(From Forest Tree Breeding Institute Ekebo, Källstorp, Sweden)

Development of Triploid and Diploid Populus tremula during the juvenile period

By HELGE JOHNSSON

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As is well known autotriploid clones and single trees of Populus tremula appear spontaneously in nature. The first find was made by NILSSON-EHLE (1936), and thereafter a number of similar occurrences have been found (JOHNSSON 1940). To judge by observations on the spontaneous habitats the triploids represent rapid-growing, robust types (giant aspen). By crossing diploids with triploids, tetrapluid individuals have been obtained (BERGSTRÖM 1940, JOHNSSON 1940). The tetraploids obviously possess slower development and reduced vitality in comparison with the diploids. None the less the tetraploids are of the greatest interest owing to their potential possibility of producing auto- and allopolyploids with different genic constitution, and of mass producing triploid seed. The oldest artificially produced tetraploid tree — a male tree — flowered for the first time in 1944, and was then exploited for crosses with diploids. The fertility of the crosses was good and a number of triploid progenies could be raised. The first discription of these triploid progenies was given by the author (1945). According to this the numbers of chromosomes of the progeny is not fully constant but varies between 2n = 47, and 2n = 59. Within the interval 2n = 54—59 lie, however, 86.9% of the populations, and 46.3% possess the exact triploid number, i. e., 2n = 57. If the corresponding values = 100 be placed for the diploid progenies, the following values are obtained for the different properties investigated in the triploids at the age of 1 year.

Leaf size	156
Leaf thickness	114
Stomata length	126
No. of stomata per unit area	65
Wood cell length	117
Wood cell diameter	120
Plant height	94
Stem diameter	98
Stem volume	82
Osmotic sugar value	98
Transpiration per leaf area	93
Transpiration per g dry matter	111
CO_2-assimilation per leaf area	92
CO_2-assimilation per g dry matter	102
Dry matter content in leaves	91
Wood's specific weight	91
Wood's dry matter content	97
Wood's cellulose content	102
Wood's furfural content	99
Wood's lignin content	99

Especially striking is the fact that the growth of the triploid was lower than that of the diploids during the first year with relative figures 94, 98 and 82 for plant height stem diameter and stem volume, respectively. Dats concerning subsequent quantitative development during the succeeding eight years will be given below.

Material

The triploid and diploid progenies raised in 1944 have been incorporated in different tests, of which, however. only one was intended for a long-term experiment, especially aimed at studying the triploid-diploid relation. This

Tab. 1. The development in the experiment

	Families	Height					Volume 1952		Numbers of individual		Mortality	Thinning	Remaining population	m³ / hectare 1952	
NO.	Parentage	1944	1947	1950	1952 b. t.	1952 a. t.	b. t.	a. t.	b. t.	a. t.	%	%	%	b. t.	a. t.
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
44-5	Möckelsnäs Småland × tetraploid	124	109	111	112	115	136	135	83.3	49.8	16.7	40.2	49.8	22.1	17.6
44-7	Sätra No. 4 Västergötland × „	88	102	98	97	99	101	105	95.8	54.5	4.2	43.1	54.5	18.8	14.9
44-9	Häggeby Uppland × „	102	107	109	110	109	112	112	91.3	55.5	8.7	39.2	55.5	19.9	16.3
44-11	Skeppmora Västmanland X „	86	106	102	104	108	119	124	87.8	51.5	12.2	41.3	51.5	20.4	16.7
44-13	Våle Medelpad X „	93	100	101	100	108	113	131	89.8	47.5	10.2	47.1	47.5	19.8	16.2
Mean triploids		99	105	104	105	108	117	121	89.6	51.8	10.4	42.2	51.8	20.2	16.3
44-8	Sätra No. 4 Västergötland × Sätra No. 1 Västergötland	99	103	100	97	92	86	78	98.0	71.5	2.0	27.0	71.5	16.9	14.5
44-10	Häggeby Uppland × Hamra Östergötland	126	93	100	102	96	82	73	97.8	72.5	2.2	25.8	72.5	15.6	13.7
44-12	Skeppmora Västmanland × Sätra No. 1 Västergötland	82	79	78	78	74	50	44	92.0	71.5	8.0	22.3	71.5	8.9	8.2
Mean diploids		102	92	93	92	87	73	65	95.9	71.8	4.1	25.0	71.8	13.8	12.1
Means		53.2 cm	141 cm	283 cm	403 cm	468 cm	2.81 dm³	3.77 dm³	91.9	59.3	8.0	35.8	59.3	17.8	14.8
Mean errors difference %		—	5.7	5.9	4.9	5.1	13.2	17.7	2.5	8.2	2.5	—	—	—	—

trial was planted out in the spring of 1945 at Mykinge experimental farm, where the Swedish Match Company had kindly placed ground at our disposal. The place of cultivation — in the Jönköping district — is situated on 57° 53' lat., and at 250 m above sea-level. The plantation is located in cultivated fields, consisting of clayish moraine.

Five triploid and three diploid families are included in the test, see Table 1. The three diploid families and three of the triploids were included in the 1945 test material (Johnsson 1945). The families are connected with each other in pairs in the following manner:

Mother:	Sätra No. 4		Häggeby		Skeppmora	
Father:	tetraploid	Sätra No.1	tetraploid	Hamra	tetraploid	Sätra No.1
Family No.	44-7	44-8	44-9	44-10	44-11	44-12

Thus in these cases the triploid and diploid families possess a common origin, in that they have a common mother.

The experiment is designed with randomised blocks according to Fisher with four replicates. Each plot consists of four rows with 25 planted plants per row, i. e., 100 plants per plot. Thus 400 plants per family are included in the experiment, and the total number of plants is 3,200. The spacing is 1.2 × 1.2 m, and the experiment's total area is 0,46 hectares.

The result of the plantation has been very satisfactory with an average mortality of only 8.0% (see Table 1, col. 12). The losses, however, have been fairly dissimilar in different families; highest in the triploid 44-5, with 16.7%, and lowest in diploid 44-8, with only 2%. The variety differences are a significant source of variation with regard to the mortality. The analysis of variance gives:

Sources of variation	*D. F.*	*Sum of squares*	*Mean squares*
Blocks	3	7	
Varieties	7	734	104.9
Errors	21	225	10.7

The quotient of significance varieties/errors is 9.804***. On an average the mortality has been considerably greater in the triploids — 10.4% — than in the diploids — 4.1% —.

Partition of variance for varieties in inter- and intraclass variation gives:

	D. F.	*Sum of squares*	*Mean squares*
Between triploid and diploid families:	1	304	304
Between families with same chromosome number:	6	430	71.7

If the quotients for both these mean squares and the mean squares for errors be formed, there is obtained for the difference between triploids and diploids 28.411***, and for the differences between families with the same number of chromosomes 4.299***. Thus triploidy has been established as occasioning an increased mortality at the same time as significant differences exist within strains with same chromosome numbers.

In Sweden young aspen plants are almost without exception attacked by leaf-destroying fungus diseases, *Melampsora sp.* and *Fusicladium radiosum,* which prove highly injurious to development and growth. Especially the attacks of *Fusicladium* exert a highly retarding influence during the first years, when not only the leaves are destroyed but also the upper parts of the annual shoots. Gradually the attacks of the disease lessen in violence and their influence becomes of less importance. This experimental plantation, like all others, has been strongly infected. During the last few years, however, the attacks have been comparatively weak. Slight attacks of aspen wood borers (*Saperda populnea*) have also occurred. In the autumn of 1952 the plantation had a mean height of 4.03 m. The mean height of the best family was 4.50 m, the highest plot mean 5.27 m, and the tallest tree 8.10 m. The plantation was almost entirely closed (Fig. 1), and it was considered that the first thinning could be suitably undertaken in the autumn of 1952. All suppressed trees were removed as well as those considered likely to be suppressed in the following three years (the thinning interval is calculated to be three years). In the tables *b. t.* indicates the situation before thinning, and *a. t.* after thinning.

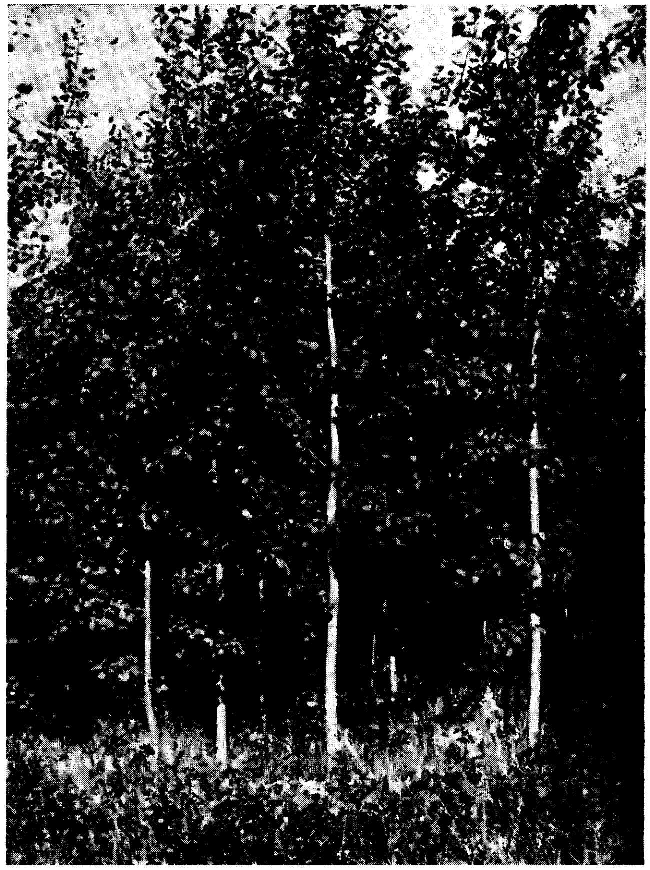

Fig. 1. From the experimental plantation before thinning, autumn 1952.

The relations in mean height between triploids and diploids have developed in the following manner (Table 1, columns 3—6):

	1944	1947	1950	1952
triploids	99	105	104	105
diploids	102	92	93	92

Thus the mean height of the triploids before the 1952 thinning was 11.4% greater than that of the diploids. Thinning increased the divergence to 108:87, i. e., the mean height of the triploids is 24.1% greater than that of the diploids after thinning (Table 1, col. 7). As the triploids are also somewhat thicker than the diploids, their stem volume is greatly superior. Before thinning the relation stood at 117:73 (col. 8), which means that the stem volume in the triploids was 60.3% greater than in the diploids.

Tab. 2. Partition of variance for varieties 1952

Source of variation	D. F.	Sum squares				Mean squares				M. S. / M. S. error			
		Height		Volume		Height		Volume		Height		Volume	
		b. t.	a. t.	b. t.	a. t.	b. t.	a. t.	b. t.	a. t.	b. t.	a. t.	b. t.	a. t.
Varieties:	7	49.076	103.102	15.5537	41.4594	7.011	14.729	2.2220	5.9228	8.709***	13.023***	7.973***	6.841***
Between 3x and 2x	1	17.702	67.379	10.7551	33.9788	17.702	67.379	10.7551	33.9788	21.990***	59.575***	38.590***	39.246***
Within strains	6	31.374	35.723	4.7987	7.4807	5.229	5.954	0.7998	1.2468	6.496***	5.264**	2.870*	1.440
Error	21	16.899	23.745	5.8532	18.1818	805	1.131	0.2787	0.8658				

Thinning widened the rift to 121:65 (col. 9). Consequently after thinning the stem volume in the triploids is 86.2% greater than in the diploids.

In Table 2 a partition has been made of the variety variance for height and stem volume before and after the 1952 thinning. The quotients of significance give an entirely convincing proof of the superiority of the triploids both as regards height and stem volume. Furthermore, occurrences of significant differences in height between families with the same chromosome number were verified but not as regards stem volume. The production, calculated in m^3 per hectare (Table 1, col. 15) has been on an average 20.2 m^3 for the triploids, and 17.8 m^3 for the diploids. After thinning there remains 16.3 m^3 for the triploids, and 14.8 m^3 for the diploids (col. 16).

The number of trees on an average per plot before and after thinning is reported in Table 1, columns 10 and 11, and in column 13 the thinning intensity is calculated in per cent of the number of stems. These data at once show that the thinning intervention in the triploid plots has been more intense, with 42.2% trees removed, than in the diploid plots, where the thinning intensity does not amount to more than 25.0%. As mentioned above the thinning was carried out so that all suppressed trees were removed as well as trees considered as going to be suppressed within the following three years. Thus it is quite clear that the rate of suppressed and half suppressed trees was higher for the triploids than for the diploids. In other words, the absolute variation was greater for the triploid progeny. In order to examine more closely the differences in variability, the relative plant height and stem volume within the plots were given a variational analytical treatment. The measurement of the arbitrary variate, v, has thus been expressed with its plot mean, M_p as unit. The variate's measurement thus becomes $= \frac{v}{M_p}$. The difference, δ, becomes $\delta = (\frac{v}{M_p} - 1)$. The sum of squares of the differences within a plot becomes $\Sigma\ \delta^2 = (\frac{\Sigma\ v^2}{M_p{}^2} - n_p)$, which expression is easily worked out with simple calculating machines (n_p = number of individuals within the plot). In Table 3 the results are given of this analysis of variance for the relative height. The standard deviation (S. D.) for the entire triploid material before thinning was 0.345, compared with 0.260 for the diploid material, thus demonstrating an essentially greater variability for the triploids. Thinning considerably reduced the relative variability — to 0.216 for the triploids and 0.183 for the diploids. Furthermore, thinning reduced the differences in variability between triploids and diploids from 1.33:1 to 1.18:1.

Tab. 3. The variance within plots for relative height

Family	Number of plants		D. F.		Sum squares		Mean squares		S. D.	
	b. t.	a. t.	b. t.	a. t.	b. t.	a. t.	b. t.	a. t.	b. t.	a. t.
Triploids										
44-5	345	198	341	194	49.2709	10.0261	0.1445	0.0517	0.380	0.227
44-7	390	218	386	214	38.5506	7.9114	0.0999	0.0370	0.316	0.192
44-9	375	223	371	219	36.9638	11.1368	0.0996	0.0509	0.316	0.226
44-11	362	207	358	203	45.0777	9.7643	0.1259	0.0481	0.355	0.219
44-13	367	190	363	186	45.9658	8.4073	0.1266	0.0452	0.356	0.213
Sum 3x	1839	1036	1819	1016	215.8288	47.2459	0.1187	0.0465	0.345	0.216
Diploids										
44-8	395	286	391	282	23.4287	7.6317	0.0599	0.0271	0.245	0.165
44-10	393	289	389	285	26.2279	9.7839	0.0674	0.0343	0.260	0.185
44-12	376	286	372	281	28.3366	10.9699	0.0762	0.0388	0.276	0.197
Sum 2x	1164	861	1152	848	77.9932	28.3855	0.0677	0.0334	0.260	0.183

Tab. 4. The variance within plots for relative volume

Family	Number of plants		D. F.		Sum squares		Mean squares		S. D.	
	b. t.	a. t.	b. t.	a. t.	b. t.	a. t.	b. t.	a. t.	b. t.	a. t.
Triploids										
44-5	333	199	329	195	195.9184	63.1037	0.5955	0.3236	0.772	0.569
44-7	383	218	379	214	214.0580	63.9899	0.5648	0.2990	0.752	0.547
44-9	365	222	361	218	257.1849	83.7238	0.7124	0.3841	0.844	0.620
44-11	351	206	347	202	258.5848	80.8512	0.7452	0.4003	0.863	0.633
44-13	359	190	355	186	259.6012	67.1636	0.7313	0.3611	0.855	0.601
Sum 3x	1791	1035	1771	1015	1185.3473	358.8322	0.6693	0.3535	0.818	0.595
Diploids										
44-8	392	286	388	282	152.7942	74.0800	0.3938	0.2627	0.626	0.513
44-10	391	290	387	286	183.4680	91.7103	0.4741	0.3207	0.689	0.566
44-12	368	286	364	282	154.6719	81.5942	0.4249	0.2829	0.652	0.538
Sum 2x	1151	862	1139	850	490.9341	247.3845	0.4310	0.2910	0.657	0.539

Corresponding data for the stem volume are found in Table 4. Before thinning, S. D. is this time for the triploids 0.818, and for the diploids 0.657, which gives the relation 1.25:1. Also after thinning the triploids are characterized by a higher variability, S. D. being 0.595 against 0.539. The relation, however, has, dimished to 1.10:1. If the S. D. values for relative height and relative volume are compared, the greater variability of the volume is clearly seen.

If the quotients of significance mean squares triploids/mean squares diploids are calculated, the following is obtained:

Height before thinning	1.753***
Height after thinning	1.392***
Volume before thinning	1.553***
Volume after thinning	1.215***

The 0.1% point is approximately 1.2 with the existing large number of degrees of freedom.

Discussion

The experiment here described has clearly demonstrated that the triploid families possess a larger variability than the diploids. This relation is probably due to the variation in chromosome number, which undoubtedly exists in the triploid populations and which is caused by the meiotic instability in the tetraploid parent. On being planted out in the field the triploid varieties contain aberrant aneuploids, of which a good number suffer from reduced vitality and entail a higher mortality in the triploids than in the diploids. In the course of subsequent development a greater differentiation arises in the triploids, since even after loss in connection with planting out there still remain some slow-growing individuals. In spite of this disadvantage the triploid families possess a more rapid average growth than the diploids. At the first thinning it is overwhelmingly minusvariants that fall, and the average increase in relation to that of the diploids. As the differentiation is greater for triploids than for diploids the first thinning is more intense for the former than for the latter. In the experiment there remained after the first thinning 51.8% on an average of the triploid families' original populations against 71.8% for the diploids. In spite of the lower number of stems per hectare (3,597 against 4,986), the remaining volume after thinning is 10.1% higher for the triploids, and the production per unit area up to 9 years of age has been 13.5% higher. If the diploid plots are thinned down to the same number of individuals as the triploid plots (which silviculturally would be incorrect), the difference in volume would of course be still more to the advantage of the triploids.

It should be observed that the mean of the triploids, already before thinning, lay considerably higher than that for the diploids, 14.1% in height and 60.3% in volume, which differences were increased by thinning to 24.1% and 86.1%, respectively. A selective thinning down of the diploid plots to the stem number of the triploids would of course reduce the differences somewhat, but would nowhere near restore the relations obtaining before thinning owing to the smaller differentiation in the diploids. To judge by the development up till now the relations in the future will be still more shifted to the advantage of the triploids, and there is reason to suppose that there will be a not unimportant increase in production per unit area during the rotation period for triploids. How great the increase in production can eventually be is scarcely possible to predict until a number of years have elapsed.

In very many cases it has been asserted that triploids possess a lower content of dry matter than their diploid forms of origin, and there has been talk of „waterbreeding". A tendency in this direction also appeared in this aspen material, in any case at the one-year stage. It may, therefore, be conceivable that a comparision based on the production of wood matter would not result in such a great difference between triploids and diploids as that existing in the volume of timber produced. As, however, aspen timber is especially used for mechanical purposes, the production of wood matter is of less immediate interest. The mechanical properties of the timber, however, claim primary attention. Unfortunately, the test material is still too undeveloped for wood-technical investigation.

A problem worthy of attention is to what degree the results obtained in this special experiment can be generalized. It is, of course, not only the number of chromosomes that separates the triploid and diploid families, but also their genic constitution. It is practically impossible to produce a triploid population with the same genic constitution as a diploid of a dioecious organism. The nearest approach that can be made in that respect is to raise the triploid by crossing a C_0-individual with a diploid sibling individual and to raise the diploid progeny of comparision by crossing the diploid parent of the triploid family and another diploid sibling plant. In the material that has been treated there does not even approximately exist such a close connection between triploids and diploids. Mating between sisters and brothers in the manner mentioned can, moreover, be thought to complicate the relations by the effect of inbreeding. In the experiment, however, there are three pairs of progenies so related that they have a common mother. It is of extreme importance, as regards the aspen in these northerly latitudes, that the parent material should possess about the same geographical origin. In *P. tremula* there exists a marked clinal differentiation, which is expressed in an increasingly retarded growth the more northerly the material of origin be in relation to the place of cultivation (Sylvén 1940). If the diploid parents are considered it cannot be said that the triploid progeny are favoured. The northernmost parent is, on the contrary, found as mother of the triploid family 44-13. The tetraploid father, however, is to a certain degree southern. The latter has been obtained by crossing Sätra no. 4 with the triploid, Bosjökloster, Skåne (Skåne is Sweden's southernmost province, and the Bosjökloster location lies exactly two degrees of latitude more to the south than the Mykinge experimental farm). Thus the tetraploid, from a geographical viewpoint, possesses a constitution of (1 genome Sätra no. 4 + 3 Bosjökloster genomes). Consequently, the triploids must have 19—38 southern Bosjökloster chromosomes, mostly around 29. It should, therefore, be remembered that the triploid families can be somewhat favoured by the origin of the tetraploid father. This influence, however, cannot be considered great, as it is only a question of difference of a few degrees of latitude. To be absolutely conclusive, the test should have embraced a larger number of both triploid as well as diploid families with different origin, and, as regards pairs, as similar as possible. It has, however, not yet been possible to arrange experiments of such multiple character. For the moment we must content ourselves with the existing data. In any case it should be possible to maintain that these data permit of a strong tendency in favour of the triploids.

Consequently, the triploids, as far as one can see, entail an increase of production in *Populus tremula.* Apart from this, it is quite possible that triploid aspen will not acquire any great silvicultural significance, seeing that a number of species hybrids — especially *P. tremuloides*×*tremula* — would appear to offer a far superior material for cultivation (Johnsson 1953). Triploidy can, however, be also exploited in species hybridisation, which has occurred with good results precisely as regards the hybrid mentioned, from which triploid families have been raised (Johnsson 1953). Data also exist for other tree species that point to a growth-increasing influence on the part of triploidy — especially in *Alnus glutinosa* (Johnsson 1950). In agriculture the first artificially produced tetraploid varieties have begun to be exploited in commercial cultivation. Even if we cannot attain through polyploidization such powerful effects as, for instance, through species hybridization, yet we have every reason to pay attention to the potential possibilities of polyploidy in silvicultural plantbreeding, and we are fully justified in making a thorough investigation of the properties and value of polyploid forest tree strains.

Summary

A survey is given of the development of a 9-year old experiment in triploid and diploid populations of *Populus tremula.* The test comprises 5 triploid and 3 diploid families. Their origin and development are summarized in Table 1. The triploid families have a greater growth in height and volume than the diploids. Significances for triploid-diploid comparisions are given in Table 2. The variation is greater in the triploid than in the diploid families both as regards height (Tab. 3) and volume (Tab. 4). The greater variation in the triploid families is considered mainly to depend on the occurrence of individuals with somewhat deviating chromosome numbers, viz., aneuploids. The results are considered as an encouragement to continue investigating the properties of polyploid forest tree.

Zusammenfassung

Die Entwicklung eines neun Jahre alten Versuches mit triploiden und diploiden Populationen von *Populus tremula* wird beschrieben. Der Versuch besteht aus 5 triploiden und 3 diploiden Familien. Ihre Herkunft und Entwicklung sind in Tabelle 1 zusammengefaßt. Die triploiden Familien haben größeren Höhen- und Volumzuwachs als die diploiden. Die Signifikanzen zum Vergleich Triploidie-Diploidie sind in Tabelle 2 angegeben. Die Variation der Höhe (Tab. 3) und des Volumens (Tab. 4) ist größer in den triploiden als in den diploiden Familien. Die größere Variation der triploiden Familien ist durch das Vorkommen von Individuen mit etwas abweichender Chromosomenzahl — Aneuploiden — erklärt. Das Resultat wird für weitere Untersuchungen der Eigenschaften triploider Forstpflanzen als anregend bezeichnet.

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Über anomale Zwitterblüten eines Klones der Gattung Populus, Sektion Leuce

Von F. W. Seitz

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Die Arten der Familie der *Salicaceae* sind normalerweise zweihäusig (diözisch). Ihre Individuen tragen Kätzchen, die sich alle aus eingeschlechtigen Blüten zusammensetzen. Gemeinhin wird deshalb in der Praxis des Pappel- und Weidenbaus von männlichen Bäumen und weiblichen Bäumen gesprochen. Es widerspricht allerdings nomenklatorischen Gepflogenheiten, wenn in früheren Jahren vegetativ vermehrbaren eingeschlechtigen Individuen euroamerikanischer Schwarzpappelbastarde und aus ihnen gezogenen Klonkollektiven botanische Namen von Artcharakter verliehen worden sind, die heute noch vielfach gebraucht werden (Beispiel: *Populus serotina* nur ♂; *Populus marilandica* nur ♀ u. a.). Die individuelle Unterscheidbarkeit des Habitus solcher Klon-Angehöriger verschiedener Geschlechter allein berechtigt dazu nicht.

Sowohl innerhalb der Gattung *Populus* wie auch in der Gattung *Salix* sind von der Norm der Diözie Ausnahmefälle im Laufe der Zeit bekanntgeworden. Dabei handelt es sich um Individuen, in deren Blüten eine mehr oder weniger vollständige Ausprägung beider Geschlechter in Erscheinung trat. Wir haben bereits früher entsprechende Literaturbeispiele zitiert (Seitz 1952, vgl. desgl. Runquist 1951, Rainio 1927). Ein weiterer Ausnahmefall (ein 4½ m hoher Baum im Ann-Arboretum, Michigan, USA) bei *Populus tremuloides* wird von Erlanson and Hermann (1927) diskutiert.

Aus allen derartigen Beobachtungen innerhalb der Gattung *Populus* wird meist geschlossen, daß in solchen Fällen die Norm der Diözie durchbrochen und jeweils in wechselnder Anzahl innerhalb der Kätzchen neben eingeschlechtigen auch „vollkommene" Zwitterblüten entwikkelt worden sind. Die erste Charakterisierung des von uns selbst aufgefundenen zwittrigen aspenähnlichen Wurzelbrutklones bei Dillingen an der Donau gründete sich auf ähnlichen Feststellungen. Wir beschrieben damals auch die speziellen morphologischen Eigentümlichkeiten der