ヒリュウ(Poncirus trifoliata var. monstrosa (T. Ito) Swingle)にみられる枝ととげの屈曲性の遺伝

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Inheritance of the Crooked Twig and Thorn Trait from Flying Dragon Trifoliate Orange (*Poncirus trifoliata* var. *monstrosa* (T. Ito) Swingle)

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Summary

The inheritance of the crooked twig and thorn trait from Flying Dragon (Hiryu) trifoliate orange was studied by utilizing one-year-old seedlings obtained from selfings and crossings of trifoliate orange cultivars and strains, including the Flying Dragon and *Citrus* plants. The segregation patterns of crooked-type and straight-type seedlings were different in reciprocal crosses: crooked-type seedlings occurred only in progenies from seed parents with cytoplasm inherited from Flying Dragon but not in the progenies from seed parents without that cytoplasm. As straight-type seedlings segregated in the progeny in which crooked-type ones occurred, it was considered that the cytoplasmic and the nuclear genes would play roles in the inheritance of crookedness of twigs and thorns and that a crooked-type seedling occurs when both the cytoplasmic and the nuclear genes are of the crooked-type. The hypothesis regarding the nuclear gene, namely, that the expression of crookedness is controlled by three pairs of complementary genes, Cr_1, Cr_2 and Cr_3, and that the genotype of the Flying Dragon is $Cr_1cr_1Cr_2cr_2Cr_3cr_3$, was consistent with the observed segregation ratios, except for that in one advanced population of Flying Dragon.

Key Words: crookedness, Flying Dragon, inheritance, *Poncirus*, trifoliate orange.

Introduction

Trifoliate orange (*Poncirus trifoliata* Raf.), a near relative of *Citrus* plants, is inedible because its fruit has a peculiar bad smell and a very sour taste. However, it adapts to the Japanese climate and soil conditions and is the most commonly used citrus rootstock in Japan. It is also used to some extent in Australia, New Zealand, Korea, and other countries. Citrus trees on this rootstock form a relatively compact tree shape that produce high-quality fruits (Iwasaki, 1966; Phillips and Castle, 1977). Trifoliate orange is cold-hardy and highly resistant to foot-rot disease and the citrus nematode (Baines et al., 1957; Hutchison, 1985). Moreover, it is generally immune to the Citrus tristeza virus (CTV), which is widely distributed in citrus-growing areas in the world, although susceptible strains have been found. The inheritance of CTV-immunity has been reported (Yoshida, 1985, 1996), and, therefore, it has been frequently used as a parental material for rootstock breeding (Hutchison, 1985).

In Japan, trifoliate orange has been used without any regard to the strains. In recent years, however, the interest in rootstocks has increased, with a diversity of cultivars and cultivation methods. A list of rootstocks including types that are more dwarfing and more vigorous than the common trifolitate orange based on the response of the grafted scion cultivars is required. Therefore, Flying Dragon (*Poncirus trifoliata* var. *monstrosa* (T. Ito) Swingle) with crooked twigs and thorns (Fig. 1) has attracted considerable attention. This rootstock dwarfs trees and, thus, reduces the labor required for orchard management in addition to improving fruit quality (Kobayashi et al., 1995; Roose, 1986).

To expand the variation in characteristics for desirable rootstocks, the author has carried out selfing and crossing of trifoliate orange cultivars and strains including Flying Dragon, small-leaved strains (Iwasaki, 1943; Iwasaki and Nishiura, 1963) and a thornless strain (Kawase and Hirai, 1985). The inheritance modes of two types of dwarfism (Yoshida, 1994) and a thornless trait (Yoshida et al., 1999) in the populations from these selfings and crossings have been reported. Cheng and Roose (1995) reported the inheritance of the dwarfing ability and curved thorn and trunk trait of Flying Dragon. In this paper, the segregation patterns and the inheritance of crookedness of twigs and thorns observed in many progeny populations of Flying Dragon are reported.

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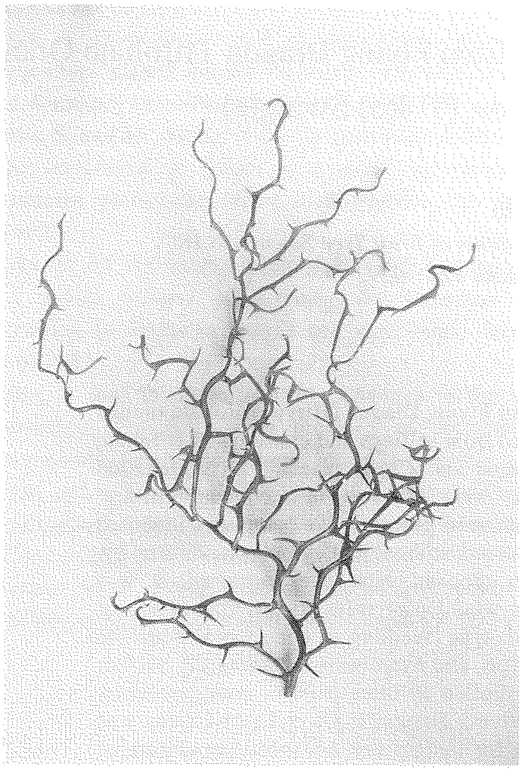

Fig. 1. A shoot of Flying Dragon trifoliate orange.

Materials and Methods

Parentage of plant materials

Flying Dragon was introduced from the Shizuoka Prefectural Citrus Experiment Station to the Horticultural Research Station (the present Department of Citrus Research, Okitsu, National Institute of Fruit Tree Science, NARO) in 1950. Small leaf A and Small leaf C were selected from a seedling population of trifoliate orange at the Citrus Branch, Oita Prefectural Agricultural Experiment Station (presently, the Tsukumi Branch, Oita Prefectural Citrus Experiment Station) and introduced to the then Okitsu Branch, Fruit Tree Research Station in 1937 (Iwasaki, 1943). In addition, Natsudaidai (*Citrus natsudaidai* Hayata), Hyuganatsu (*C. tamurana* hort. ex Tanaka) and Hassaku (*C. hassaku* hort. ex Tanaka) were used as parents. Among these parental materials, Flying Dragon has crooked twigs and thorns, whereas the others have straight twigs and thorns. Flying Dragon and Natsudaidai are polyembryonic; the others are monoembryonic.

Progeny segregation

The following seedlings were produced from 1977 to 1983 and from 1990 to 1993: selfed progenies (S_1) of Small leaf A, Small leaf C and Flying Dragon, F_1 progenies of reciprocal crosses between Small leaf A × Small leaf C and those derived from Small leaf A × Flying Dragon and Small leaf C × Flying Dragon. Moreover, the following seedlings of advanced generations were produced from 1989 to 2001: F_2 progenies obtained from selfings of F_1 selections, back-cross progenies (BC_1) of F_1 selections with Flying Dragon, S_2 progenies from selfings of S_1 selections and progenies of S_1 selections crossed with Small leaf A, Small leaf C and Flying Dragon. Selfed progenies of Hyuganatsu and Hassaku were produced in 1983, whereas, F_1 progenies of Flying Dragon crossed with Hyuganatsu, Hassaku and Natsudaidai were produced from 1990 to 1995. In

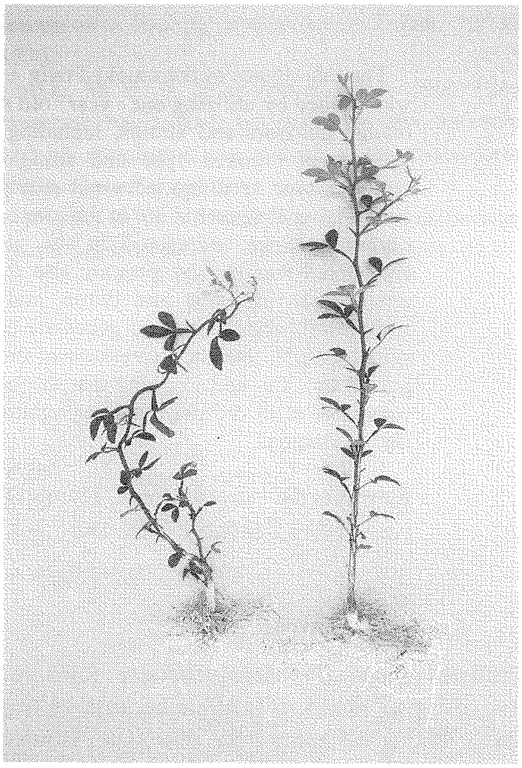

Fig. 2. Crooked-type (left) and straight-type (right) seedlings of trifoliate orange.

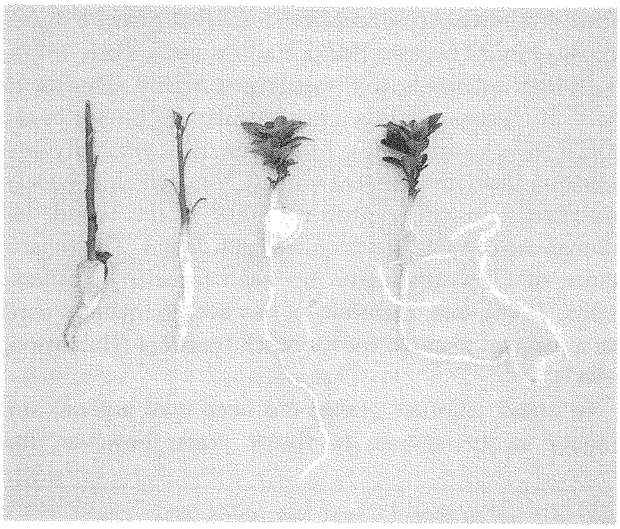

Fig. 3. Match-type (left two) and rosette-type (right two) seedlings of trifoliate orange.

nearly half of these populations, it took 2 to 4 years to produce the seedlings used. Of the above F_1 and S_1 selections, F_1 selections were all monoembryonic, while the S_1 selections segregated into monoembryonic and polyembryonic ones.

The 1-year-old seedlings that were grown in a greenhouse kept above 20℃ during winter were classified into four types: "straight", "crooked" (Flying Dragon-like), "rosette", and "match" (Figs. 2 and 3). Rosette-type seedlings have small trifoliate leaves, extremely short internodes (less than 1 mm) and thick roots. Match-type seedlings grow a little during the germination period and do not develop the typical trifoliate leaves (Yoshida, 1994). All rosette-type seedlings in a selfed progeny of Flying Dragon and parts of rosette-type seedlings in selfed progenies of 2 S_1 selections (Flying Dragon selfed 90-62 and Flying Dragon selfed 90-86) were sprayed with a 100 ppm gibberellin solution (Kyowa Hakko Kogyo Co., Ltd., Tokyo) 7 to 9 months after the germination to force elongation of their internodes to determine whether they were straight or crooked. The zygotic seedlings were distinguished from nucellar ones by an isozyme analysis of glutamate oxalacetate aminotransferase (GOT) in selfed populations of Flying Dragon and progenies of Flying Dragon × Natsudaidai. In a population from Flying Dragon × Small leaf C, isozyme analyses of GOT, phosphoglucose isomerase (PGI) and leucine aminopeptidase (LAP) were used to identify zygotic seedlings. The seedlings from Natsudaidai × Flying Dragon were distinguished by the presence or absence of trifoliate leaves.

Results

Progenies from seed parents without the cytoplasm of Flying Dragon

Among the progenies from seed parents without the cytoplasm of Flying Dragon (Table 1), there were no crooked-type in the S_1 progenies of Small leaf A and

Table 1. Segregation pattern of seedling form in progenies from seed parents without cytoplasm of Flying Dragon.

Population	No. of seedlings investigated	No. of zygotic seedlings					No. of Nucellar seedlings
		Crooked	Straight	Rosette	Match	Unknown (poor growth)	
<S_1 progeny>							
Small leaf A selfed	380	0	379	0	0	1	0
Small leaf C selfed	292	0	257	0	35	0	0
Hyuganatsu selfed	79	0	79	0	0	0	0
Hassaku selfed	50	0	50	0	0	0	0
<F_1 progeny>							
Small leaf A × Small leaf C	150	0	150	0	0	0	0
Small leaf C × Small leaf A	284	0	284	0	0	0	0
Small leaf A × Flying Dragon^{z}	20	0	20	0	0	0	0
Small leaf C × Flying Dragon	98	0	91	0	7	0	0
Hyuganatsu × Flying Dragon	53	0	53	0	0	0	0
Hassaku × Flying Dragon	23	0	23	0	0	0	0
Natsudaidai × Flying Dragon	262	0	18	0	0	0	244
<F_2 progeny>							
(Small leaf C × Flying Dragon) No. 1 selfed	4	0	4	0	0	0	0
(Small leaf C × Flying Dragon) No. 9 selfed	11	0	8	3	0	0	0
(Small leaf C × Flying Dragon) No. 16 selfed	57	0	54	0	3	0	0
(Small leaf C × Flying Dragon) No. 21 selfed	221	0	162	41	18	0	0
(Small leaf C × Flying Dragon) No. 30 selfed	125	0	97	28	0	0	0
<BC_1 progeny>							
(Small leaf C × Flying Dragon) No. 1 × Flying Dragon	22	0	22	0	0	0	0
(Small leaf C × Flying Dragon) No. 3 × Flying Dragon	5	0	5	0	0	0	0
(Small leaf C × Flying Dragon) No. 5 × Flying Dragon	5	0	5	0	0	0	0
(Small leaf C × Flying Dragon) No. 8 × Flying Dragon	1	0	1	0	0	0	0
(Small leaf C × Flying Dragon) No. 9 × Flying Dragon	3	0	1	2	0	0	0
<Others>							
Small leaf A × Flying Dragon selfed 90-66^{z}	71	0	68	0	0	3	0
Small leaf A × Flying Dragon selfed 90-83^{z}	8	0	8	0	0	0	0
Small leaf C × Flying Dragon selfed 90-63^{z}	219	0	190	0	29	0	0
Small leaf C × Flying Dragon selfed 90-66	189	0	161	0	25	3	0

Among seed parents, Natsudaidai is polyembryonic and the others are monoembryonic.

^{z} Crooked-type.

Table 2. Segregation pattern of seedling form in progenies from seed parents with cytoplasm of Flying Dragon.

Population	No. of seedlings investigated	No. of seedlings							Expected ratio of crooked: straight^{y}	χ^2	Probability of fitness
		Zygotic					Nucellar	Unknown^{z}			
		Crooked	Straight	Rosette	Match	Unknown (poor growth)	Crooked	Crooked			
<S_1 progeny>											
Flying Dragon selfed	320	20+(7)^{x}	53+(4)^{x}	12	3	3+(1)^{x}	0	229 (8)^{w}	27:37	0.65	0.42
<F_1 progeny>											
Flying Dragon × Small leaf C	67	10	16	0	1	2	0	38	–^{v}	–	–
Flying Dragon × Natsudaidai	116	44	33	0	0	2	37	0	9:7	0.03	0.87
<S_2 progeny>											
(Flying Dragon selfed 90-51) selfed	73	26	33	0	0	14	0	0	27:37	0.09	0.77
(Flying Dragon selfed 90-62) selfed	199	40+(4)^{x}	79	35	1	45	0	0	27:37	2.08	0.15
(Flying Dragon selfed 90-86) selfed	196	54+(2)^{x}	76+(8)^{x}	42	7	17	0	0	27:37	0.28	0.60
(Flying Dragon selfed 91-101-2) selfed	18	3	12	1	0	2	0	0	27:37	3.03	0.08
(Flying Dragon selfed No. 5^{u}) selfed	20	0	20	0	0	0	0	0	0:1	–	–
(Flying Dragon selfed No. 6^{u}) selfed	306	0	213	83	7	3	0	0	0:1	–	–
<F_2 progeny>											
(Flying Dragon × Small leaf C) 92-16 selfed	26	15	9	0	1	1	0	0	–^{v}	–	–
<Others>											
(Flying Dragon selfed No.6^{u}) × Flying Dragon	460	0	340	102	8	10	0	0	0:1	–	–

Among seed parents, Flying Dragon is polyembryonic and the others are monoembryonic.

[z] Unknown whether a nucellar seedling or a zygotic one.

[y] Segregation ratio on the assumption that crookedness is controlled by three pairs of complementary nuclear genes Cr_1,Cr_2 and Cr_3, and genotype of Flying Dragon is $Cr_1cr_1Cr_2cr_2Cr_3cr_3$.

[x] Investigated after stems of rosette-type seedlings are elongated by gibberellin treatment.

[w] Estimated to be zygotic based on theoretical segregation ratio of GOT genotypes.

[v] Many cases are assumed.

[u] Straight-type. The other seed parents are crooked-type.

Table 3. Segregation pattern of seedling form in progenies from polyembryonic seed parents with cytoplasm of Flying Dragon.

Population	No. of seedlings investigated	No. of seedlings				
		Crooked[z]	Straight	Rosette	Match	Unknown (poor growth)
< S_2 progeny >						
(Flying Dragon selfed 90-63) selfed	12	3	5	3	0	1
(Flying Dragon selfed 90-66) selfed	50	41	5	0	0	4
(Flying Dragon selfed 90-82) selfed	22	15	6	0	0	1
(Flying Dragon selfed 90-83) selfed	5	3	2	0	0	0

All parents are crooked-type.

[z] Discrimination between zygotic and nucellar seedlings was not carried out.

Small leaf C and in the F_1 progenies of reciprocal crossings between them, or among the progenies of Small leaf A × Flying Dragon and Small leaf C × Flying Dragon. Moreover, no crooked-type seedlings segregated in a) the 5 F_2 progenies produced by selfings of straight-type F_1 selections from Small leaf C × Flying Dragon, b) the 5 BC_1 progenies of straight-type F_1 selections from Small leaf C × Flying Dragon with Flying Dragon, c) the 2 hybrid progenies between Small leaf A and crooked-type S_1 selections of Flying Dragon and d) the 2 hybrid progenies between Small leaf C and crooked-type S_1 selections of Flying Dragon. Likewise, no crooked-type seedlings segregated in the S_1 progenies of Hyuganatsu and Hassaku and the intergeneric F_1 progenies of Hyuganatsu × Flying Dragon, Hassaku × Flying Dragon and Natsudaidai × Flying Dragon. Rosette-type and/or match-type seedlings segregated in some of the above progenies.

Progenies from seed parents with the cytoplasm of Flying Dragon

The segregation patterns of seedling forms in the progenies from seed parents with the cytoplasm of Flying Dragon (Table 2) reveal that rosette-type seedlings treated with gibberellin were classified into straight-type and crooked-type. The stem type of one seedling could not be determined because of poor stem elongation. Crooked-type and straight-type seedlings segregated in the S_1 progeny of Flying Dragon and the F_1 progenies of Flying Dragon × Small leaf C and Flying Dragon × Natsudaidai. Moreover, in a) the 4 S_2 progenies from crooked-type and monoembryonic S_1 selections of Flying Dragon, and b) the F_2 progenies produced by selfing of a crooked-type and monoembryonic F_1 selection from Flying Dragon × Small leaf C, both crooked-type and straight-type seedlings segregated. However, no crooked-type seedlings segregated in the 2 S_2 progenies from straight-type and monoembryonic S_1 selections of Flying Dragon and those derived from a straight-type and monoembryonic S_1 selection of Flying Dragon × Flying Dragon. The seed parents of these progenies have the cytoplasm of Flying Dragon. Not only did rosette-type and/or match-type seedlings segregated among some of the above progenies, seedlings with crooked and straight stems segregated in the 4 S_2 progenies from crooked-type and polyembryonic S_1 selections of Flying Dragon. No discrimination between zygotic and nucellar seedlings was attempted (Table 3).

Discussion

Crooked-type seedlings did not segregate from the progenies of Small leaf C × Flying Dragon and Natsudaidai × Flying Dragon, but they did from the progenies of Flying Dragon × Small leaf C and Flying Dragon × Natsudaidai. Therefore, it was clear that the segregation patterns differed in reciprocal crossings. Crooked-type seedlings occurred only in the progenies from seed parents with the cytoplasm of Flying Dragon, but not in the progenies from seed parents without it. As both straight- and crooked-type seedlings occurred among the progenies, I considered that cytoplasmic and nuclear genes play important roles in the inheritance of the two morphological traits. Grosser et al. (1988) reported that intergeneric somatic hybrid plants of the 'Hamlin' orange (*Citrus sinensis* Osbeck) and Flying Dragon expressed crookedness of stems and thorns in addition to trifoliate leaves. Cheng and Roose (1995) reported that in a population of open-pollinated seedlings of Flying Dragon in which all seedlings were thought to have originated from selfing based on molecular marker genotypes, the segregation ratio of the crooked-type to the straight-type was consistently 3:1; the crooked-type was dominant, while the straight-type was recessive. The segregation ratio that they reported does not agree with the result concerning the S_1 progeny of Flying Dragon. Moreover, the segregation ratio in the 4 S_2 progenies of Flying Dragon does not agree with the hypothesis that the expression of crookedness is controlled by a single dominant gene for which Flying Dragon is heterozygous. On the assumption that the expression of crookedness is controlled by three pairs of complementary nuclear genes, Cr_1, Cr_2 and Cr_3, and that the genotype of Flying Dragon is $Cr_1cr_1Cr_2cr_2Cr_3cr_3$, the segregation ratio of the crooked-type to the straight-type in the S_1 progeny of Flying Dragon, except for the seedlings with poor growth, such as those of the match-type, was consistent with an expected ratio of 27:37. Among the crooked-type seedlings with GOT genotypes identical to Flying Dragon, 8 seedlings were estimated to be zygotic based on the theoretical segregation ratio of the GOT genotypes. Although crooked-type S_1 selections of Flying Dragon, (Flying Dragon × Small leaf C) 92-16, Small leaf C and Natsudaidai have some possibilities of genotypes according to this hypothesis, the segregation ratios of the crooked-type to the straight-type, except for the seedlings with poor growth in populations produced by selfing or crossing of these parents, were consistent with this hypothesis (Table 2). It is considered that no crooked-type seedling segregated in the selfed progenies of straight-type Flying Dragon selfed No. 5 and Flying Dragon selfed No. 6 because they have a crooked-type cytoplasm but not the crooked-type genotypes. Among the progenies from Flying Dragon selfed No. 6 × Flying Dragon, crooked-type seedlings are expected to segregate whatever genotype Flying Dragon selfed No. 6 has. However, no crooked-type seedling segregated, which is inconsistent with the hypothesis, even though the number of seedlings in this population was not small. The reason for the inconsistency needs further investigation.

Cheng and Roose (1995) reported that no recombinants were found between the trunk and thorn characteristics which is in agreement with the results of this report. The trunk and thorn characteristics are considered to be similarly expressed because citrus thorns are morphologically abortive branches that develop from one of the lateral buds in the leaf axil (Frost, 1938; Schroeder, 1953).

The rosette-type is in an indistinguishable state whether the twig is straight or crooked because of its extremely short internodes. It is possible to elongate internodes of rosette-type seedlings with gibberellin treatment and to classify them into two types, straight and crooked (Yoshida, 1994). It is considered that the rosette- and crooked-types are under the control of different genes that are mutually unrelated. In addition to rosette- and match-type seedlings, there were many seedlings whose traits were unidentifiable because of their poor growth in the populations, such as the S_2 progenies of Flying Dragon. Cheng and Roose (1995) reported an inbreeding depression resulting from the selfing of trifoliate orange. Most of the seedlings with poor growth in this study are considered to be dwarfs that resulted from recombination through inbreeding, which differs from that in the rosette- and match-types.

Cheng and Roose (1995) reported that curved thorn and stem growth were closely linked to, or pleiotropic effects of, the dwarfing gene, and estimated that Flying Dragon was differentiated from the non-dwarfing cultivars of trifoliate orange by the accumulation of one or more mutations without any sexual recombination. Russo and Starrantino (1988) reported three mutants with crooked twigs, which originated as a mutant seedling or a bud sport of the citranges (*Citrus sinensis* × *Poncirus trifoliata*) 'Troyer' and 'Carrizo'. The author also discovered a bud sport with crooked twigs and thorns such as Flying Dragon in 2001, and named it RP-137M, which originated from a progeny of trifoliate orange named RP-137 ('Kiyomi' (*Citrus unshiu* Marc. var. *praecox* Tanaka 'Miyagawa wase' × *C. sinensis* 'Trovita') × 'US119' ((*C. paradisi* Macf. 'Duncan' × *Poncirus trifoliata*) × *C. sinensis* 'Succory')) (Fig. 4). If the crookedness of these mutants is inherited as Flying Dragon, the mutation(s) that accompany a cytoplasmic mutation from the straight- to crooked-types might have occurred in the mother trees from which these mutants originated because their cytoplasms are not the Flying Dragon-type.

Flying Dragon is regarded as a promising dwarfing rootstock. However, the population from its seed includes a high percentage of zygotic seedlings (0 to 76% (Khan and Roose, 1988) and 47% (Yoshida, 1994)). Therefore, the high percentage makes it difficult to obtain uniform seedlings. The average embryo number (an average of 50 seeds) of Flying Dragon in this study was about 5. The crooked-type seedlings in the progenies of Flying Dragon were monoembryonic and polyembryonic; their embryo count among polyembryonic seedlings varied from 1.6 to 8.6. It is possible that some of the seedlings produce zygotic ones at a low rate. Among the progeny seedlings of Flying Dragon planted in the field, all crooked-type seedlings were dwarfish and had a smaller canopy than those of the common trifoliate orange, whereas the vigor of straight-type seedlings varied from strong to weak. Among the straight-type seedlings, the polyembryonic ones should be evaluated to determine whether they should be used as dwarfing or vigorous rootstocks, according to the top growth of the grafted scion cultivars.

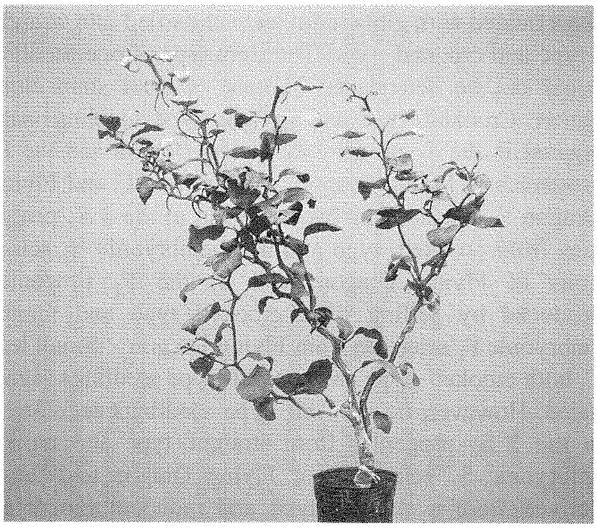

Fig. 4. Grafted tree of RP-137M, a bud sport with crooked twigs and thorns.

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ヒリュウ (*Poncirus trifoliata* var. *monstrosa* (T. Ito) Swingle) にみられる枝ととげの屈曲性の遺伝

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摘　要

ヒリュウにみられる枝ととげの屈曲性の遺伝様式について検討するため，ヒリュウを含むカラタチの品種・系統やカンキツ属植物の自殖や交雑により生じた実生個体群について，1年生時に枝ととげの形態を調査した．枝ととげの屈曲型と直立型の分離状況は正逆交雑で違いが認められ，屈曲型の個体は種子親がヒリュウの細胞質を持つ個体群のみで生じた．屈曲型を分離した個体群では直立型も分離したことから，枝ととげの屈曲性の遺伝には細胞質と核遺伝子が関与し，細胞質と核遺伝子が共に屈曲型の場合に屈曲型が発現すると考えられた．核遺伝子について，枝ととげの屈曲を促す3対の補足遺伝子 (Cr_1, Cr_2, Cr_3) を想定し，ヒリュウの遺伝子型を $Cr_1cr_1Cr_2cr_2Cr_3cr_3$ とする仮説は，1個体群を除いて供試した個体群における分離比と矛盾しなかった．