THE DUTCH ELM DISEASE

Summary of fifteen years hybridisation and selection work (1937–1952) [1][2]

Met een samenvatting: De iepenziekte; 15 jaar iepenselectie

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1. *Introduction*

In 1938 an account was published of the work on selection of elms resistant to the Dutch elm disease (Went, 1938). The present publication, dealing with hybridisation and selection during the period 1937–1952, is a continuation of the earlier paper.

Between 1928 and 1938 a collection was formed from various countries, consisting not only of grafts of different species, varieties and forms, but also of about 10.000 seedlings. They were tested for their susceptibility to *Ophiostoma ulmi* (Buisman) Nannf., the fungus causing the Dutch elm disease.

In 1937 hybridisation was started, in order to combine factors for desirable growthform with those for resistance. This work was carried out at the Institute of Genetics at Wageningen, under the supervision of the late Professor Honing (1942 and 1943). Krijthe (1938–1941) did important work at the start; in 1941 Bakker took it over, followed by Haspers (1944 and 1946) from 1942–1944. In the meantime the selection work was continued in the laboratory „Willie Commelin Scholten" at Baarn by the author (Went 1939–1944) under the direct supervision of Professor Westerdijk. From 1945 on the author also took over the work on hybridisation (Went 1946–1952), which was moved to Baarn.

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(Comité ter Bestudering en Bestrijding van ziekten in Iepen en andere Boomsoorten), which was incorporated in 1946 in the Institute for Biological Field Research (I.T.B.O.N.) of the Central National Council for Applied Scientific Research in the Netherlands (T.N.O.).

2. *Spread of the Dutch elm disease in the Netherlands*

From 1930 until 1944 the State Forest Service (Staatsbosbeheer) kept a count of elms in the Netherlands which had to be felled because they were badly diseased or dying (table 1), (BURGER, 1938; VAN STEYN, 1940–1946).

TABLE 1. Decrease of the number of elms in the Netherlands from 1930–1946. (*Afname van het aantal iepen in Nederland gedurende de jaren 1939 t/m 1946*)

Year (*Jaar*)	Total number of elms in the Netherlands (*Totaal aantal iepen*)	Elms felled because of Dutch elm disease (*Iepen gerooid i.v.m. de iepenziekte*)	% felled because of Dutch elm disease (*Percentage gerooid i.v.m. iepenziekte*)	Estimated number of trees felled for other reasons *Schatting van het aantal iepen gerooid om andere redenen*)
1930	1.228.000	11.000	0.9	15.000
1931	1.202.000	26.000	2.2	15.000
1932	1.161.000	24.000	2.1	10.000
1933	1.127.000	70.000	6.2	15.000
1934	1.042.000	33.000	3.2	15.000
1935	994.000	44.000	4.4	20.000
1936	930.000	38.000	4.1	15.000
1937	877.000	30.000	3.4	15.000
1938	832.000	22.000	2.6	15.000
1939	795.000	23.000	2.9	15.000
1940	757.000	40.000	5.3	50.000
1941	667.000	26.000	3.9	45.000
1942	596.000	19.000	3.2	25.000
1943	552.000	15.000	2.7	37.000
1944	500.000			45.000 [1])
1945	455.000			30.000 [1])
1946	425.000			

[1]) From 1944 onwards the Forest Service ceased to register diseased elms. The numbers are the total of elms cut down for all reasons.

Table 1 shows that the number of elms in the Netherlands decreased from 1.228.000 in 1930 to 425.000 in 1946. This means that two thirds of the elms in the Netherlands were cut down in a period of 16 years. The percentages of elms felled show that the disease did not decrease. Thus one can anticipate that all the elms will eventually disappear from our country.

Not only was the total number of elms removed counted but also, seperately, the number of trees felled on different soil types. For the province of Groningen it was shown, that 7.7 % of 39.913 elms on clay soil were felled between 1932 and 1937; on peat soil and sandy soil the numbers were, respectively, 34.0 % of 6525 elms, and 37.2 % of 9939. Everywhere in the country the elms on sandy soil have almost disappeared.

In the clay areas beautiful stands of elms survived. Many of these trees, however, were destroyed during the second world war. On the peat soil in Friesland and along the canals of Amsterdam a great many of the elms are still in good condition. An explanation of these facts may probably be found in the beneficial effect of a high water table and the quick wilting of elms attacked by the Dutch elm disease on soils which dry out easily.

As almost all the elms planted along the roads and canals in the Netherlands belong to the same susceptible variety, *U. hollandica belgica*, it is obvious that the disease will spread rapidly. Only along the coast in the sand dunes are other varieties of elms found. Here the elms including *U. hollandica belgica* are less diseased, because along our coast a strong westerly wind prevails, which protects the elms from attack by the elm bark beetle, the vector of the disease.

In the lower lying parts of our country, the polder, where only few tree species will grow well, the elm is one of the most important trees. This explains why it is necessary to find a substitute for the very susceptible Dutch elm.

3. *Methods*

a. *Hybridisation*

In 1937, when hybridisation was started, nothing was known about the susceptibility of elm hybrids. For that reason all available species, varieties and forms were, as far as possible used as parents. The height of some of the trees and non-flowering condition in others, were restrictions on the varieties used.

Pollination is performed after emasculation of the elmflowers, which grow in clusters. The flowers do not ripen simultaneously. Depending on the weather, it takes from several days to two weeks to finish the emasculation of one cluster. Paperbags, enclosing the clusters, have to be opened anew every day, which may give an undesired opportunity for wind fertilization. To counterbalance this possibility, all emasculated flowers are fertilized with an excess of pollen, every time the bags are opened.

Emasculation takes a long time. Before continuing this time-absorbing method, the question had to be answered, whether self-pollination would occur under natural conditions and if so, to what extent, it resulted in fertile seeds. It turned out that after self-pollination fertility of the seeds could range from 0–100 %. Big differences in percentages of fertility occurred among different hybrids in the same year, as well as among the seeds of one variety in different years. Table 2 gives the results of selfpollination of trees which produced more than 10 % fertile seeds. During the periods 1938–1941 and 1945–1952, flowers of 189 trees were self-pollinated. From these trees 23 or about 12 % gave more than 10 % fertile seeds.

The conclusion can be drawn, that emasculation is neccessary if we are to be sure of the identity of the parents of the fertile seeds.

LELIVELD (1935) studied the development of the embryosac of the Dutch elm. Her conclusion was that the abnormality she found in the development of the embryos of the greater part of the seeds was due to the impossibility of fertilization by pollen of the same type and the incompatibility of pollen produced by other types of *Ulmus*. The impossibility of fertilization by pollen of the same type was due to the shedding of all the pollen at the same time and the non-simultaneous ripening of the pollen and the embryosac.

LELIVELD's conclusions would probably have been different, if she had studied seeds developing in paperbags. Under these conditions fertilization can take place. In nature in Holland the flowers are mostly damaged by frost and for this reason no seeds develop. Only in years with exceptionally favourable

TABLE 2. Seeds obtained after self-pollination. Results of the twenty-three trees which produced more than 10% fertile seeds.[1]) (*Zaden ontstaan na zelfbestuiving*)

Selfpollinated elm-species and varieties (*Iepensoorten en variëteiten*)	Number of years during which the trees were selfed (*Aantal jaren waarin de zelfbestuiving plaats vond*)	Year of hybridisation (*Jaar van kruising*)	Number of seeds (*Aantal zaden*)	Fertile seeds (*fertiele zaden*)	
				Number (*Aantal*)	%
Wallichiana	5	1939	112	12	10.7
Wallichiana	5	1952	824	256	31.1
laciniata	3	1938	128	50	39.1
242 (Wallich. × glabra pend.)	3	1947	370	72	19.4
242 (Wallich. × glabra pend.)	3	1949	69	10	14.5
hollandica vegeta	8	1938	141	27	19.1
148 (holl. veg. × carp. nr 28)	2	1952	202	33	16.3
125 (holl. veg. × carp. nr 1)	3	1952	191	20	10.5
glabra fastigiata	1	1941	335	52	15.5
glabra nr 49	9	1940	46	6	13.1
6.2 (glabra nr 49 × carp. nr 1)	6	1950	316	32	10.1
carpinifolia nr 1	11	1938	92	11	11.9
carpinifolia nr 1	11	1945	5	5	100
carpinifolia nr 1	11	1947	160	20	12.5
carpinifolia nr 1	11	1952	27	4	14.8
carp. Christine Buisman	5	1945	11	11	100
carpinifolia nr 43	2	1945	12	11	91.8
carpinifolia nr 43	2	1946	3	2	66.6
263 (glabra nr 49 × carp. nr 1)	1	1948	584	135	23.3
240 (gl. fast. × Wallichiana)	1	1950	582	114	19.6
L 10.10 (carp. nr 53 × holl. veg.)	1	1950	847	272	32.2
O.W. 5 (holl. veg. × carp. Damp.)	1	1948	5	1	20.0
hollandica Fjerrestad	2	1938	411	48	11.7

[1]) During 1942, 1943 and 1944 no counts of sterile seeds were made. More than 10% fertile seeds obtained by self-pollination were found four times in 1938 and 1952; three times in 1945 and 1950; twice in 1947 and 1948; once in 1939, 1940, 1941, 1946 and 1949, and not at all in 1951.

weather conditions, will seeds ripen in abundance in nature; this was the case in 1942. In more southern regions, such as France, many viable seeds develop.

The pollen is normally collected from cut branches placed in the laboratory. Nearly all attempts to germinate the pollen in vitro failed. For that purpose, the following solutions were used: 2.5 %–10 % mannite; 0.5 %–0.005 % boric acid; 0.1 %–0.001 % ascorbic acid and 0.5 %–0.25 % dextran or combinations of these chemicals. The chemicals were dissolved either in distilled water or in purified agar. The best results were obtained when the pollen was not in contact with agar or water. As the pollen germinated only in a few cases and without consistancy, no conclusions could be drawn about its viability and its ability to fertilize. Neither was triphenyltetrazoliumchloride (used to differentiate between living and dead tissues of seeds) of any use. All the pollen-grains, even those which had been boiled, turned red.

Save for some elm species flowering in autumn (e.g. *U. crassifolia*, *U. parvifolia* and *U. Sieboldiana*), all other species, which flower in spring, can be used for hybridizing. When the weather is favourable the earliest species will flower at the beginning of February, the latest at the beginning of April. If there is a late freezing period these dates may be delayed in such a way that early and late trees start flowering at the same time.

In most years free-pollinated trees will not produce fertile seed. Only in years with favourable weather (no frost just before, during or after the flowering period) will fruits ripen on these trees. In the paperbags, however, the flowers are somewhat protected and only severe frost, or freezing just before the flowers open, will interfere with seed development.

If the paperbags are removed during the process of ripening the seeds will be eaten by birds. Therefore, either the paperbags must be left to protect the seeds, or they must be replaced by bags of cheesecloth to increase the aeration of the fruits.

TABLE 3. Percentage fertile and germinated seeds from the same trees used either as male- or as female parents. (*Percentage fertiele en gekiemde zaden, wanneer dezelfde boom als vader- dan wel als moederboom werd gebruikt*)

Used tree (*Gebruikte boom*)	Year (*Jaar*)	Female parent (*Moederboom*)			Male parent (*Vaderboom*)		
		total seeds (*aantal zaden*)	% fertile	% germinated (*% gekiemd*)	total seeds (*aantal zaden*)	% fertile	% germinated (*% gekiemd*)
U. carpinifolia nr 1 .	1938	1019	23.7	87.5	3298	41.5	56.7
,,	1939	238	2.1	80.0	1487	37.1	43.3
,,	1940	81	17.3	78.5	1768	56.1	54.4
,,	1941	142	4.2	83.3	904	31.7	70.3
,,	1945				158	67.1	74.5
,,	1946	84	8.3	14.3	1123	42.8	21.2
,,	1947	27	40.7	0	984	51.3	29.3
,,	1948	100	40.0	57.5	181	60.8	28.2
,,	1949	70	31.4	68.2	423	36.2	19.6
,,	1950	403	62.8	75.0	2369	43.5	45.5
,,	1951	733	7.6	75.0	2337	15.1	38.4
,,	1952	453	13.4	78.7	2075	35.5	62.9
Total	1938/1952	3350	21.3	67.8	17107	39.0	47.8
U.carp. Chr. Buisman	1945	174	96.0	67.7			
,,	1946	103	87.4	42.2	419	40.8	11.7
,,	1947	201	52.7	36.5	488	51.6	24.6
,,	1948	3	100	0	205	36.6	33.3
,,	1949				163	14.1	65.2
,,	1950	42	100	59.0	323	42.4	41.6
,,	1951	132	40.0	46.5	332	26.8	39.3
,,	1952	135	97.0	77.1	1013	58.5	65.0
Total	1945/1952	790	68.3	62.9	2943	45.5	44.8

To avoid the freezing of the flowers, emasculation and pollination was, at one time, performed on detached branches in the greenhouse. As the results were poor, this method was abandoned after 1944.

Some trees gave more fertile seeds if used as female than as male parents, e.g. *U. carpinifolia* CHRISTINE BUISMAN; with others the reverse was the case e.g. *U. carpinifolia* nr 1 (table 3). As the percentage of fertile seeds varied greatly statistical methods were used to compare these counts.[1]) The behaviour of *U. carpinifolia* nr 1 may be explained by the damage done to the flowers during the emasculation. As soon as the filaments start to elongate the anthers open and therefore the stamens have to be removed before they protrude from the flowers. At this early stage emasculation may easily damage the pistil, which will not then develop.

b. *Sowing and planting*

The seeds of elm ripen during the second half of May. They are sown singly at regular distances in square flats of porous clay filled with sieved leafmold. Germination may vary from 0% to 100%, but in many years the average was around 35%. Ungerminated seeds, left in the soil, may germinate after one and even after two years. The best results are obtained if the seed was collected and sown immediately after counting. As BARTON (1939) improved the germination percentage greatly by soaking the seed, this method was tried with seeds of different elm species (WENT 1950; 1951), but as many good results as bad were obtained. That the full seeds were in fact viable was shown by germination tests. On wet filterpaper about 95% of the seeds germinated. If these germinated seeds were planted, many were lost. It was considered therefore, that this method was no improvement on direct sowing in soil.

Elm seeds sown in the greenhouse have to be kept extremely wet. Germination may take place gradually during the summer, but most seeds germinate one week after sowing. Temperatures are kept at an average of 28 °C during the day and at 19 °C during the night. When the seedlings have developed about four leaves the seed pans are put in the open. Between the middle of July and the middle of August the seedlings are planted out in open ground. In the autumn of the next year they are transplanted to their final site, at a spacing of one metre by one metre.

Many plants are lost in the open ground. This may be due to insects, damping off fungi, or frost. The first two factors are eliminated, as far as possible, but the last factor is considered a help in selection. Though usually only a proportion of the seedlings is lost, once all 64 seedlings of the hybrid *U. pumila pinnato ramosa* × *U. hollandica superba* and all 4 seedlings of the hybrid *U. pumila* × *U. hollandica superba* were killed by frost during the first three winters, before they had been inoculated.

If the seeds are sown in the open, more seedlings are lost during the first year, than if they are sown in the greenhouse and slowly hardened off.

c. *Inoculation and selection*

The method of testing the elms against *Ophiostoma ulmi* has not been changed since Dr CHRISTINE BUISMAN started these investigations in 1928. The stem of the young tree is inoculated with a spore suspension of the fungus, using a hypodermic syringe with a short needle. For older trees lateral branches are used as the needle of the syringe gets clogged with bits of the thicker bark of the main stem.

[1]) Different methods i.e. the tests of „STUDENT" or WILCOXON, as well as the sign test of FISHER, showed that there was a real difference between the percentages of the male- and female parents.

Each year between May 15 and July 15 every seedling is inoculated twice. If the tree remains healthy for five successive years, grafts are made which are inoculated again for five successive years, together with the original seedling. If, in this way, enough inoculated grafts remain healthy and show a satisfactory growth type, the trees are distributed to nurserymen.

It was found that if inoculation followed transplanting or grafting, the tree did not become diseased. As it was necessary, for practical reasons, to transplant seedlings twice during the first three years, they were only inoculated for the first time in their fourth year. This means that a tree is at least 15 years old, before one can be sure about its resistance.

In one elm variety the susceptibility of grafts was compared with that of layers. As no difference was found between grafts, consisting of different stock and scion, and layers, the possible influence of the stock on the scion was in future neglected.

4. *Results*

a. *Hybridisation*

During the past 15 years 1397 crosses have been made, of which 874 had a different combination of parents.[1])

The elms used for hybridisation are:

Asiatic species

U. pumila L.,
,, *pinnato ramosa* HENRY,
,, *arborea* LITV.,
U. laciniata MAYR,
,, *nikkoensis* REHD.,
U. Wallichiana PLANCH,
U. japonica SARG.,
U. Wilsoniana SCHNEID.

American species

U. americana L.,
,, *pendula* AIT.,
U. fulva MICHX.

European species

U. carpinifolia GLEDITSCH nrs. 1, 16, 24 (CHRISTINE BUISMAN), 28, 31, 40, 42, 43, 53, 61, 62 (BEA SCHWARZ), 134,
,, *Dampieri* (WESM.) REHD.,
,, *Haarlemensis* HORT.
,, *Horsholmii* (HORT.) MELVILLE,
,, *Koopmannii* HORT.
,, *suberosa* (MOENCH) REHD. pendula HORT.,
,, *Wentworthii* HORT.
,, *Wredei* (JUEHLKE) REHD.,

[1]) It is not possible to give a list of all the combinations used here. A duplicated list of all the data is available on request.

U. glabra Huds.	nrs. 49, 50,
,,	*aurea* Hort.,
,,	*camperdownii* (Hervey) Rehd.,
,,	*cornuta* (David) Rehd.,
,,	*crispa* (Loud.) Rehd.,
,,	*Escaillardii* Hort.,
,,	*exoniensis* (K. Koch) Rehd.,
,,	*major* Hort.,
,,	*microphylla* Hort.,
,,	*nigricans* Hort.,
,,	*pendula* (Loud.) Rehd.,
,,	*suberosa alata* Hort.,
,,	*tricuspis* Hort.
U. hollandica Mill.,	*belgica* (Burgsd.) Rehd.,
,,	*Dauvessei* (Henry) Rehd.,
,,	*Fjerrestad* Hort.,
,,	*gigantea* Hort.,
,,	*macrophylla* Hort.,
,,	*Pitteursii* (Kirchn.) Rehd.,
,,	*superba* (Henry) Rehd.,
,,	*vegeta* (Loud.) Rehd.
U. laevis Pall.,	*celtidea* Hort.
U. procera Salisb.,	*betulaefolia* Hort.,
,,	*purpurea* (Kirchn.) Rehd.,
U. stricta Lindl.	*sarniensis* (Loud.) Moss.

In 1945 the first hybrids started to flower and from then on these hybrids have also been used as male- or female parent.

If one of these parents has very strongly developed characters, some of the offspring will show these characters too, but mostly the parentplants are extremely heterozygotic and the differences in character between the seedlings are too small to be distinguished. Often big groups of seedlings of the same parent may show a special character.

Among the European elms used for hybridising, *U. glabra* can easily be recognized by the form of the leaf which has its broadest part above the middle. This character is often found in its hybrids too. If *U. glabra* is hybridized with *U. carpinifolia* many intermediate forms may turn up, but also the real *glabra* type.

In the Netherlands *U. hollandica belgica* was the elm most frequently planted. This form, as were all the other *hollandica*-types, was supposed to be a hybrid between *U. glabra* and *U. carpinifolia*. Table 4 gives the results of the hybridisation of the *glabra*-, *hollandica*- and *carpinifolia* types with each other and among themselves.

TABLE 4. Occurrence of *glabra* forms when *U. glabra, U. hollandica, U. carpinifolia* and their varieties were hybridized over the period 1938 to 1952. (*Optreden van glabra vormen wanneer U. glabra, U. hollandica en U. carpinifolia als ouderplanten bij het kruisingswerk werden gebruikt*)

Female parent (*Moederboom*)	Pollination with forms of (*bestuiving met*)					
	glabra		hollandica		carpinifolia	
	number of seedlings (*aantal zaailingen*)	% glabra type	number of seedlings (*aantal zaailingen*)	% glabra type	number of seedlings (*aantal zaailingen*)	% glabra type
glabra	3	100			19	42.2
glabra pendula	28	71.4	20	70.0	47	6.4
glabra suberosa alata . . .	9	66.6	126	54.8	57	4.7
glabra major	3	33.3	36	41.7	29	6.9
glabra exoniensis	65	32.3	51	3.9	171	5.3
272(gl. microph. × carp. nr 1)	41	7.3	7	0	31	0
glabra 49	256	0.8	116	0	416	0
242(Wallichiana × gl. pend.)	1	0	25	0	103	0.9
glabra aurea					2	0
glabra microphylla					50	0
hollandica Fjerrestad . . .			67	37.3	29	20.7
hollandica Dauvessei . . .	44	43.2	17	23.5	18	5.5
hollandica vegeta	67	16.4	142	2.8	655	0.3
hollandica belgica	180	15.5	405	1.5	744	0
hollandica Pitteursii . . .			16	0	31	0
hollandica major			1	0		

The first column of table 4 gives the forms used as female parent. Different types of pollen parents are grouped under the heads *U. glabra, U. hollandica* and *U. carpinifolia*. If all the *glabra* forms were true to type, they should produce 100 % *glabra*-type plants if crossed with each other. From the third column of table 4 it is clear that this was not the case as the percentage of *glabra-type* plants varied from 0 % to 100 %. However, those forms giving the greatest number of *glabra*-type plants after pollination with *glabra* forms gave also the highest number of *glabra* types if hybridised with *U. hollandica* or *U. carpinifolia.*

The most interesting hybrids are those of *U. hollandica.* If *U. hollandica Fjerrestad, U. hollandica Dauvessei, U. hollandica vegeta* or *U. hollandica belgica* are hybridised with each other or with other forms of *U. hollandica,* 37 % to 1.5 % of the hybrids are *glabra* types. The first three even give *glabra* types when hybridised with *U. carpinifolia.* This affirms the theory that one of the parents of *U. hollandica* is *U. glabra.*

That *U. hollandica vegeta* was a hybrid of *U. glabra* and *U. carpinifolia* was already suggested by HENRY (1910). His seedlings of *U. glabra* developed two pairs of opposite leaves followed by alternate leaves on the stem above the cotyledons. *U. carpinifolia* had all its leaves in pairs, while *U. hollandica vegeta* gave seedlings of both kinds in a proportion three of the opposite-leaved type to one of the alternate-leaved type.

The first year after germination many seedlings showed opposite leaves. The leaf pairs were standing on opposite sides of the stem (decussate). This symptom mostly disappeared in the second year. Another group of seedlings had alternate leaves, often lying on one side of the stem (distichous), while the tip of the shoot bent over. In between all characters from opposite to alternate leaves and from decussate to parastichous and distichous placed leaves could be found. According to MELVILLE (1937) elm seedlings show their hybrid nature in this way. When KRIJTHE (1939, p.16) tried to identify her elm seedlings, it turned out that it was impossible to distinguish between these *glabra-* and *carpinifolia* characters. Probably the parent trees had been highly heterozygotic.

All the seedlings are described according to leafshape. As they are mostly inoculated from their third or fourth year onward and as afterwards all diseased trees are discarded, the descriptions have to be made in the second year of growth.

The elms with *carpinifolia* leaf-types were divided according to, whether they had small, normal or large leaves. The hope of finding a correlation between leaf character and susceptibility to *Ophiostoma ulmi* was not realised. [1]) It was found, however, that the most vigorous growing, and often large-leaved elms showed a greater tendency to become heavily diseased than the slower growing ones.

Earlier investigations (WENT 1938) have already proved that all the American species as well as the European species *U. glabra, U. laevis* and most forms of *U. hollandica* are highly susceptible. None of the hybrids of these elms showed any degree of resistance. When it became evident that susceptible elms gave susceptible offspring, only the most resistant forms were used for breeding.

It was not possible to give the complete results of the hybridisation work done since 1937, but as an example the results obtained with *U. hollandica vegeta* are given in table 5 (see page 119). The hybrids of this elm with *U. carpinifolia* nr 1 were in particular very resistant to *Ophiostoma* and also showed good growth forms.

Therefore every year from 1946 onwards these elms were used as parents. For pollination one or more branches with many flowers were usually chosen. The results show that only in 1950 and 1952 was a satisfactory number of seeds obtained. This emphasises the fact that it is extremely difficult to produce one special hybrid.

Table 6 gives the results of the inoculation of those elms, obtained by hybridisation from 1937 till 1945, which showed a high degree of resistance and a good or fairly good growth form. The seedlings raised from seed gathered in 1945 were the latest lot, of which grafts were inoculated. The seedlings raised in later years have not yet been tested long enough to select them for grafting.

If the list of all the elms used for hybridizing is compared with the elms that show resistance (table 6), it is clear that only a few elm varieties produced more or less resistant offspring.

Taking the female parents into account the elms in table 6 can be divided into 5 groups viz. *U. pumila, U. Wallichiana, U. glabra, U. hollandica* and *U. carpinifolia.* With the exception of *U. glabra,* these female parents are themselves more or less resistant. However, in this table *U. glabra* is represented only by nr 49, a hybrid seedling from England, itself showing some resistance. As only 2 out of 256 seedlings of this number showed the *glabra* leaf-form, the identification is doubtful, though the original elm had many *glabra* characteristics.

[1]) From 1937 until 1940 the highest percentage of diseased trees was found among the large-leaved elms, the lowest among the small-leaved ones (WENT 1943). These results were not repeated in the seedlings of elms sown between 1941 and 1945 (WENT 1948).

TABLE 5. Number of hybrids with *U. hollandica vegeta* as female plants. Crosspollinations, which gave no seedlings, are not included [1]). (*Aantal kruisingen uitgevoerd met U. hollandica vegeta als moederplant*)

Pollen-parent (*Pollen-plant*)	1937		1938		1939		1940		1941		1944		1946		1947		1948		1949		1950		1951		1952	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	c	a	c	a	c
selfed	31	0	21	0	14	0			9	0	6	1											3	3		
pumila			2	0																						
pumila arborea			2	0	8	0																				
laevis					1	0																				
Wallichiana					7	0	1	0																		
procera betulaefolia			1	0																						
procera purpurea	4	0					6	0																		
glabra	4	0																								
glabra cornuta							8	0																		
glabra pendula							4	0																		
glabra Escaillardii			22	0																						
glabra nr 49													1	0	6	3	2	1			32	32	7	7		
hollandica belgica	18	0	11	0																						
hollandica macrophylla	1	0																								
hollandica Pitteursii			25	0																						
hollandica superba			2	0																						
carpinifolia	7	0																								
carpinifolia nr 1	6	0	52	3	19	0	64	2					15	2	28	14	1	0	13	8	107	107	8	8	52	52
carp. Christ. Buisman															18	1					5	5	1	1	41	41
carpinifolia nr 28			19	0											15	5	1	0			33				89	89
carpinifolia nr 53							4	0														33				
carpinifolia nr 61																					86	86			66	66
carpinifolia nr 62															1	0							1	1		
carp. Dampieri	20	0	14	0	20	0	52	0																		
carp. Haarlemensis	2	0																								
carp. Wentworthii			2	0																						
carpinifolia nr 43																										
260 (pum. p. r. × holl. veg.)													2	0							2	2				
148 (holl. veg. × carp. 28)																							4	4		

[1]) a = number of seedlings; b = number of seedlings still resistant in 1952; c = number of seedlings not yet inoculated.

The hybrids with different *U. pumila* forms as parents still showed the undesirable growth-form of the original *U. pumila*. As the hybrids with the other elms as female parents seem to be more hopeful in this respect, trees of *pumila*-parentage are no longer used for hybridizing.

TABLE 6. Hybrids which were grafted and where both seedling and graft showed a high degree of resistance in 1952. (*Hybriden, waarvan afgeënt werd en waarbij zowel de oorspronkelijke zaailing als de enten in 1952 een hoge graad van resistentie vertoonden*)

Hybrid	Number of hybrids on which each male parent appears (*optreden van een zelfde vorm als pollenplant*)	Year of hybridisation (*Jaar van hybridisatie*)	Number of seedling (*Aantal zaailingen*)	Seedlings resistant in 1952 (*Aantal zaailingen resistent in 1952*)	Number of grafts (*Aantal afgeente nummers*)	Grafts resistant in 1952 (*Enten resistent in 1952*)
pumila hybr. × selfed	1	1943	6	3	2	1
pumila × japonica	1	1940	7	2	1	1
pumila × gl. sub. alata	1	1940	11	1	1	1
p. pinn. ram. × holl. veg.	6	1939	80	1	7	4
p. pinn. ram. × carp. Hoers.	1	1939	29	3	6	3
p. pinn. ram. × carp. nr 1	12	1940	35	5	3	1
p. pinn. ram. × carp. Damp.	1	1940	194	6	4	2
pum. arborea × carp. nr 28	6	1941	7	1	1	1
Wallichiana × carp. nr 1	12	1939	69	1	5	2
Wallichiana × carp. nr 1	12	1942	27	3	1	1
glabra 49 × selfed	2	1942	32	6	1	1
glabra 49 × selfed	2	1944	185	55	1	1
glabra 49 × holl. vegeta	6	1941	54	8	3	2
glabra 49 × carp. nr 1	12	1938	21	2	5	3
glabra 49 × carp. nr 1	12	1941	63	3	1	1
glabra 49 × carp. nr 28	6	1938	5	1	4	3
holl. belg. × selfed	1	1937	29	0	1	1
holl. belg. × holl. veg.	6	1939	17	1	1	1
holl. belg. × carp. nr 28	6	1938	120	0	3	1
holl. veg. × carp. nr 1	12	1937	6	0	1	1
holl. veg. × carp. nr 1	12	1938	52	3	10	4
holl. veg. × carp. nr 1	12	1940	64	2	7	4
holl. veg. × carp. nr 28	6	1938	19	0	3	1
carp. nr 1 × carp. nr 28	6	1944	373	42	11	11
carp. nr 61 × selfed	1	1942	47	3	1	1
carp. nr 61 × carp. nr 1	12	1942	114	7	9	7
carp. nr 61 × carp. nr 28	6	1944	41	9	1	1
carp. nr 62 × selfed	1	1942	112	24	10	9
carp. nr 62 × carp. nr 1	12	1942	125	20	16	15
carp. nr 28 × holl. veg.	6	1938	4	0	1	1
carp. nr 28 × carp. nr 1	12	1938	164	1	16	3
carp. nr 40 × selfed	1	1942	1136	44	2	1
carp. nr 53 × holl. veg.	6	1942	85	11	2	2
Christ. Buism. × holl. veg.	6	1945	28	3	1	1
Christ. Buism. × carp. nr 1	12	1942	40	2	1	1

When it was clear that susceptible species and varieties gave susceptible offspring, more stress was laid on continuing the work with resistant varieties. The results over the last years show clearly that the seedlings obtained in this way are as a whole much more resistant, than the seedlings collected freely in nature at the beginning of the investigations. This general increase in resistance of the seedlings makes the future of the research much more hopeful.

Every year virtually all the elms in the trial ground at Baarn are inoculated with *Ophiostoma*. The only exceptions are trees which have been recently transplanted. In the earlier years of the investigation, the elms in late summer showed everywhere wilting, yellowing of foliage, and dieback of twigs, which gave a very „diseased" aspect to the trial grounds as a whole. Recently, although a little yellowing and occasional dieback can still be found, the general appearance of the elms in late summer is of greenness and health. This alone is some measure of the general increase in resistance, which was resulted from hybridization and selection over a long period.

If the male parents in table 6 are taken into account it is obvious that as a result of using *U. carpinifolia* nr 1, which happened twelve times, many highly resistant seedlings of good growth form turned up. With *U. carpinifolia* nr 28 and *U. hollandica vegeta* this only happened on six occasions.

The last column of table 6 gives the number of highly resistant grafts of satisfactory growth which are still present in 1953. The highest numbers are found among the hybrids: *U. hollandica vegeta* × *U. carpinifolia* nr 1 (9), *U. carpinifolia* nr 62 selfed (9), *U. carpinifolia* nr 1 × *U. carpinifolia* nr 28 (11) and *U. carpinifolia* nr 62 × *U. carpinifolia* nr 1 (15). Except for those with *U. hollandica vegeta* as female parent, all the selections with a great number of grafts had *U. carpinifolia* either as female or as male parent. It is clear, bearing these results in mind, that the different varieties of *U. carpinifolia* are especially useful for hybridizing.

In successive years pollination of the same elm varieties gave different quantities of viable seed, a fact partly due to the weather conditions during or just before the time of flowering (see page 111). This was the case with U. *pumila* and *U. pumila pinnato ramosa*, and their hybrids, which start to flower as early as the beginning of February. Often the flowers are already damaged by frost before they open and if a period of very low temperatures occurs during pollination, the flowers may even be damaged in the paperbags. As a result only a small amount, or even no fertile seeds at all, develop. The chancé of freezing is much less for late flowering trees like *U. Wallichiana*. For this reason, and also because its hybrids have an undesirable growth habit, *U. pumila* and its hybrids are no longer used for hybridization.

Already hybrids have been used as parents in the hybridizing scheme. The results of the inoculations of the offspring of these crossings are not ready for publication.

b. *Resistant selections*

Up till now no hybrids have been distributed to growers, only two seedlings of *U. carpinifolia* with a high degree of resistance have been given to Dutch nurserymen. The first seedling originated from Spain and was called after „CHRISTINE BUISMAN", who started the hybridisation work. The second came from France and was called after „BEA SCHWARZ" (fig. 1), who first described the fungus causing the Dutch elm disease.

After the elm „CHRISTINE BUISMAN" had been cultivated for several years, it was found to be so heavily attacked by the fungus *Nectria cinnabarina*, that its planting could no longer be recommended. From then on all trees, which showed a high degree of resistance to the Dutch elm disease, were tested for their susceptibility to *Nectria cinnabarina*. Unfortunately the method used did not give

Fig. 1. Top-grafted U. carpinifolia „Bea Schwarz" in the Hague
(*Hoog opgeënte U. carpinifolia „Bea Schwarz" in den Haag*)

reliable results. However, it is certain that the elm „BEA SCHWARZ" is resistant to attack by *Nectria cinnabarina*.

c. *Cytology*

LELIVELD (1934) counted the chromosomes of different elm species. In *U. hollandica belgica, U. hollandica Pitteursii, U. carpinifolia suberosa alata, U. Wilsoniana, U. pumila pinnato ramosa* and *U. glabra suberosa* she found 14 chromosomes as the haploid number. No irregularities could be found in the reduction division. KRIJTHE (1939, p. 17) stained material from 15 different elm species and varieties. They all had 14 chromosomes in the haploid stage, with the exception of *U. pumila arborea* (*U. turkestanica*), where sometimes 28 chromosomes were found in the metaphase of the pollengrain.

KRAUSE (1930) counted 14 chromosomes in *U. glabra, U. carpinifolia* and *U. americana,* while WALKER (1932) counted 15 chromosomes for *U. pumila* and *U. fulva* (KRIJTHE counted 14 for these species) and 28–30 chromosomes for *U. americana.*

The Swedish Forest Tree Breeding Association at Källstorp produced triploid and tetraploid forms of *U. glabra.* As these forms proved to be just as susceptible to the Dutch elm disease as *U. glabra,* it was considered useless to include them in the hybridisation scheme. It might well be useful to try out triploid and tetraploid forms of the most resistant *carpinifolia* types, if they could be produced.

In elm flower-initiation takes place in the year previous to flowering. For *U. pumila pinnato ramosa* KRIJTHE (1940, p. 15) found that flowerdevelopment started on May 10th; by the 1st of August the flowers had fully developed. For *U. hollandica belgica* these dates were respectively June 14th and August 1st.

d. *Chemotherapy*

In 1946 ZENTMEYER et al. (1946) published a list of chemicals which gave a protective effect against the Dutch elm disease. Three of these chemicals which seemed to give the best results were used in our experiments.

One of them, paranitrophenol, was poured into holes in the stems of elms (WENT 1948). The results were not very convincing, though it did appear that resistance had been slightly increased by the treatment. However, this chemical was not tried again, as the bark above and below the point of injection was killed for quite a long way up and down the tree. In later years (WENT 1949, 1951 and 1952) 8-oxychinolinebenzoate and -sulphate were used. In the first years these chemicals were poured into holes in the trees. The next two years they were mixed into the soil around the trees by subsurface injection, as described by DIMOND et al. (1949). All the results were negative.

In 1952 DIMOND et al. (1952) published a short note on the protective effect of 2-carboxymethylmercaptobenzothiazole. This chemical was also tried by mixing it into the soil around the tree, and by injecting small quantities into chisel holes in the stem of the tree (WENT 1953). After inoculation all treated and untreated trees became diseased.

Up to the present time no chemical has been found that can be used as a treatment for protecting elms from, or curing elms attacked by, the Dutch elm disease.

5. *Conclusion*

Selection of elms resistant to the Dutch elm disease, has already resulted in the finding of two highly resistant types; *U. carpinifolia* CHRISTINE BUISMAN and *U. carpinifolia* BEA SCHWARZ.

Hybridisation of the most resistant trees with types showing a desirable growth-form has given rise to a group of seedlings with a much higher resistance against *Ophiostoma* than the originally tested seedlings. Many individuals with high resistance have been found among these hybrid seedlings.

Probably within a few years it will be possible to select elms with a high degree of resistance in combination with desirable habit of growth.

6. *Samenvatting*

1. *Inleiding*

In de *inleiding* wordt vermeld waar en door welke personen het onderzoek is uitgevoerd.

2. *Verspreiding van de iepenziekte in Nederland*

In dit hoofdstuk zijn de gegevens verwerkt, die het Staatsbosbeheer van 1930 t/m 1946 over het optreden van de iepenziekte in Nederland verzamelde (tabel 1).

Van de 1.228.000 iepen, die in 1930 in Nederland werden geteld waren er in 1946 nog 425.000 over. Dus in verloop van 16 jaar is 2/3 van onze iepenopstand verdwenen.

De tellingen uitgevoerd in de provincie Groningen laten zien dat iepen op zand en veengrond veel eerder ten offer vallen aan de iepenziekte dan iepen op klei.

In Friesland echter staat het grootste deel van de nog aanwezige iepenlanen op veengrond. Het is dus vermoedelijk toe te schrijven aan het hogere vochtgehalte van de klei en van de Friese veengronden, dat de verwelkingsverschijnselen van de iepenziekte minder snel het afsterven van de bomen tengevolge hebben. Dit verklaart ook de grotere resistentie van de iepen langs de Amsterdamse grachten ten opzichte van die in de buitenwijken met opgespoten grond.

3. *Methodiek*

a. Hybridisatie

De methode van castreren en bestuiven is beschreven.

In de loop der jaren is bij 189 bomen zelfbestuiving uitgevoerd[1]; 12 % hiervan leverde meer dan 10 % fertiele zaden op. Dit kan bij verschillende soorten optreden, maar ook in een enkel jaar bij een soort, die meerdere jaren voor zelfbestuiving werd gebruikt. Als voorbeeld (tabel 2) zou ik de bomen L 10.10 (*U. carpinifolia* no 53 × *U. hollandica vegeta*) willen nemen, waar in 1950 32 % of 272 van 847 zaden fertiel waren. Daar het niet mogelijk is van te voren aan te geven of zelfbestuiving al dan niet zal optreden is castratie noodzakelijk om zeker te zijn van de vaderplant.

Sommige iepen-vormen leveren meer fertiel zaad op, wanneer zij gebruikt worden als moederboom, bij anderen is dit juist het geval wanneer zij als pollenplant worden gebruikt (tabel 3).

b. Zaaien en planten

Methoden om het percentage kieming bij de zaden op te voeren worden besproken. Zaaien in zeer nat te houden bladaarde in zaaibakken in de kas levert de beste resultaten op.

c. Inoculatie en selectie

Nog steeds wordt op dezelfde wijze geïnoculeerd als in 1928 door CHRISTINE BUISMAN werd aangegeven. De zaailingen worden ongeveer vanaf hun vierde jaar gedurende vijf achtereenvolgende jaren tweemaal per jaar geïnoculeerd. Vertonen zij dan nog geen ziekteverschijnselen en is de groei bevredigend dan worden er enten van gemaakt. Deze enten van de oorspronkelijke zaailingen moeten dan weer voor minstens 5 jaar op hun resistentie worden onderzocht. Is het aantal onderzochte enten dan groot genoeg en is de resistentie voldoende (hoogstens 10 %–15 % zieke exemplaren), dan kan een dergelijke boom voor afgifte aan de kwekers in aanmerking komen.

4. *Resultaten*

a. Hybridisatie

Ten minste 48 verschillende soorten, variëteiten en vormen van iepen zijn bij het kruisingswerk gebruikt. Het vermoeden dat verschillende variëteiten van *U. hollandica* ontstaan zouden zijn uit kruising van *U. glabra* met andere vormen (tabel 4), bleek juist te zijn. Wanneer *U. hollandica Fjerrestad* met andere *hollandica*-vormen werd gekruist trad in 37 % van de gevallen een *glabra*-nakomeling op. Bij *U. hollandica Dauvessiï* was dit 23 %, bij *U. hollandica vegeta* 3 % en bij *U. hollandica belgica* 1.5 %. De eerste 3 gaven ook na kruising met *carpinifolia*-vormen *glabra*-nakomelingen en wel resp. 21 %, 5 % en 0.3 %.

[1]) Ieder jaar, waarin bij een boom zelfbestuiving werd uitgevoerd, is als eenmaal zelfbestuiving geteld.

U. hollandica belgica leverde geen *glabra* planten op na kruising met *carpinifolia* vormen, doch na zelfbestuiving traden nog tweemaal *glabra*-vormen op, dit is 0.5 % van de 1.5 % *glabra*-vormen die *U. hollandica belgica* gaf na kruising met willekeurige *hollandica*-vormen.

De hybriden waarbij gevoelige soorten als moeder- of vaderplant werden gebruikt bleken alle vatbaar te zijn voor de iepenziekte.

In tabel 6 zijn die hybriden opgenomen waarbij tot 1952 zowel bij de zaailingen als bij de enten een hoge graad van resistentie tegen de iepenziekte werd aangetroffen.

Het blijkt, dat men de moederplanten kan onderverdelen in de groepen *U. pumila, U. Wallichiana, U. glabra* no 49, *U. hollandica belgica, U. hollandica vegeta* en 7 verschillende zaailingen van *U. carpinifolia*. Daar de meest gevoelige iepen o.a. *U. glabra*, direct afvielen als ouderplant, valt het op dat *U. glabra* no 49 bij de resistente ouderplanten hoort. Dit is echter een *U. glabra*, die zeker geen zuivere *glabra*-eigenschappen heeft. Bij zelfbestuiving trad slechts bij 2 van de 256 zaailingen de zuivere *glabra*-vorm op.

De hybriden met *U. pumila* of vormen daarvan als moederplant vertoonden alle de te wilde *pumila*-groei.

Daar het kruisen van deze vorm vaak mislukte door de zeer vroege bloei, waardoor grote kans op vorstschade ontstond, is deze soort geschrapt als ouderplant. Wel zou als ouderplant nog doorgewerkt kunnen worden met enkele hybriden van deze soort.

Hybriden met *U. Wallichiana* als moederplant geven bijzonder mooi groeiende bomen. Tot nu toe vertoonden deze echter een grote gevoeligheid voor *Nectria cinnabarina*. Deze schimmel veroorzaakt bijna steeds het afsterven van *U. Wallichiana*. De hybriden van *U. hollandica vegeta* met *U. carpinifolia* no 1, zijn zeer veelbelovend. Van 9 nummers wordt thans nog doorgekweekt.

Ditzelfde kan gezegd worden van de nakomelingen van *U. carpinifolia* no 62 (de iep BEA SCHWARZ) zelfbestoven en gekruist met *U. carpinifolia* no 1.

Wanneer men naar de pollenplanten kijkt dan blijkt, dat in tabel 6 *U. carpinifolia* no 1 alleen 12 maal voorkomt, *U. hollandica vegeta* en *U. carpinifolia* no 28 beide 6 maal. Deze pollenplanten zullen dus bij het verdere onderzoek steeds gebruikt moeten worden.

b. Resistente selecties

Tot op dit ogenblik zijn nog geen hybriden aan de kwekers afgestaan. Dit was ook nauwelijks te verwachten, daar het kruisen pas in 1937 is begonnen en 15 jaar het minimum is voor selectie van een nummer. Wanneer men het percentage resistente zaailingen, thans uit de kruisingen verkregen, vergelijkt met het percentage resistentie van de uit het wild verzamelde zaailingen, dan blijkt dat er enorme voortgang is gemaakt in de loop van het onderzoek.

De twee thans verkregen resistente iepen zijn beide afkomstig van zaailingen waarvan het zaad in het wild werd verzameld. Het zijn de iep CHRISTINE BUISMAN (*U. carpinifolia* no 24) afkomstig uit Spanje en de iep BEA SCHWARZ (*U. carpinifolia* no 62) afkomstig uit Frankrijk. De eerste wordt echter hevig aangetast door de schimmel *Nectria cinnabarina* en is daardoor niet bruikbaar.

c. Cytologie

Een kort overzicht is gegeven van het onderzoek naar het aantal chromosomen voorkomende bij iepen. Het haploïde aantal was bij de meeste onderzochte soorten 14. Slechts bij *U. americana* bleek dit aantal 28 te zijn. Ook bij *U. turkestanica* werden een enkele maal in de metaphase van de pollenkorrel 28 chromosomen aangetroffen.

d. Chemotherapie.

Geen van de door ons onderzochte middelen leverde een vermindering van de aantasting op. De onderzochte stoffen zijn: paranitrophenol, 8 oxychinoline-benzoaat, 8 oxychinoline-sulphaat en 2-carboymethyl-mercapto-benzo-thiazol.

5. Conclusie

Het is waarschijnlijk dat over enkele jaren bomen met een hoge graad van resistentie en een goede groei geselecteerd zullen kunnen worden.

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Versl. W. = Verslag over de werkzaamheden voor het Iepenziektecomité verricht op het Laboratorium voor Erfelijkheidsleer te Wageningen.
Versl. B. = Verslag van de onderzoekingen over de Iepenziekte verricht op het Phytopathologisch Laboratorium W. C. Scholten, te Baarn.
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