Paraquat Resistance in Erigeron *philadelphicus* L.

By KAZUYUKI ITOH

Project Research Team 1st, National Agriculture Research Center
(Tsukuba, Ibaraki, 305 Japan)

Introduction

Shortly after the introduction of herbicides for weed control, Harper[4] predicted that repeated use of the same herbicide would be almost inevitably followed by the development of a resistant biotype of weed, as often happened with pesticides and insecticides. Many reports have been published concerning variations within weed species in response to herbicides. However, the development of resistance due to repeated herbicide treatment was not as rapid as expected. In 1968, the first case of resistance development was reported by Ryan[8] in Washington State on *Senecio vulgaris* grown in a nursery where atrazine and simazine had been used once or twice annually since 1958. Now, we know that repeated use of herbicides causes herbicide resistant biotypes by new selection pressure in weedy plants.

Discovery of the biotype resistant to paraquat and diquat

In 1980, the present author and his co-workers obtained information that the control of *Erigeron philadelphicus* (Philadelphia fleabane) has become increasingly difficult in mulberry fields located on the river land of the Arakawa River at Fukiage, Saitama Prefecture. Replies to questionnaires distributed to mulberry growing farmers in that area revealed that paraquat had been applied 2 or 3 times annually during the preceding 8–11 years. Then, we presumed that the new biotype resistant to paraquat comes to appear approximately 5–6 years after paraquat was introduced to their mulberry fields[10].

In the field experiments conducted at the sites infested with *E. philadelphicus* resistant to paraquat, the resistant plants were killed by generally recommended dosages of bentazon,

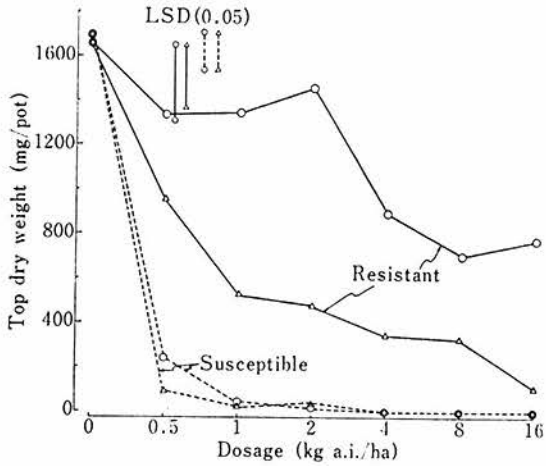


Fig. 1. Relationship between doses of paraquat (○) and diquat (△) applied and top dry weight of tested plants 10 days after application (Y. Watanabe et al., 1982)

Table 1. Control of paraquat resistant *Erigeron philadelphicus* in a mulberry field with several herbicides applied at recommended doses

Herbicide	Rate (kg a. i./ha)	Top dry weight (g/m²)
Paraquat-dichloride	0.96	93.9
Paraquat-dimethylsulphate	1.14	102.7
Bentazon	6.00	8.1
MCP-sodium	0.39	25.9
Glyphosate	4.10	0
Check	—	92.8

(Y. Watanabe et al., 1982)

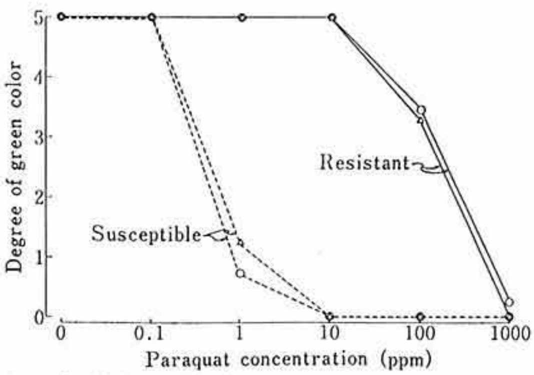


Fig. 2. Relationship between paraquat concentration and retention of green color of radical leaf (○) and stem leaf (△) disks, after dipping in herbicide solution for 48 hr (Y. Watanabe et al., 1982)

glyphosate and MCPA, showing that they are non-resistant to these herbicides (Table 1).

Then, the response to paraquat and diquat was compared between the paraquat resistant plants and the normal susceptible plants originated from a site where paraquat had not been sprayed. As shown in Fig. 1 and Plate 1, the susceptible plants were quite sensitive to paraquat and to diquat. The dosage of 1 kg a.i./ha was sufficient to kill completely green leaves of the susceptible plants. On the other hand, resistant plants treated with paraquat at a rate of 0.5 to 2.0 kg a.i./ha showed none of the symptoms observed in the susceptible plants. They retained a few green leaves even at a rate of 16 kg a.i./ha. The paraquat resistant plants had also developed the resistance to diquat.

An experiment to examine the response of leaf disks to various concentrations of paraquat solution was carried out. The result given in Fig. 2 clearly shows that the extent of the resistance to paraquat of the resistant plants of *E. philadelphicus* is 100 times higher than that of susceptible plants.

Distribution and ecological fitness of the resistant biotype

The survey of mulberry fields on the river land of the Arakawa River conducted in April 1981 clarified the distribution of paraquat resistant biotype as shown in Fig. 3. The

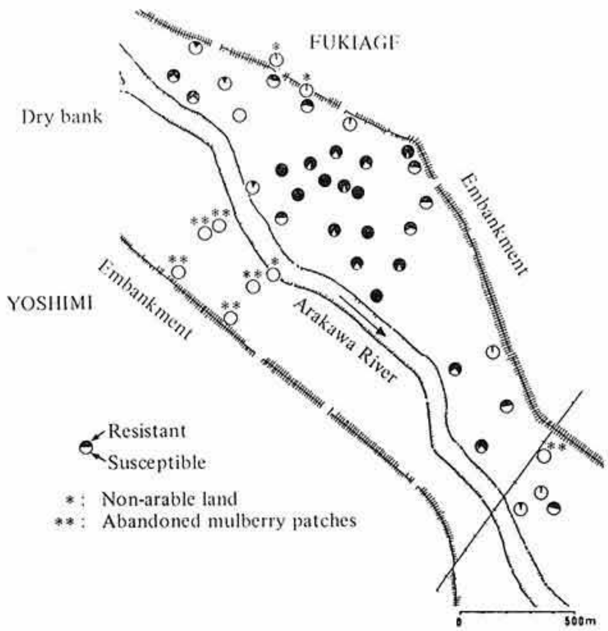


Fig. 3. Distribution of paraquat resistant biotype of *Erigeron philadelphicus* in mulberry fields on the river land of the Arakawa River in April 1981 (Watanabe et al., 1982)[11]

Table 2. The mean ratio of the occurrence of paraquat resistant biotype to the total number of plants examined of *Erigeron philadelphicus* under different frequencies of paraquat application

Paraquat application	Land utilization	No. of samples	Mean ratio of resistant biotype
Never applied	Vacant[a)]	10	2.1 (%)
2–3 years ago	Abandoned mulberry patches	2	0.0
Sometimes[b)]	Vicinity of mulberry patches	14	47.5
2–3 times every year	Mulberry patches	24	80.5

Determined in April, 1982.
a): Embankment, unused land, etc.
b): Sometimes receiving paraquat due to drift or boundary application in adjacent mulberry patches.

existence of the paraquat-resistant biotype was clearly demonstrated as shown in Plates 2 and 3. It seems that this area was a center of the resistant biotype development. After this time, the distribution has spread all over the whole area. The resistant biotype of *E. philadelphicus* has come to be detected not only in mulberry fields but also in chestnut fields, tea fields and abandoned fields due to repeated application of paraquat. And now, the resistance comes to be observed even in other species of weed such as *Erigeron canadensis* L.[7)], *E. sumatrensis* Retz.[3)] and *Youngia japonica* D.C.[3)]. It suggests that their resistance occurred concurrently and in many places.

On the basis of the information obtained by interviews with mulberry growers, the relation between the number of paraquat-resistant plants (in percentage to the total number of plants examined) and the frequency of paraquat application was determined as shown in Table 2. In the mulberry patches where paraquat was applied every year, the percentage of paraquat resistant biotype population was the highest (Plate 3), while in areas which had been left unused without paraquat application the percentage was very low. It is very interesting that the paraquat-resistant biotype was not detected in areas where mulberry cultivation was abandoned only 2–3 years ago. This fact seems to suggest that the resistant biotype is less competitive with the normal susceptible one in the absence of paraquat application. It implies that the resistant biotype is lower in ecological fitness than the normal biotype, similar to the case of atrazine resistant biotypes of *Senecio vulgaris* and *Amaranthus retroflexus*[1)]. Since a competitive study has not been carried out between the two biotypes of *E. philadelphicus* in the absence of paraquat, future studies are needed to determine whether the competitive ability of the susceptible biotype is superior to the resistant one.

Inheritance of the resistance

Seedlings at the 1.5 leaf stage, derived from resistant* or susceptible plants of *E. philadelphicus* were treated (foliar spray) with varying concentrations of paraquat. For the susceptible seedlings, the range of the concentration from 0.0039 to 0.5 kg a.i./ha was used, while that from 0.031 to 16.0 kg a.i./ha was used for resistant seedlings. The number of seedlings killed was given in Fig. 4. The dose of paraquat to kill the resistant seedlings was 250 times higher than that for the susceptible seedlings. The paraquat solution at a concentration of 0.5 kg a.i./ha was sufficient to classify the seedlings as resistant or susceptible (Fig. 4).

Preliminary experiments on the manner of reproduction of *E. philadelphicus* showed that

* Paraquat resistant plants were sampled from mulberry patches on the river land of the Arakawa River.

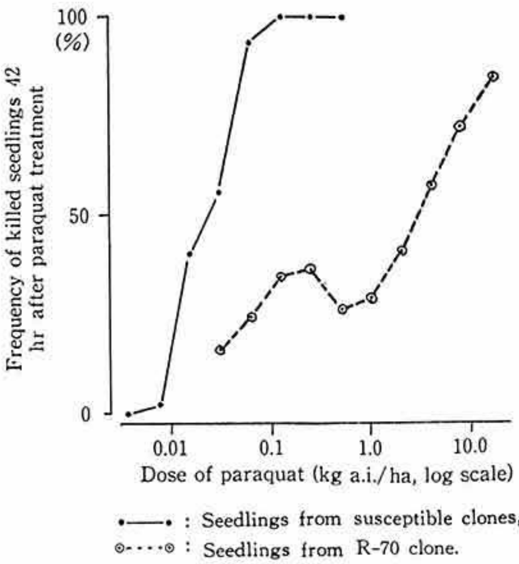


Fig. 4. Mortality of *Erigeron philadelphicus* seedlings derived from a resistant clone and from susceptible clones after foliar spray of paraquat

the percentage of self-pollination and apomixis was less than 1.0% in (1), (2-b) and (2-c) in Table 3. In contrast, values for the cross between different clones of the same biotype (2-d) and between different biotypes (2-e), were 34.7 and 39.7, respectively. The percentage values were high, and the number of developed seedlings per head averaged 115.

Segregation of the phenotype in the F_1 population of the crosses, S × S, S × R, R × S and R × R, in 1982 and 1983 (Table 4 and Plate 4) and that in the test crosses in 1983, furnished good evidence that a single dominant gene is responsible for the paraquat resistance in *E. philadelphicus*, although many species of weed show uniparental (maternal) inheritance of *s*-triazine resistance[2,9]. Thus, the occurrence of paraquat resistant biotype might not be due to an original intraspecific variation, but due to mutation of a gene.

The present study showed clearly that the

Table 3. Germination rate of progenies derived from selfing and allogamy in *Erigeron philadelphicus*

Crossing treatments	(1) In a head	(2-a) No crossing	(2-b) In a plant	(2-c) In a clone	(2-d) Between clones	(2-e) Between biotypes
No. of heads used	18	20	13	7	26	15
Mean no. of florets/head	517*	309	329	278	323	306
Mean no. of germination achenia/head	0.1	0.6	2.2	1.9	112.2	119.6
Mean germination ratio**(%)	0.02	0.2	0.7	0.7	34.7	39.7

* Disk- and ray-florets. ** Mean number of germination achenia/mean number of florets.

Table 4. Segregation ratio in F_1 population of four kinds of crosses between paraquat resistant (R) and susceptible (S) clones of *Erigeron philadelphicus* in 1982 and 1983

Parental clone Female Male	No. of F_1 heads	Total no. of seedlings	No. of survived seedlings	No. of dead seedlings	Expected ratio* (R : S)
S × S	15	1882	1	1881	0 : 1
S × R hetero	3	433	211	222	1 : 1
S × R homo	2	242	238	4	1 : 0
R hetero × S	15	1791	893	898	1 : 1
R homo × S	1	138	138	0	1 : 0
R hetero × R hetero	17	1939	1449	490	3 : 1
R hetero × R homo	11	1193	1179	14	1 : 0
R homo × R homo	9	1216	1211	5	1 : 0

* Single dominant gene.
S : Part or total of S–8, 15, 17, 22 and 45 clone.
R hetero : Part or total of R–31, 50, 70 and 74 clone.
R homo : Part or total of R–13 and 60 clone.

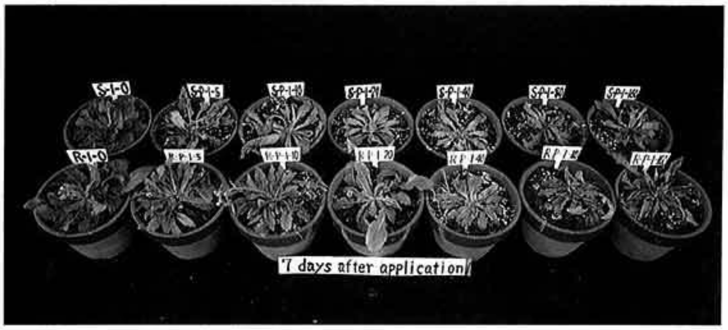
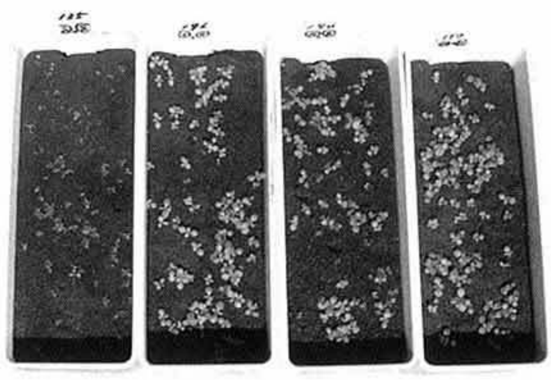


Plate 1. Relationship between doses of paraquat and damage of resistant plants (lower) and susceptible ones (upper) 7 days after application
Doses of paraquat (from left to right):
Upper line; 0, 5, 10, 20, 40, 80, 160 (g a.i./a)
Lower line; 0, 5, 10, 20, 40, 80, 160 (g a.i./a)

Plate 2. The state of weeds in a mulberry patch 2 or 3 days after paraquat spray
Green plants at the center are resistant biotype.

Plate 3. *E. philadelphicus* survived under repeated application of paraquat. All weeds disappeared except the resistant biotype of *E. philadelphicus*.



S x S S x R R x S R x R

Plate 4. The state of F_1 population of indicated crosses 3 days after the paraquat treatment (0.5 kg a.i./ha) showing the inheritance of paraquat resistance

resistant plants are developed not only from the achenia or ramets of resistant clones but also from the pollination with pollens from resistant plants which can be done by various insects.

In the field where the resistant biotype of *E. philadelphicus* exists, other kinds of herbicides or other methods of weed control must be employed.

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