Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

ASPECTS OF RESISTANCE TO PHENOXY HERBICIDES

IN NODDING THISTLE (*CARDUUS NUTANS* L.)

A thesis
presented in partial fulfilment
of the requirements
for the degree of
Doctor of Philosophy
at
Massey University

Kerry Charles Harrington

1992

ABSTRACT

A nodding thistle (*Carduus nutans* L.) population had been reported from Argyll in Hawkes Bay, New Zealand, which had poor susceptibility to MCPA and 2,4-D. Plants from the Argyll population were grown beside another Hawkes Bay nodding thistle population in a glasshouse and their dose response curves for MCPA were compared in three separate experiments. The Argyll population was significantly less susceptible to MCPA in all experiments, though the magnitude of resistance varied between experiments from 5-fold to 14-fold. When grown beside each other in the field, the Argyll population was 7 times more resistant to MCPA than the other population.

A range of other herbicides was applied to the Argyll nodding thistle population. Cross-resistance was detected for 2,4-D and MCPB, but no significant decreases in susceptibility were detected with mecoprop, clopyralid, picloram, dicamba, paraquat/diquat or glyphosate. A significant reduction in susceptibility to tribenuron-methyl was measured in a field experiment, but this difference was not apparent when the experiment was repeated in a glasshouse. The cross-resistance to MCPA, MCPB and 2,4-D meant selective control of nodding thistle at Argyll in clover-based pastures was now very difficult to achieve.

Nodding thistle populations from 20 Hawkes Bay and 7 Waikato properties were tested for resistance to MCPA, and significant levels of resistance were detected in 14 of these populations. Interviews of property owners indicated that resistance had developed where 2,4-D or MCPA had been applied annually for many years, whereas properties without resistance had been sprayed less regularly.

Resistant and susceptible nodding thistle seedlings were grown together at a 1:1 ratio under conditions of nutrient stress to determine whether herbicide-resistant nodding thistle plants are less competitive than normal. No difference was detected between the resistant and susceptible biotypes used.

Under some conditions, susceptible plants were more likely to have high trichome densities on their leaves, but this trait was found to be too variable and not correlated closely enough with herbicide susceptibility to be useful in distinguishing between resistant and susceptible biotypes.

Significant differences in susceptibility to MCPA were maintained between resistant and susceptible biotypes even when leaf surfaces were damaged to allow better foliar penetration of the herbicide, or when herbicide was applied to plants via the root system. Thus the mode of resistance did not appear to involve difficulties with foliar uptake.

Studies with radiolabelled 2,4-D confirmed that resistance did not relate to poor leaf penetration. These experiments indicated that 2,4-D was broken down more rapidly in resistant plants. Other findings were that 2,4-D or its metabolites were released in greater quantities from the root systems of susceptible plants, and that herbicide molecules were more difficult to extract from the interior of susceptible plants, possibly due to increased binding.

Reasons why resistance to phenoxy herbicides has developed in nodding thistle are discussed, and techniques for controlling resistant populations selectively in pastures and preventing further resistance from developing are also analysed.

ACKNOWLEDGEMENTS

I wish to express my sincere gratitude to my two supervisors, Assoc Prof A.G. Robertson (Agronomy Department) and Dr A.I. Popay (MAFTech), for their invaluable advice, encouragement, constructive criticism and assistance during the course of this study and preparation of this manuscript. Their continued support despite their respective changes in circumstances has been particularly appreciated.

I would also like to thank:

- Dr H.G. McPherson (DSIR) for his considerable advice and support as a supervisor in the earlier stages of the project

- Prof B.R Watkin and Dr G.W. Ivens for their supervision and assistance in the first few months of the project before they both retired from the Agronomy Department

- Dr D.J. Woolley (Horticultural Science Department) for his invaluable assistance and advice with the radiolabelled herbicide experiments

- Mr D.T. Sollitt and Ms F.J. Brown (Agronomy Department) for their useful technical advice

- Mr R.L. Bolter (Agricultural Engineering Department) for building the "box sprayer" used in most of the trials, and Mr I.A. Painter (Agricultural Engineering Department) for building the atomiser used in the later radiolabelled herbicide experiments

- Dr W.D. Stirling (Mathematics and Statistics Department) for his assistance with the probit analysis, Dr C.D. Lai and Mr G.C. Arnold (Mathematics and Statistics Department) for their assistance with the chi-square analysis, and Dr I.L. Gordon (Agronomy Department) for his help with analysing the fitness experiment data

- all the staff of DowElanco (formerly Ivon Watkins-Dow) who provided me with information, advice and data, especially Mr B. Harris

- all of the farmers who gave me access to their farms and provided information on past spraying practices

- the Ministry of Agriculture and Fisheries, the Massey University Agricultural Research Fund and DowElanco for their financial assistance

- Massey University for employing me as a full-time lecturer throughout the project

- the staff of the Agronomy Department for their advice and encouragement

- my wife Janice and our children for their support and tolerance during the project which began before any of them even knew me.

TABLE OF CONTENTS

TITLE PAGE i
ABSTRACT ii
ACKNOWLEDGEMENTS iv
TABLE OF CONTENTS vi
LIST OF TABLES xii
LIST OF FIGURES xv
LIST OF PLATES xix
LIST OF PESTICIDES xxi

1 INTRODUCTION 1
1.1 OBJECTIVE 1
1.2 NODDING THISTLE (*CARDUUS NUTANS* L.) 1
1.2.1 **Importance in New Zealand** 1
1.2.2 **Biology of nodding thistle** 3
1.2.2.1 Seed physiology 3
1.2.2.2 Growth and development 4
1.2.2.3 Reproduction and dispersal 6
1.2.2.4 Habitat 7
1.2.3 **Non-chemical control of nodding thistle** 8
1.2.3.1 Pasture management techniques 9
1.2.3.2 Biological control 11
1.2.3.3 Mechanical control 12
1.2.3.4 Summary 13
1.2.4 **Chemical control of nodding thistle** 13
1.3 MCPA AND 2,4-D 16
1.3.1 **Properties** 16
1.3.2 **History and uses** 17
1.3.3 **Absorption into plants** 19
1.3.4 **Movement within plants** 20
1.3.5 **Symptoms and mode of action** 22
1.3.6 **Degradation within plants** 23
1.4 FACTORS INFLUENCING EFFECTIVENESS OF FOLIAR-APPLIED HERBICIDES 24
1.4.1 **Environmental factors** 24
1.4.1.1 Climate 24
1.4.1.2 Other environmental factors 26

1.4.2 **Genetic factors** 26
1.5 CONCLUDING COMMENTS 28

2 TECHNIQUES FOR COMPARING THE SUSCEPTIBILITY OF POPULATIONS TO HERBICIDES 29
2.1 INTRODUCTION 29
2.2 DESIGN OF A SPRAYER 31
2.2.1 **Introduction** 31
2.2.2 **Requirements for field trials** 31
2.2.3 **Requirements for glasshouse trials** 33
2.2.4 **Details of sprayer** 33
2.3 SCOTCH THISTLE FIELD TRIAL 37
2.3.1 **Introduction** 37
2.3.2 **Methods and materials** 38
2.3.3 **Results and discussion** 39
2.3.3.1 Plant identification 39
2.3.3.2 Quantitative responses 39
2.3.3.3 Quantal responses 39
2.3.4 **Conclusions** 43
2.4 NODDING THISTLE FIELD EXPERIMENT 44
2.4.1 **Introduction** 44
2.4.2 **Methods and materials** 44
2.4.3 **Results and discussion** 45
2.5 NODDING THISTLE GLASSHOUSE EXPERIMENT 48
2.5.1 **Introduction** 48
2.5.2 **Methods and materials** 49
2.5.3 **Results and discussion** 50

3 GLASSHOUSE COMPARISONS OF POPULATIONS 52
3.1 INTRODUCTION 52
3.2 FIRST GLASSHOUSE COMPARISON 52
3.2.1 **Methods and materials** 52
3.2.2 **Results and discussion** 53
3.3 SECOND GLASSHOUSE COMPARISON 55
3.3.1 **Introduction** 55
3.3.2 **Methods and Materials** 56
3.3.3 **Results and discussion** 56
3.4 THIRD GLASSHOUSE COMPARISON 58
3.4.1 **Introduction** 58

3.4.2 **Methods and materials** 58
3.4.3 **Results and discussion** 58
3.5 CONCLUDING DISCUSSION 60

4 FIELD COMPARISONS OF POPULATIONS 61
4.1 INTRODUCTION 61
4.2 METHODS AND MATERIALS 61
4.3 RESULTS AND DISCUSSION 64
4.3.1 **Influence of plant age** 64
4.3.2 **Tolerance of the Argyll population** 68
4.4 CONCLUSION 70

5 TESTING FOR CROSS-RESISTANCE 71
5.1 INTRODUCTION 71
5.2 CLOPYRALID EXPERIMENT 71
5.2.1 **Introduction** 71
5.2.2 **Methods and materials** 72
5.2.3 **Results and discussion** 72
5.3 HERBICIDE SCREENING TRIAL 74
5.3.1 **Introduction** 74
5.3.2 **Methods and materials** 74
5.3.3 **Results and discussion** 77
5.3.3.1 MCPA 77
5.3.3.2 2,4-D 79
5.3.3.3 Mecoprop 79
5.3.3.4 MCPB 82
5.3.3.5 Clopyralid 82
5.3.3.6 Picloram and dicamba 83
5.3.3.7 Herbicides with other modes of action 84
5.4 SECOND TRIBENURON-METHYL TRIAL 86
5.4.1 **Introduction** 86
5.4.2 **Methods and materials** 87
5.4.3 **Results and discussion** 87
5.5 CONCLUDING DISCUSSION 89
5.5.1 **Alternative chemical control strategies** 89
5.5.2 **Mechanism of resistance** 89

6 OTHER SITES WITH PHENOXY-RESISTANT NODDING THISTLE 92
6.1 INTRODUCTION 92
6.2 FIRST POPULATION SCREENING TRIAL 92
6.2.1 **Introduction** 92
6.2.2 **Methods and materials** 93
6.2.3 **Results and discussion** 93
6.3 SECOND POPULATION SCREENING TRIAL 96
6.3.1 **Methods and materials** 96
6.3.2 **Results and discussion** 98
6.4 SPRAYING HISTORIES 103
6.4.1 **Introduction** 103
6.4.2 **Methods and materials** 103
6.4.3 **Results** 104
6.4.3.1 Resistant sites 104
6.4.3.2 Susceptible sites 105
6.4.4 **Discussion** 106
6.5 CONCLUSIONS 109

7 FITNESS OF RESISTANT NODDING THISTLE 111
7.1 INTRODUCTION 111
7.2 METHODS AND MATERIALS 112
7.3 RESULTS AND DISCUSSION 112
7.4 CONCLUSIONS 116

8 INITIAL PHYSIOLOGICAL INVESTIGATIONS 117
8.1 INTRODUCTION 117
8.2 LEAF TRICHOMES 117
8.2.1 **Introduction** 117
8.2.2 **1987 field trial** 119
8.2.2.1 Introduction 119
8.2.2.2 Methods and materials 119
8.2.2.3 Results and discussion 119
8.2.3 **1988 glasshouse trial** 120
8.2.3.1 Introduction 120
8.2.3.2 Methods and materials 121
8.2.3.3 Results and discussion 121
8.2.4 **Conclusions** 122
8.3 CUTICLE DAMAGE AND SOIL APPLICATION 123
8.3.1 **Introduction** 123

8.3.2 **Methods and materials** 124
8.3.3 **Results and discussion** 127
8.3.3.1 Effect of cuticle damage 127
8.3.3.2 Effect of root uptake 128
8.3.4 **Conclusion** 129

9 PHYSIOLOGICAL STUDIES USING RADIOLABELLED 2,4-D 130
9.1 INTRODUCTION 130
9.2 FIRST PENETRATION AND TRANSLOCATION EXPERIMENT 131
9.2.1 **Introduction** 131
9.2.2 **Methods and materials** 132
9.2.2.1 Preparation of herbicide 132
9.2.2.2 Application to plants 132
9.2.2.3 Recovery of radioactivity 133
9.2.3 **Results and discussion** 134
9.2.3.1 Foliar penetration 134
9.2.3.2 Translocation 137
9.2.3.3 Insoluble residues 139
9.2.4 **Conclusions** 140
9.3 SECOND PENETRATION AND TRANSLOCATION EXPERIMENT 140
9.3.1 **Introduction** 140
9.3.2 **Methods and materials** 141
9.3.2.1 Preparation of herbicide 141
9.3.2.2 Application to plants 141
9.3.2.3 Recovery of radioactivity 142
9.3.3 **Results and discussion** 143
9.3.3.1 Foliar penetration 143
9.3.3.2 Translocation 145
9.3.3.3 Insoluble residues 147
9.3.4 **Conclusions** 150
9.4 METABOLISM EXPERIMENTS 150
9.4.1 **Introduction** 150
9.4.2 **Methods and materials** 151
9.4.2.1 Ether partitioning 151
9.4.2.2 Separation of the ether soluble components 151
9.4.2.3 Separation of the water soluble components 153

9.4.3 **Results and discussion** ... 154
9.4.3.1 Ether partitioning ... 154
9.4.3.2 Separation of the ether soluble components ... 155
9.4.3.3 Separation of the water soluble components ... 158
9.4.4 **Conclusions** ... 159
9.5 DISCUSSION ... 160
9.6 CONCLUSION ... 162

10 CONCLUDING DISCUSSION
10.1 INTRODUCTION ... 164
10.2 REASONS FOR RESISTANCE DEVELOPING ... 164
10.2.1 **Introduction** ... 164
10.2.2 **Selection pressure of herbicides** ... 165
10.2.3 **Initial frequency of resistance gene** ... 167
10.2.4 **Seed bank** ... 168
10.2.5 **Fitness of resistant individuals** ... 169
10.2.6 **Conclusions** ... 170
10.3 PREVENTING FURTHER DEVELOPMENT OF RESISTANCE TO PHENOXY HERBICIDES ... 171
10.3.1 **Nodding thistle** ... 171
10.3.2 **Other pasture species** ... 173
10.3.3 **Other land uses** ... 174
10.4 CONTROL OF PHENOXY-RESISTANT NODDING THISTLE ... 175
10.4.1 **Introduction** ... 175
10.4.2 **Alternative herbicides** ... 175
10.4.3 **Improving effectiveness of phenoxy herbicides** ... 176
10.4.4 **Non-chemical techniques** ... 177
10.5 FURTHER RESEARCH ... 177

BIBLIOGRAPHY ... 179

LIST OF TABLES

1.1 Effect of MCPA and 2,4-D on the control of nodding thistle grown at Argyll and Matapiro 15

2.1 The percentage of herbicide solution injected into the chamber of the sprayer which was subsequently collected directly below the nozzle in a 250 ml flask with a horizontal surface area of 57 cm^2 36

2.2 Estimates of the LD50 values for nodding thistle tolerance to MCPA at the five Maraekakaho and Colyton sites, with 95% confidence limits 47

2.3 Estimates of the LD50 (with confidence limits) for the glasshouse-grown nodding thistle populations, and the Massey University Scotch thistle population 51

3.1 A summary of the four glasshouse experiments conducted to assess the tolerance of Ohiti and Argyll nodding thistle populations to MCPA 60

4.1 Summary of results from the three glasshouse experiments and one field experiment comparing the susceptibility of Argyll and Ohiti nodding thistle populations to MCPA 66

4.2 Summary of average plant size measurements taken at time of treatment for the glasshouse and field experiments conducted between September 1986 and May 1987 67

5.1 Herbicide treatments applied to Argyll and Ohiti nodding thistle populations at Massey University in May 1988 75

6.1 Measurements of plants harvested on 17 August 1988 to characterize the size of treated plants 100

8.1 The percentage of glasshouse-grown plants from 14 different original sites assigned to various trichome density scores on 18 August 1988 122

8.2 The number of Argyll and Ohiti nodding thistle plants treated at the various MCPA concentrations on 23 February 1987 125

8.3 The effect of damaging plant cuticles on the susceptibility to MCPA of phenoxy-resistant (Argyll) and phenoxy-susceptible (Ohiti) nodding thistle plants .. 128

9.1 The quantity of radioactivity (kBq) recovered from two plants which had their leaves rinsed with water then chloroform immediately following application of ^{14}C-2,4-D 134

9.2 The percentage of radioactivity applied to leaves of herbicide-resistant and susceptible nodding thistle plants as ^{14}C-2,4-D ammonium salt that was recovered by rinsing the treated leaves 7 days after application 135

9.3: Estimates of herbicide penetration derived from comparing quantities of ^{14}C found within plants with those located on leaf surfaces 136

9.4 The distribution of ^{14}C within nodding thistle plants to which ^{14}C-2,4-D was applied to a young leaf and a mature leaf 7 days earlier 138

9.5 The percentage of the radioactivity located within plant organs which was not soluble in ethanol 139

9.6 Estimates of the percentage of ^{14}C-2,4-D applied to Argyll (resistant) and Matapiro (susceptible) nodding thistle plants which penetrated into the foliage 144

9.7 The percentage of ^{14}C recovered from the potting mixture, presumably due to exudation from roots, expressed relative to total ^{14}C recovered from the plant following absorption, and relative to total ^{14}C translocated down into the root system 146

9.8 The percentage of recovered ^{14}C absorbed by plants that was translocated into the root system of herbicide-resistant and susceptible plants 148

9.9 The percentage of ^{14}C located within foliage or roots of treated resistant and susceptible nodding thistle plants which was not removed by extraction with 95% ethanol 149

9.10 The percentage of radioactive material extracted by ethanol from the roots of phenoxy-resistant and susceptible nodding thistle plants which was soluble in ether 154

9.11 The percentage of radioactive ether soluble compounds isolated from the roots of herbicide resistant and susceptible nodding thistle plants which had Rf values similar to 2,4-D (0.8), or with Rf values below 0.1, following chromatographic separation on thin layer silica gel G plates using a diethyl ether / petroleum ether / formic acid (70 : 30 : :2) solvent.........................156

9.12 Estimation of the differences in absolute quantities of active radiolabelled 2,4-D in the roots of resistant and susceptible nodding thistle plants 7 days after foliar application 157

9.13: Losses of radioactivity recorded during the processing of samples containing water soluble compounds from two replicates of resistant and susceptible nodding thistle plants 159

LIST OF FIGURES

1.1 Line drawings of a nodding thistle (a) seedling, (b) rosette and (c) flowering branch.......5

1.2 The structure of MCPA and 2,4-D molecules.......16

2.1 The dose response curve for two populations, I and II.......30

2.2 A diagramatic representation of the sprayer designed for applying herbicide solutions to nodding thistle plants in this project.......35

2.3 Mortality data for Scotch thistle plants sprayed with various concentrations of MCPA in the field near Massey University in October 1985.......40

2.4 Probit transformation of Scotch thistle mortality data, and the computer-fitted regression line for these data.......42

2.5 Computer fitted dose response curve of Scotch thistle for MCPA with the upper and lower 95% confidence limits for this curve.......42

2.6 The traditional presentation of a dose response curve for Scotch thistle susceptibility to MCPA with the 95% confidence limits for the LD50 dose 43

2.7 The dose response data obtained for nodding thistle at Maraekakaho (Sites 1-4) and Colyton (Site 5) in 1985.......47

2.8 Computer fitted dose response curves for nodding thistle susceptibility to MCPA at Maraekakaho (combination of all four sites) and Colyton.......48

2.9 The percentage of glasshouse grown plants killed by MCPA applied in December 1985.......50

3.1 Percentage of nodding thistle plants killed from Argyll, Colyton and Ohiti populations grown and treated with MCPA in a glasshouse in September 1986.......53

3.2 Percentage of nodding thistle plants killed from Argyll and Ohiti populations grown and treated with MCPA in a glasshouse in December 1986 57

3.3 Percentage of nodding thistle plants killed from Argyll and Ohiti populations grown and treated with MCPA in a glasshouse in February 1987 59

4.1 The percentage of Argyll and Ohiti nodding thistle plants killed by various concentrations of MCPA when grown in a pasture at Massey University and treated when four and six months old 64

4.2 Dose response curves fitted using probit analysis for the Argyll and Ohiti nodding thistle populations grown in the field at Massey University and treated when four months old 65

4.3 Dose response curves fitted using probit analysis for the Argyll and Ohiti nodding thistle populations grown in the field at Massey University and treated when six months old 65

5.1 The effect of clopyralid on Argyll and Ohiti nodding thistle populations treated in October 1987 when 9-11 months old 73

5.2 The control obtained of Argyll and Ohiti nodding thistle populations when sprayed with phenoxy herbicides at recommended rates in May 1988 77

5.3 The hypothesized relationship between results obtained from applying MCPA to Argyll and Ohiti nodding thistle populations in May 1987 and May 1988 ... 78

5.4 Molecular structures of herbicides tested for cross-resistance in May 1988 80

5.5 A diagram relating the application rate at which nodding thistle is normally controlled by mecoprop to the lowest application rate at which the trial result could have occurred if Argyll nodding thistles were resistant to this herbicide 81

5.6 The control obtained of Argyll and Ohiti nodding thistle populations when sprayed in May 1988 with 150 g ai/ha of clopyralid, 2.4kg ai/ha of MCPB (iso-octyl ester) and a mixture of 14 g ai/ha of clopyralid and 500 g ai/ha of MCPB (butyl ester) 83

5.7 The control obtained of Argyll and Ohiti nodding thistle populations when treated with herbicides at the rates listed in Table 5.1 in May 1988 84

5.8 Histograms of nodding thistle plant size at treament and the subsequent fate of these plants when sprayed with tribenuron-methyl at 150 mg ai/litre in May 1988 for the Argyll and Ohiti populations 86

5.9 The effect of tribenuron-methyl on phenoxy-resistant (Waotu) and phenoxy-susceptible (Ohutu) nodding thistle populations treated in a glasshouse in October 1990 88

5.10 The effect of clopyralid on nodding thistle and clovers at Argyll applied by Dow-Elanco staff in June 1989 (B. Harris, unpublished data) 90

6.1 Location of sites in Hawkes Bay from which nodding thistle populations were tested for resistance to MCPA. 94

6.2 The percentage of plants killed by 3.0 mg ai MCPA / 5 ml for seven nodding thistle populations grown and treated in a glasshouse in February 1988 95

6.3 The statistical significance of differences in mortality between Argyll (if mortality is 10%) and six hypothetical populations if 10, 20 or 30 plants were tested per population 96

6.4 Location of sites in Waikato from which nodding thistle populations were tested for resistance to MCPA 99

6.5 The percentage of plants killed by 3.0 mg ai MCPA / 5 ml for 23 nodding thistle populations grown and treated in a glasshouse in August 1988 101

7.1 Average shoot dry weight of phenoxy-resistant (Argyll) and susceptible (Matapiro) nodding thistle plants grown at two densities for 10 weeks 114

8.1 The percentage of field-grown Argyll and Ohiti plants assigned to each of the trichome density scores on 1 October 1987, where 0 = few trichomes on upper leaf surfaces and 5 = high trichome density 120

8.2 The relationship between the average foliar trichome density of 14 nodding thistle populations and the percentage of plants killed within each population when treated with 3.0 mg ai MCPA / 5 ml immediately following assessment of trichome density 123

8.3 The percentage of nodding thistle plants assigned to each of the trichome density score categories which were subsequently killed by 3.0 mg ai MCPA / 5 ml 124

8.4 The unfitted dose response curves for glasshouse-grown Ohiti (solid lines) and Argyll (broken lines) nodding thistle populations sprayed with MCPA on to intact (light lines) and damaged (heavy lines) cuticles in February 1987 ... 127

8.5 The fitted dose response curves for glasshouse-grown Argyll and Ohiti nodding thistle populations to which MCPA was applied by injection into the potting mixture of individual plants in February 1987 129

9.1 A summary of the procedures used in this project to study the possible metabolism of radiolabelled 2,4-D within resistant and susceptible nodding thistle plants 152

LIST OF PLATES

2.1 The sprayer, pressurised in a laboratory by compressed air, being used to treat a nodding thistle plant from a glasshouse....................34

2.2 Use of carbon dioxide to pressurise the sprayer for treating a nodding thistle plant in the field....................34

2.3 A plastic label marking the position of a treated nodding thistle plant 20 cm from its tip (at end of pen) which has since died....................46

2.4 Potted nodding thistle plants in irrigation trays immediately prior to treatment in the experiment described in Section 2.5....................46

3.1 Nodding thistle plants immediately prior to treatment in the first glasshouse comparison (Section 3.2)....................54

3.2 Plants from the second glasshouse comparison (Section 3.3) immediately prior to treatment....................54

4.1 View of the field trial site at the time of treatment....................63

4.2 A typical nodding thistle plant at the time of treatment in the field comparison of the Argyll and Ohiti populations....................63

5.1 The screens used to enclose each plot during boom-application of the various herbicide treatments with a precision plot sprayer....................76

5.2 An Argyll nodding thistle plant 7 weeks after being treated with the MCPB ester and clopyralid mixture. The plant was dead at the final assessment 5 months after application....................76

6.1 The paddock from which seed of the Raukawa population was collected in January 1988. It had been sprayed with 2,4-D while the plants were vegetative, so all plants visible had survived that application....................97

6.2 The plants from the Waotu and Matapiro populations 4 months after application of MCPA....................97

7.1 Argyll (*eg* numbers 8 and 22) and Matapiro (*eg* numbers 1, 15 and 29) plants after 2 months of growing together in a tray at a density of 35 plants per tray ... 115

7.2 Argyll (A1 and A2) and Matapiro (M1 and M2) plants after 2 months of growing together in a tray at a density of 4 plants per tray ... 115

8.1 A nodding thistle leaf with few trichomes ... 118

8.2 A nodding thistle leaf with a high trichome density ... 118

8.3 A nodding thistle plant placed into position through a hole in the top of a wooden box ready to be scarified by the collection of wire brushes shown in the foreground ... 126

8.4 Immediately after the scarifier had been dropped 5 cm on to the nodding thistle plant ... 126

LIST OF PESTICIDES

The chemical names of pesticides mentioned in this text are:

amitrole	3-amino-1,2,4-triazole
bentazone	3-isopropyl-2,1,3-benzothiadiazin-4-one 2,2-dioxide
bromofenoxim	3,5-dibromo-4-hydroxybenzaldehyde 2,4-dinitrophenyloxime
bromoxynil	3,5-dibromo-4-hydroxybenzonitrile
chlorsulfuron	*N*'-(2-chlorobenzenesulfonyl)-*N*-(4-methoxy-6-methyl-1,3,5-triazin-1-yl)urea
clopyralid	3,6-dichloropyridine-2-carboxylic acid
cyanazine	2-chloro-4-(1-cyano-1-methylethylamino)-6-ethylamino-1,3,5-triazine
2,4-D	2,4-dichlorophenoxyacetic acid
dicamba	3,6-dichloro-2-methoxybenzoic acid
dichlorprop	(±)-2-(2,4-dichlorophenoxy)propionic acid
dinoseb	2-(1-methylpropyl)-4,6-dinitrophenol
diquat	9,10-dihydro-8a,10a-diazoniaphenanthrene
DNOC	2-methyl-4,6-dinitrophenol
etridiazole	5-ethoxy-3-trichloromethyl-1,2,4-thiadiazole
glyphosate	*N*-(phosphonomethyl)glycine
ioxynil	4-hydroxy-3,5-di-iodobenzonitrile
MCPA	4-chloro-2-methylphenoxyacetic acid
MCPB	4-(4-chloro-2-methylphenoxy)propionic acid
mecoprop	(±)-2-(4-chloro-2-methylphenoxy)propionic acid
metsulfuron	2-[3-(4-methoxy-6-methyl-1,3,5-triazin-2-yl)ureidosulfonyl]benzoic acid
paclobutrazol	(2*R*,*S* 3*R*,*S*)-1-(4-chlorophenyl)-4,4-dimethyl-2-(1*H*-1,2,4-triazol-1-yl) pentan-3-ol
paraquat	1,1'-dimethyl-4,4'-bipyridylium
picloram	4-amino-3,5,6-trichloropicolinic acid
simazine	2-chloro-4,6-bisethylamino-1,3,5-triazine
tribenuron	2-[4-methoxy-6-methyl-1,3,5-triazin-2-yl(methyl)carbamoylsulfamoyl]benzoic acid
trifluralin	2,6-dinitro-*N*,*N*-dipropyl-4-trifluoromethylaniline