INSTITUTE OF ECOLOGY-POLISH ACADEMY OF SCIENCES

EKOLOGIA POLSKA

Vol. XIX Warszawa 1971 No. 36

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THE ROLE OF SOME ECOLOGICAL FACTORS IN THE DEVELOPMENT OF PESTICIDE RESISTANCE IN *SITOPHILUS ORYZAE* L. AND *TRIBOLIUM CASTANEUM* HERBST.

(Ekol. Pol. 19: 563–616). The author studied the effect of some factors such as: temperature, relative humidity, diet, sex and age, on the process of development of resistance to Metasystox, Azotox and Pybuthrin in *Sitophilus oryzae* L. and *Tribolium castaneum* Herbst. Pesticide tests were carried out at the level LC_{50} for 10, up to 25 generations of beetles.

Contents

I. INTRODUCTION

The resistance of insects to pesticides has been known since the last years of the 19th century, but it was only after World War II that it became important. The resistance forming phenomenon is an ever-growing process due to the rapid development of plant protection by pesticides. The number of insect species with signs of insecticide resistance increases from year to year and in consequence the actual task of plantprotection becomes more difficult. Search has been continued, for many years, for ways of counteracting the disastrous consequences of the pesticide resistance developing phenomenon. To gain some success it is necessary to know the mechanisms of resistance formation, and the related enzymatic processes of breaking up the insecticides. Research works, which in fact started in this area, have not hitherto given a complete solution to this extremely difficult and complex problem.

In recent years more and more attention has been given to the role of ecological factors in the development of insecticide resistance in insects. This line of investigations seems to be particularly important.

In the literature papers can be found concerned with the effect of ecological factors on the resistance of insects to insecticides. Godan's investigations (1964) of *Drosophila melanogaster* Mg. have shown that population density has a clear effect on the susceptibility of the different developmental stages to insecticides. Gilbert, Couch and Mc Duffie (1953) found that in autumn the flies were more resistant to DDT and Lindan than in spring and summer. Wiesmann (1957) attributed this fact to the effect of temperature. According to him the break.up of DDT into DDE to a great extent depends on temperature. Other authors, e.g. Johnston, Bogart and Linquist (1954) relate the influence of temperature to its effect on the length of the life cycle. Other effects of the environment have also been described. Bacon, Reley and Zweig (1964), who studied the susceptibility of *Lygus hesperus* Knight to DDT and Toxaphen, have found that insects collected in fields with alfalfa in flower were less susceptible to DDT than insects collected from harvested crops.

Another factor influencing the susceptibility of insects to insecticides is diet. The experiments carried out by Rivera and Steinhauer (1962) and Zscheintzsch (1966) with *D. melanogaster* Mg. have shown that when cultvated in different media, this species revealed a variable insecticide tolerance in regard to halogen-derivatives. Similar data has been reported in Henneberry's study (1964) concerning *Tetranychidae.*

Insecticide resistance in insects depends also on the developmental stages, sex and age. In their studies on the effect of different pesticides on various insect species Saikeld and Potter (1953) and Largenmüller (1957) have found that eggs are more resistant than the larvae. Krohne and Lindgren (1958), who carried out tests with *S. oryzae*, have found that the most resistant in relation to methyl bromide are eggs, pupae, adults, larvae being the least resistant of all. Kerr (1954) found that *Drosophila melanogaster* Mg. females were more resistant than males, and that in this species susceptibility increases with the age of the individuals.

Pest control methods should be based on the practical application of the achievements of ecology, one of which is the possibility of modifying the environment so as to make it less favourable to the pests. Of particular importance are studies on the effectiveness of pesticides in relation to some ecological factors such as population factors and environmental factors.

The aim of the studies here presented was to establish the effect of some ecological factors such as environmental factors temperature, relative air humidity, diet, and population factors: age and sex, on the development of insecticide resistance. The author intended to find whether there exists any difference in resistance, related to different ecological conditions of laboratory cultures, as well as to the sex and age of the insects.

II. METHODS

1. Culture of test insects

For the tests individuals of the following two beetle species were used: *Sitophilus oryzae* L. and *Tribolium castaneum* Herbst. The beetles used for the experiments came from populations which had been cultured in the Institute of Ecology for many years. Thus the original material was uniform. During the setting of the cultures different conditions were applied, whereas the test conditions were the same in all experiments.

S. oryzae and *S. granarius* cultures were carried out according to the method published by Sandner (1960). The beetles were kept in bakelite boxes, 40 adult individuals per a box. Each box contained 50 g of food. In the series used for diet experiments the following kinds of food were used: wheat, rye, barley, hulled barley, and in the remainder of experiments only wheat. The imagines were kept in the food-containing boxes for 25 days. After removing the individuals of the original generation the boxes were examined every two days and the beetles of the daughter generation were selected for tests.

T. castaneum was also cultured in bakelite boxes, each box containing 50 g of medium consisting of 95 parts of flour and 5 parts of dry yeast (Park 1934). In each of these boxes 30 adult *T. castaneum* were placed and 25 days there after all the members of the original generation were removed. To test the effect of temperature and humidity the cultures were placed in thermostats, where 3 different variants of temperature and relative air humidity were maintained. Variant I: 25°C and 75% relative air humidity; Variant II: 30°C and 75% relative air humidity; Variant III: 30°C and 55% relative air humidity. Under these conditions the beetles were cultured (depending on the species) for 10 up to 25 generations.

To study the relationship between the development of resistance and sex the sex of the pupae of *T. castaneum* was determined, and the adult forms that emerged from them were treated with the pesticide, males and females separately.

To find the relationship between the development of resistance and age 2 lines of adult *T. castaneum*, aged 1–3 days, and 15 days, were tested with Pybuthrin.

In every generation of *S. oryzae* and *T. castaneum* selection of imagines was carried out using Metasystox, Azotox and Pybuthrin. The selection of all the insects was carried out at the level of LC_{50}. As controls, in all the variants non-treated cultures were continued in three repetitions. These represented a continuation of the insecticide susceptible original population.

2. Description of the pesticide used

The following pesticides were used: a) Azotox 33, containing 33% of technical DDT in an organic solvent with an addition of backing substances, b) Metasystox "i", containing about 50% of thiolic methyl-demeton isomer, c) Pybuthrin 6/60, containing 6% of pyrethrins and 60% of piperonyl butoxide.

The reason for selecting the three pesticides was that they represent three different groups of compounds: 1. phosphoric organic insecticides – Metasystox, 2. chlorinated hydrocarbons – Azotox, 3. pyrethrins – Pybuthrin. Azotox and Pybuthrin are used as grain-store pest control substances.

3. Testing techniques

The insects were treated with water emulsions of the pesticide at concentrations from 0.001 up to 2%. Following Goos' recommendations (1961), the pesticide was transferred onto qualitative filter paper of average filtration rate, placed in Petri dishes 10 cm in diameter. In each dish 50 adult *S. oryzae* or *T. castaneum* were kept. Tests were carried out in 3–5 dishes, 50 imagines in each. Every generation was subjected to 3–5 pesticide concentrations. In control dishes the beetles were placed on filter paper moistened with 1 ml water. The insects remained in contact with the pesticide, or water, for 72 hours. Subsequently, dead individuals were counted and removed. All tests were carried out under identical conditions at room temperature and at the same time of the day. Mortality values were corrected by using Abbot's (1925) formula:

$$S_{sk} = \frac{100\,(P_o - P_k)}{100 - P_k}$$

where: S_{sk} – corrected mortality rate, P_o – observed mortality rate, P_k – mortality rate of the controls.

During the 4-year period 164 thous. individuals of *S. oryzae* and 117 thous. *T. castaneum* were tested.

For the elaboration of the results the statistical method of Litchfield and Wilcoxon (1949), developed by Bojanowska (1961), was used. Mortality lines for individual generations were drawn on logarithm-probits paper, and LC_{50} was determined. Then the last generations of the insect populations concerned were compared in regard of the level of their resistance. For the straight lines Pearson's criterion, the so-called empirical Chi^2 (which was then compared with the tentative Chi^2) was evaluated, and the slope of lines "*S*" was calculated. That is how the real position of the straight lines was found. The level of resistance of individual populations, according to the formula:

$$R = \frac{LC_{50}\,R}{LC_{50}\,W}$$

was calculated, where: *R* – resistant population, *W* – susceptible population. The confidence limits were then found for LC_{50} and *R* for $P = 0.95$.

The effect of the variable parameters of individual experiments was determined by the ratio of the average lethal concentrations of the populations compared:

$$PR = \frac{LC_{50}\, I}{LC_{50}\, II}$$

Elsewhere in the paper *PR* will be referred to as susceptibility ratio. Further on, the significance of the differences was determined as follows:

If $PR \geqslant f_{PR}$ then the difference is significant

If $PR \leqslant f_{PR}$ then the difference is not significant

Where: *f* is the suceptibility ratio factor (as read from the nomogram).

Differences in susceptibility were calculated and interpreted in relation to the dose that caused 50% mortality among the insects, i.e. the average lethal concentration. This approach was also applied in all those cases where the regression lines were not parallel, and the dose ratios for different mortality rates (16%, 50% and 84%) varied.

In accordance with the interpretation commonly accepted by toxicologists it has been assumed that if the straight lines representing mortality are parallel, i.e. do not differ in slope "*S*" then the cause of mortality is even.

Two straight lines are considered to be parallel if their slope ratio (*SR*) is less or equal to the factor for the straight line slope ratio (f_{SR}). If $SR \leqslant f_{SR}$ then with probability 0.95 the straight lines were assumed to be parallel.

III. THE COURSE OF TESTS AND THE RESULTS

1. The effect of temperature on the development of resistance in insects

In the temperature series tests were performed with the following two species used as tests insects: *Sitophilus oryzae* L. and *Tribolium castaneum*

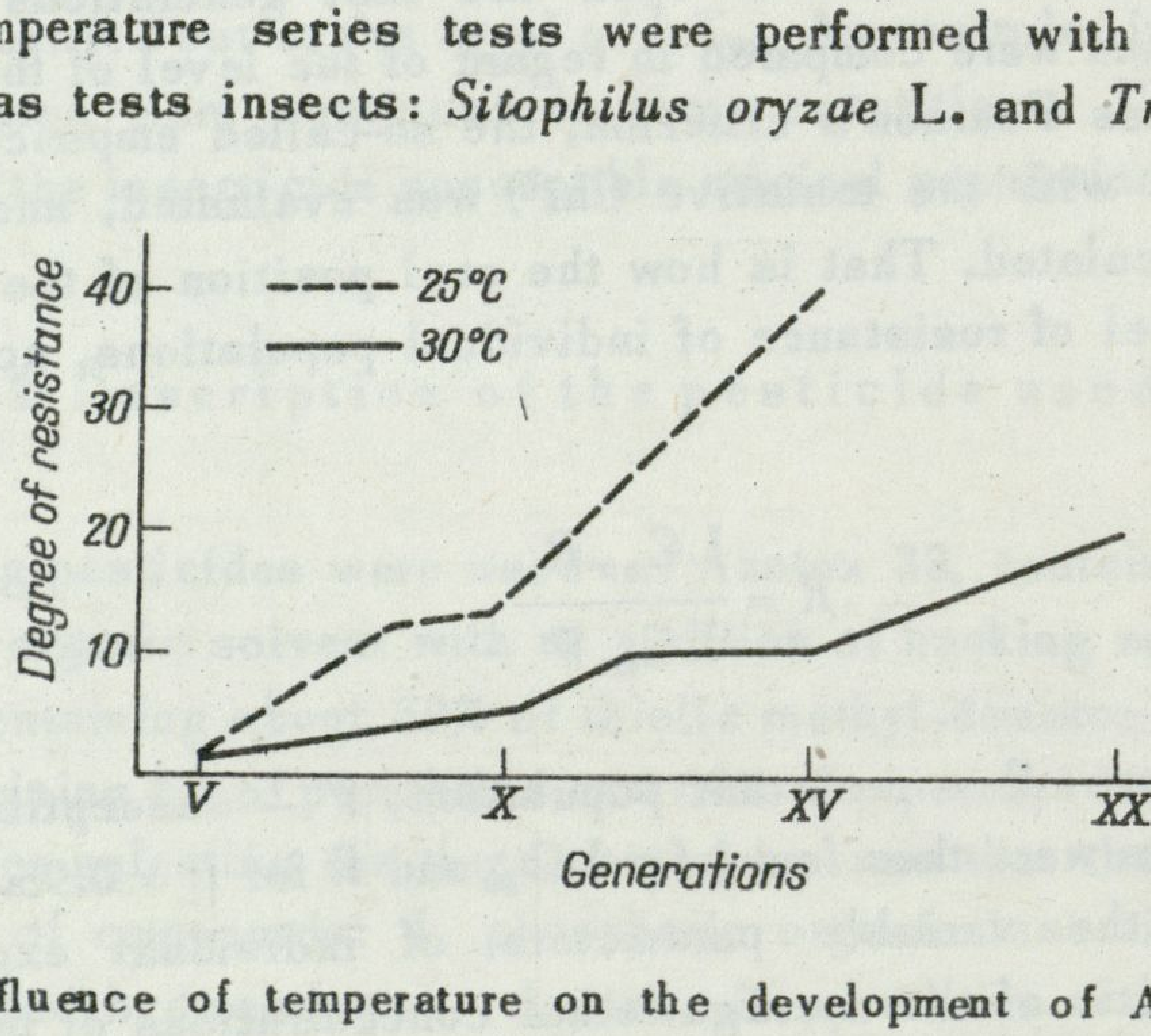

Fig. 1. The influence of temperature on the development of Azotox resistance in *S. oryzae*

Course of development of Azotox resistance in *S. oryzae* in relation to temperature

Tab. I

Generation	Temperature 25°					Temperature 30°				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance
Original population	0.0005	0.0006–0.0005	2.28	2.62–1.98		0.0005	0.0006–0.0005	2.28	2.62–1.98	
V	0.0012	0.0013–0.0011	1.54	1.61–1.39	2.40	0.0009	0.0009–0.0008	1.47	1.57–1.38	1.80
VIII	0.0068	0.0075–0.0062	2.24	2.53–2.04	13.60	0.0018	0.0019–0.0017	1.76	1.88–1.64	3.60
X	0.0070	0.0073–0.0066	1.69	1.79–1.59	14.00	0.0025	0.0026–0.0024	2.13	2.98–1.52	5.00
XII	0.0140	0.0149–0.0130	1.78	1.88–1.67	28.00	0.0044	0.0046–0.0042	1.62	1.78–1.47	9.20
XV	0.0200	0.0220–0.0182	2.16	2.41–1.93	40.00	0.0050	0.0054–0.0045	2.18	2.40–1.98	10.00
XX						0.0100	0.0110–0.0090	2.31	2.54–2.10	20.00

Susceptibility ratio of 15th generations – 4 (4.40–3.70); f/PR – 1.10.

Herbst. Permanent relative humidity of air was maintained at 75% (±1). The development of resistance to Azotox, Metasystox and Pybuthrin at 25°C and 30°C (±1°C) was investigated.

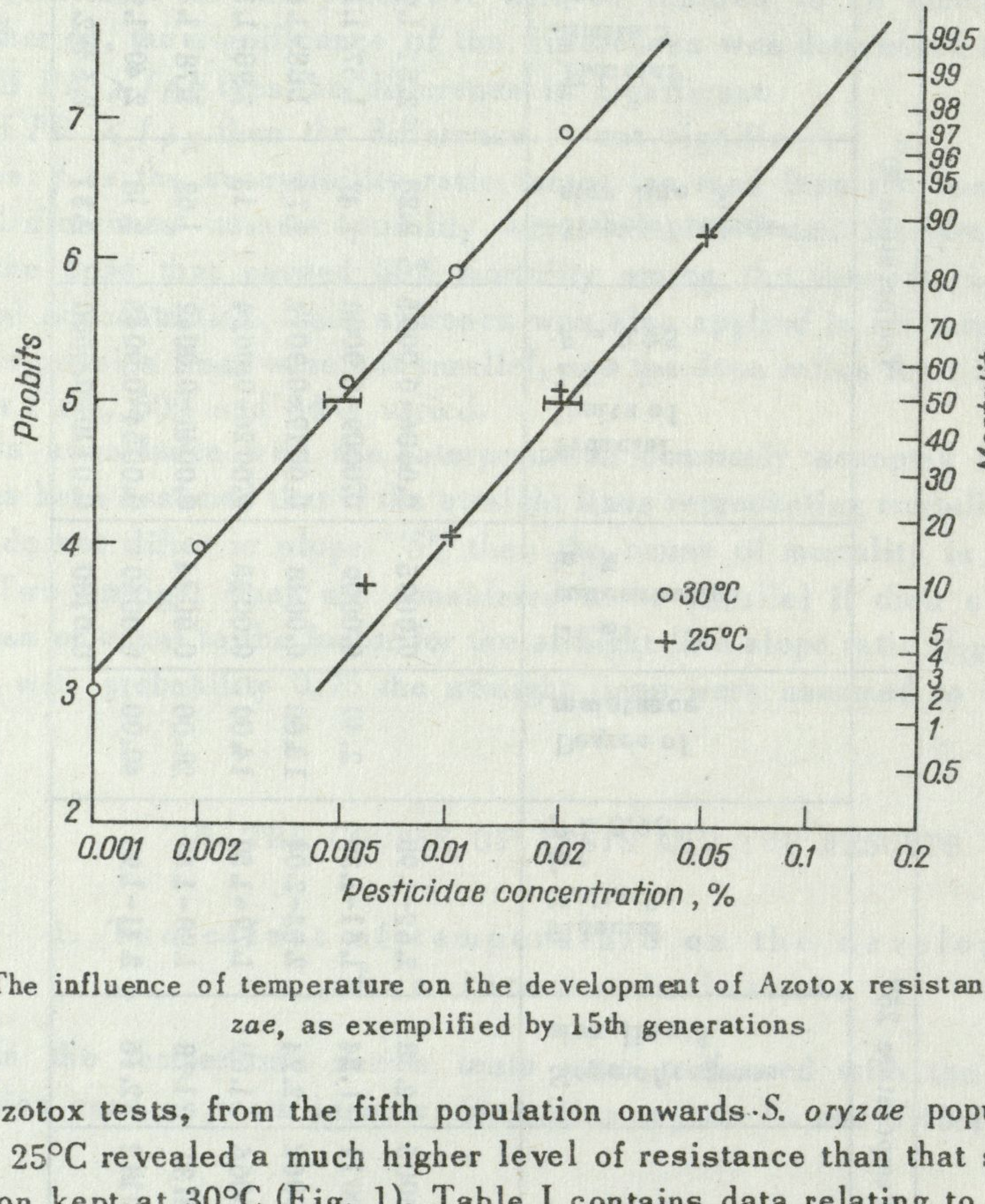

Fig. 2. The influence of temperature on the development of Azotox resistance in *S. oryzae*, as exemplified by 15th generations

In Azotox tests, from the fifth population onwards *S. oryzae* population cultures at 25°C revealed a much higher level of resistance than that seen in the population kept at 30°C (Fig. 1). Table I contains data relating to changes in LC_{50}, course of the straight lines illustrating the changes in susceptibility of the individuals of particular generations, and changes in resistance levels. The straight lines in Figure 2 show changes of susceptibility in *S. oryzae* adults, Azotox-treated for 15 generations at two different temperatures. The lines are parallel, that is their slope "*S*" is the same, which indicates that the course of mortality was the same. The susceptibility of the population kept at 30°C is accordingly higher than that of the population cultured at 25°C. The susceptibility ratio of the beetles if the fifteenth generations in both variants of the experiment is 4. As it follows from this data, at 25°C the development of Azotox resistance in *S. oryzae* is much more faster that at 30°C. Similar to that is the development of Metasystox resistance in this species. The graph (Fig. 3)

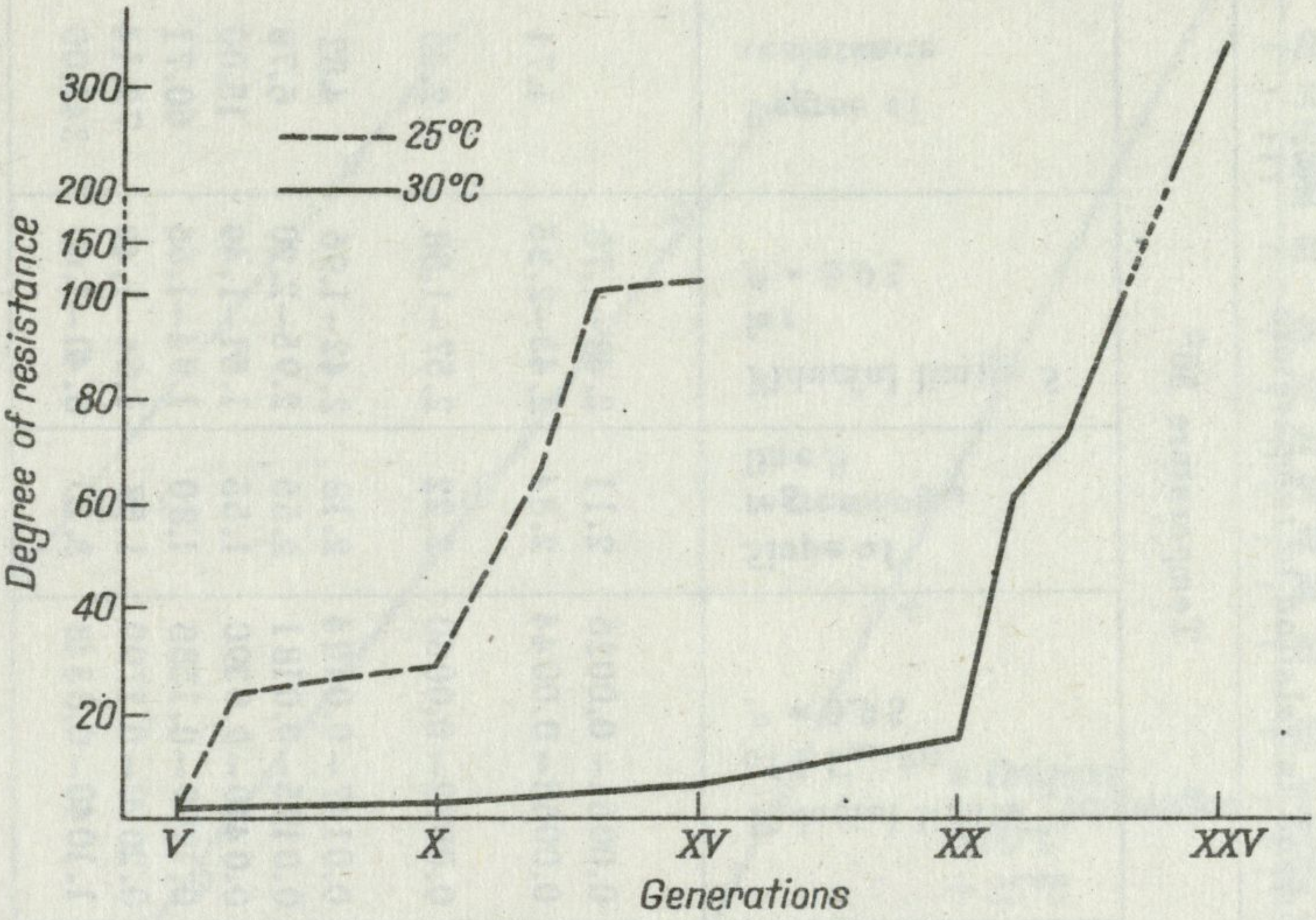

Fig. 3. The influence of temperature on the development of Metasystox resistance in *S. oryzae*

illustrates the effect of temperature on the development of Metasystox resistance in adult *S. oryzae*, and Table II – the changes of LC_{50} value, regression lines, and the resistance in the two populations investigated (cultured at 25°C and at 30°C). Figure 4 shows regression lines representing changes in resistance in the adults of the fifteenth generations of the two populations concerned, in relation to Metasystox concentration. As can be assumed from the data in Table II, Metasystox resistance of adult *S. oryzae* cultured at 25°C is produced at a much higher rate than in the populations cultured at 30°C. The degree of resistance for the fifteenth generations of the population cultured at 25°C is 114.28, and for the population cultured at 30°C only 6.78. The susceptibility ratio for the fifteenth generations is 16.84.

The effect of temperature on the production of Pybuthrin resistance in *S. oryzae* is much less pronounced than in the case of Azotox and Metasystox, but some effect no doubt exists.

The curves in Figure 5 represent the effect of temperature on the development of Pybuthrin resistance in *S. /oryzae.* In Table III are presented LC_{50} values, the course of regression straight lines and resistance levels for both populations. The graph (Fig. 6) shows the susceptibility of the populations treated with Pybuthrin for eighteen generations. The respective straight lines are not parallel, which indicates that the course of mortality at the given temperatures was not even. When the straight lines are compared at the level of

Tab. II

Course of development of Metasystox resistance in *S. oryzae* in relation to temperature

Generation	Temperature 25°					Temperature 30°				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance
Original population	0.0028	0.0031–0.0026	2.11	2.48–1.78		0.0028	0.0031–0.0026	2.11	2.48–1.78	
V	0.0050	0.0053–0.0048	1.64	1.97–1.37	1.78	0.0048	0.0053–0.0044	2.34	2.43–2.25	1.71
VI	0.0660	0.0713–0.0611	1.68	1.84–1.53	23.57					
X	0.0830	0.0888–0.0776	1.54	2.08–1.14	29.64	0.0066	0.0072–0.0060	2.22	2.57–1.88	2.36
XII	0.1900	0.2109–0.1711	1.67	2.17–1.36	67.85					
XIII	0.2850	0.3078–0.2549	1.83	1.99–1.67	101.79	0.0135	0.0147–0.0124	2.18	2.42–1.96	4.82
XV	0.3200	0.3392–0.3019	1.68	1.79–1.48	114.28	0.0190	0.0195–0.0181	2.55	2.95–2.20	6.78
XX						0.0420	0.0440–0.0390	1.55	1.61–1.49	15.00
XXI						0.1700	0.1809–0.1588	1.80	1.94–1.66	60.71
XXII						0.1850	0.2020–0.1700	1.58	1.64–1.49	72.14
XXV						0.9600	1.1040–0.8348	3.20	6.40–1.60	343.00

Susceptibility ratio of 15th generation – 16.84 (18.52–15.31); *f/PR* – 1.1.

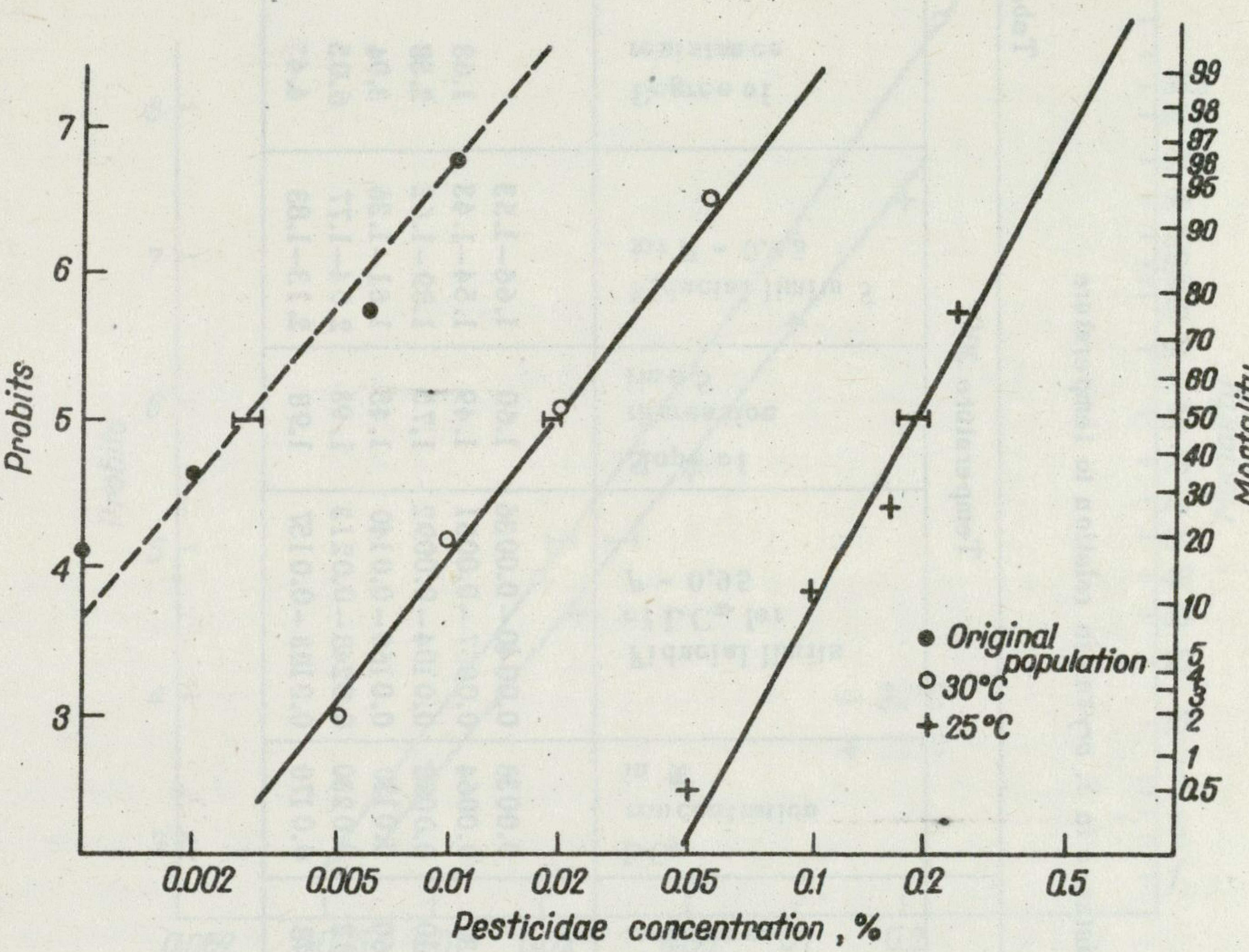

Fig. 4. The influence of temperature on the development of Metasystox resistance in *S. oryzae*, as exemplified by 15th generations

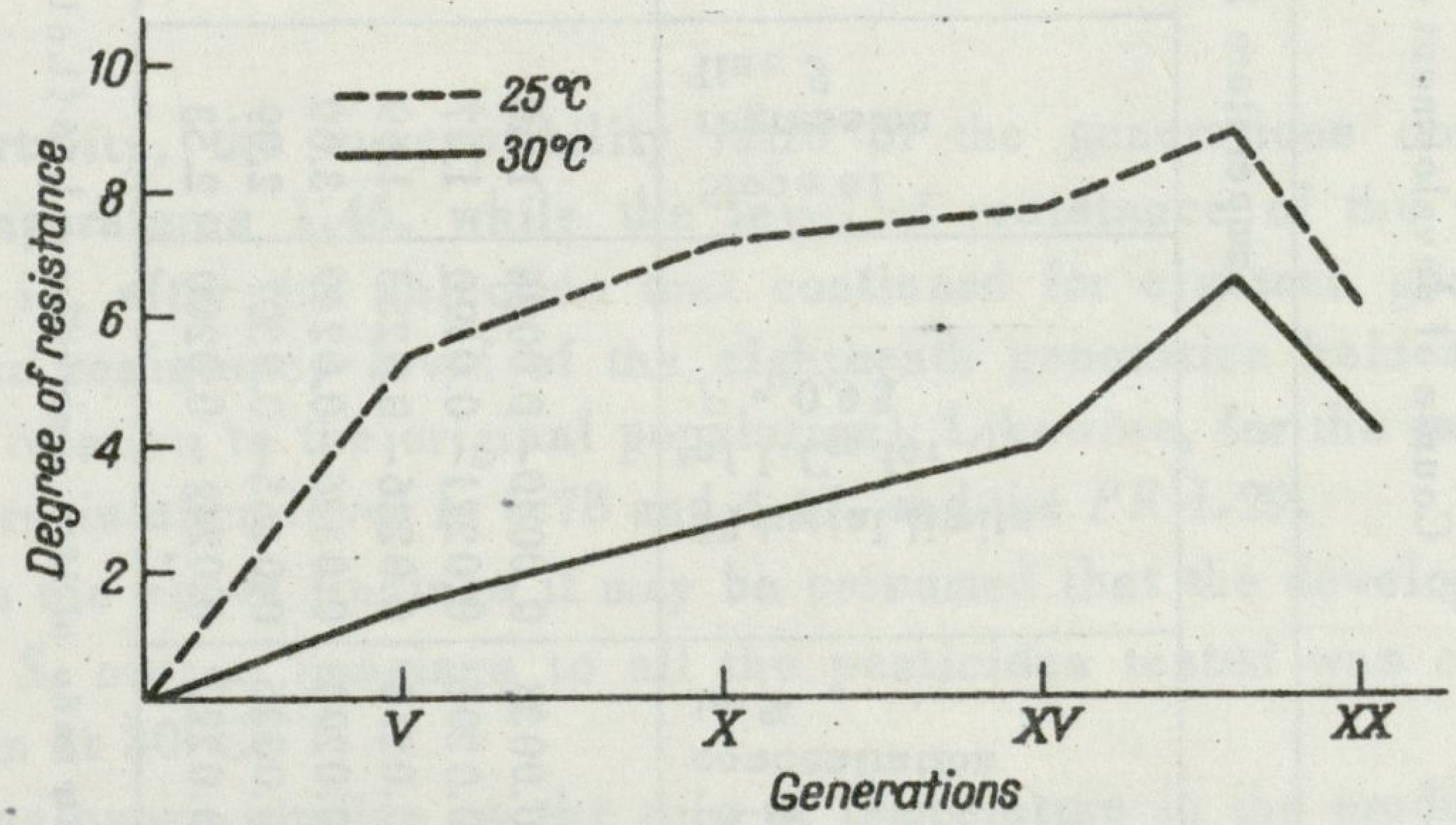

Fig. 5. The influence of temperature on the development of Pybuthrin resistance in *S. oryzae*

Course of development of Pybuthrin resistance in *S. oryzae* in relation to temperature

Tab. III

Generation	Temperature 25°					Temperature 30°				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance
Original population	0.0038	0.0040–0.0036	1.60	1.66–1.53		0.0038	0.0040–0.0036	1.60	1.66–1.53	
V	0.0205	0.0221–0.0190	1.97	2.21–1.76	5.39	0.0064	0.0067–0.0061	1.49	1.54–1.43	1.68
X	0.0270	0.0286–0.0253	1.69	1.75–1.54	7.10	0.0098	0.0104–0.0092	1,75	1.89–1.62	2.58
XV	0.0290	0.0336–0.0249	3.60	4.50–2.88	7.60	0.0150	0.0160–0.0140	1.45	1.61–1.36	3.94
XVIII	0.0335	0.0365–0.0307	2.09	2.30–1.90	8.82	0.0230	0.0248–0.0213	1.93	2.04–1.77	6.05
XX	0.0220	0.0242–0.0200	2.53	2.83–2.26	5.78	0.0170	0.0183–0.0157	1.98	2.13–1.83	4.47

Susceptibility ratio of 18th generation – 1.46 (1.61–1.33); *f/PR* – 1.1.

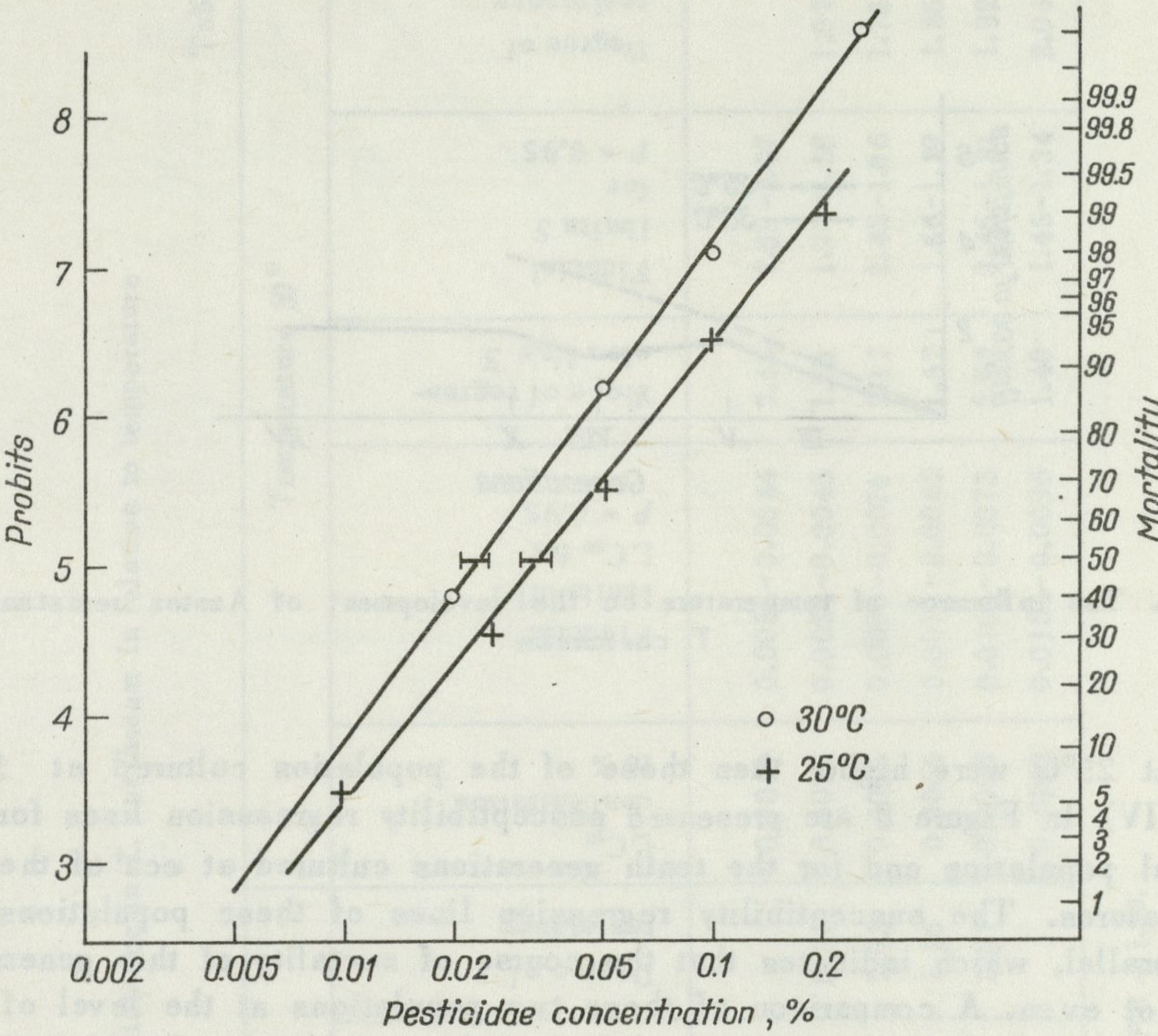

Fig. 6. The influence of temperature on the development of Pybuthrin resistance in *S. oryzae*, as exemplified by 18th generations

50% mortality, the susceptibility ratio of the generations considered is for both temperatures 1.46, while the level of resistance of the population kept at 25°C is, after the selection that continued for eighteen generations, 8.82, while the resistance level of the eighteenth generation held at 30°C is only 6.05 (in relation to the original population). Likewise, for the twentieth generation the resistance level is 5.78 and 4.47, and the *PR* 1.29.

From the above findings it may be presumed that the development of resistance in *S. oryzae* imagines to all the pesticides tested was clearly faster at 25°C than at 30°C.

In analogous studies on the role of temperature in the production of resistance to Azotox, Metasystox and Pybuthrin in adult *T. castaneum* in cultures at 25°C only 10 generations were obtained. The graph in Figure 7 shows the course of Azotox resistance development in adult *T. castaneum* at 25°C and 30°C. From the fifth generation onwards the resistance levels of the population

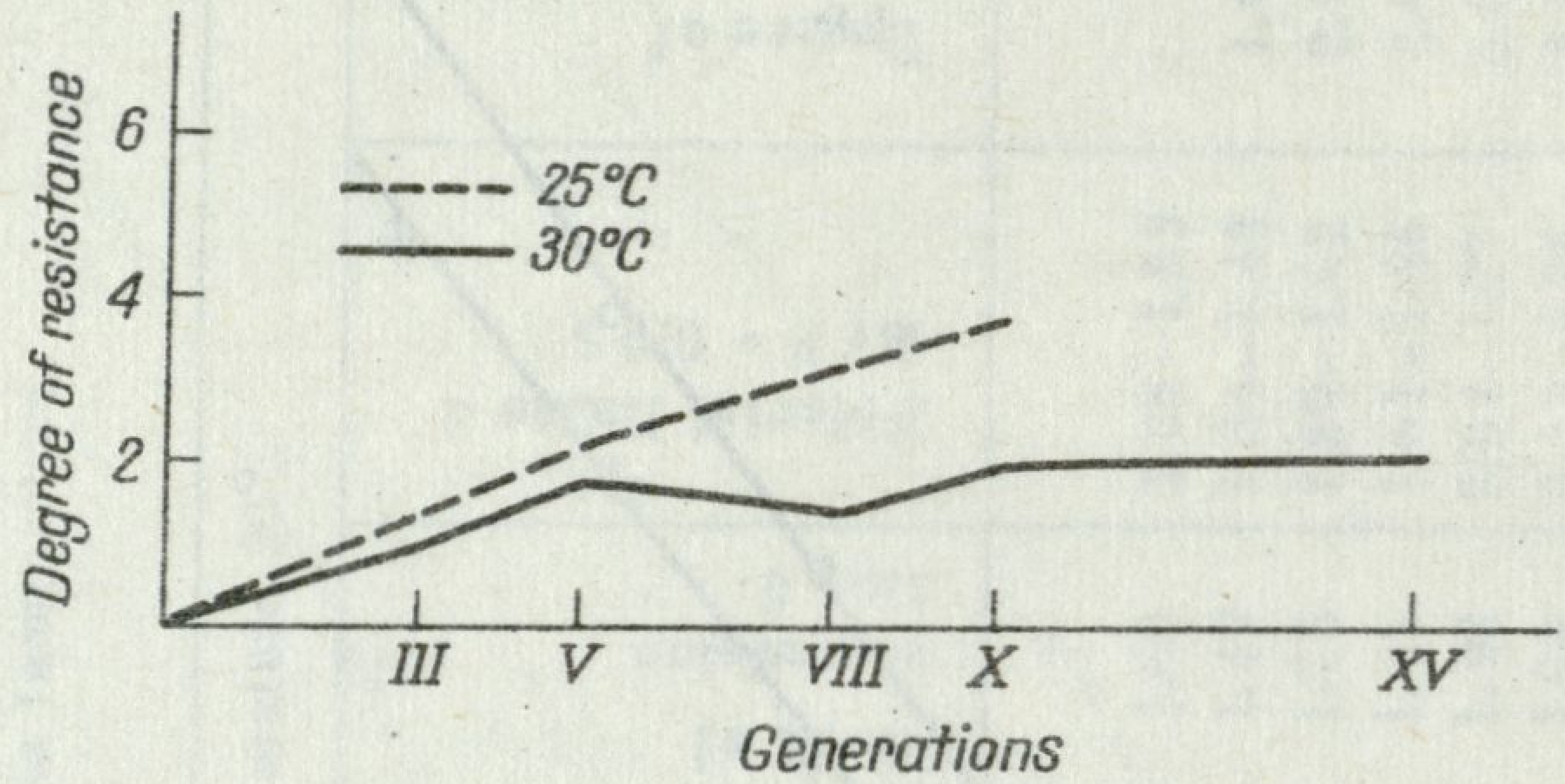

Fig. 7. The influence of temperature on the development of Azotox resistance in *T. castaneum*

kept at 25°C were higher than those of the population cultured at 30°C (Tab. IV). In Figure 8 are presented susceptibility regresssion lines for the original population and for the tenth generations cultured at ech of the two temperatures. The susceptibility regression lines of these populations are not parallel, which indicates that the course of mortality of this generation was not even. A comparison of these two populations at the level of 50% mortality shows that the resistance level of the population cultured at 25°C, as compared with the original population, is 3.67, and that of the population cultured at 30° C – 1.82. The susceptibility ratio for the populations compared was 2.

The influence of temperature on the production of Metasystox resistance in *T. castaneum* imagines is more evident than in the experiments with Azotox. The development of Metasystox resistance in adult *T. castaneum* kept at 25°C is much faster than that in the insects cultured at 30°C (Fig. 9). LC_{50} of the tenth generation of the population cultured at 25°C is 0.058, while LC_{50} of the tenth gerenation of the population cultured at 30°C is 0.0121. The course of Metasystox resistance development in *T. castaneum* is shown in Table V. Figure 10 presents the regression straight lines illustrating the susceptibility of the tenth generations of the two populations in which Metasystox resistance was developing. The slopes of the regression lines are very similar, and we assume that the lines are parallel, which indicates that the course of mortality was even. The resistance level for the tenth generation of the population cultured at 25°C is 27.62, and that for the analogous generation kept at 30°C only 5.8. The susceptibility ratio for the tenth generations is 4.79. As indicated by the data in Table V and in the graph (Fig. 10), the development of resistance in the population cultured at 25°C is much faster than at 30°C.

Course of development of Azotox resistance in *T. castaneum* in relation to temperature

Tab. IV

Generation	Temperature 25°					Temperature 30°				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance
Original population	0.0049	0.0055-0.0044	2.45	2.89-2.07		0.0049	0.0055-0.0044	2.45	2.89-2.07	
III	0.0064	0.0070-0.0059	2.19	2.43-1.97	1.31	0.0050	0.0054-0.0045	1.75	1.94-1.58	1.02
V	0.0125	0.0141-0.0110	2.38	3.33-1.70	2.55	0.0082	0.0090-0.0074	2.12	2.42-1.86	1.76
VIII	0.0155	0.0169-0.0155	2.17	2.39-1.97	3.16	0.0066	0.0070-0.0062	1.52	1.66-1.39	1.36
X	0.0180	0.0193-0.0168	1.75	1.82-1.59	3.67	0.0090	0.0108-0.0075	2.52	3.46-1.81	1.82
XV						0.0100	0.0104-0.0096	1.40	1.45-1.34	2.04

Susceptibility ratio of 10th generations – 2.00 (2.78–1.44); *f/PR* – 1.39.

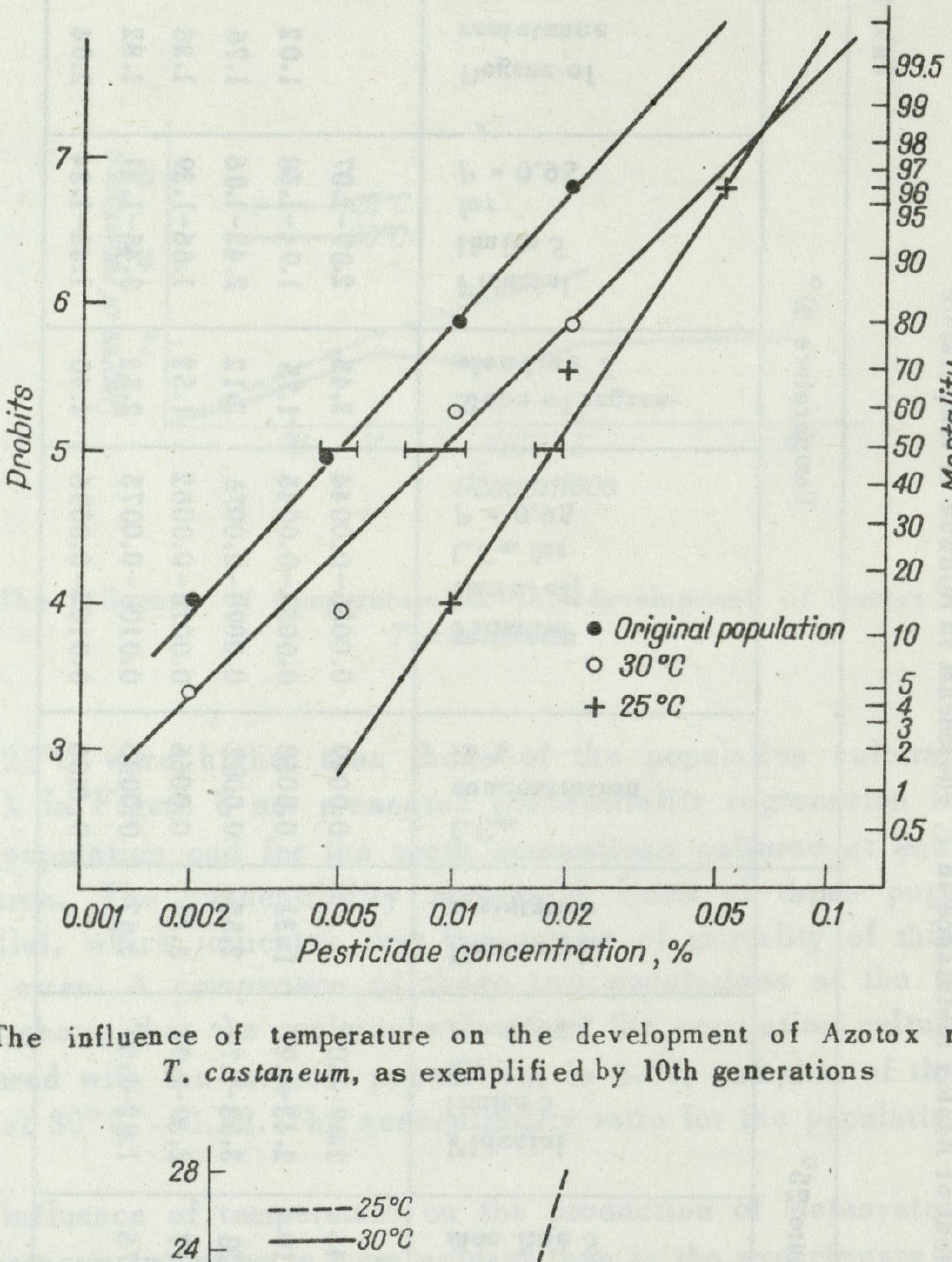

Fig. 8. The influence of temperature on the development of Azotox resistance in *T. castaneum*, as exemplified by 10th generations

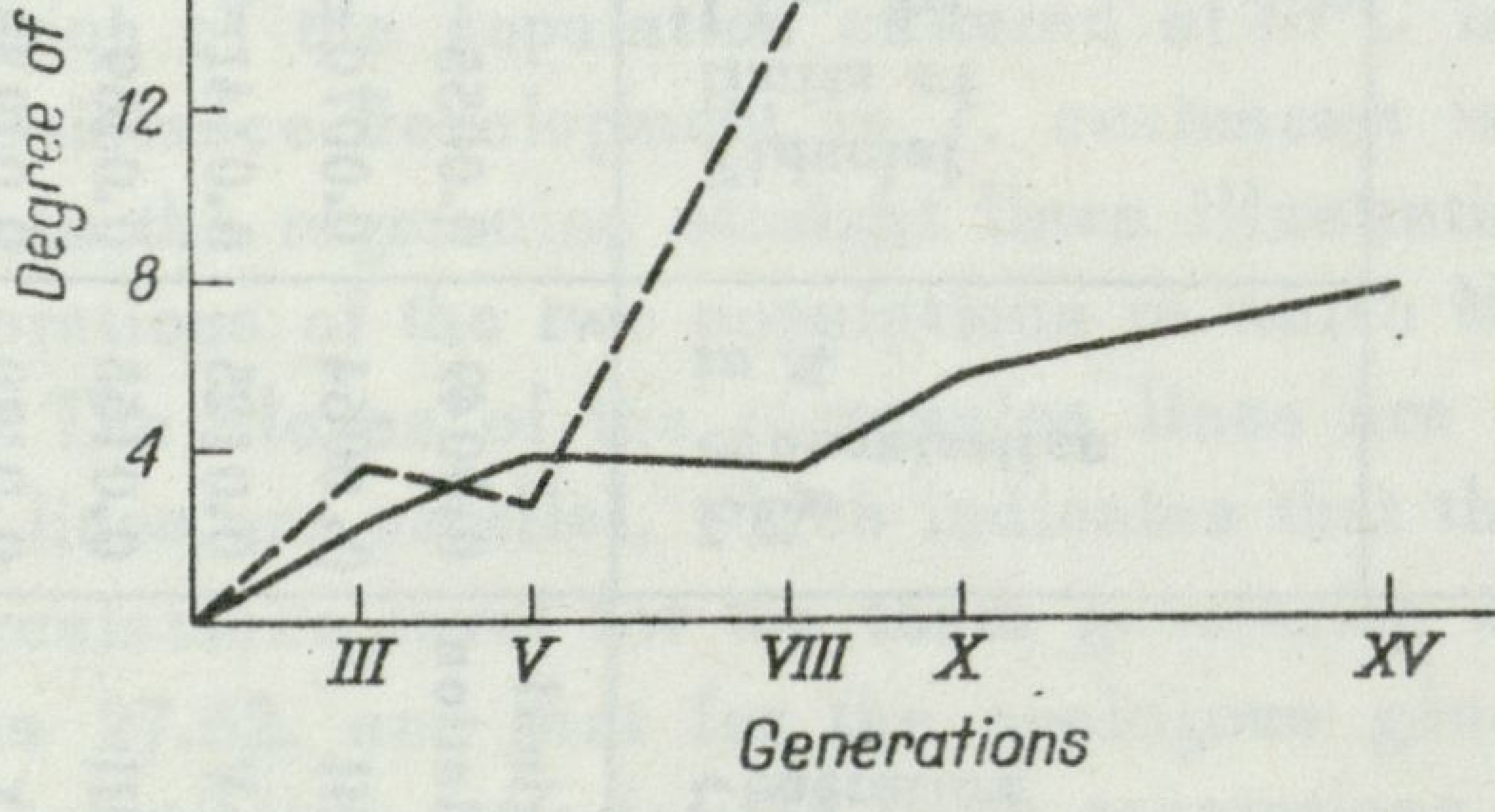

Fig. 9. The influence of temperature on the development of Metasystox resistance in *T. castaneum*

Course of development of Metasystox resistance in *T. castaneum* in relation to temperature

Tab. V

Generation	Temperature 25°					Temperature 30°				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression Line S	Fiducial limits S for $P = 0.95$	Degree of resistance
Original population	0.0021	0.0022–0.0020	1.79	1.93–1.66		0.0021	0.0022–0.0020	1.79	1.93–1.66	
III	0.0074	0.0079–0.0069	1.70	1.81–1.59	3.52	0.0052	0.0063–0.0042	2.48	2.62–2.25	2.48
V	0.0049	0.0051–0.0047	1.78	1.97–1.60	2.33	0.0081	0.0088–0.0073	1.82	1.96–1.69	3.85
VIII	0.0300	0.0320–0.0283	1.43	1.50–1.36	14.28	0.0070	0.0075–0.0064	1.78	1.90–1.66	3.33
X	0.0580	0.0603–0.0558	1.41	1.47–1.35	27.62	0.0121	0.0128–0.0114	1.63	1.72–1.54	5.80
XV						0.0160	0.0171–0.0149	1.75	1.87–1.63	7.62
XX						0.0250	0.0260–0.0240	1.47	1.55–1.39	11.90

Susceptibility ratio of 10th generation – 4.79 (5.26–4.35); f/PR – 1.1.

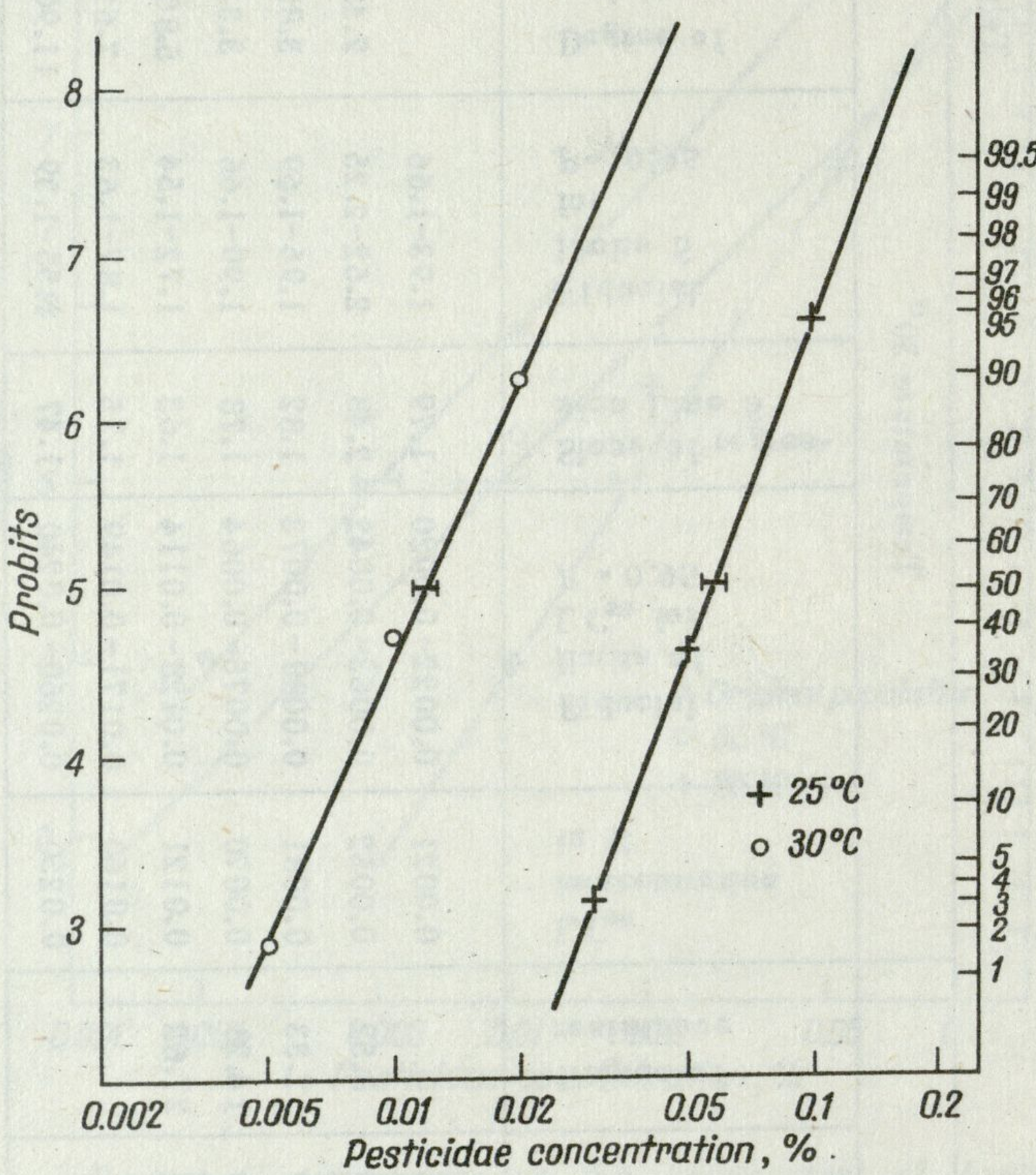

Fig. 10. The influence of temperature on the development of Metasystox resistance in *T. castaneum*, as exemplified by 10th generations

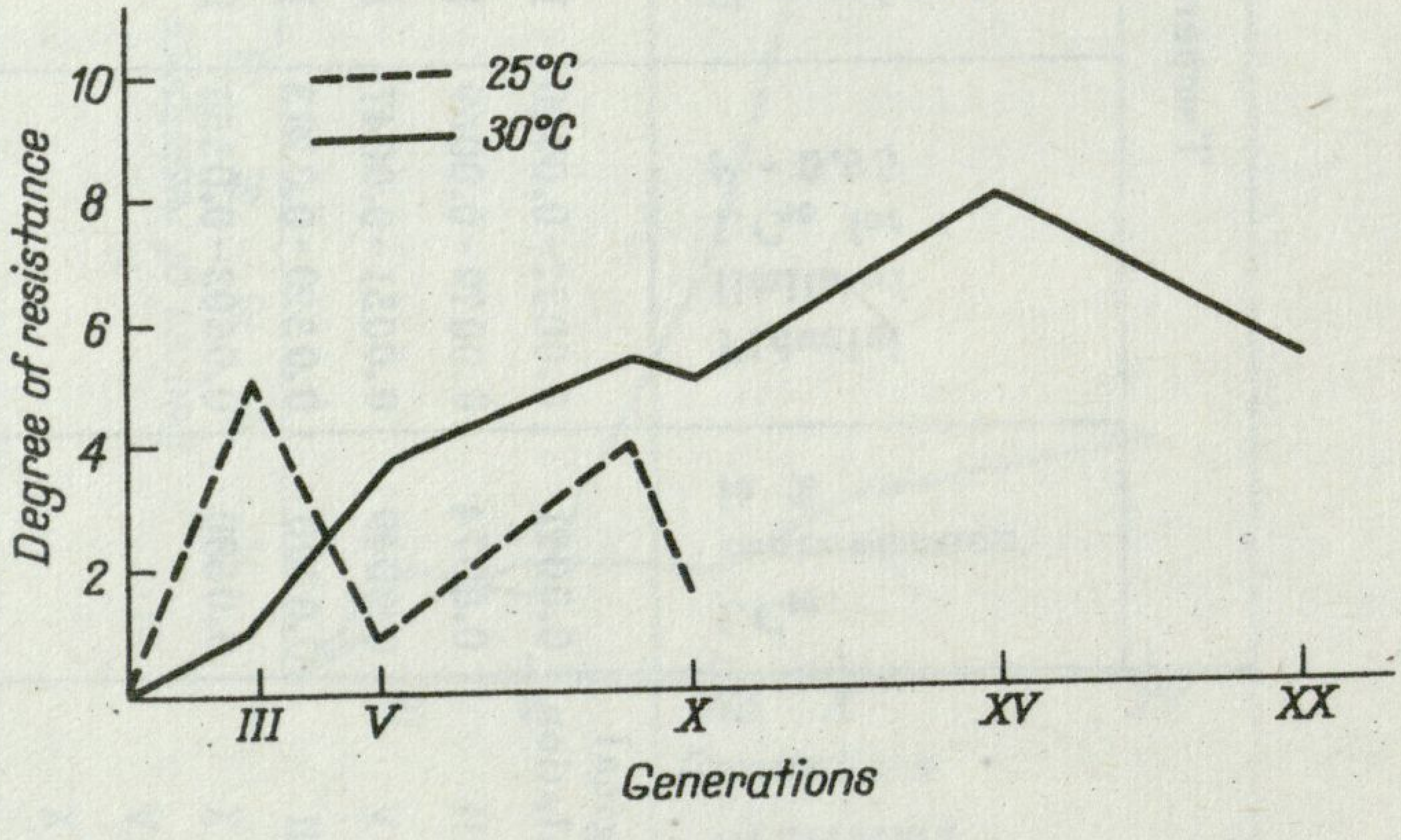

Fig. 11. The influence of temperature on the development of Pybuthrin resistance in *T. castaneum*

Course of development of Pybuthrin resistance in *T. castaneum* in relation to temperature

Tab. VI

Generation	Temperature 25°					Temperature 30°				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance
Original population	0.0038	0.0046-0.0031	2.58	3.04-2.13		0.0038	0.0046-0.0031	2.58	3.04-2.13	
III	0.0190	0.0209-0.0173	2.72	3.59-2.06	5	0.0038	0.0042-0.0033	2.00	2.22-1.81	1.00
V	0.0035	0.0038-0.0032	2.04	2.24-1.85	0.92	0.0130	0.0142-0.0110	2.08	2.21-1.74	3.68
IX	0.0130	0.0140-0.0120	2.00	2.26-1.77	3.42	0.0200	0.0220-0.0182	2.20	2.42-2.00	5.24
X	0.0056	0.0062-0.0051	2.23	2.30-2.16	1.47	0.0190	0.0205-0.0176	2.05	2.46-1.71	5.00
XV						0.0300	0.0327-0.0275	2.08	2.24-1.89	7.89
XX						0.0210	0.0231-0.0191	2.05	2.37-1.76	5.53

Susceptibility ratio for 10th generations – 3.39 (3.45–3.25); *f/PR* – 1.05.

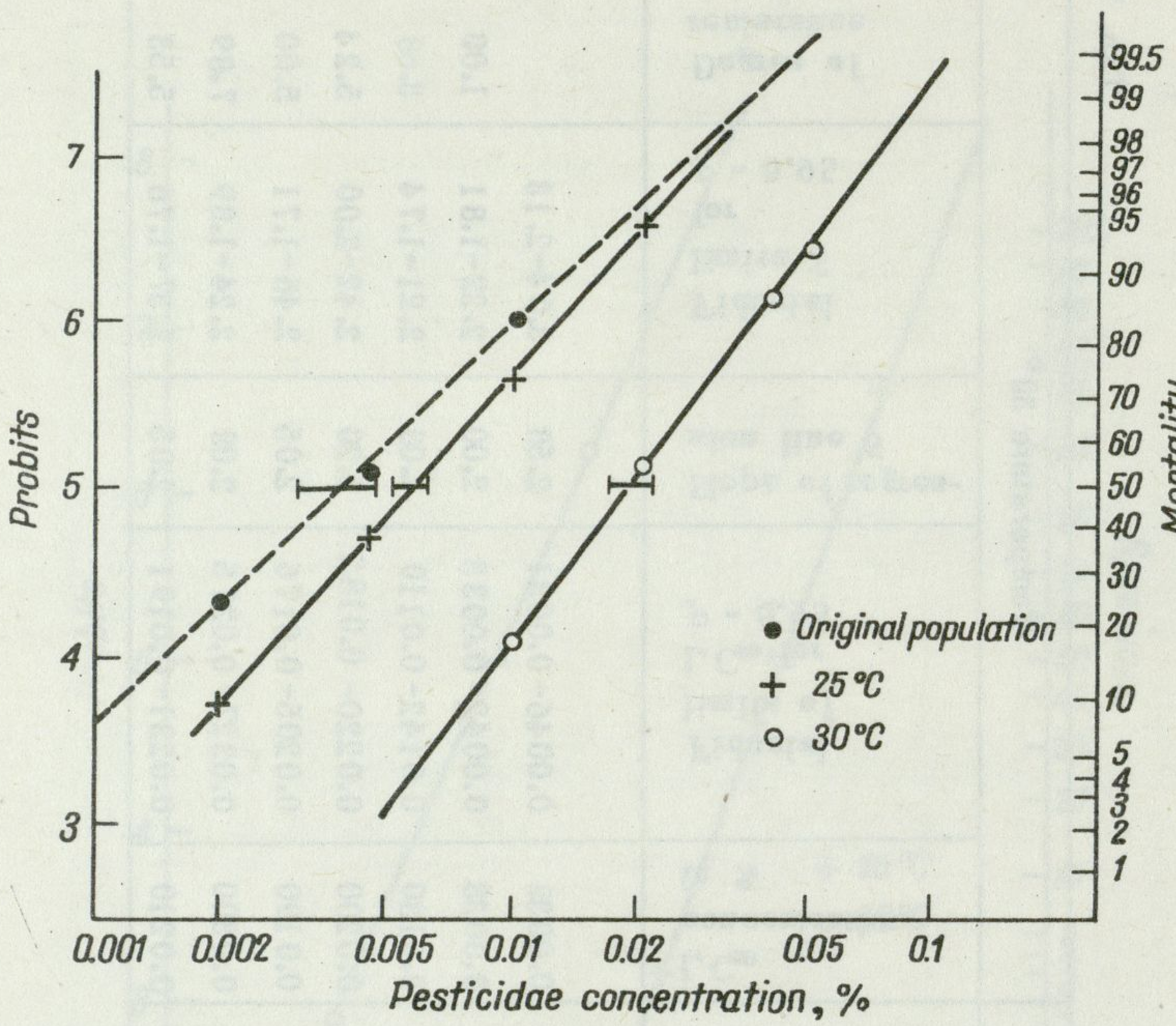

Fig. 12. The influence of temperature on the development of Pybuthrin resistance in *T. castaneum*, as exemplified by 10th generations

The effect of temperature on the production of Pybuthrin resistance in adult *T. castaneum* is different. Up to the fourth generation (Fig. 11) the population cultured at 25°C shows a much lower susceptibility to the pesticide tested than does the population cultured at 30°C. Between the fifth and the tenth generations the population kept at 30°C reveals a higher resistance. The course of development of Pybuthrin resistance in *T. castaneum* is shown in Table VI. For purposes of comparison, in Figure 12 are given susceptibility regression lines of the tenth generations of populations cultured at 25°C and 30°C, and the susceptibility regression line of the original population. These lines indicate that the mortality of the beetles under study was not uniform. The results presented above indicate that the population cultured at 30°C develops resistance at a much higher rate than the population cultured at 25°C. The LC_{50} value of the tenth generation of the population cultured at 25°C is 0.0056, and the LC_{50} of the insects cultured at 30°C – 0.019. The susceptibility ratio for the tenth generations equals 3.39.

2. The effect of relative humidity of air on the resistance developing process in insects

Experiments aimed at establishing the effect of relative humidity of air on the development of insecticide resistance were carried out with adult *S. oryzae* and *T. castaneum* at constant temperature 30°C. The development of resistance to the following three insecticides: Azotox, Metasystox and Pybuthrin was studied at two different relative air humidity levels 75% and 55%.

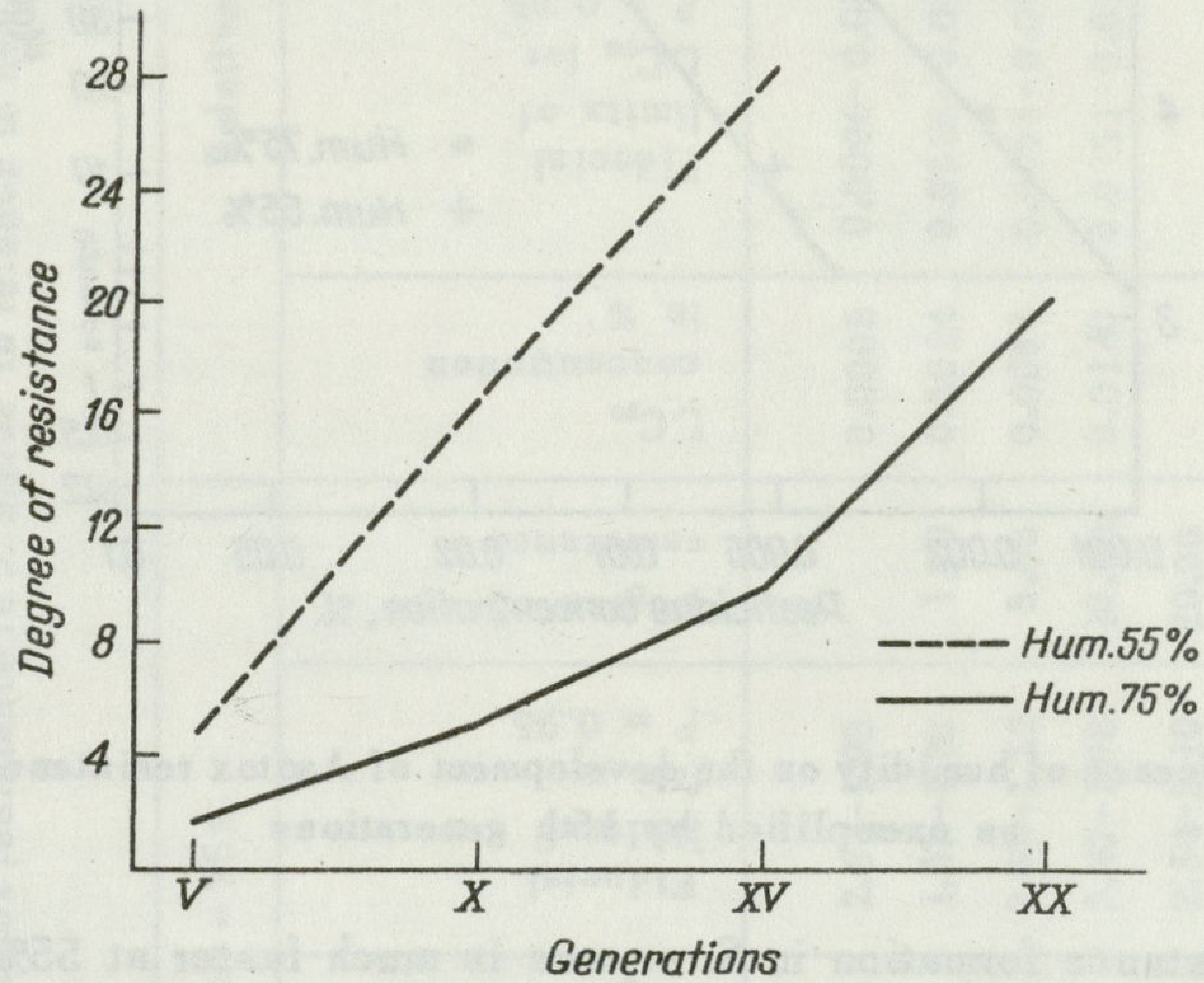

Fig. 13. The influence of humidity on the development of Azotox resistance in *S. oryzae*

Adult *S. oryzae* cultured at 55% air humidity appeared to develop Azotox resistance at a much higher rate than the population cultured at 75% (Fig. 13). To compare the susceptibility of the populations under study straight lines of regression are shown in Figure 14, representing the susceptibility of the fifteenth generations of Azotox-treated beetles. The lines are parallel, which indicates that the course of mortality under the different humidity conditions was the same. The comparison of LC_{50} values for different humidity levels (Tab. VII) shows that the fifteenth generation cultured at 55% humidity is more resistant than the fifteenth generation cultured at 75% humidity. The level of resistance of the population kept at 75% humidity, as compared with the original population, is 10, and that of the population cultured at 55% humidity – 28. The susceptibility ratio for the fifteenth generations is 2.80. The process

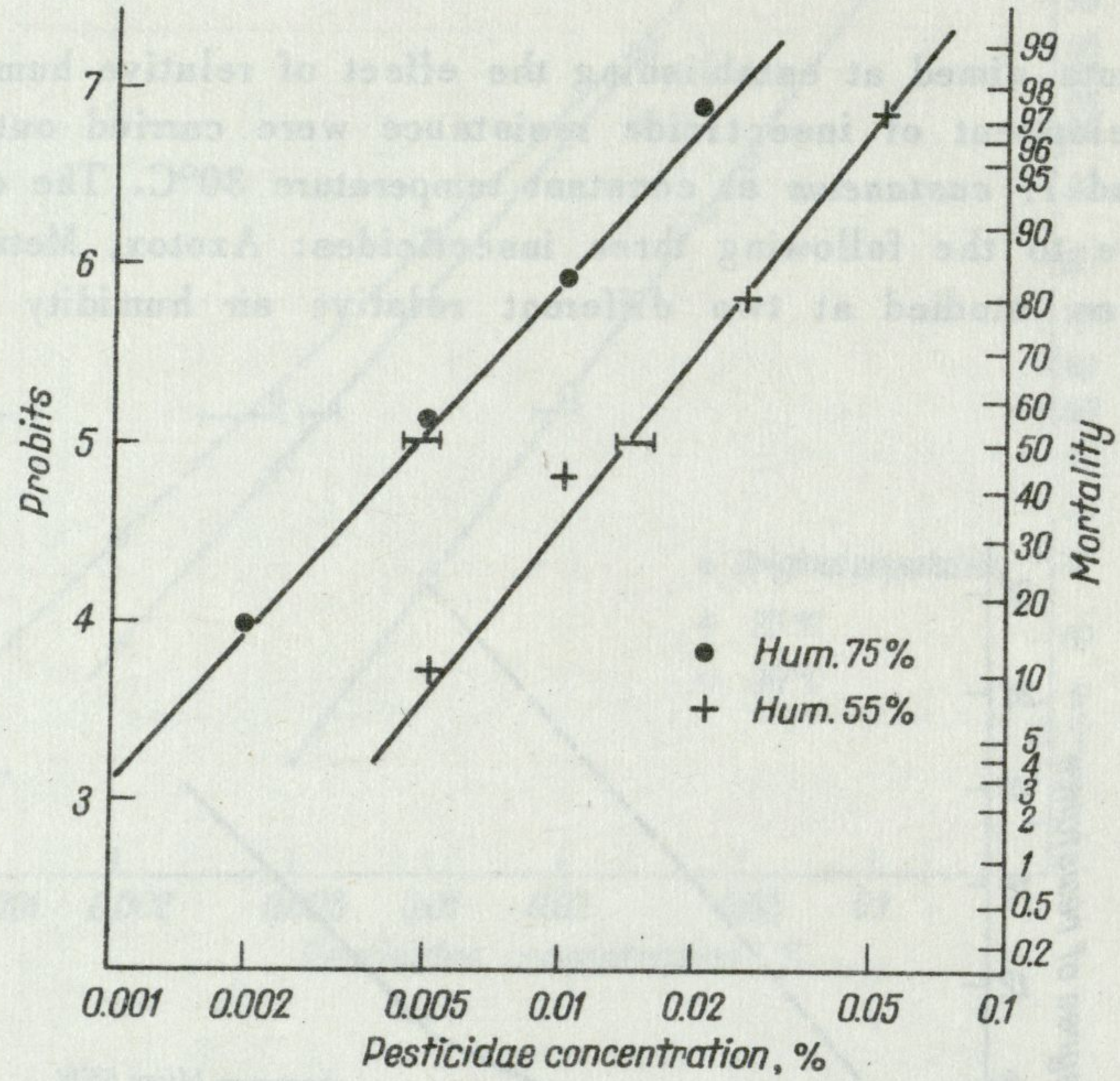

Fig. 14. The influence of humidity on the development of Azotox resistance, in *S. oryzae* as exemplified by 15th generations

of Azotox resistance formation in *S. oryzae* is much faster at 55% air humidity than at 55%. A similar effect of humidity on the course of resistance doveloping in the same species (*S. oryzae*) could be observed in tests with Metasystox. The curves in Figure 15 represent the increase of Metasystox resistance over twenty beetle generations. Changes of the LC_{50} value for *S. oryzae* populations cultured at the two different humidity values are presented in Table VIII. The LC_{50} value of the fifteenth generation of the population cultured at 55% is 0.062, and that of the fifteenth generation of the population cultured at 75% humidity – 0.019. The resistance level values, as compared with the original population, were 21, 14 and 6.78. The susceptibility ratio of the fifteenth generations was 3.23. The regression lines illustrating the susceptibility of the adults of the fifteenth generations are presented in Figure 16. For purposes of comparison, in the same graph regression lines have been drawn for the twentieth generation cultured at 75% humidity, and for the original population. The comparison of the straight lines shows that the *S. oryzae* population cultured at 55% air humidity produced Metasystox resistance much faster than the population cultured at 75% humidity.

Course of development of Azotox resistance in *S. oryzae* in relation to humidity

Tab. VII

Generation	Relative humidity of air = 75%					Relative humidity of air = 55%				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance
Original population	0.0005	0.0006–0.0005	2.28	2.62–1.98		0.0005	0.0006–0.0005	2.28	2.62–1.98	
V	0.0009	0.0009–0.0008	1.47	1.57–1.38	1.80	0.0024	0.0026–0.0022	2.51	3.01–2.09	4.8
X	0.0025	0.0026–0.0024	2.13	2.98–1.52	5.00	0.0084	0.0091–0.0077	2.29	2.56–2.05	16.8
XV	0.0050	0.0054–0.0043	2.18	2.40–1.98	10.00	0.0140	0.0151–0.0138	2.00	2.24–1.78	28.0
XX	0.0100	0.0110–0.0090	2.31	2.54–2.10	20.00					

Susceptibility ratio of 15th generations – 2.80 (3.08–2.54); f/PR – 1.1.

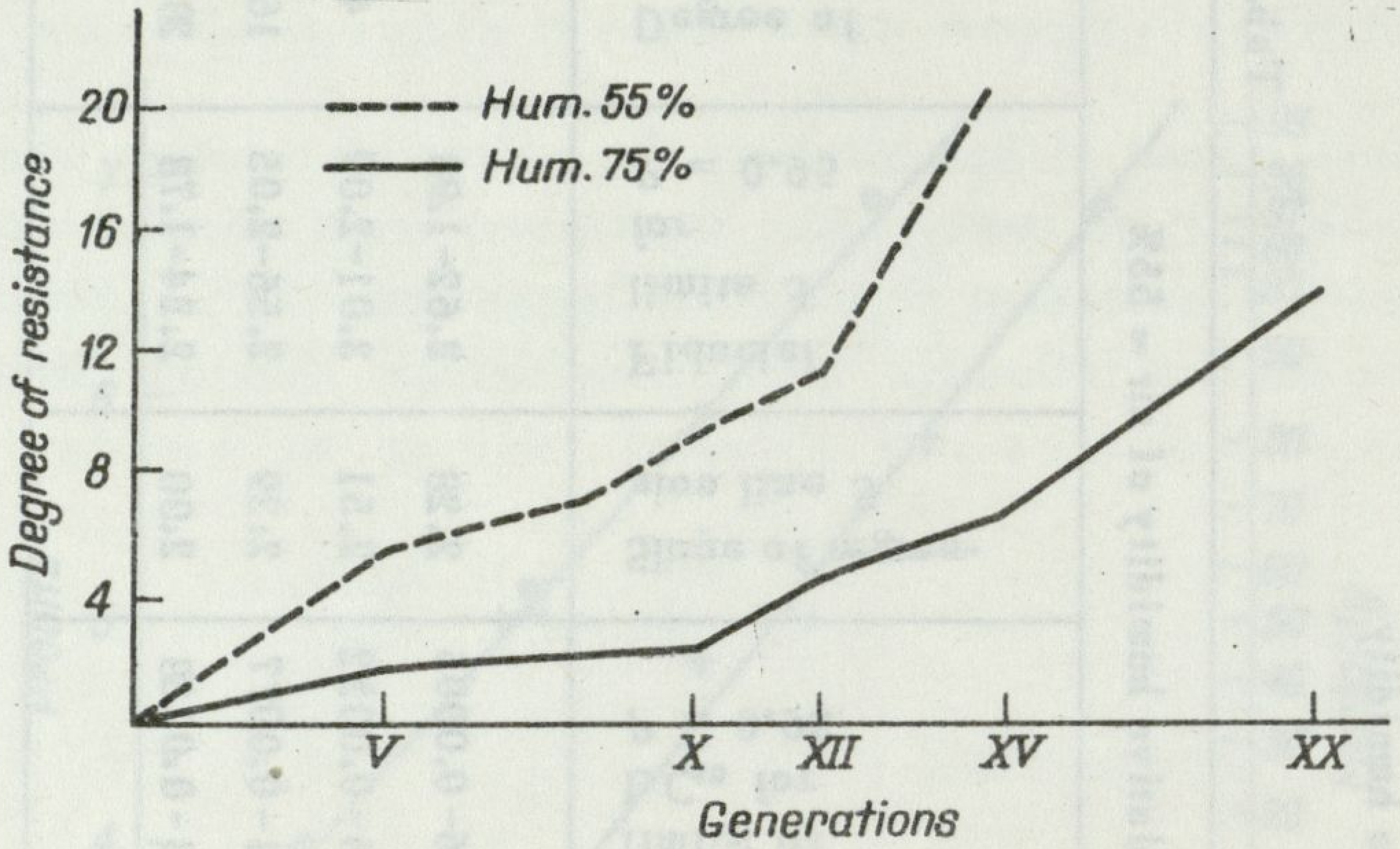

Fig. 15. The influence of humidity on the development of Metasystox in *S. oryzae*

The effect of the two humidity levels on the production of Pybuthrin resistance in *S. oryzae* is considerable. In the graph (Fig. 17) curves have been drawn to illustrate the process of resistance development in the two populations considered. A slight increase in resistance can be seen in the population cultured at 55% humidity, as compared with the population cultured at 75% humidity. The differences, as presented in Table IX, are not statistically significant. This is obvious also from the graph (Fig. 18). The straight lines of regression for the fifteenth generations of the two populations intersect, while the limits of confidence of LC_{50} value are very near each other. For comparison, the straight line of regression has been drawn for the twentieth generation of the population cultured at 75% humidity. The LC_{50} value of this generation also approaches the LC_{50} value of the fifteenth generations. In each of the populations considered the course of mortality appears to be different. The results presented above indicate that the humidity levels used in the experiments had only a slight effect on the development of Pybuthrin resistance in *S. oryzae*.

The effect of humidity on the development of resistance was also tested on adult *T. castaneum*, but the humidity levels used (75% and 55%) did not exert any significant influence on the production of Azotox resistance in *T. castaneum*. The curves in the graph (Fig. 19) show an increase in the rate of resistance development in the population considered. From the eighth generation onwards a slight increase of resistance could be seen in the population cultured at 55% relative air humidity, as compared with the population cultured at 75%. This is further confirmed by the values of LC_{50} for the populations considered, and the slopes of the straight lines of regression illustrating the susceptibility of the populations compared (Tab. X). In the graph (Fig. 20)

Course of development of Metasystox resistance in *S. oryzae* in relation to humidity

Tab. VIII

Generation	Relative humidity of air = 75%					Relative humidity of air = 55%				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance
Orygınal population	0.0028	0.0031-0.0026	2.11	2.48-1.78		0.0028	0.0031-0.0026	2.11	2.48-1.78	
V	0.0048	0.0053-0.0044	2.34	2.43-2.25	1.71	0.0150	0.0159-0.0141	1.84	1.98-1.70	5.36
VIII	0.0059	0.0064-0.0054	2.13	2.41-1.88	2.14	0.0190	0.0203-0.0178	1.75	1.89-1.63	6.78
X	0.0066	0.0072-0.0060	2.22	2.57-1.88	2.36	0.0270	0.0302-0.0241	2.30	6.40-1.21	9.64
XII	0.0135	0.0147-0.0124	2.18	2.42-1.96	4.82	0.0325	0.0364-0.0288	2.65	6.09-2.50	11.60
XV	0.0190	0.0195-0.0181	2.55	2.95-2.20	6.78	0.0620	0.0651-0.0590	1.49	1.55-1.44	21.14
XX	0.0420	0.0440-0.0390	1.55	1.61-1.49	15.00					
XXV	0.9600	1.1041-0.8348	3.20	6.40-1.60	343.00					

Susceptibility ratio of 15th generations 3.23 (3.39–3.08); f/PR – 1.05.

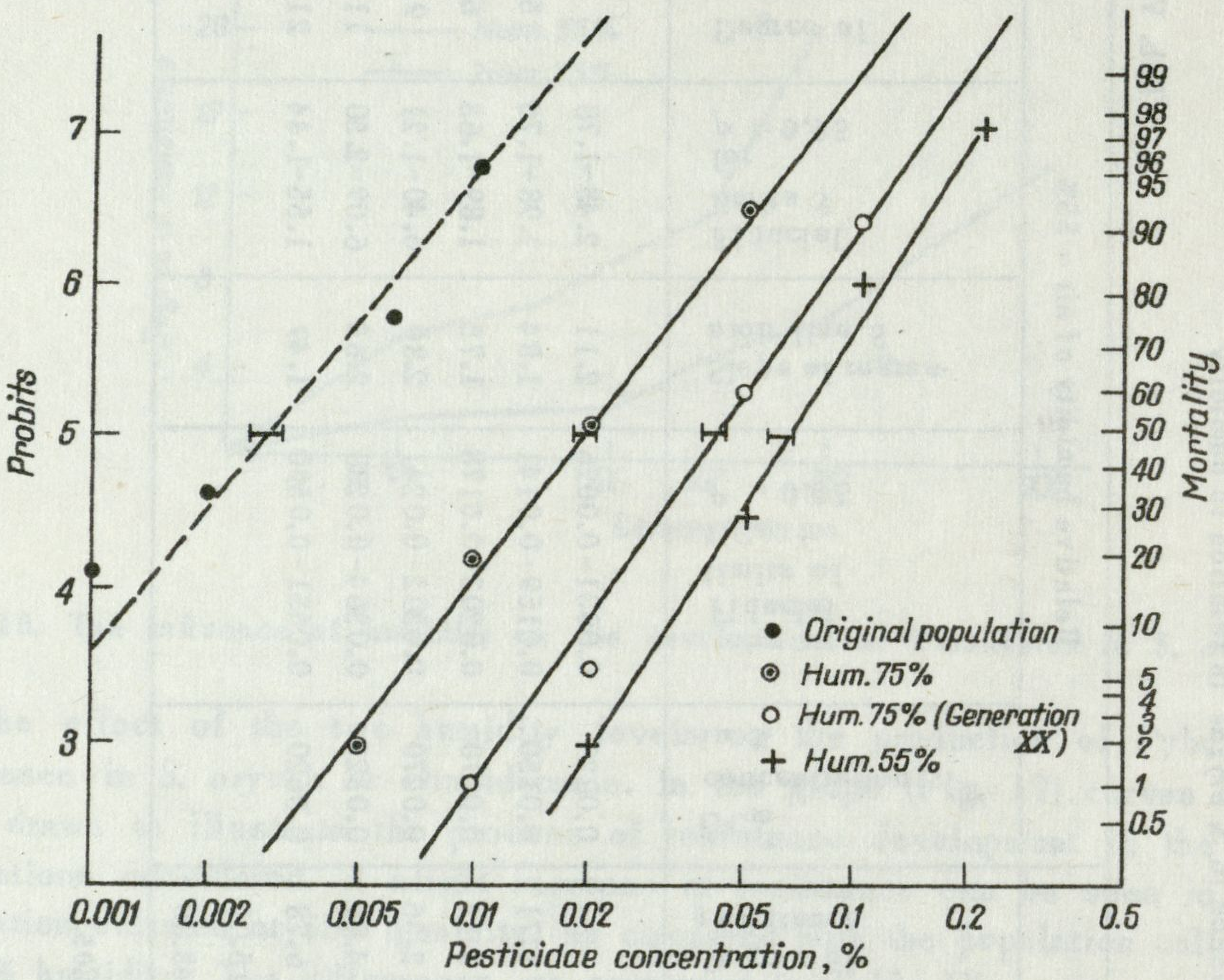

Fig. 16. The influence of humidity on the development of Metasystox resistance, in *S. oryzae* as exemplified by 15th generations

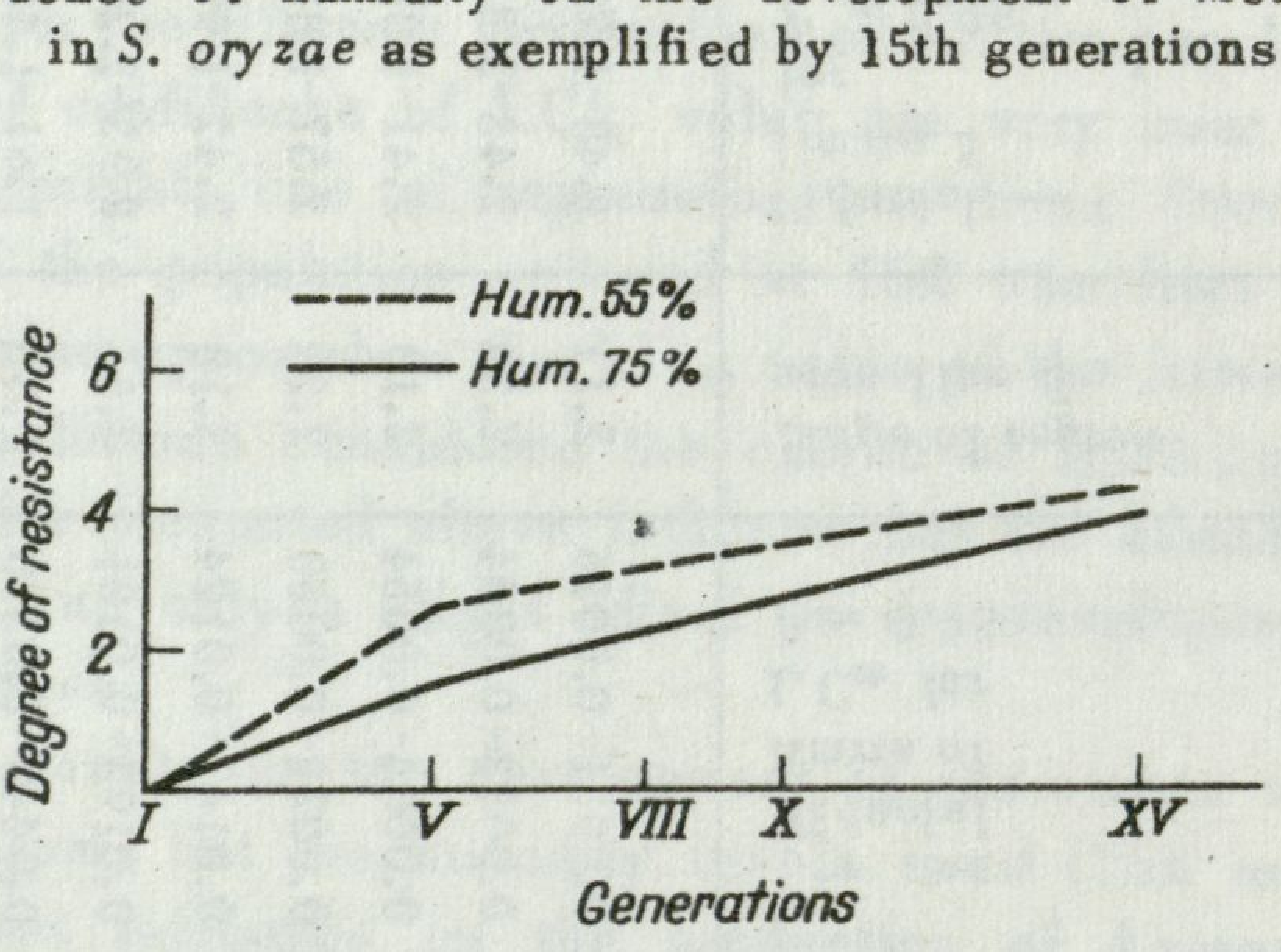

Fig. 17. The influence of humidity on the development of Pybuthrin resistance in *S. oryzae*

the course of the straight lines of regression of the twentieth generations is shown. These lines depict the mortality of these Azotox-treated generations. The lines are parallel, which permits the conclusion that the course of mortality among the beetles of the populations under study was not uniform.

Course of development of Pybuthrin resistance in *S. oryzae* in relation to humidity

Tab. IX

Generation	Relative humidity of air = 75%					Relative humidity of air = 55%				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance
Original population	0.0038	0.0040–0.0036	1.60	1.66–1.53		0.0038	0.0040–0.0036	1.60	1.66–1.53	
V	0.0064	0.0067–0.0061	1.49	1.54–1.43	1.42	0.0096	0.0104–0.0089	1.81	2.01–1.63	2.53
VIII	0.0080	0.0086–0.0073	1.95	2.11–1.80	2.10	0.0120	0.0129–0.0120	1.93	2.10–1.76	3.16
X	0.0098	0.0104–0.0092	1.75	1.89–1.62	2.58	0.0128	0.0138–0.0119	2.00	2.20–1.82	3.37
XV	0.0150	0.0160–0.0140	1.45	1.61–1.36	3.94	0.0160	0.0173–0.0148	1.97	2.06–1.79	4.21
XVIII	0.0230	0.0248–0.0213	1.93	2.04–1.77	6.05					
XX	0.0170	0.0183–0.0157	1.98	2.13–1.83	4.47					

Susceptibility ratio of 15th generation – 1.06 (1.17–0.96); f/PR – 1.1.

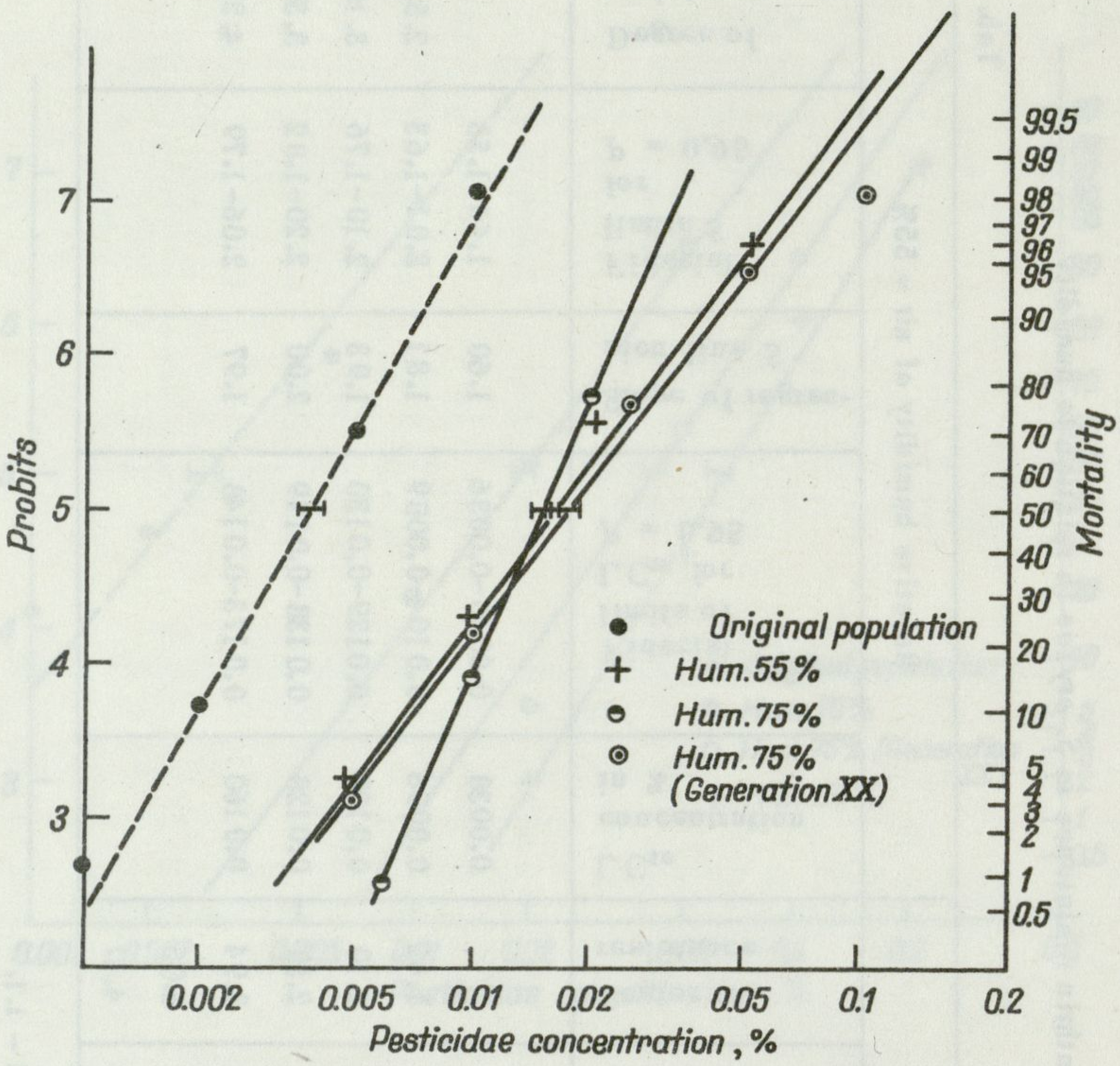

Fig. 18. The influence of humidity on the development of Pybuthrin resistance in, *S. oryzae*, as exemplified by 15th generations

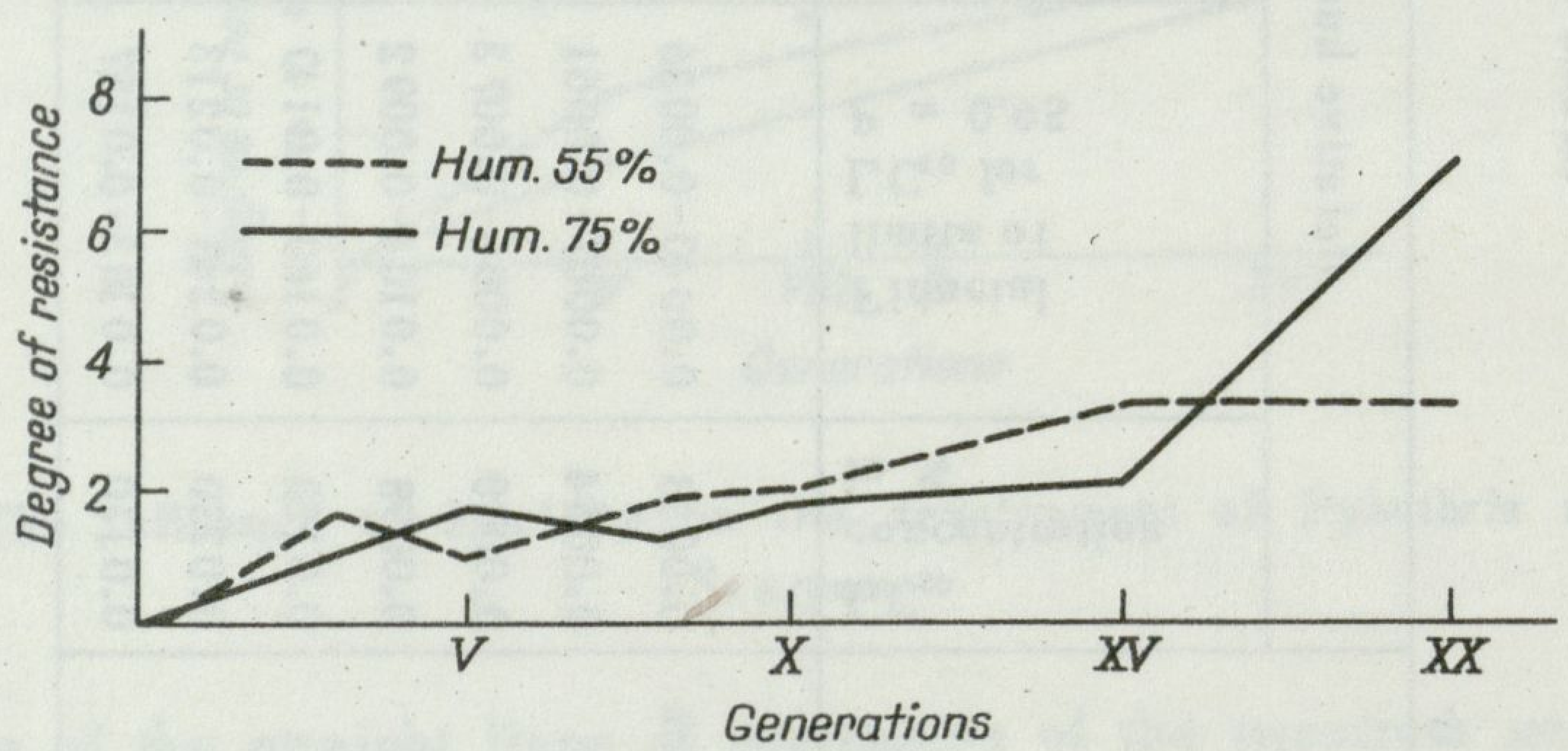

Fig. 19. The influence of humidity on the development of Azotox resistance in *T. castaneum*

Tab. X

Course of development of Azotox resistance in *T. castaneum* in relation to humidity

Generation	Relative humidity of air = 75%					Relative humidity of air = 55%				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance
Original population	0.0041	0.0055–0.0044	2.45	2.89–2.07		0.0041	0.0055–0.0044	2.45	2.89–2.07	
III	0.0050	0.0054–0.0045	1.75	1.94–1.58	1.02	0.0080	0.0088–0.0073	2.27	2.51–2.04	1.63
V	0.0082	0.0090–0.0074	2.12	2.42–1.86	1.76	0.0049	0.0053–0.0045	1.77	1.96–1.50	1.00
VIII	0.0066	0.0070–0.0062	1.52	1.66–1.39	1.36	0.0090	0.0098–0.0083	2.06	2.29–1.85	1.84
X	0.0090	0.0108–0.0075	2.52	3.46–1.81	1.82	0.0094	0.0098–0.0090	1.42	1.48–1.36	1.91
XV	0.0100	0.0104–0.0096	1.40	1.45–1.34	2.04	0.0165	0.0168–0.0162	1.25	1.31–1.19	3.30
XX	0.0320	0.0342–0.0299	1.87	2.07–1.69	7.00	0.0160	0.0171–0.0149	1.74	1.86–1.62	3.26

Susceptibility for 20th generations – 2.00 (2.16–1.85); f/PR – 1.08.

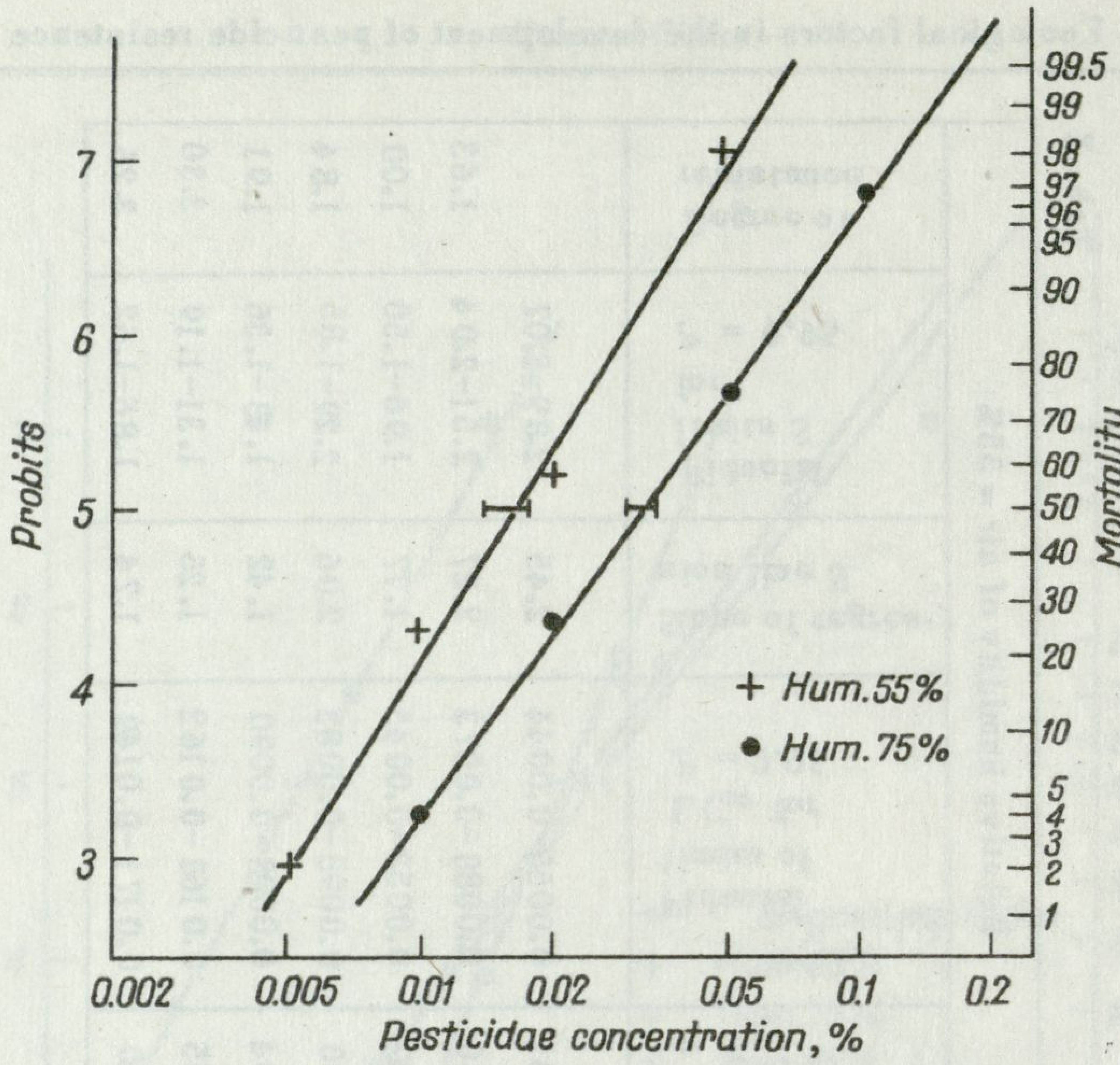

Fig. 20. The influence of humidity on the development of Azotox resistance in *T. castaneum*, as exemplified by 20th generations

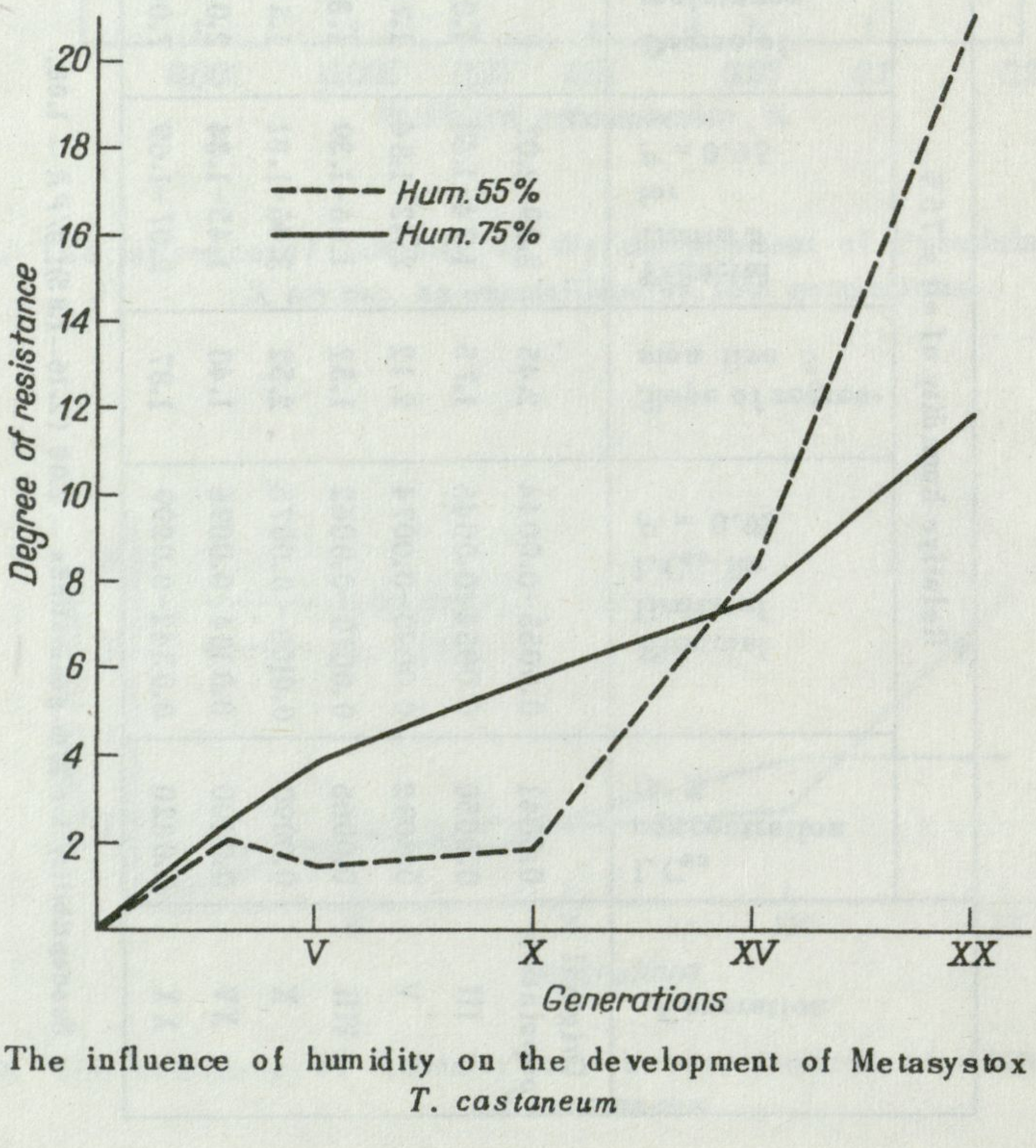

Fig. 21. The influence of humidity on the development of Metasystox resistance in *T. castaneum*

Course of development of Metasystox resistance in *T. castaneum* in relation to humidity

Tab. XI

Generation	Relative humidity of air = 75%					Relative humidity of air = 55%				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits S for $P = 0.95$	Degree of resistance
Original population	0.0021	0.0022–0.0020	1.79	1.93-1.66		0.0021	0.0022–0.0020	1.79	1.93-1.66	
III	0.0052	0.0063–0.0042	2.48	2.62-2.25	2.48	0.0045	0.0048–0.0042	1.55	1.69-1.42	2.14
V	0.0081	0.0088–0.0073	1.82	1.96-1.69	3.85	0.0032	0.0035–0.0030	1.80	1.94-1.66	1.50
X	0.0121	0.0128–0.0114	1.63	1.72-1.54	5.80	0.0040	0.0042–0.0038	1.78	1.89-1.68	1.90
XV	0.0160	0.0171–0.0149	1.75	1.87-1.63	7.62	0.0175	0.0187–0.0162	1.71	1.81-1.52	8.33
XX	0.0260-	0.0260–0.0240	1.47	1.55-1.39	11.90	0.0460	0.0492–0.0428	1.61	1.72-1.54	21.10

Susceptibility for 20th generations – 1.84 (2.02–1.67); *f/PR* – 1.1.

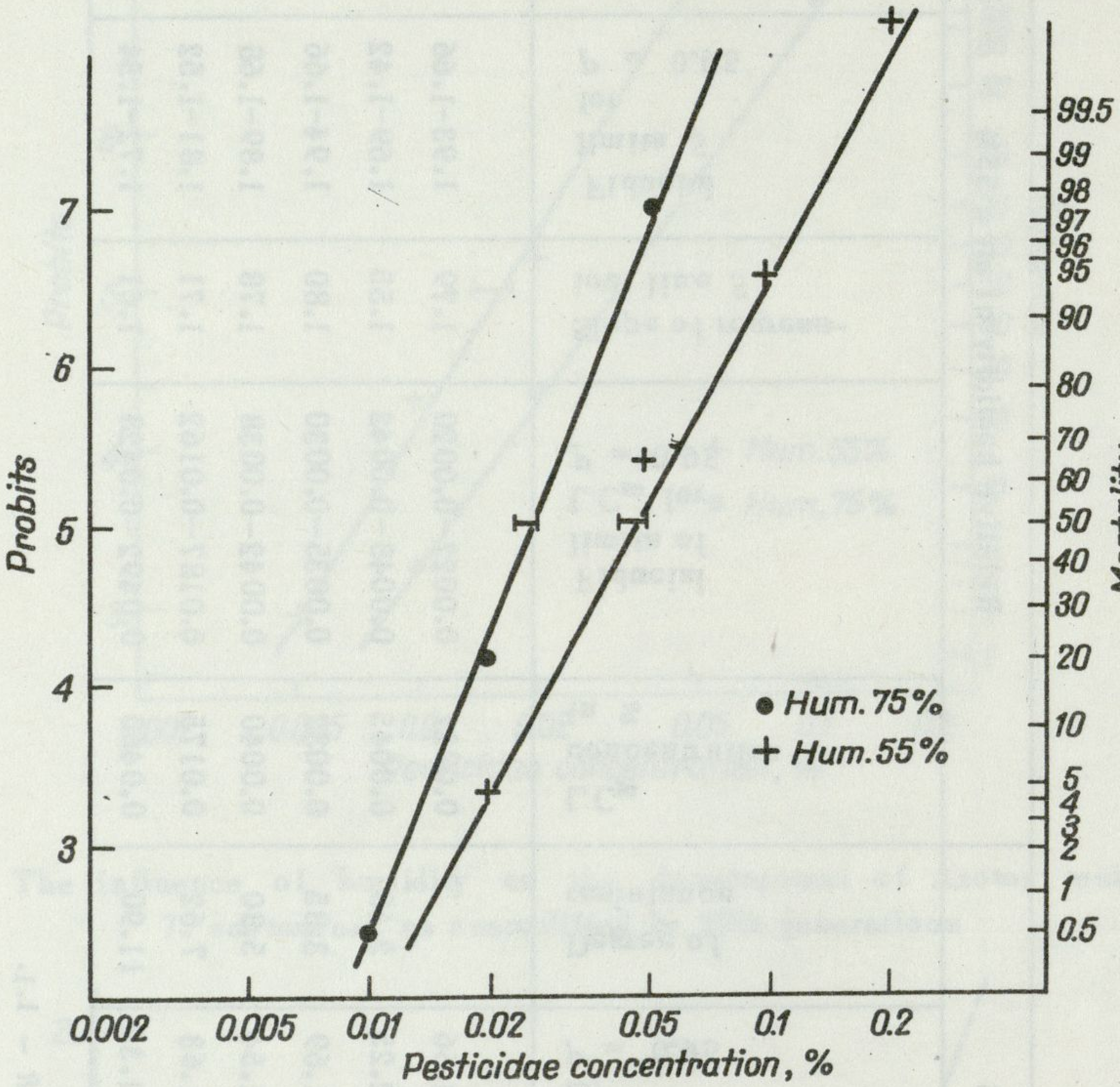

Fig. 22. The influence of humidity on the development of Metasystox resistance in *T. castaneum*, as exemplified by 20th generations

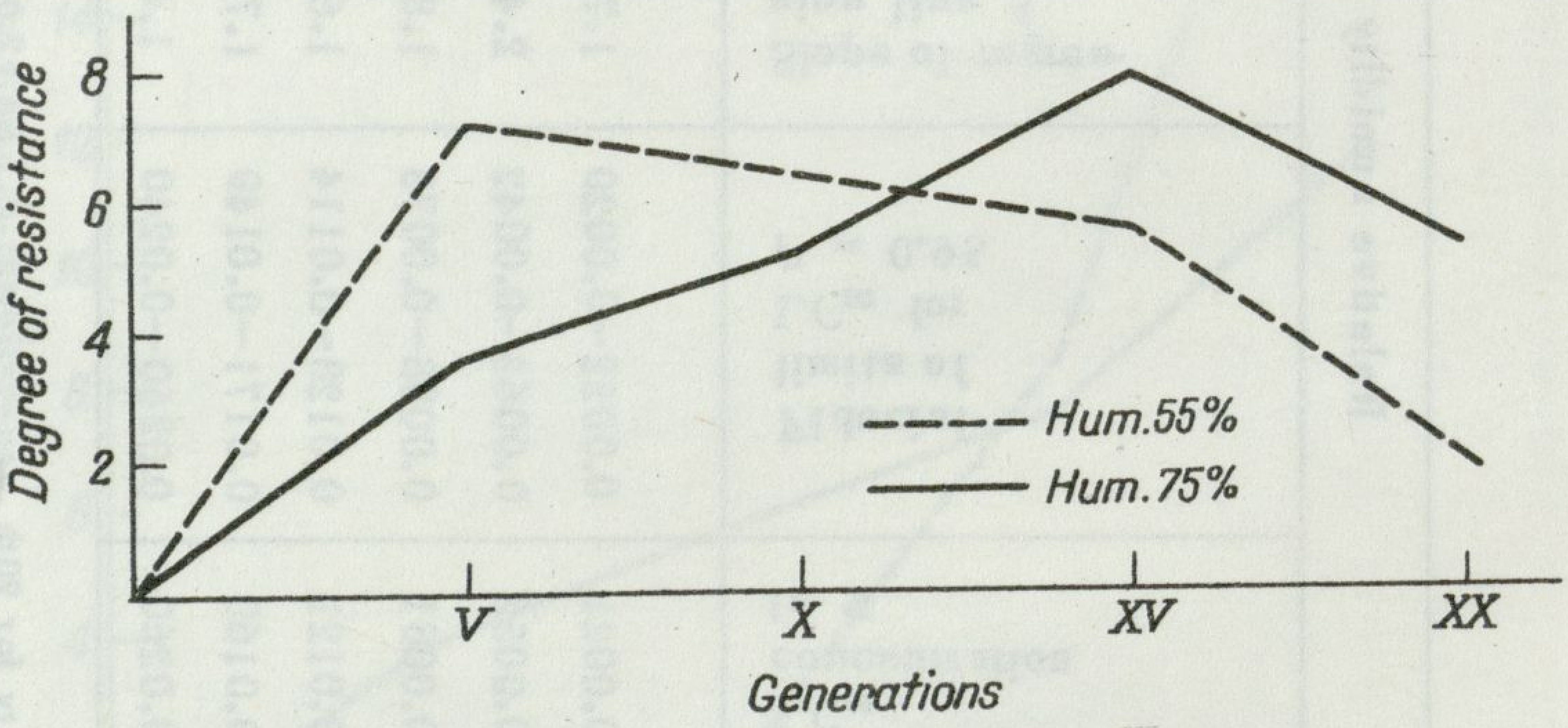

Fig. 23. The influence of humidity on the development of Pybuthrin resistance in *T. castaneum*

The process of Metasystox resistance formation in *T. castaneum* appears to be different. As can be inferred from the changes that occurred during the first thirteen generations, the higher humidity level of the air (75%) speeds

Course of development of Pybuthrin resistance in *T. castaneum* in relation to humidity

Tab. XII

Generation	Relative humidity of air = 75%					Relative humidity of air = 55%				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for P = 0.95	Slope of regression line S	Fiducial limits S for P = 0.95	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for P = 0.95	Slope of regression line S	Fiducial limits S for P = 0.95	Degree of resistance
Original population	0.0038	0.0046–0.0031	2.58	3.04–2.13		0.0038	0.0046–0.0031	2.58	3.04–2.13	
III	0.0038	0.0042–0.0033	2.00	2.22–1.81	1.00	0.0160	0.0166–0.0153	1.65	1.81–1.50	4.21
V	0.0130	0.0142–0.0110	2.08	2.21–1.74	3.42	0.0270	0.0297–0.0245	2.44	2.83–2.10	7.10
X	0.0190	0.0205–0.0176	2.05	2.46–1.71	5.00	0.0240	0.0300–0.0192	4.55	6.82–2.93	6.32
XV	0.0300	0.0327–0.0275	2.08	2.24–1.89	7.89	0.0210	0.0229–0.0192	2.20	2.59–1.86	5.53
XX	0.0210	0.0231–0.0191	2.05	2.37–1.76	5.53	0.0080	0.0089–0.0072	2.65	3.02–2.23	2.10

Susceptibility for 20th generation – 2.63 (2.89–2.39); f/PR – 1.1.

up the process of Metasystox resistance development in *T. castaneum*, as compared with the lower humidity (55%). From the fourteenth generation on the relationship is altered (Fig. 21). The development of resistance in this species at 55% humidity is accelerated. LC_{50} value, and the slopes of the straight lines of susceptibility regression of the generation tested are presented in Table XI. The graph (Fig. 22) shows the straight lines of susceptibility regression of the twentieth generation of both the populations investigated. The position of the straight lines also indicates that they are not parallel and the conclusion from this is that under different humidity conditions the mortality of the populations under study is different. The susceptibility ratio of the twentieth generations is 1.84.

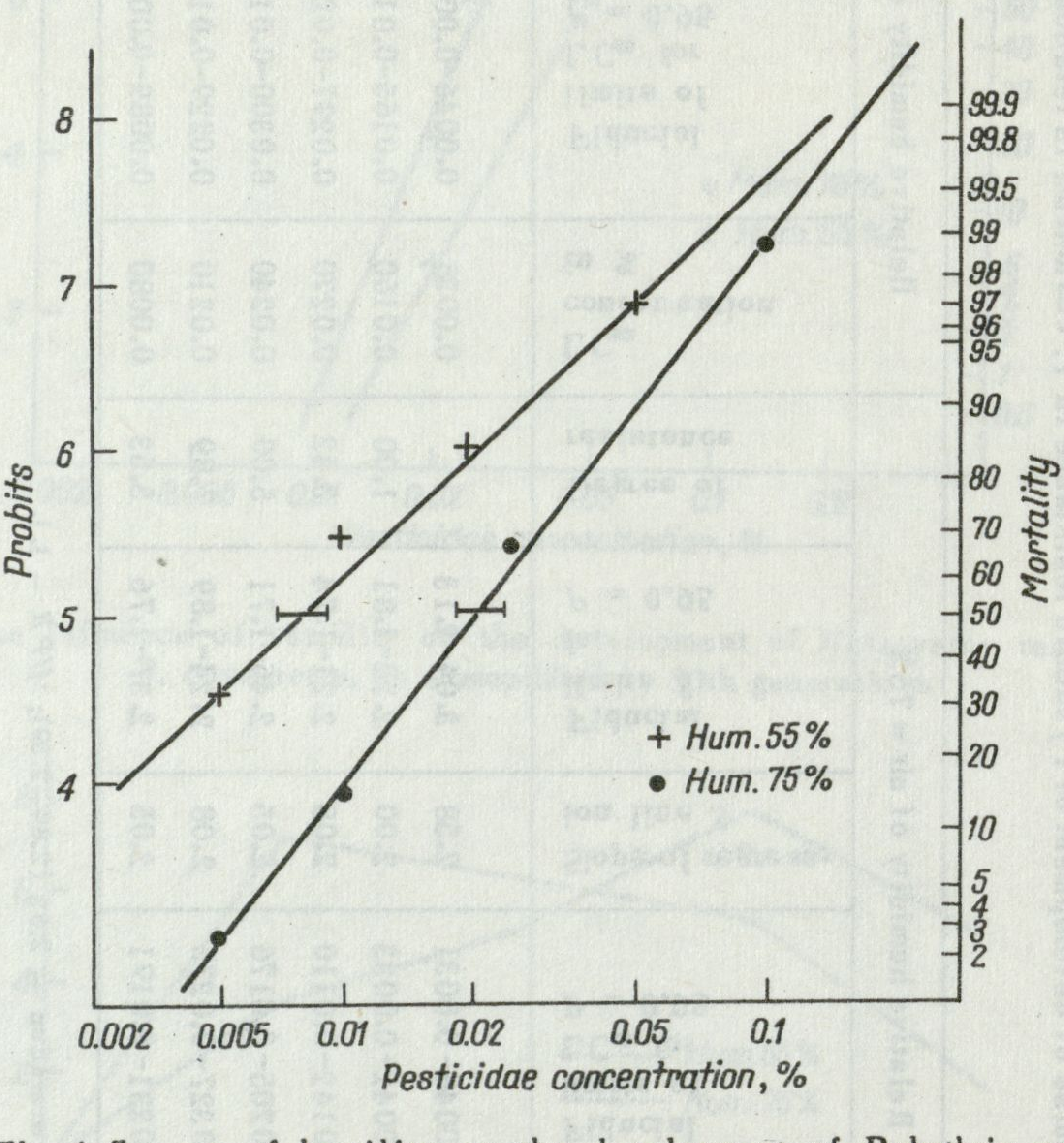

Fig. 24. The influence of humidity on the development of Pybuthrin resistance in *T. castaneum*, as exemplified by 20th generations

By contrast to Metasystox treatment, in Pybuthrin-treated populations up to the twelfth generation a much higher resistance could be observed at lower humidity level (55%). As can be seen in Figure 23, from the thirteenth generation on in the population cultured at 75% a growth of resistance occurred. Table XII shows the values of LC_{50} and the slopes of the straight lines of regression for the two Pybuthrin-treated populations. In Figure 24 are shown the straihgt lines of regression of susceptibility of the twentieth generations of the population studied. The lines are not parallel, which indicates that the course of mortality of the beetles was not the same under the humidity levels allowed. The susceptibility ratio of the twentieth generations is 2.63.

The results presented above do not indicate any clear relationship between the relative air humidity levels used and the production of resistance in *T. castaneum* to Azotox, Metasystox and Pybuthrin.

3. The effect of diet on the resistance developing process in *Sitophilus oryzae*

In the diet series *S. oryzae* was used as the test insect. Individuals of this species were cultured at 30°C and 75% air humidity on different diets.

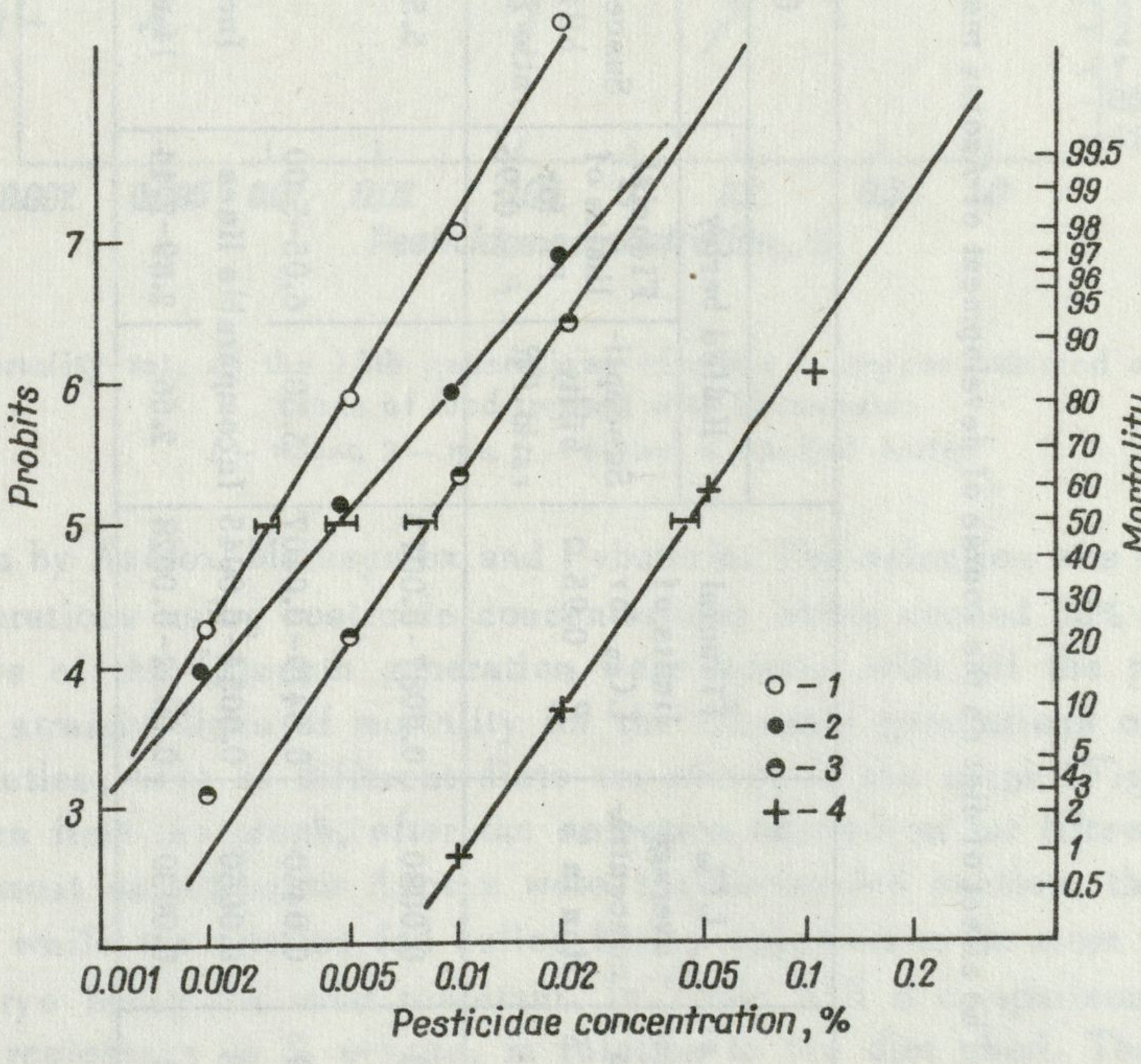

Fig. 25. Mortality rate of the 15th generations of adult *S. oryzae* cultured on different kinds of food treated with Azotox

1 – barley, *2* – wheat, *3* – hulled barley, *4* rye

They were fed: wheat, rye, barley and hulled barley. Prior to the experiment each amount of food was kept for three weeks under constant air humidity. The individual experiments differed only in respect of the food given to the beetles. As in the other experiments, the 1–3 days' old beetles were subjected

The effect of diet on the course of development of Azotox resistance in *S. oryzae*

Tab. XIII

Kind of food	Generation	Slope of regression line S	LC_{50} average concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Compared with					
					Hulled barley		Rye		Wheat	
					Susceptibility ratio PR	Fiducial limits of PR for $P = 0.95$	Susceptibility ratio PR	Fiducial limits of PR for $P = 0.95$	Susceptibility ratio PR	Fiducial limits of PR for $P = 0.95$
Hulled barley	XV	1.93	0.0080	0.0087-0.0073			5.50	6.05-5.00	Incomparable lines	
Rye	XV	1.89	0.0440	0.0479-0.0407	5.50	6.05-5.00			Incomparable lines	
Wheat	XV	2.18	0.0050	0.0054-0.0045	Incomparable lines		Incomparable lines			
Barley	XV	1.74	0.0030	0.0032-0.0028	2.66	2.89-2.44	14.66	15.83-13.57	Incomparable lines	

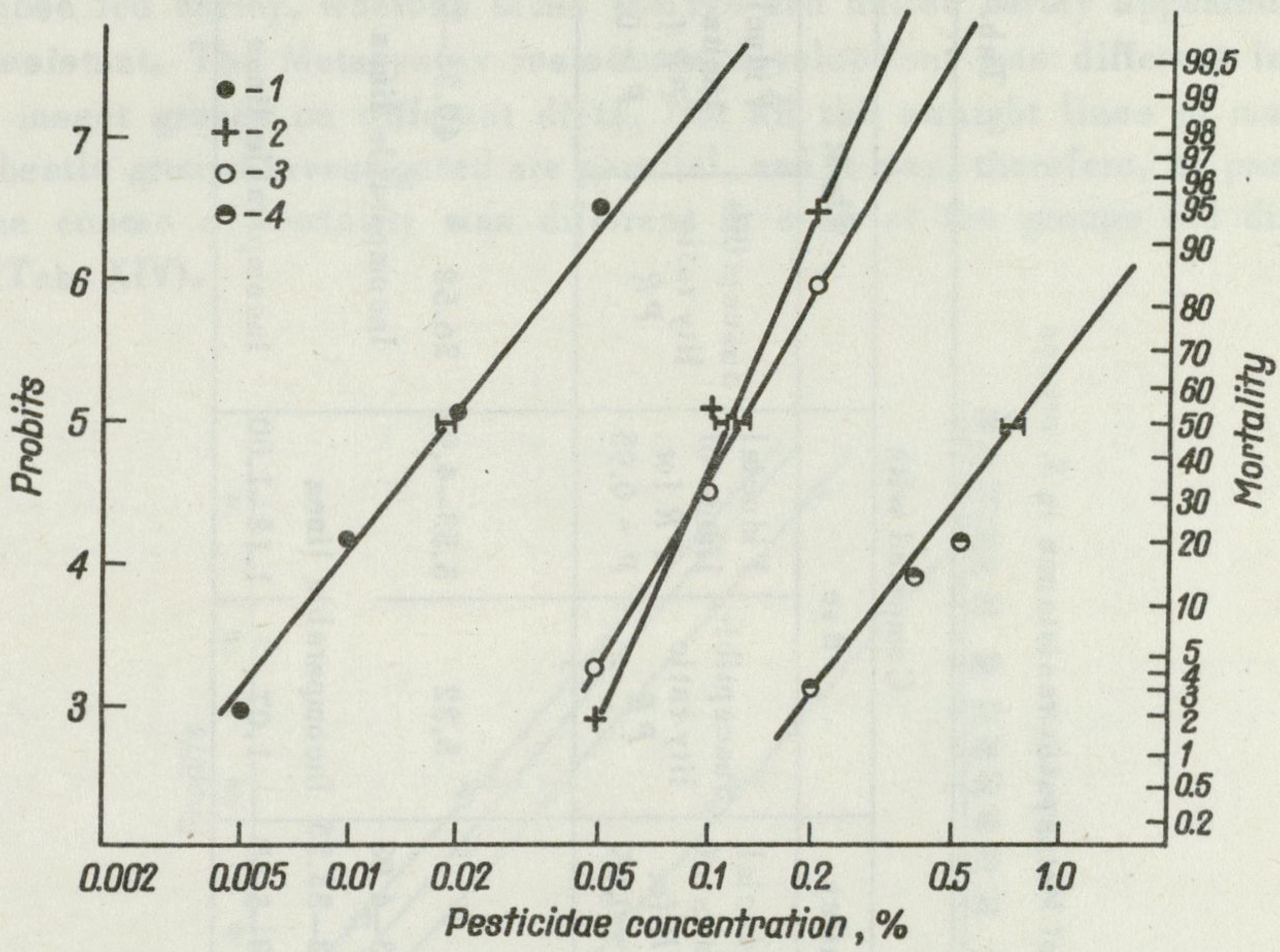

Fig. 26. Mortality rate of the 15th generations of adult *S. oryzae* cultured of different kinds of food treated with Metasystox
1 – wheat, *2* – rye, *3* – barley, *4* – hulled barley

to selection by Azotox, Metasystox and Pybuthrin. The selection was continued for 15 generations using pesticide concentrations which caused 50% mortality. The beetles of the fifteenth generation were treated with all the pesticides used. The straight lines of mortality for the fifteenth generations of Azotox--treated beetles, kept on different diets are shown in the graph (Fig. 25). As can be seen from the graph, after the selection carried on for fifteen generations the most sensitive to Azotox were the barley-fed beetles, then those fed wheat, while the beetles fed hulled barley appeared to be more resistant, those fed rye being the most resistant. In Table XIII a comparison is made of Azotox resistance in *S. oryzae*, in relation to the diet used. The straight line of mortality for the wheat-fed beetles is not parallel with the remaining lines representing the course of mortality of insects fed other kinds of food. It may be presumed that the development of Azotox resistance in wheat-fed beetles proceeds in a way which is different from that observed in the beetles cultured on the remainder of diets.

The course of development of Metasystox resistance in beetles fed the above-mentioned foods is different. In Figure 26 are shown the straight lines of mortality for the fifteenth generations of Metasystox-treated beetles fed wheat, barley, rye, and hulled barley. As can be inferred from the analysis

The effect of diet on the course of development of Metasystox resistance in *S. oryzae*

Tab. XIV

Kind of food	Generation	Slope regression line *S*	LC_{50} Regression line *S*	Fiducial limits of LC_{50} for $P = 0.95$	Compared with					
					Hulled barley		Rye		Wheat	
					Susceptibility ratio *PR*	Fiducial limits of *PR* for $P = 0.95$	Susceptibility ratio *PR*	Fiducial limits of *PR* for $P = 0.95$	Susceptibility ratio *PR*	Fiducial limits of *PR* for $P = 0.95$
Hulled barley	XV	1.81	0.7050	0.7473–0.6650			5.22	5.53–4.93	36.58	40.23–33.25
Rye	XV	1.65	0.1135	0.1203–0.1071	5.22	5.53–4.93			Incomparable lines	
Wheat	XV	2.55	0.0190	0.0195–0.0181	36.58	40.23–33.25	Incomparable lines			
Barley	XV	1.71	0.1220	0.1295–0.1151	5.78	6.13–5.45	1.07	1.13–1.00	Incomparable lines	

of LC_{50} valeus, the most susceptible to Metasystox were the wheat-fed beetles, then those fed barley, whereas those fed rye and hulled barley appeared to be more resistant. The Metasystox resistance development was different in each of the insect groups on different diets. Not all the straight lines of mortality of the beetle groups investigated are parallel, and it may, therefore, be presumed that the course of mortality was different in each of the groups fed different foods (Tab. XIV).

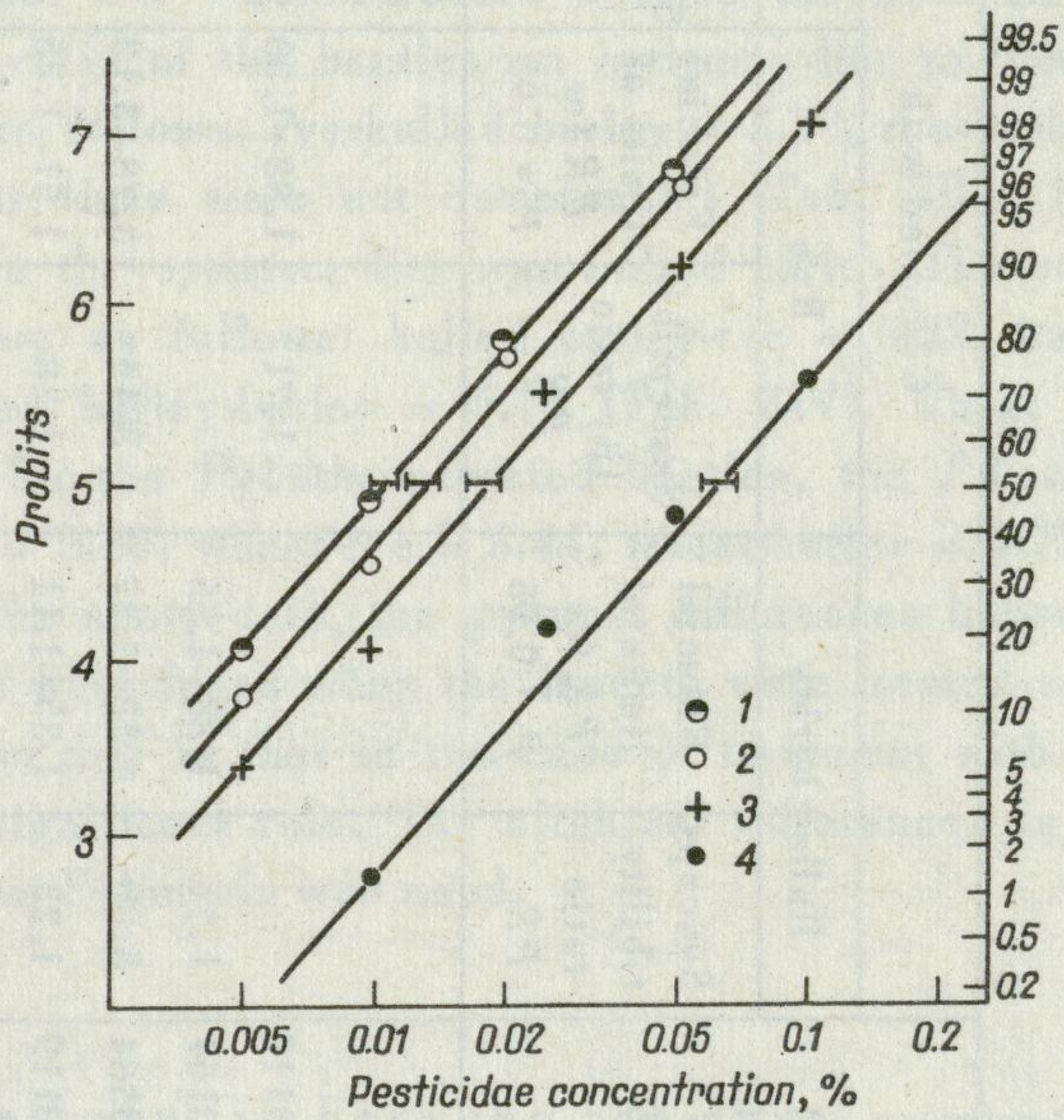

Fig. 27. Mortality rate of the 15th generations of adult *S. oryzae* cultured on different kinds of food treated with Pybuthrin
1 – hulled barley, *2* – barley, *3* – rye, *4* – wheat

The straight lines of mortality of the beetles cultured on different diets for fifteen generations treated with Pybuthrin are shown in Figure 27. The beetles fed hulled barley appeared to be the most susceptible of all, then those fed barley, whereas those fed rye were found to be more resistant, and those fed wheat – the most resistant. As indicated by the LC_{50} values (Tab. XV) and the slope of the straight lines of mortality, the mortality of the beetles was fairly similar and comparable in all the beetle groups cultured on different foods treated with Pybuthrin.

To sum up the following statement can be made: Azotox resistance is most easily produced in beetles fed rye, and less easily in those fed hulled barley, The effect of diet on the course of development of Pybuthrin resistance in *S. oryzae*

Tab. XV

Kind of food	Generation	Slope regression line S	LC_{50} regression line S	Fiducial limits of LC_{50} for $P = 0.95$	Compared with					
					Hulled barley		Rye		Wheat	
					Susceptibility ratio PR	Fiducial limits of PR for $P = 0.95$	Susceptibility ratio PR	Fiducial limits of PR for $P = 0.95$	Susceptibility ratio PR	Fiducial limits of PR for $P = 0.95$
Hulled barley	XV	2.28	0.0105	0.0115–0.0110			1.71	1.88–1.55	5.80	6.38–5.27
Rye	XV	2.26	0.0180	0.0198–0.0164	1.71	1.88–1.55			3.44	3.78–3.13
Wheat	XV	2.27	0.0620	0.0682–0.0564	5.80	6.38–5.27	3.44	3.78–3.13		
Barley	XV	2.15	0.0130	0.0142–0.0119	1.23	1.35–1.11	1.38	1.51–1.25	4.77	5.25–4.34

wheat or barley. The levels of Metasystox resistance (in descending order) were as follows: beetles fed hulled barley, rye, barley, wheat. The degree of Pybuthrin resistance in descending order was as follows: beetles fed wheat, rye, barley, hulled barley.

To be able to compare the effect of the different pesticides on the resistance of the population the optimum diet (giving the highest level of resistance to the pesticide) was taken as the basis, and then the susceptibility ratio for the optimum diet was compared with those obtained for the other diets and insecticides used. For Azotox-treated beetles the optimum diet was rye. The susceptibility ratio of the beetles on optimum diet to those on the remainder of diets was as follows: rye-hulled barley = 5.50, rye-barley = 14.66 (the rye--wheat straight lines were not comparable) (Tab. XIII). For the Metasystox--treated beetles the optimum diet was hulled barley. The susceptibility ratio — *PR* values were as follows: hulled barley-rye = 5.22, hulled barley-wheat = = 36.58, hulled barley-barley = 5.78 (Tab. XIV). Wheat appeared to be the optimum food for the Pybuthrin-treated beetles, the *PR* values being: wheat--hulled barley = 5.80, wheat-rye = 3.44, wheat-barley = 4.77 (Tab. XV). As can be seen from the above-data, the greatest differences between the optimum and the other diets were found when the insects were treated with Metasystox. The conclusion from this is that in the case of treatment with this insecticide the diet plays a significant role. The slightest differences in the *PR* ratio value were found when Pybuthrin was used.

4. The relationship between the development of resistance and the sex of the insects

For studies on the relationship between the sex and the development of resistance in insects, individuals of *T. castaneum* were used. Adult individuals of successive generations were treated with Metasystox. The pupae of every fifth generation were divided into sex groups. The adult forms that emerged from the pupae were treated, males and females separately, to check their resistance. As has been found, from the fifth generation onwards females and males clearly differ in resistance. Females show a greater resistance than the males. Between the tenth and the fifteenth generation no change in resistance can be seen in females or males (Fig. 28). The LC_{50} values for the twentieth generation is 0.05 in females, and 0,03 in males. Likewise, the level of resistance is 20.83 and 16. The *PR* values for the twentieth generations is 1.56. The values of LC_{50}, the straight lines of susceptibility regression and the levels of resistance for both sexes in individual generations are given in Table XVI.

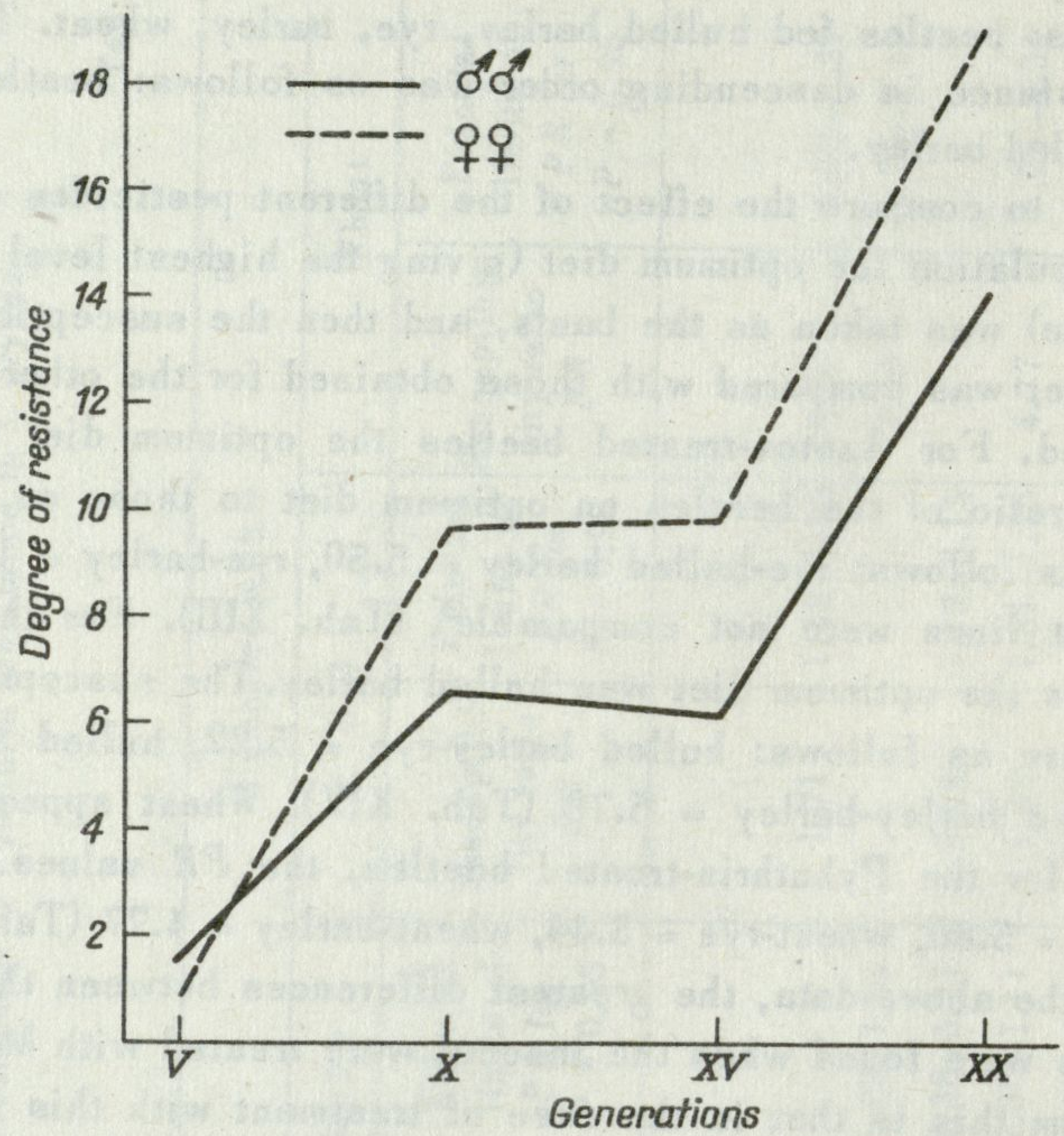

Fig. 28. Relationship between the development of Metasystox resistance in *T. castaneum* and sex

5. The relationship between the development of resistance and the age of the insects

In the age series *T. castaneum* beetles were treated with Pybuthrin. Selection was carried out among 1–3 days' and 15-days' old insects. To be able to compare the process of resistance development, in Table XVII are presented LC_{50} values, the slopes of regression lines and the levels of resistance for 1–3 days' and 15-days' old beetles. As can be seen from the table, the 1–3 days' old beetles of the original generation are more susceptible than the 15-day beetles. The LC_{50} value for the 1–3 days' old beetles is 0.0038, and for the 15 days' old ones – 0.0160. From the fifth generation on the resistance of the 1–3 days' old beetles appears to be higher than that of the original population, but the susceptibility of the 15 days' old beetles remains unchanged. The level of resistance of the fifteenth generations for the 1–3 days' old group is 7.89, and for the 15 days' old group – 1.25. The susceptibility ratio for the 1–3 days' group is 1.67. The results of selection in the populations investigated are shown in Figure 29. In Figure 30 are presented the straight lines of regression illustrating the mortality of the fifteenth generation of the 1–3 days' and the 15 days' old groups.

Course of development of Metasystox resistance in male and female *T. castaneum*

Tab. XVI

Generation	Males					Females				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits of S for $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits of S for $P = 0.95$	Degree of resistance
Original population	0.0020	0.0020–0.0018	1.76	1.97–1.57		0.0024	0.0026–0.0022	1.84	2.09–1.53	
V	0.0072	0.0075–0.0069	1.23	1.30–1.16	3.60	0.0070	0.0077–0.0064	1.67	1.77–1.55	2.91
X	0.0172	0.0189–0.0157	1.63	1.76–1.50	8.60	0.0280	0.0308–0.0254	1.73	1.83–1.54	11.66
XV	0.0160	0.0176–0.0145	1.80	1.96–1.65	8.00	0.0280	0.0310–0.0250	2.00	2.26–1.79	11.66
XX	0.0320	0.0346–0.0296	1.86	2.19–1.58	16.00	0.0500	0.0545–0.0459	1.90	3.04–1.64	20.83

PR – susceptibility for 20th generations – 1.56 (1.72–1.42); *f/PR* – 1.1.

Tab. XVII

Course of development of Pybuthrin resistance in adult *T. castaneum* at various ages

Generation	1–3 days old imagines					15 days old imagines				
	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope of regression line S	Fiducial limits of S for $P = 0.95$	Degree of resistance	LC_{50} concentration in %	Fiducial limits of LC_{50} for $P = 0.95$	Slope regression line S	Fiducial limits of S for $P = 0.95$	Degree of resistance
Original population	0.0038	0.0046–0.0031	2.58	3.04–2.13		0.0160	0.0171–0.0149	1.55	1.64–1.46	
III	0.0038	0.0042–0.0033	2.00	2.22–1.81	1.00	0.0165	0.0181–0.0150	2.25	2.52–2.00	1.03
V	0.0130	0.0142–0.0110	2.08	2.21–1.74	3.68	0.0100	0.0106–0.0094	1.38	1.39–1.36	0.62
X	0.0190	0.0205–0.0176	2.05	2.46–1.71	5.00	0.0150	0.0165–0.0136	2.27	2.54–2.03	0.94
XV	0.0300	0.0327–0.0275	2.08	2.24–1.89	7.89	0.0180	0.0196–0.0164	2.00	2.18–1.83	1.25

PR susceptibility for 20th generations – 1.67 (1.83–1.44); *f/PR* – 1.09.

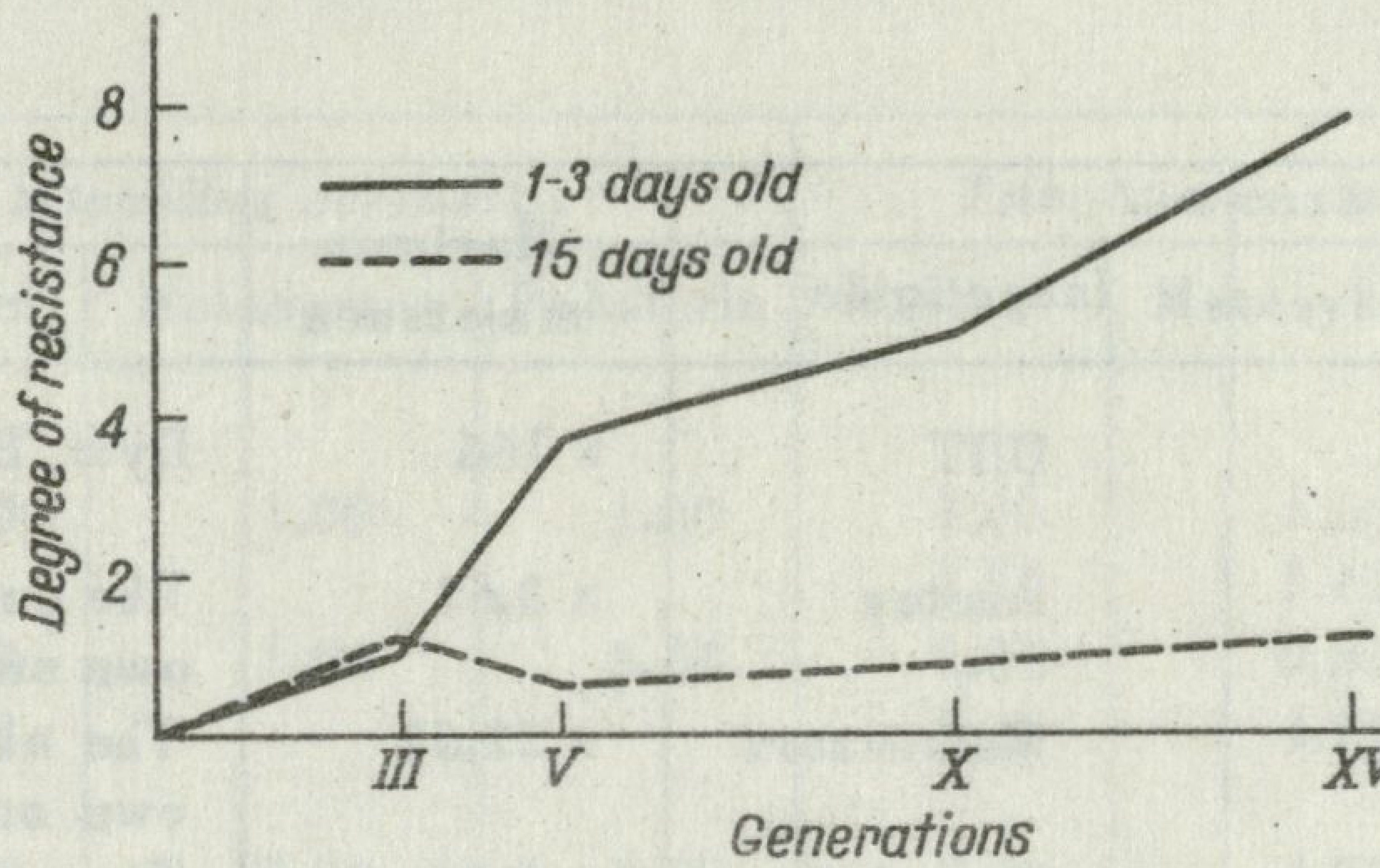

Fig. 29. Relationship between the age of *T. castaneum* and the development of Pybuthrin resistance

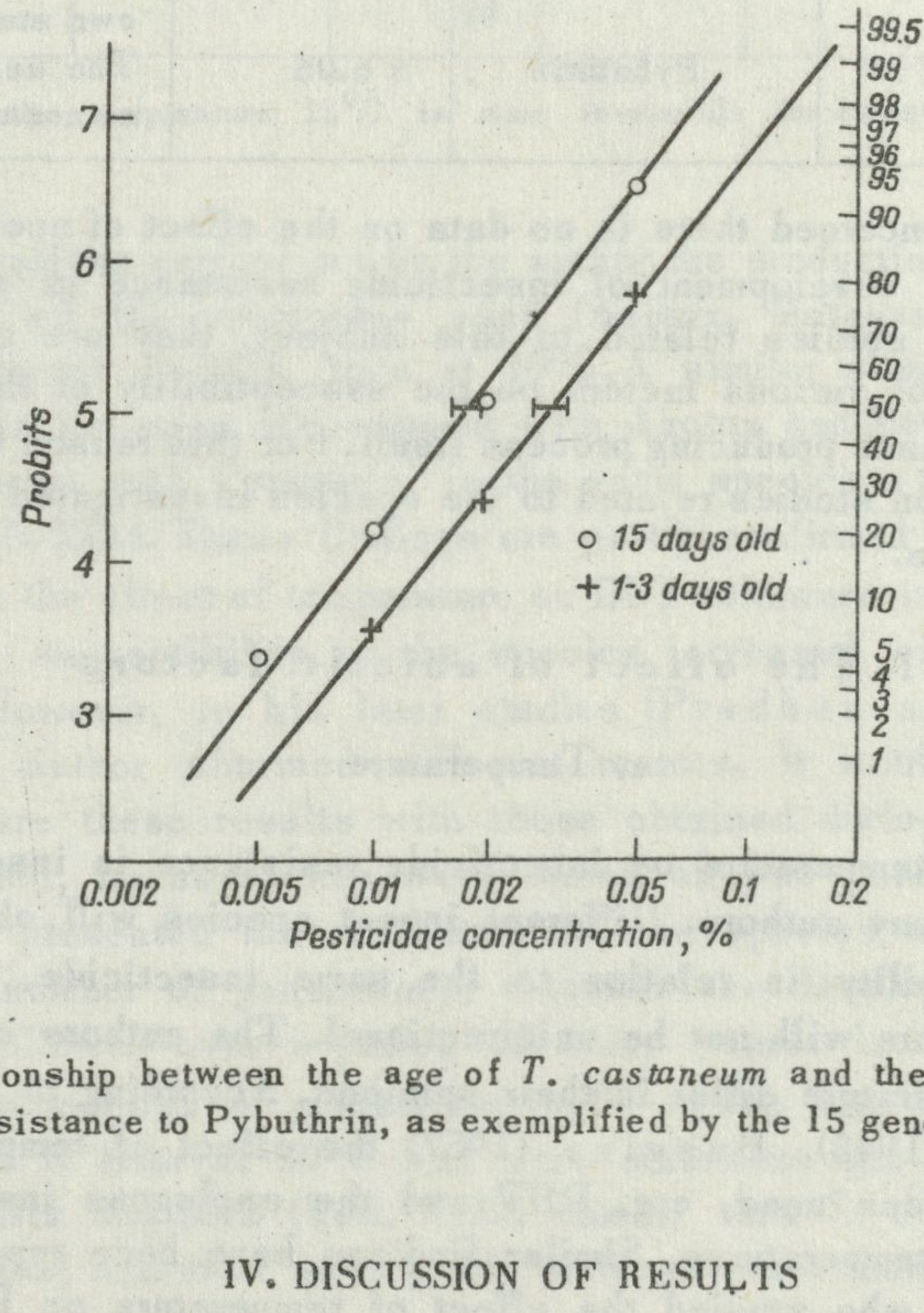

Fig. 30. Relationship between the age of *T. castaneum* and the development of their resistance to Pybuthrin, as exemplified by the 15 generations

IV. DISCUSSION OF RESULTS

The existence of insecticide resistance in *S. oryzae* and in *T. castaneum* has been described by but a few authors, and most of the studies concerned deal with one or two generations only. Table XVIII contains a summary of studies on the development of resistance in *S. oryzae* and *T. castaneum*.

Resistance of laboratory strains of *T. castaneum* and *S. oryzae* to different insecticides

Tab. XVIII

Species	Insecticide	Maximum resistance	Author
T. castaneum Herbst.	DDT	× 166	Dyte, Blackman(1967)
T. castaneum Herbst.	Azotox	× 3.67	The author's own studies
T. castaneum Herbst.	Metasystox	× 27.62	The author's own studies
T. castaneum Herbst.	Pybuthrin	× 7.86	The author's own studies
S. oryzae L.	Azotox	× 40	The author's own studies
S. oryzae L.	Metasystox	× 434.00	The author's own studies
S. oryzae L.	Pybuthrin	× 6.05	The author's own studies

In the literature concerned there is no data on the effect of ecological factors on the process of development of insecticide resistance in granary pests. Even if there are studies related to this subject, they are concerned with the direct effects of various factors on the susceptibility of the species and not with the resistance producing process itself. For this reason the discussion is based not only on studies related to the species investigated by the author, but also on others.

1. The effect of abiotic factors

a. Temperature

The effect of temperature on insecticide resistance in insects has been investigated by many authors. Different insect species will obviously show different susceptibility in relation to the same insecticide, therefore the effect of temperature will not be unidirectional. The authors concerned with the effect of temperature differ in their opinions. According to Fan, Cheng and Richards (1948), Busvine (1957) the effect of temperature varies with the insecticides used, e.g. DDT and the anologous insecticides are toxical at higher temperatures. Similar findings have been reported by Styczyńska (1966) who studied the effect of temperature on DDT tolerance in the body louse. Similar results have been described by David (1946) who treated *Aëdes aegypti* (L.) with pyrethrin. Strong and Sbur (1964), who studied the effect of temperature on the activity of Diazinon, DDVP, Dibrom, Gusathion and Ronnel on *S. oryzae*, found that as the temperature increased, the mortality of this species decreased.

Susceptibility ratio of the beetles during development of resistance at 25°C and 30°C

Tab. XIX

Generation	*Sitophilus oryzae* L.			*Tribolium castaneum* Herbst		
	Azotox	Metasystox	Pybuthrin	Azotox	Metasystox	Pybuthrin
Original population	1.00	1.00	1.00	1.00	1.00	1.00
III				1.28	1.42	5.00
V	1.33	1.04	3.20	2.35	0.60	0.27
VIII	3.78			2.35	4.29	
IX						0.65
X	2.80	12.58	2.75	2.00	4.79	0.29
XII	3.18					
XIII		21.11				
XV	4.00	16.84	1.93			
XVIII			1.46			
XX			1.29			

PR $>$ 1, then the temperature 25°C is more favourable for resistance development in insects.

In the investigations carried out by the author the production of resistance in *S. oryzae* to all the pesticides used (Azotox, Metasystox, Pybuthrin) proceeded much faster at 25°C than at 30°C. A similar situation was found in *T. castaneum* in the case of treatment with Azotox and Metasystox, but in the case of treatment with Pybuthrin, in the same species a reverse process was observed (Tab. XIX). These findings are partly confirmed by Pradhan's studies (1949a) on the effect of temperature on DDT tolerance in *T. castaneum.* He found that the susceptibility of the species increased with an increase of temperature. However, in his later studies (Pradhan and Rangarao 1958) the same author obtained different results. It would, however, be difficult to compare these results with those obtained during the investigation here described, bacause they were based on one generation only. In the series here presented the resistance of the species under study was observed over a number of generations, therefore the development of resistance could be followed over a period of many years. In addition to the finding that the production of resistance in *S. oryzae* and *T. castaneum* is much faster at 25°C than at 30°C one more statement can be made, on the basis of the results obtained (Tab. XIX), namely that *S. oryzae* is a much more plastic species, and more susceptible to temperature than *T. castaneum.*

b. Humidity

As indicated by many studies (Barlow and Hadaway 1952, Busvine 1957), relative humidity of the environment has no significant effects on the toxic activity of the contact poisons in relation to the housefly, mosquitoes and other insects. Similar findings have been described by Berfrand 1919, Chapman and Johnson 1925, Lindgren and Shepard 1932 (quot. after Pradhan 1949b), who did not find any effect of humidity on chloropicrin tolerance in *S. oryzae*, *S. granarius* and *T. confusum*, as well as by David (1946), who studied the effect of humidity on pyrethrin susceptibility in *A. aegypti* (L.). As regards this problem, there is a discrepancy of opinions. Strong and Sbur (1960, 1964) observed that an increase in the grain humidity was accompanied by a higher mortality of *S. granarius*, *S. oryzae*, treated with a number of different pesticides. The same authors also found that the effect humidity varied with the pesticides used. Pradhan (1949b), who investigated the effect of humidity on pesticide tolerance in *T. castaneum*, found that at a higher humidity level (84%) the species was more susceptible to DDT than at lower humidity levels (30–50%). Fisk and Shepard 1938, and Parkin 1944 (quot. after Pradhan 1949b) found that at lower humidity lecels the mortality among *T. confusum* treated with methyl bromide was lower. During her studies on the effect of relative air humidity on DDT tolerance in *Pediculus humanus humanus* L. Styczyńska (1966) found that with increasing humidity the tolerance of the insects decreased.

Susceptibility ratio of the beetles during development of resistance at humidity 55% and 75%

Tab. XX

Generation	*Sitophilus oryzae* L.			*Tribolium castaneum* Herbst.		
	Azotox	Metasystox	Pybuthrin	Azotox	Metasystox	Pybuthrin
Original population	1.00	1.00	1.00	1.00	1.00	1.00
III				1.60	0.87	4.21
V	2.67	3.13	1.50	0.60	0.40	2.08
VIII		3.20	1.50	1.36		
X	3.36	4.09	1.31	1.04	0.33	1.26
XII		2.60				
XV	2.80	3.21	1.07	1.65	1.09	0.70
XX				0.50	1.84	0.34

If $PR > 1$, then humidity 55% is more favourable for resistance development.

The investigation presented in this paper indicates that humidity exerts a clear effect on the susceptibility to Azotox and Metasystox in *S. oryzae*, and only a slight one in relation to Pybuthrin. The species appeared to be more resistant when cultured at 55% than at 75% humidity (Tab. XX). *T. castaneum* was found to be less susceptible to the humidity of the environment. As can be inferred from the results, humidity does not exert a significant influence on the production of resistance in *T. castaneum* in relation to Azotox, Metasystox and Pybuthrin. It is impossible, however, to compare the results of the present investigation and those reported by the above authors, since these authors studied the effect of humidity on the susceptibility of the species only once, in one or two generations, taking into account only the toxicity of the pesticide and not the resistance developing process in the insects. Nevertheless, it should be emphasized that the author's results concerning *S. oryzae* populations agree with the general conclusions published by Pradhan (1949b) and Styczyńska (1966), who think that at lower humidity levels the insects are less susceptible (Fig. 14, 16, 18). The results of the present experiments, the aim of which was to establish the effect of humidity on the development of resistance in *T. castaneum* in relation to Azotox, Metasystox and Pybuthrin, indicate that in this case we are not dealing with a general ecological regularity. It may be inferred from the results that the effect of the environment to a large extent depends on the species studied, and its susceptibility to the action of the abiotic factors. It has also been found that the effect of the environmental factors on the population depends on the kind of pesticide. In all the experimental series in which Pybuthrin was used the rate of resistance development was slow in both the insect species tested. This may be attributed to the fact that Pybuthrin consists of piperonyl butoxide — a synergistic substance which enhances the action of pyrethrins. Resistance to Metasystox and Azotox is developed at a much faster rate. After a Metasystox selection that continued for several generation, the population tested responds to the pesticide by a rapid increase in resistance (Fig. 4, 10, 22).

c. Diet

The effect of diet on the resistance developing process is very complex, and it is difficult to ascertain the existence of some direct relationship without simultaneously studying the resistance producing mechanisms. Some authors (Gordon 1961, Henneberry 1964) have found that diet generally affects the insecticide susceptibility in insects. As indicated by the data in Gordon's paper (1961): after being cultured for 12 generations on beans, carnations and plum trees, the mites *Tetranychus urticae* L. showed a low TEPP resistance (5–10-fold), while those cultured on dead nettle and the common hop showed a high (50–200-fold) resistance. In their investigations Rivera and Steinhauer (1962) found that the DDT susceptibility in *Drosophila melanogaster* Mg. depended on nitrogen content in the food, an increase in nitrogen content was accompanied by an increased DDT susceptibility in these dipterans. In earlier investigations (Cichy 1969) on the effect of different kinds of food on Pybuthrin susceptibility in *T. castaneum* the authors of this study has found that beetles cultured on different diets differ in their susceptibility to this insecticide.

The research on the effect of different diets on the development of resistance in *S. oryzae* to Azotox, Metasystox and Pybuthrin, carried out by the author, shows that in populations cultured for several generations on different diets the resistance developing process proceeds in different ways, and the particular diets have different effects, depending on the insecticide used. This probably is related to the direct effect of food on the size (weight) of the imagines (Sandner 1968). The results obtained (Tab. XIII, XIV, XX) permit the conclusion that in the development of resistance in *S. oryzae* to Metasystox and Azotox the role of diet is very important, but diet has a much less effect on the development of Pybuthrin resistance. Thus also in this case Pybuthrin appears to be the most advantageous means of avoiding the adverse consequences of producing insecticide resistance.

2. The effect of population factors

a. Sex

The relationship between insecticide susceptibility and the sex of insects has been studied by many authors. Loschiavo (1955) finds that female *T. confusum* are more susceptible to DDT than the males treated with the same dose. Similar results have been obtained by the author (Cichy 1969) from studies on the relationship between the development of Pybuthrin resistance and the sex of *T. castaneum*. Tielecke (1960) studied the susceptibility to DDT, HCH, Chlordan, and Toxaphen in male and female *S. granarius*. Males appeared to be more resistant to all these pesticides than were the females. The above studies covered one generation only. It was for this reason that the author of the present paper decided to follow these interesting relationships in resistance developing processes over a number of generations. Selection of *T. castaneum* by Metasystox was continued for twenty generations. In the original population the females were more resistant than the males. Their susceptibility ratio – *PR* was 1.2. During further selection the *PR* ratio increased to reach the value 1.56 for the twentieth generation. The results permit the conclusion that the rate of development of Metasystox resistance in *T. castaneum* depends on the sex of the individuals, females being more resistant than the males.

b. Age

In their investigation of the relationship between pesticide susceptibility and the age of the housefly Byrdy and Górecki (1961) found that 1–5 days' old adults were less DDT tolerant than 15 days' old individuals. Similar results have been published by Goos (1961) from studies on the effect of this insecticide on *Calandra granaria.* In the investigations carried out by the author also young individuals of *T. castaneum* appeared to be less Pybuthrin tolerant than the older ones. It has been found that Pybuthrin resistance in *T. castaneum* develops at a much faster rate if the selection is carried out among young individuals.

V. CONCLUSIONS

1. Temperature exerts a clear influence on the development of resistance to Azotox, Metasystox and Pybuthrin in *S. oryzae* and *T. castaneum.* It has been found that at a lower temperature (25°C) the rate of ressistance development was in both species much faster than at higher temperature (30°C), an exception to this being the Pybuthrin resistance developing process in *T. castaneum.*

2. Humidity appears to have an appreciable effect on the rate of resistance development in *S. oryzae* in relation to all the pesticides tested. At 55% humidity the rate of development of resistance to Azotox, Metasystox and Pybuthrin was faster than at 75% humidity.

3. No appreciable effect of humidity could be observed in regard of the development of resistance to the pesticides tested in *T. castaneum.*

4. *S. oryzae* has been found to be susceptible to environmental factors. It seems therefore advisable to attempt trials aimed at controlling this species by combining insecticide treatment with environment modification by varying the temperature and humidity.

5. In *T. castaneum* some relationship can be seen between Metasystox resistance and the sex of the individuals. After the selection that was continued for a number of generations, the females appeared to be more resistant than the males.

6. The rate of development of Pybuthrin resistance in *T. castaneum* is faster when selection is carried out among younger individuals.

7. The role of diet appears to be very significant in the case of development of resistance to Metasystox and Azotox in *S. oryzae.* The effect of food is much less evident in relation to the development of Pybuthrin resistance. Therefore also in this case Pybuthrin appears to be the best insecticide as far as the control of granary pests is concerned.

The author wishes to express her cordial thanks to Prof. Dr. Henryk Sandner for guidance and kind assistance, to Doc. Dr. Adam Goos for his kind and valuable comments, also to Małgorzata Pankanin, M. Sc., and Elżbieta Kosewska for their kind help with the laboratory work.

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WPŁYW NIEKTÓRYCH CZYNNIKÓW EKOLOGICZNYCH NA POWSTAWANIE ODPORNOŚCI *SITOPHILUS ORYZAE* L. I *TRIBOLIUM CASTANEUM* HERBST. NA INSEKTYCYDY

Streszczenie

Celem badań było stwierdzenie wpływu niektórych czynników ekologicznych takich jak: temperatura, względna wilgotność powietrza, pokarm, płeć i wiek na proces powstawania odporności owadów na insektycydy.

Do badań użyto dwóch gatunków chrząszczy: *Sitophilus oryzae* L. i *Tribolium castaneum* Herbst. oraz trzech preparatów Azotox ,,33'', Metasystox ,,i'' i Pybuthrin

6/60. Doświadczenia prowadzono w trzech wariantach temperatury i wilgotności. Wariant I: 25°C i 75% względnej wilgotności powietrza; II: 30°C i 75% względnej wilgotności powietrza; III: 30°C i 55% względnej wilgotności powietrza. W takich warunkach hodowano chrząszcze przez 10 do 25 pokoleń. Chrząszcze do eksperymentów nad wpływem pokarmu hodowano na pszenicy, życie, jęczmieniu, kaszy-pęczaku. Do innych doświadczeń hodowano tylko na pszenicy.

Zależność powstawania odporności od płci chrząszczy badano na *T. castaneum*. Określano płeć poczwarek, a następnie po wyjściu z nich imagines, osobno traktowano samce i samice preparatem Metasystox. Dla stwierdzenia zależności powstawania odporności od wieku testowano Pybuthrinem dwie linie chrząszczy *T. castaneum* w wieku 1–3 dni i 15 dni.

Selekcję wszystkich owadów prowadzono na poziomie LC_{50}. Przy opracowaniu wyników zastosowano graficzną metodę statystyczną Lichtfielda i Wilcoxona 1949, w opracowaniu Bojanowskiej 1961. Na podstawie przeprowadzonych badań stwierdzono, że:

1. Temperatura wywiera wyraźny wpływ na powstawanie odporności *S. oryzae* i *T. castaneum* na Azotox, Metasystox i Pybuthrin. W niższej temperaturze 25°C u obu badanych gatunków odporność rozwijała się znacznie szybciej niż w temperaturze wyższej 30°C z wyjątkiem powstawania odporności u *T. castaneum* na Pybuthrin.

2. Wilgotność ma wyraźny wpływ na powstawanie odporności u *S. oryzae* na wszystkie badane preparaty. Chrząszcze hodowane w wilgotności 55% uodporniły się na Azotox, Metasystox, i Pybuthrin szybciej niż w wilgotności 75%.

3. Nie zaobserwowano wyraźnego wpływu wilgotności na powstawanie odporności na badane preparaty u *T. castaneum*.

4. *S. oryzae* jest gatunkiem podatniejszym na wpływ środowiska i wydaje się, że byłoby celowe przeprowadzenie prób zwalczania tego gatunku drogą modyfikowania środowiska temperaturą i wilgotnością, przy stosowaniu insektycydów.

5. Odporność *T. castaneum* na Metasystox zależy od płci. Po selekcji prowadzonej przez szereg pokoleń samice okazały się bardziej odporne niż samce.

6. Powstawanie odporności na Pybuthrin u *T. castaneum* przebiega znacznie szybciej jeśli selekcje prowadzimy na osobnikach młodszych, niż na starszych.

7. Przy powstawaniu odporności u *S. oryzae* na Metasystox rola pokarmu jest bardzo istotna. Znacznie mniejszy wpływ wywiera pokarm na powstawanie odporności na Pybuthrin, a zatem Pybuthrin i w tym przypadku okazał się środkiem najkorzystniejszym z punktu widzenia zwlaczania szkodników magazynowych.

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