of B-chromosomes in the offspring. In a single 3B plant as female parent there was a moderate loss of B-chromosomes in the offspring.

(vii) When only the male parent has 1 or 2 B-chromosomes there is variable behaviour but without marked gain or loss of B-chromosomes in the offspring.

(viii) When both parents carry B-chromosomes fewer of them are transmitted to the offspring than is predicted from the behaviour of the same parents in crosses with plants lacking B-chromosomes.

(ix) Non-disjunction occurs at a similar rate in both male and female germ lines but is not responsible for the accummulation mechanism.

(x) Accummulation is probably due to preferential migration of B-chromosomes at the first meiotic division in the female to the pole giving rise (after the second division) to the single functional megaspore.

(xi) The significance of these results for the natural distribution of Sitka spruce B-chromosomes is discussed.

Key words: Sitka spruce, B-chromosome, preferential transmission, flower development.

Zusammenfassung

An Picea sitchensis wurde die Vererbung der B-Chromosomen, sowie ihr Einfluß auf den Blühtermin der ♂ und ♀ Blüten untersucht. Obgleich die B-Chromosomen in der Meiose zufällig verteilt werden, scheinen sie jedoch durch die ♀ Gameten gehäuft übertragen zu werden, insbesondere wenn 1—2 B-Chromosomen vorhanden sind. Es wird daher angenommen, daß sie nach der Meiose, die zur Bildung der ♀ Gameten führt, bevorzugt an dem Pol liegen, an dem die Eizelle gebildet wird. Eine derartige gehäufte Übertragung der B-Chromosomen durch den ♂ Elter wurde nicht beobachtet.

Introduction

The chromosome complement of a diploid species generally shows little variation in number. Occasionally mistakes are made in the segregation of chromosomes at cell division which result in aneuploid daughter cells. Such gain or loss of regular members of the chromosome complement has a dramatic and deleterious effect on the phenotype if present in all cells.

Stevens (1908) and Longley (1927) first described animals and plants that contained supernumerary chromosomes which were not extra members of the normal diploid complement and which had little effect on growth, development and reproduction. Randolph (1928) coined the term "B-chromosome" for these extra chromosomes and they have now been described in more than 700 species (Rees, 1974).

B-chromosomes often, but not always, show somatic instability, structural differences from A-chromosomes including extensive heterochromatinisation, failure to pair with A-chromosomes, lack of major genes and non-Mendelian inheritance.

B-chromosomes were first described in Sitka Spruce by Moir and Fox (1972) and are limited in their distribution to the southern half of the species range (Moir and Fox, 1977). They have no effect on growth rate (Moir and Fox, 1976; Kean, 1981). Moir (1975) in a limited number of crosses showed that B-chromosomes accumulate through the female germ line. The main purpose of the present study is to extend these observations and to investigate the effect of the B-chromosome on male and female flower development.

Materials and Methods

For this study all the Sitka spruce trees contained in the Forestry Commission tree banks at Wauchope and Ledmore, Scotland were used. To determine the number of B-chromosomes in these clones we collected vegetative buds from two or more trees per clone in February or March. These were slit longitudinally, fixed in Carnoy's fluid for 24 hours and stored in 70% ethanol. Meristematic cells were squashed in lactopropionic orcein after brief hydrolysis in 5M HCl and 100 well-squashed interphase nuclei scored for chromocentre number, shape and size. This process takes about 5 minutes and B-chromosome number can then be estimated from the chromocentre scores (Moir and Fox, 1972, 1977; Kean, 1981).

Seeds from crosses were germinated in Petri dishes at room temperature. When the primary root was 5—10 mm long the seedling was immersed in 0.5% colchicine for 5 hours prior to fixation and scanning as for the vegetative buds. We attempted to score 5 colchicine (C-) metaphases per seedling but in cases where this was not possible 100 interphase nuclei were also scored for chromocentres.

*) Department of Genetics, University of Aberdeen.
**) Forestry Commission Northern Research Station, Edinburgh.
+) Present address: Faculty of Medicine, Memorial University of Newfoundland.

Male flower buds from clones having at least 1 B-chromosome were collected on 17th and 21st April 1978 and fixed/stained by the technique of SNOW (1963). Squash preparations were then analysed for meiotic stages present. The meiotic and post-meiotic stages recognised were as follows

1	Leptotene	11	Interkinesis
2	Zygotene	12	Prophase-II
3	Pachytene	13	Metaphase-II
4	Diffuse diplotene	14	Anaphase-II
5	Early diplotene	15	Telophase-II
6	Late diplotene	16	Postmeiotic interphase
7	Diakinesis	17	Tetrads
8	Metaphase-I	18	Microspores
9	Anaphase-I	19	Pollen grains
10	Telophase-I		

In 1977 and 1978 crosses were made among clones for which the number of B-chromosomes was known. We obtained seeds from 49 different tree × tree combinations. The crosses were made by isolating upright female strobili with controlled pollination two weeks afterwards. The cones were collected for seed extraction in mid-September.

On 18th May 1977, during the period of isolation of female flowers prior to artificial pollination, the appearance of these flowers in most of the Wauchope clones was assessed according to the following classification.

1. Unflushed — bud scales completely enclose buds.
2. Just flushed — buds beginning to burst through scales.
3. Half-flushed — more scales broken.
4. Fully-flushed with tusk — cap of scales remaining at apex.
5. Fully-flushed without tusk — apex exposed and ovuliferous bracts about to open.
6. Half-open — bracts partly reflexed.
7. Fully-open — bracts fully reflexed.

Results

(i) Male meiotic development

Because of asynchrony of meiosis within the buds the mean meiotic developmental stage present in microsporocytes taken from the middle of the male strobilus (1977)

or the two ends (1978) was used as an index of meiotic development. The mean values for the apex are reported for the Wauchope trees on 17th and 21st April 1978 (Table 1). It can be seen that meiotic development is progressively retarded by increasing B-chromosome number. Data from other dates and sites (not reported) were in general agreement. Analyses of variance showed that, except at the latest collection dates, there were highly significant differences between the indices of the different B-classes.

(ii) B-chromosome behaviour during male meiosis

Even in diffuse diplotene (Fig. 1a) the B-chromosomes are condensed and unpaired either with each other or with the A-chromosomes. At metaphase-I they tend to lie off the equatorial plate in an apparently random manner (Fig. 1b, c, d) and presumably segregate to the adjacent pole at anaphase-I.

(iii) Female flowering

Female flowering was assessed by comparing the rank values for the state of flowering in each clone of each B-
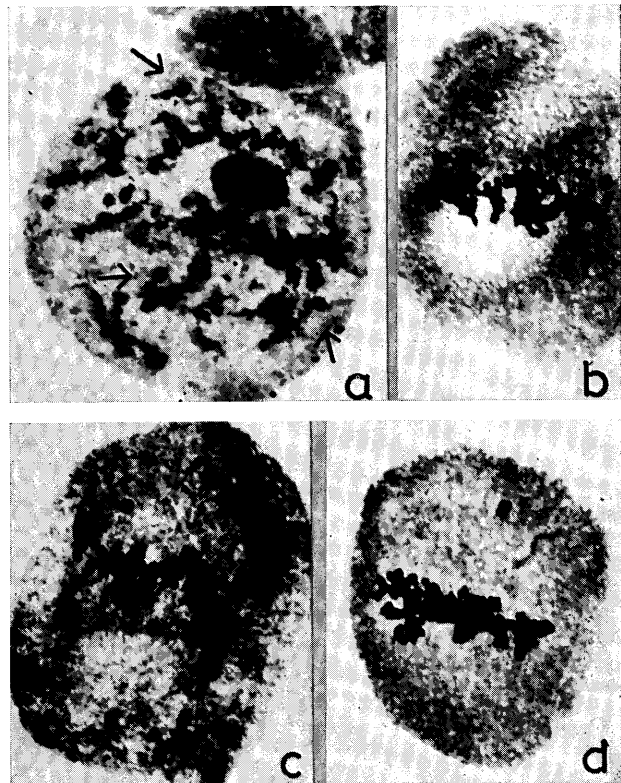

Fig. 1. — Male meiosis in plants with one (d) or three (a, b and c) B-chromosomes. a - diffuse diplotene; b, c and d metaphase-I. Note the unpaired, heterochromatic nature of the B-chromosomes (→). The B-chromosomes lie off the spindle equator and appear to lie at random with respect to each other (Mag. × 800).

Table 1. — Mean stage of meiotic development (1 = Leptotene, 19 = Pollengrains — see KEAN, 1981) for male buds with different numbers of B-chromosomes at Wauchope in the 1978 meiotic season.

DATE	B-CHROMOSOMES AND NO. OF BUDS							
	OB	n	1B	n	2B	n	3B	n
17th April	17.8	3	17.3	14	14.2	11	1.0	2
21st April	19.0	1	18.5	5	18.1	14	12.5	1

Table 2. — Frequency distribution of female flowering stage for clones of differing B-chromosome number at Wauchope on 18th May, 1977. (1 = Unflushed, 7 = Flushed — see KEAN, 1981). Numbers of clones are: 0B - 656, 1B - 93, 2B - 27, 3B - 1.

B-chromosome number	% FLOWERS AT EACH STAGE OF FEMALE FLOWER DEVELOPMENT						
	1	2	3	4	5	6	7
0	1.9	15.0	29.5	21.4	14.8	10.8	6.6
1	4.3	23.7	34.4	18.3	10.8	7.5	1.1
2	18.5	25.9	37.0	11.1	7.4		
3	100.0						

Table 3. — Predicted distribution of B-chromosomes in the progeny of crosses of B-chromosome with 0B plants according to the Mendelian and binomial hypotheses. Note that for 0B × 1B the predictions of the two models are identical.

PARENTS	Hypothesis	Predicted Percentage of Progeny with			
		0B	1B	2B	3B
0B, 1B	Mendelian	50	50		
	Binomial	50	50		
0B, 2B	Mendelian		100		
	Binomial	25	50	25	
0B, 3B	Mendelian		50	50	
	Binomial	12.5	37.5	37.5	12.5

class at Wauchope on 18th May 1977. The data are summarised in Table 2. It can be seen, in spite of the reducing number of observations, that as the number of B-chromosomes increases there is a progressive retardation of female flower development.

(iv) B-chromosome Inheritance

Table 3 indicates the expected frequencies of B-chromosomes in the progeny of crosses where only one parent carried B-chromosomes. The Mendelian hypothesis assumes normal pairing and disjunction of B-chromosomes and the binomial hypothesis is a consequence of no pairing and random distribution at meiosis. The actual results of the crosses performed in 1976—1978 are contained in Tables 4—

Table 4. — Distribution of B-chromosomes in progeny of the crosses between 0B females × 1B males. χ^2 refers to the fit to either the Mendelian or the binomial hypothesis. 2B plants were pooled with 1B. L.c. tests for the net gain or loss of B-chromosomes. * - P < 0.05.

PARENTS 0B females x 1B males	B-FREQUENCY IN OFFSPRING			χ^2 (1)	Mean B's Per Plant	z
	0	1	2			
2 x 3	41	25		3.88*	0.38	1.99*
810 x 685	54	45	1	0.64	0.47	0.58
1088 x 685	53	50	1	0.04	0.50	0.00
338 x 423	52	70		3.83	0.41	1.95
800 x 421	68	47		3.25	0.43	1.38
946 x 672	65	44	2	0.42	0.47	0.64
1036 x 495	62	55		5.73*	0.39	2.24*
337 x 328	67	41	1	2.66	0.57	1.56

Table 5. — Distribution of B-chromosomes in progeny of the crosses between 1B females × 0B males. * - P < 0.05; ** - P < 0.01; *** - P < 0.001.

PARENTS 1B females x 0B males	B-FREQUENCY IN OFFSPRING			χ^2 (1)	Mean B's Per Plant	z
	0	1	2			
3 x 2	6	8		0.29	0.57	0.51
255 x 94	53	45	2	0.36	0.49	0.18
685 x 1088	34	72	1	14.22***	0.69	4.06***
1106 x 422	18	82	1	41.83***	0.83	8.26***
1106 x 148	11	44		19.80***	0.80	5.51***
1350 x 541	30	68		14.73***	0.69	4.06***
821 x 987	35	76		15.14***	0.68	4.06***
1101 x 967	41	72		8.50**	0.64	3.08**
1108 x 594	30	91	2	32.27***	0.77	5.32***
1080 x 113	23	93		42.24***	0.80	6.07***
841 x 683	53	60	6	1.05	0.61	2.05*
1107 x 683	10	10		0.00	0.50	0.00

Table 6. — Distribution of B-chromosomes in progeny of the crosses between 0B females × 2B males. χ^2 tests the fit of the binomial hypothesis. Other symbols as for table 5. N. C. - Not computed.

PARENTS 0B females x 2B males	B-FREQUENCY IN OFFSPRING						χ^2 (2)	Mean B's Per Plant	z
	0	1	2	3	4	5			
140 x 256	31	66	27	2			0.35	1.00	0.00
1088 x 560	14	32	8				3.19	0.89	1.27
237 x 324	10	37	50	11		1	60.85***	1.61	7.40***
543 x 324	4	5					N.C.	0.56	2.50*
795 x 324	15	26	12	1			0.22	0.93	0.19
803 x 324	33	49	27				1.76	0.94	0.84
795 x 1	28	64	25	1			0.92	0.99	0.16
1035 x 1	33	54	23	1			1.54	0.93	1.00

Table 7. — Distribution of B-chromosomes in progeny of the crosses between 2B females × 0B males. Symbols as for Table 5.

PARENTS 2B females x 0B males	B-FREQUENCY IN OFFSPRING					χ^2 (2)	Mean B's Per Plant	z
	0	1	2	3	4			
1 x 2	4	24	64	2		104.30***	1.68	11.16***
156 x 94	4	36	59			68.47***	1.56	9.68***
259 x 94	6	37	57			58.78***	1.51	8.54***
560 x 1088	11	61	48	2		24.93***	1.34	5.66***
1 x 427	6	30	63	9		102.00***	1.69	10.20***
560 x 494	10	43	73	1		88.17***	1.53	9.41***
324 x 394	7	41	52	1	1	47.24***	1.49	7.22***

Table 8. — Distribution of B-chromosomes in progeny of the crosses between the single 3B plant (781) as female parent and 0B males. Symbols as for Table 5.

PARENTS 3B females x 0B males	B-FREQUENCY IN OFFSPRING					χ^2 (3)	Mean B's Per Plant	z
	0	1	2	3	4			
781 x 1231[++]	16	44	33	7	3	2.97	1.39	1.20
781 x 1371	12	49	30	9		6.03	1.36	1.73
781 x 338[+++]	32	77	66	15	1	6.21	1.35	2.38*
781 x 980	23	60	38	16	2	6.86	1.38	1.50

8. It is immediately clear that the results conflict with the predictions of the Mendelian hypothesis but are similar to the predictions of the binomial hypothesis.

Many crosses were performed which involved both parents carrying B-chromosomes. However, in view of the general lack of agreement with the Mendelian model and the detailed deviation from the binomial model only the results of those crosses are reported where each B-chromosome parent had also been crossed, as the appropriate sex, with other plants lacking B-chromosomes. This allows the prediction of the zygotic frequencies in the present crosses from the (presumed) gametic frequencies of the other crosses. Some B-clones produced similar distributions irrespective of their 0B partners and consequently the overall gametic frequencies were derived by pooling the data from each representative replicate (e.g. 781 × 0B). However, others such as 324 and 560 produced inconsistent results and thus each type of response was used to derive a number of expectations. This meant that for the most complicated prediction (560 × 324) there were four possible expected outcomes. Table 9 summarises the data for the relevant crosses.

Discussion

Although B-chromosomes generally lack major genes, many instances of quantitative genetic effects have been described. The Sitka B-chromosome is relatively inert with regard to its influence on somatic growth and development (KEAN, 1981) but it has been clearly demonstrated here that it has a retarding effect on either the rate of male meiosis and the rate of development of female flowers or on the time of initiation. In both cases the effect appears to be additive with greater B-frequencies having greater effects. A delay in flowering time has also been reported in B-chromosome containing plants of Narcissus (FERNANDES, 1952), Crepis capillaris (RUTISHAUSER, 1963), Japanese and experimental rye varieties (KISHIKAWA, 1965; JONES and REES, 1968) and maize (KATO, 1970 cited by JONES, 1975). Similarly, the B-chromosomes of Anthoxanthum

aristum (OESTERGREN, 1947), Sorghum purpureosericeum (DARLINGTON and THOMAS, 1941) and rye (MÜNTZING, 1946, 1949) have been found to retard pollen grain development.

On the basis of the B-classes predicted for the offspring alone, a Mendelian mode of inheritance for the B-chromosome can be completely excluded. For 1B × 0B crosses the predictions of the Mendelian and binomial hypotheses do not differ (Table 3) but for the 2B × 0B and 3B × 0B crosses the departure between observed and expected is very large. This is not surprising in view of the failure of the B-chromosomes to pair with each other in the male (Fig. 1). On the other hand the predictions of the random model are largely supported. The predicted classes are all represented and, especially in the case of B's passing through the male gametes, the class proportions are predicted fairly well. However on three counts, which may not be independent, the binomial hypothesis too is inadequate as a full explanation of the transmission behaviour of the B-chromosome·

(a) In many cases (see Tables 4—8) higher B-chromosome classes are represented in the offspring than are predicted by this model, though with only a low frequency.

(b) Individual classes may not agree with the frequencies predicted from the model.

(c) There may be an overall gain or loss of B-chromosomes and this is especially marked in crosses of 1B or 2B female parents with 0B males (Tables 5 and 7).

The presence of extra B-chromosome categories indicates that non-disjunction must be occurring in both male and female germ lines. However, accumulation is almost entirely a property of the female germ line when 1 or 2 B-chromosomes are present. If we compare the frequency of plants which must have undergone non-disjunction with those which may not have for the reciprocal cross types 1B × 0B and 2B × 0B, we find that their frequencies are not significantly different between male and female germ lines ($\chi^2_{(1)}$ = 1.4634, P = 0.3—0.2 and $\chi^2_{(1)}$ = 0.1985, P = 0.7—0.5 respectively). Thus mitotic or second meiotic non-disjunction cannot be responsible for the accumulation

Table 9. — Distribution of B-chromosomes in progeny of crosses in which both parents carry B-chromosomes. O - observed, E - expected. Expected values are derived from the results of the same parents crossed with 0B plants of the opposite sex. χ^2 tests the significance of the deviation of observed from expected. * - P < 0.05, ** - P < 0.01, *** - P < 0.001.

PARENTS	O or E	B-FREQUENCY IN OFFSPRING						DF	χ^2	MEAN B's PER PLANT
		0	1	2	3	4	≥5			
1B 1B 255 x 421	O	44	66	31						0.91
	E	43.3	66.7	28.5	2.4	0.1		2	0.02	0.93
2B 1B 1 x 3	O	3	12	35	13					1.92
	E	2.0	11.7	31.1	17.0	1.2		2	2.10	2.06
2B 1B 1 x 423	O	3	28	50	20					1.86
	E	3.0	18.1	48.7	29.1	2.1		2	8.53*	2.09
2B 1B 560 x 685	O	5	31	52	19					1.79
	E1	4.9	31.9	47.0	21.7	1.5	0.02	3	1.32	1.84
	E2	4.4	21.6	48.7	31.2	1.1	0.01	2	9.55**	2.03
2B 2B 560 x 324	O	6	16	32	43	9	1			2.34
	E1	0.9	8.1	26.4	40.0	25.3	6.3	4	35.75***	2.92
	E2	2.8	19.9	39.0	32.8	11.5	1.1	3	4.95	2.31
	E3	0.8	6.0	21.3	38.2	32.8	8.0	4	63.48***	3.14
	E4	2.5	13.9	36.1	37.6	16.0	1.0	3	5.97	2.50
3B 1B 731 x 685	O	13	30	43	23	8				1.95
	E	8.9	34.7	43.4	23.3	6.0	0.8	4	2.79	1.87
3B 1B 781 x 423	O	25	63	63	42	10	1			1.76
	E	18.0	65.5	74.1	36.8	8.7	0.9	4	5.42	1.78
3B 1B 781 x 459	O	15	37	42	16	6				1.66
	E	10.6	37.8	41.5	20.5	5.0	0.6	4	2.87	1.77
3B 2B 781 x 1	O	10	29	43	26	11	2			2.04
	E	4.9	23.6	41.1	33.4	14.3	3.7	4	9.66*	2.33
3B 2B 781 x 324	O	1	12	13	2					1.57
	E1	0.4	2.5	6.9	9.3	6.1	2.8	2	41.41***	2.98
	E2	1.2	5.5	9.2	7.7	3.5	0.9	2	15.92***	2.34

mechanism as it is in many other species such as rye (MUNTZING, 1946) and maize (ROMAN, 1947).

It should also be noted that non-disjunction of a single B leads to a deficiency of 1B gametes compared with 0B and the presence of 2B gametes. However, in 1B females × 0B males it is the 1B category which is generally in excess (Table 5).

The fact that the accumulation mechanism is largely a characteristic of the female germ line and does not involve non-disjunction suggests that preferential (reductional) segregation at the first meiotic division, with the B-chromosomes tending to pass to the pole giving rise to the lower half of the linear tetrad, is responsible. The lowest cell in the tetrad is generally the only functional megaspore. A similar mechanism has been described in Lilium (KAYANO, 1957) and Trillium (RUTISHAUSER, 1956), though in general accumulation mechanisms operating through the male germ line are more common.

While accumulation is very marked in the female parents bearing 1 or 2 B-chromosomes, a moderate loss occurred in the single 3B individual (Table 8). In only one of the four crosses was the loss significant but there was a non-significant loss in the other three and the pooled data show a highly significant loss ($\chi^2_{(3)}$ = 16.76, P < 0.001). Although no great weight can be put on the behaviour of the single 3B tree, it remains a possibility that the accumulation behaviour of the B-chromosome may vary not only between the male and female germ lines but also within the female germ line depending upon the actual

number of B-chromosomes present. This suggestion of an interaction between the B-chromosomes is supported by the results of crosses involving B-containing parents on both sides (Table 9). Of the seven crosses for which there were only single predictions five yielded B-chromosome distributions similar to expectations. Two of the three in which there was more than one possible outcome included possibilities which did not differ significantly from observation. However, the general trend was for the mean B-frequency observed to be less than the expected value and in every case where the difference was significant the observed value was lower. In the most significant case (781 × 324) the deficiency is clearly in the higher B-classes and this implies that there is a loss of plants with higher B-numbers.

The fact that the B-chromosome does not show a random distribution between natural populations (MOIR and FOX, 1977) argues against it being a completely neutral character. However, the particular pattern of distribution shown by natural populations could be explained by the present findings. Selection against the B-chromosome in the northern half of the species range could be through the delay in meiosis and flowering which they induce. It is not known if the B-chromosome of Sitka spruce has any effects which are selectively advantageous in other circumstances but even if it does not the presence of the accumulation mechanism, coupled with more favourable growing conditions, may be sufficient to account for its southerly distribution. Although the present data on the accumulation mechanism

are provisional for high B-numbers there are several indications that it may be self-limiting and not lead inexorably to ever-increasing population B-frequencies.

(a) Accumulation on the female side may be limited to plants with one or two B's.

(b) Crosses between plants both of which carry B's lead to some unexplained loss of B's.

(c) The effect of flowering time may lead, especially in the case of individuals with three or more B-chromosomes, to reduced fecundity due to a lack of other trees with ripe pollen and receptive female flowers at the appropriate time.

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Untersuchungen zum Wachstum slowakischer Rotbuchenprovenienzen (Fagus sylvatica L.)

By L. Paule
Forstliche Fakultät der Hochschule für Forstwirtschaft
und Holztechnologie, Zvolen, Tschechoslowakei

Zusammenfassung

In der Arbeit wird die geographische Variabilität der slowakischen Provenienzen der Rotbuche *(Fagus sylvatica* L.) an Hand der Wachstumsmerkmale untersucht. Die Versuchsfläche mit 1 rumänischen und 19 slowakischen Provenienzen wurde im Jahre 1972 mit 3jährigen Pflanzen begründet. Die Arbeit umfaßt die Ergebnisse des Höhen- und Durchmesserwachstums und des -zuwachses, sowie deren Saisondynamik. Die Buchenprovenienzen aus dem Gebiet der Slowakei weisen eine beträchtliche geographische Variabilität auf. Die besten Provenienzen sind diejenigen der Nordostslowakei und die lokale Provenienz — Zvolen. Aus mehrjährigen Untersuchungen ergibt sich, daß im Frühjahr (bis 15. Juni) 77%, im Sommer (bis 15. August) 16% und im Spätsommer 7% des Höhenzuwachses und 34%, 54%, bzw. 12% des Durchmesserzuwachses realisiert werden.

Schlagworte: Fagus sylvatica L., geographische Variabilität, Provenienzforschung, Höhenwachstum, Höhenzuwachs, Durchmesserwachstum, Durchmesserzuwachs, Saisondynamik des Zuwachses.

Summary

The geographical variability of Slovak provenances of Beech *(Fagus sylvatica* L.) was studied on the basis of their growth characteristics. Provenance trial was established in 1972 with 3 years old plants of 1 Roumanian and 19 Slovak provenances. The paper deals with the evaluation of height and diameter growths and increments and their seasonal dynamics. Beech provenances from the region of Slovakia manifested a relatively high geographical variation. The best of them are those from the North-Eastern Slovakia and that of local origin — Zvolen. Investigations lasting more years showed that in spring (till June 15th) has been realized 77%, in summer (till August 15th) 16% and in late summer 7% of the height increment and 34%, 54% and 12% of the diameter increment, respectively.

Key words: Fagus sylvatica L., geographical variation, provenance investigations, height growth, height increment, diameter growth, diameter increment, seasonal dynamics of increment.

Einleitung

In der Vergangenheit wurde in der Slowakei die genetische und züchterische Forschung mehr auf die Nadel- als auf die Laubholzarten ausgerichtet. Dies ist dadurch bedingt, daß den Nadelholzarten eine beträchtlich größere Wertigkeit zugeordnet wurde. Auch ist ihre Fläche bei Begründung der Waldbestände beträchtlich größer. Erst in den letzten Jahrzehnten wendet sich die Forschung mehr den Laubholzarten, vor allem der Buche, deren Flächen-