Resistance to Rust (*Puccinia antirrhini*) in *Antirrhinum majus*

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Frances Mary Gawthrop
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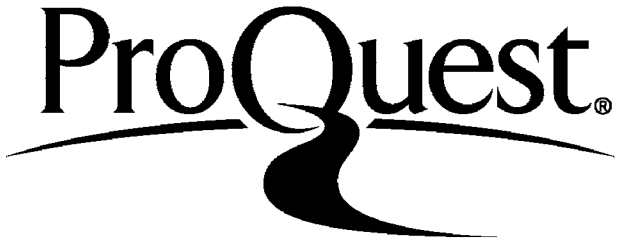

FRANCES GAWTHROP

RESISTANCE TO RUST (*PUCCINIA ANTIRRHINI*) IN *ANTIRRHINUM MAJUS*

ABSTRACT

A quantitative assessment of the susceptibility of 131 cultivars of *Antirrhinum majus* L. to the rust fungus *Puccinia antirrhini* Dietel and Holway by means of replicated trials over two years revealed a wide range of general resistance; there is scope for improvement of rust-resistance by breeding. The loss of immunity was due to genetic change in the fungus because variations in pathogenicity occur among geographical isolates.

An investigation of the epidemiology of the rust revealed that during the summer in Britain, uredospores are liberated through the day to germinate and establish infection after dew has fallen in the evening. The local dispersal of the pathogen is largely by wind but the spread between continents throughout the world is more likely to be due to human activity.

A breeding programme is suggested for the improvement of *A. majus* by hybridizing the more resistant cultivars. Meanwhile, some horticulturally acceptable varieties with "rate-reducing" resistance to the fungus are recommended. These varieties should not become disfigured by the disease provided they are grown away from susceptible varieties.

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CHAPTER ONE

GENERAL INTRODUCTION

Antirrhinum majus L. was in cultivation by the end of the sixteenth century. It was used as a herbal remedy for ailments of the eyes. Initially there were only three flower colours: white, purple and yellow; but during the nineteenth century the range of colours increased and antirrhinum became a popular bedding plant. The value of the snapdragon as an ornamental is summarized in this quote from Watkins and Simpson's seed catalogue in 1955: "Few plants can rival antirrhinum for summer bedding. Their bright, varied colourings, their ease of cultivation and long continued flowering period mark them out as ideal for this purpose".

Antirrhinum rust, caused by the fungus Puccinia antirrhini Dietel and Holway, was first reported from California. It soon became a serious disease of antirrhinums attacking the host plant wherever it was grown. The fungus is found on the leaves, stems, calyces and capsules, destroying ovaries, reducing seed production and often killing the host. The main damage is caused by uredia in which some teleutospores are formed towards the end of the season. The development of basidiospores has been observed but all attempts to infect antirrhinum with them have been unsuccessful. The rust is therefore thought to be heteroecious although no alternate host has been found.

Attempts to control the disease by cultural techniques and fungicides have been unsuccessful; the expense and limited control achieved by fungicides has made their use unpractical. Varieties were developed in America which were immune to the disease but in 1936 these varieties succumbed to the disease in California. The American varieties remained resistant in Britain until 1962 when they too showed symptoms of the disease. The Royal Horticultural Society's Trial of rust-resistant antirrhinums in 1969 had to be abandoned because all stocks succumbed to the rust. This trial marked a turning point in the popularity of the antirrhinum. Seed companies started to withdraw varieties and the plant began to fall from favour not only for municipal plantings but even in private gardens.

The Royal Horticultural Society has maintained an interest in the plant and joined with Royal Holloway College to investigate the

scientific background to the rust epidemics with a view to providing a basis for future development of improved lines of snapdragon. This thesis reports the results of an investigation to reveal whether the loss of immunity in the antirrhinum was due to a mutation in the rust or a loss of the gene for resistance in the host. Information relevant to this was obtained from the behaviour of cultivars of antirrhinum in plot experiments (Chapter 4), laboratory tests of rust isolates (Chapter 6) and a review of the published information on the spread of the disease and changes in host susceptibility (Chapter 2). Studies were also made of the development of rust-resistant varieties (Chapter 3), the resistance in wild species (Chapter 7) and the epidemiology of the rust (Chapter 5). A breeding strategy is suggested for the improvement of rust-resistance in Antirrhinum majus (Chapter 9).

CHAPTER TWO

SPREAD OF *PUCCINIA ANTIRRHINI*

INTRODUCTION

A brief account of the spread of *P. antirrhini* across America has been documented by Peltier (1919) and Doran (1921), across Europe by Lepik (1941) and Fikry (1937, 1939) and in Australia by Walker (1954) and Close (1958). The rust was an economically important disease in the horticultural trade, therefore many workers were watching for the disease among their seed-crops and reported it when it appeared. Consequently its distribution is well documented and has been summarized briefly by Barbe (1964b) but its spread has never been adequately reviewed. Different workers have suggested that contaminated seed, infected seedlings, cuttings and soil, insects and wind are responsible for the dispersal of the pathogen. In this chapter the chronology of the spread and the probable method of dispersal will be discussed.

HISTORY OF THE SPREAD OF THE PATHOGEN

The first report of the rust was published by Blasdale (1903) who found the disease on cultivars of *A. majus* at San Leandro, near San Francisco, California in 1895. Later it became apparent that the fungus had been collected in California as early as 1879 (Barbe, 1967); nevertheless the type specimen is the sample collected by Blasdale and described by Dietel (1897). The spread of the rust throughout the world may be traced by the first published record of the disease in each country supplemented by the dates on specimens seen at the Arthur Herbarium, Purdue University, U.S.A. by Dr. B.M.G. Jones. The chronology of the spread is shown in Table 2.1.

The disease first appeared outside California at Portland, Oregon in 1909. It continued to spread within the west coast states and was reported east of the Rockies in Illinois in 1913. Within the next four years the rust had spread over most of the mid western and eastern states and had reached the Canadian Plains (Figure 2.1). Whetzel found the rust in 1922 in Bermuda, where it caused severe losses in 1923.

Table 2.1 Chronology of the Spread of Puccinia antirrhini

Year	Country	Month	Location	Reference
1879	U.S.A.	-	California (Santa Cruz)	D.E. Farlow (A.H.) Barbe (1967)
1895	U.S.A.	-	California (San Leandro)	Blasdale (1903) Blasdale (1919)
1909	U.S.A.	- Aug.	Oregon (Portland Oregon	Peltier (1919) C.Laddon and H.S.Jackson (A.H.)
1913	U.S.A.	July	Illinois (Nr.Chicago)	Peltier & Rees (1914) Peltier (1919)
1914	U.S.A.	Sept. Nov.	Ohio Ohio (Cleveland)	Peltier & Rees(1917) C.C. Rees (A.H.)
1914	U.S.A.		Indiana	Peltier & Rees(1914)
1915	U.S.A.	Jan.	Iowa	Peltier (1919)
1915	U.S.A.	Jan.	Wisconsin Wisconsin (Mulwauhee)	Peltier (1919) C.C. Rees (A.H.)
1915	U.S.A.	Jan. - Nov.	Massechusetts Massechusetts Massechusetts(Worcester)	Peltier (1919) Doran (1921) W.J. Wood (A.H.)
1915	U.S.A.	- Oct.	Michigan Michigan (Redford)	Peltier (1919) C.K. Smith (A.H.)
1915	U.S.A.	Nov.	Connecticut(Westbrook)	Clinton (1916) Doran (1921)
1915	U.S.A.		Maine	Doran (1921)
1915	U.S.A.		New Hampshire	Doran (1921)
1915	U.S.A.		Rhode Island	Doran (1921)
1916	U.S.A.		Alabama	Peltier (1919)
1916	Canada	Aug.	Ontario (Guelph)	R.E. Stone (A.H.)
1916	Canada	-	Quebec (Ontario)	Doran (1921)
1916/7	U.S.A.	-	Nebraska	Thurston (1919) Doran (1921)
1917	U.S.A.	Nov.	Texas (College Station)	J.Taukenhaus (A.H.)
1917	U.S.A.	Sept.	Pennsylvania (State College)	C.R. Horton and W.J. Miller (A.H.)
1919	U.S.A.	-	Missouri	Thurston (1919)
1919	U.S.A.	-	Colorado (Denver)	E.L. Kirkpatrick (A.H.)
1919	U.S.A.	March	Florida (Kissimee)	J.C. Arthus (A.H.)
1919	U.S.A.	July	Utah (Salt Lake City)	A.O. Garrett(A.H.)
1920	Canada	-	Manitoba (Winnipeg)	W.P. Frazer (A.H.)
1922	U.S.A.	Sept.	Wyoming (Laramie)	E.B.Parson (A.H.)
1922	Bermuda	-	-	Whetzel (1924)
1931	Canada	May	Alberta (Birdmonton)	E.H. Moss (A.H.)

Table 2.1 continued

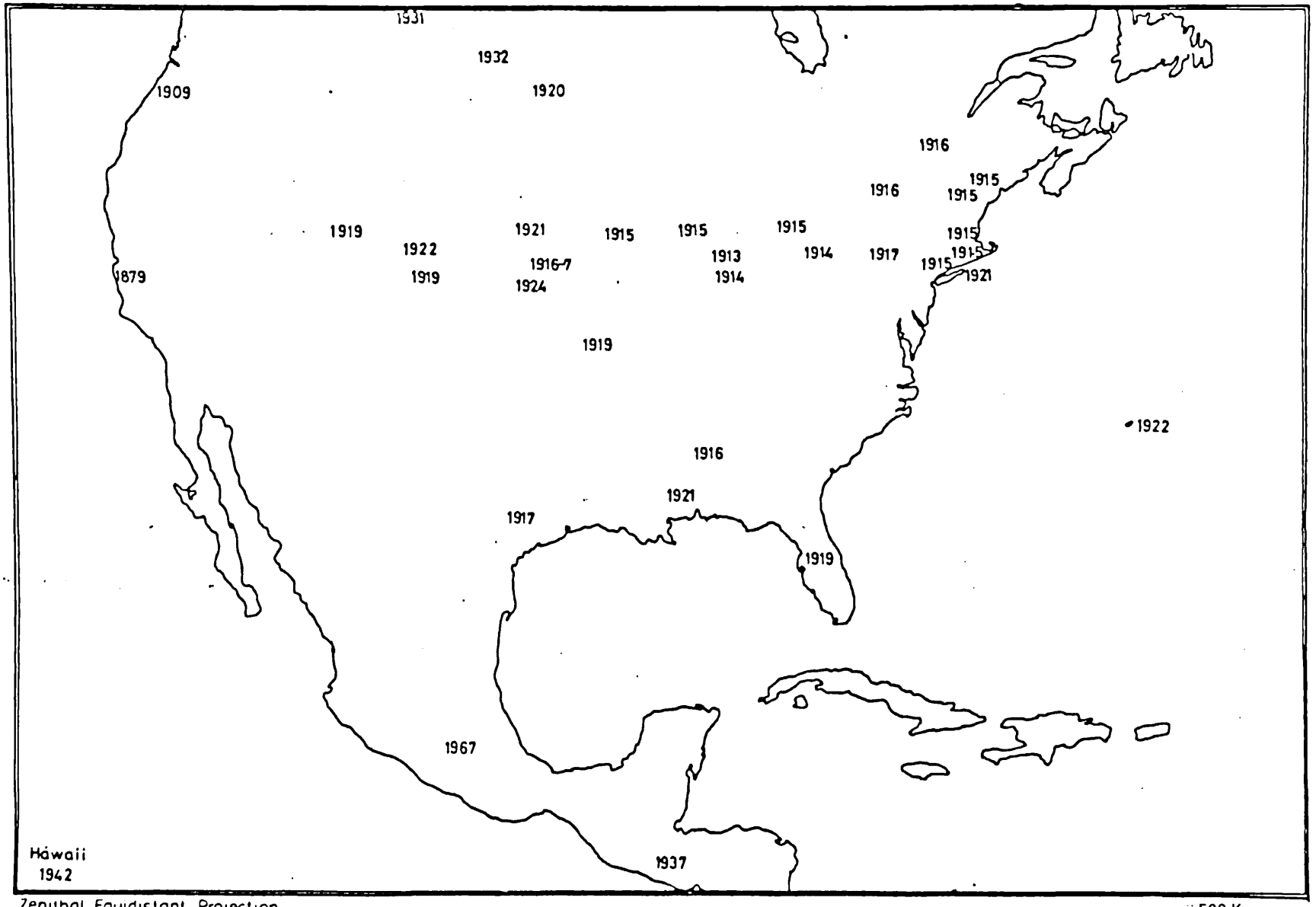
Year	Country	Month	Location	Reference
1931	France	Oct.	Grignon	Viennot Bourgin(1933)
1932	Canada	July	Saskatcheuan (Saskatoon)	W.P. Frazer (A.H.)
1933	England		Kent	Green (1933,1934) Pethybridge (1934)
1933	Netherlands		Zeist (Hilversum) Naarden	Schenk (1934) Van Poetern (1934)
1934	Germany		Bonn Cologne Essen Mulheim	Andres (1934) Laubert (1934a) Laubert (1934a) Laubert (1934b) Pape (1934) Poeverlein (1935)
1934	Denmark	Oct.	Vanlose	Buchwald (1934)
1934	Italy	Nov.	Florence	Preti (1935)
1935	Austria	Nov.	Vienna	Steiner (1936)
1935	Scotland			Dennis & Foister (1935)
1935	Sweden	Aug.	Oland	Palm (1937)
1935	Switzerland		Berne (Umgebung)	Blumer (1935)
1935	Czechoslavakia		Olmutz	Cernik (1936)
1935	Hungary	Oct.	Monor(Szekesfchervar) Budapest (Pomer)	Moesz (1940)
1936	Poland		Kornik (Nr.Poznan)	Kochman (1938)
1936	Roumania	Sept. Oct. Oct.	Brasov Bucharest Constanta	Savulescu and Savelescu (1937)
1936	Bulgaria			Christoff and Christove (1939) Kovachevsky (1938)
1936	Egypt	Nov.	Cairo	Fikry (1937)
1936	Madeira			Viennot Bourgin(1939)
1936	Estonia			Lepik (1936)
1936	Israel		Jerusalem Tel Aviv	Rayss (1937) Ballard (1938)
1937	U.S.S.R.		Leningrad (Voronezh) Odessa (The Caucasus)	Lepik (1941)
1937	Morocco	Feb.	Casablanca	Berger (1938)
1938	Turkey		Izmir (Ankara)	Bremer et al (1947)
1938	Greece		Thessalonika	Maire & Politis(1940)
1939	South Africa	Sept.	Netal (E.Cape)	Bottomley (1940)
1939	Tunisia	April		Guyot & Chevasset (1958) Guyot (1958)
1939	Portugal			Da Camara et al(1939)

Table 2.1 continued

Year	Country	Month	Location	Reference
1940	Zimbabwe (S.Rhodesia)	Oct.	Bulawayo	Hopkins (1941)
1941	Hawaii			Martin (1942)
1937-1941	Guatamala		Chimaltenango	Cummins (1943)
1941	Spain	Oct.	Coruna	Sardina (1941)
1945	Norway		Nedstrand	Jorstad (1946)
1948	Mozambique			De Carvalho(1948)
1948	Mexico	April	San Jacinto	(A.H.) Zevada et al (1955)
1950	Tanzania		Morogoro	Wallace & Wallace (1950) Wallace (1952)
1952	Australia	Oct.	Sidney	Anonymous (1953a) Walker (1954)
1952	Malawi (Nyasaland)		Blantyre	Bisby & White(1953)
1953	New Zealand	Dec.	Palmerston North Wellington Auckland	Moll (1954) Baker (1956)
1954	Kenya		Nairobi Lake Naivasha	Anon (1955b)
1954	Tasmania	March		Walker (1954) Magee (1955)
1955	Mauritius			Orian (1957)
1955	Algeria	Feb.		Guyot & Chevassut (1958)
1955	Cyprus	Dec.	Nicosia	Georghiou and Papadopoulos (1957)
1955	W.Australia			Goss (1961)
1959	Finland	July	Lansi Saksa Schoningen	Rauhala (1966)
1970	Afghanistan	June	Kabul	Brandenburger and Steiner (1972)
1977	Argentina			Rocca de Sarasola and Lindquist(1979)
1977	Brazil			Rocca de Sarasola and Lindquist(1979)

By 1931 the pathogen had crossed the Atlantic and had been seen for the first time in Europe in Northern France. It spread rapidly across the continent and during the early 1930's it had reached Great Britain, The Netherlands, Germany, Denmark, Italy, Austria, Switzerland, Czechoslavakia and Hungary; by 1938 it had reached the Mediterranean

Figure 2.1 Spread of the rust in North America



coast (Figure 2.2).

The next distant outbreak of the disease was in the southern hemisphere, in South Africa in 1939. From there it spread northwards through east Africa reaching Kenya by 1954. By this time the disease had reached Australia. It was first reported from Sidney, New South Wales but within two years had also been found in New Zealand and Tasmania. The latest outbreak of the disease was in South America where rust was reported to be in Brazil and Argentina in 1977.

The spread of the rust throughout the world is shown in Figure 2.3. There are some reports which do not fit into this scheme: for instance the first report from Mexico in 1948 was later than that for Guatamala. The rust may be present for some time in a country before it is recognised. Thus Cummins (1943) notes that the disease was generally distributed in Guatamala in 1943. Similarly the rust may have been present in Afghanistan before 1970, although it was not recognised until two mycologists visited Afghanistan in that year specifically to make collections of its fungi. Despite these anomalies, the majority of reports fit into the general scheme outlined by the isochronic arcs on Figure 2.3 which radiate from its Californian origin and secondary origins on remote continents.

Agents of dispersal.

The means by which the rust may have been dispersed around the world has been the subject of much discussion and it is unlikely that a single agent is solely responsible.

The dispersal of contaminated seed would account for a wide distribution of the rust. Uredospores adhere to the testa of the antirrhinum seed; Hopkins (1941), Helson (1953), Walker (1954) and Barbe (1967) have all found commercial seed samples contaminated with uredospores. Harman, Pfleger and Braverman (1973) found the embryos of some seeds to be replaced by mycelia, uredospores and teleutospores. Contaminated seed has been thought to be responsible for the introduction of the disease into Great Britain (Comber, 1933), South Africa (Hopkins, 1941) and Australia (anon, 1953c) because the disease was found on plants grown from imported seed. Hassebrauk (1937) considers that the disease cannot be transmitted by seed because the uredospores are not viable for a sufficient length of time and disease-free plants have been grown from contaminated seed (Hopkins, 1941; Walker, 1954; Barbe, 1967; Harman,

Figure 2.2 Spread of the rust in Europe

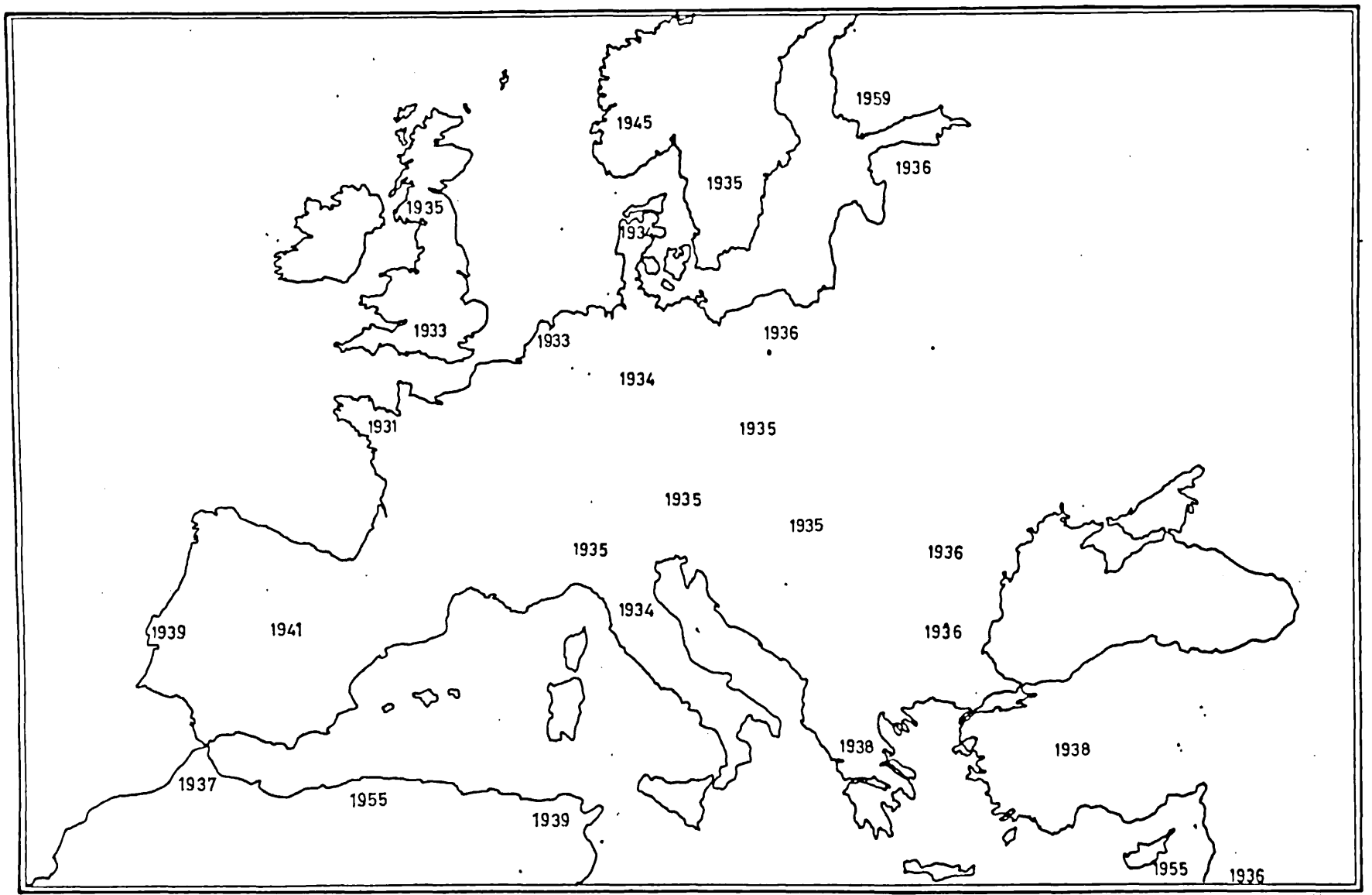
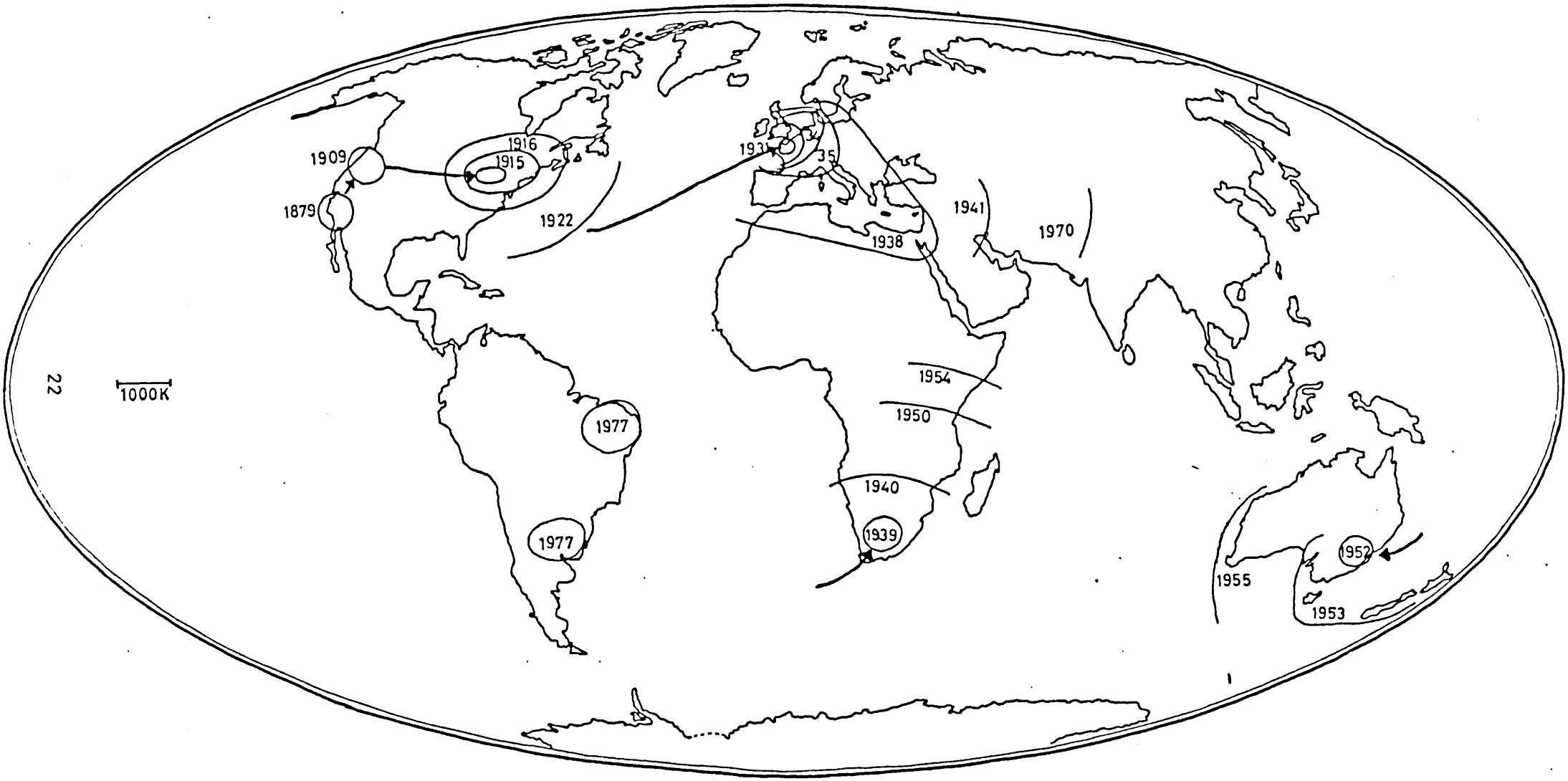


Figure 2.3 Spread of Antirrhinum Rust



Mollweide's Homolographic Projection - Areas correct. Distortion increasing towards border of map.

Pfleger and Braverman, 1973). The chronology of the spread shown in Figure 2.3 is too slow for it to be explained by viable spores in commercial seed since relatively large amounts of antirrhinum seed are shipped around the globe each year in the normal business of the seed trade; we would expect a rapid spread to all the continents. In addition the disease reached Tasmania within two years of being recorded in Australia despite strict quarantine regulations which required all seed imports to be examined (Anon 1953b, 1955a). We may therefore conclude that the rust was not widely dispersed as a seed contaminant. The transport of infected seedlings, however, may be involved in long distance dispersal.

Plants and cuttings used to be distributed much more widely than they are today. The plants may appear completely free of the disease while the fungus is in its incubation period. Thurston (1919) and Whetzel (1974) believe the disease was introduced into the eastern states of the U.S.A. and Bermuda respectively on infected seedlings. The disease may also be carried in soil since Lehoczky (1954) found uredospores of P. antirrhini remained viable and infective after overwintering. Barbe (1967) however was unsuccessful in his attempts to gain infection from uredospores which had been overwintered in the soil. Although the transport of uredospores in soil appears possible it is unlikely to be the means of long distance dispersal. Insect vectors, may be involved in some short range dispersal.

An association has been observed between the uredospores of P. antirrhini and the European earwig Forficula auricularia L. Barbe (1964a) and a species of the gall midge Mycodiplosis sp. (Green, 1936). During this study an association between bees and P. antirrhini was observed. Uredospores were found on the bodies of the bees and within their pollen-sacs. Turner (1974) noted that Apis dorsata appeared to visit the rust pustules of Puccinia polysora on maize and honey bees have been reported to forage on rust spores of Oxalis sp. (Wolfenbarger, 1977). Savile (Private communication in litt) considered that the bees collected rust spores, as a source of protein if food was scarce. The spores within the bees' pollen-sacs are unlikely to spread the disease but the spores adhering to their bodies are capable of germination and may be dislodged later and infect another susceptible plant within the flight range of the bee.

This may account for short range dispersal of the disease but long distance dispersal is more likely to be the result of wind. Uredospores

are readily disseminated in air currents and there is evidence that wind plays a major role in the dispersal of pathogens over land. When the rust was reported in Australia in 1952, Walker (1955) plotted the furthest point, from the initial outbreak, to which the disease had spread after nine, fifteen and eighteen weeks. He established that the shape of the zone of spread correlated with the prevailing wind direction.

Effective dissemination of uredospores across oceans is more difficult to demonstrate. Uredospores have been collected in spore traps on aeroplanes at heights exceeding 10,000 ft. and it seems that the spores retain their viability and may be carried for hundred of miles at this height. The presence of spores in the atmosphere has been demonstrated between Australia and New Zealand (Close, Moar, Tomlinson and Lowe, 1978), over the North Sea, (Hirst, Stedman and Hurst, 1967) and northwards across the English Channel (Hirst, Stedman and Hogg, 1967).

There does not appear to be a single explanation which can alone account for the spread of the rust throughout the world, but the two methods which are most likely to account for the long distance dispersal of the rust fungus appear to be the distribution of infected plants and in air currents. The spread across the oceans and the tropics is more likely to be on infected plants but subsequent spread may occur as a result of wind.

CHAPTER THREE

DEVELOPMENT OF RUST-RESISTANT VARIETIES

TERMINOLOGY

Since the valuable work by Van der Plank (1963, 1968) many adjectives have been used to describe the types of disease resistance exhibited by plants. The proliferation of terms has led to much confusion as workers have attempted to establish synonymies between existing and new terms (Roane, 1973).

There are basically only two types of resistance. In the first, the host resists the establishment of a successful parasitic relationship by isolating the infection site. The second kind reduces the rate of infection and thus the amount of disease which finally develops on the plants. Table 3.1 summarizes the terms which are approximately synonymous and have been used to distinguish types of resistance.

Table 3.1 Terms which have been used to describe resistance.

Resistance which reduces the amount of effective inoculum	Resistance which reduces the apparent infection rate
Specific	General
Race specific	Race non-specific
Vertical	Horizontal
Major Gene	Minor Gene
Monogenic	Polygenic
Oligogenic	Multigenic
Qualitative	Quantitative
	Generalized
	Uniform
	Field
	Partial
	Permanent
	Durable
	Slow rusting

Van der Plank (1963) classified resistance in epidemiological terms and coined the phrases "vertical resistance" to describe a host genotype which is resistant to some races of the pathogen and "horizontal resistance" for host resistance which is equally effective against all races of the pathogen. The use of these terms has been criticised principally by Nelson (1978) whose rigid interpretation makes them mutually exclusive. He redefines horizontal resistance as a "rate-

reducing resistance" because it reduces the apparent infection rate.

The term "vertical resistance" has been used to describe a plant with one or more major genes each specific to a virulence gene in the pathogen according to the "gene for gene" hypothesis proposed by Flor and reviewed by him in 1971 (Flor, 1971). More recently Van der Plank (1978) made the point that vertical resistance can occur without host-pathogen specificity. He says the essential difference between the two types of resistance, irrespective of host-pathogen specificity, is the differential interaction between the host and pathogen in vertical resistance and the absence of such an interaction in horizontal resistance. Horizontal resistance is generally conditioned by an unknown number of minor genes and has therefore frequently been called polygenic. There are a few examples of mono or oligogenic horizontal resistance. For example, the protection of compact barley varieties e.g. "Proctor" against loose smut (Ustilago nuda hordei) of barley is complete because these varieties have a long glume (Macer, 1960). Although this is really resistance by "disease escape" it is often quoted as an example of oligogenic horizontal resistance. Other examples include resistance to milo disease (Periconia circinata) of sorghum (Van der Plank, 1968) and resistance to woolly aphid (Eriosoma lanigerum) in apple (Robinson, 1976).

Nelson, MacKenzie and Scheifele (1970) proposed the concept that the genes controlling both horizontal and vertical resistance are the same. The genes act according to their genetic backgrounds; thus the genes function vertically when they are separate and horizontally when they are together. Parlevliet and Zadoks (1977) considered that all resistance and virulence genes within a given host-pathogen relationship operated in a single, integrated system. Thus, in their model the horizontal and vertical resistances sensu Van der Plank (1963) do not represent different kinds of resistance. Whilst in reality, the two types of resistance may be combined it is convenient to define each separately.

Despite attempts by Robinson (1969) to standardize the terminology in disease resistance there is still a certain amount of confusion and it seems appropriate for each worker to define his own terms. In this account three sets of terms have been used to define host-parasite relationships:

i specific resistance (antonym: general resistance)
ii immune (antonym: susceptible)
iii tolerant (antonym: intolerant)

i Specific and General Resistance

The terminology of Browning, Simons and Torres (1977) has been used to define these forms of resistance. They apply 'specific resistance' to resistance conferred by a major gene which acts by reducing the amount of effective inoculum. General resistance, on the other hand, is used for resistance which is inherited polygenically and reduces the apparent infection rate. Absolute proof of the latter resistance is impossible (Johnson, 1979). Johnson and Law (1975) proposed the term 'durable' to describe resistance which is long-lasting and where the degree of resistance is not necessarily the same to all races of the pathogen. 'Durable resistance' has the advantage that it embodies fewer assumptions than 'horizontal resistance' but can only be recognised in long-established varieties. Russell (1978) prefers to avoid the use of 'general resistance' because it is rather vague and is usually just a synonym of 'field resistance'. The term 'field resistance' might be thought to only operate in the field and to be difficult to detect in a laboratory or greenhouse. In the case of resistance to rust in antirrhinum, 'general resistance' is preferable to the above terms, at least until there is greater understanding of the inheritance of the present-day resistance and its effectiveness over several years has been assessed. It may then be possible to select more definite terms to describe the resistance.

ii Immunity and Susceptibility

Resistance is a continuously variable property, from highly susceptible to totally resistant. The term 'immunity' is used to denote 'absolute freedom from disease' i.e. 100% resistance in every plant (Nelson, 1973).

iii Tolerance and Intolerance

The final term 'tolerance' relates to the relative vigour of an infected plant. It has been included in several broader definitions of resistance (Caldwell, Schafer, Compton and Patterson, 1958; Russell, 1978) and has been defined as the 'ability of plants to endure severe disease without severe losses in yield or quality' (Schafer, 1971). There is no doubt that it is advantageous for an individual to possess a degree of tolerance where the disease will not be as damaging to the plant's growth or flowering, even though infection may be severe. It should be noted, however, that tolerance

does not reduce the rate of spread of an epidemic (Matuz, Mesterházy and Barabás, 1979). Therefore, in terms of an epidemic, the presence of tolerant plants will enhance the rate of spread of disease in the same manner as intolerant, susceptible plants and consequently reduce the effect of general resistance.

DEVELOPMENT OF RUST RESISTANT VARIETIES

The early work on the development of rust-resistant antirrhinums in America is well documented. In Britain, however, the work was not published in such detail. Nevertheless it has been possible to trace the development from the correspondence between Mr. Donald Green, then mycologist at the Royal Horticultural Society's Garden at Wisley, and Frank Simpson of W.H. Simpson and Sons, Ltd., a seed firm based in Birmingham and from Green's practical notebooks.

a) In America

The rust disease was first reported from California where practically all the American antirrhinum seed is produced. By the 1920's, the rust had become so severe that it was virtually uncontrollable. Milbrath and Emsweller and Jones (Mains, 1935) searched the Californian seed fields for individual plants with some resistance but none of these workers found plants with any degree of resistance.

The first record of resistant antirrhinums came from Indiana (Mains and Thompson, 1928). Mains (1935) noticed rust on the antirrhinums in his garden in 1922. Only two plants survived although both had moderate infection. By selfing these and selecting the most resistant plants in each generation, Mains obtained a number of lines derived from these two plants with marked resistance to the rust. As the inbreeding progressed, sterility developed and this retarded the selection of homozygous resistant lines. Mains considered the preservation of rust-resistance to be of prime importance and gave less attention to the maintenance of other qualities. Thus his breeding material produced irregular flower spikes with magenta-coloured flowers (White, 1933). Mains recognised that the plants were undesirable for commercial purposes but realised their potential value in plant breeding. Therefore he released these two lines, numbers 2-1 and 7-13 together with a resistant selection from the commercial variety "Giant White", to the plant breeders. Among those who received

seed were Milbrath and Emsweller in California and White in Massachusetts.

Emsweller and Jones developed resistant commercial strains using the backcross method to combine resistance from one of the originals in Main's garden in 1922 with desirable characters, from a susceptible commercial plant (Mains, 1935). They found that the number of backcrosses necessary to produce a line homozygous for flower colour, habit of growth and general morphological characters varied with different varieties but if the commercial parent was as homozygous as possible for colour and type before crossing started, the homozygous combination could normally be obtained in three to five backcrosses. The second backcross material was sent to Californian seedsmen and these most probably included the companies who permitted the use of their grounds for trials (Bodger Seeds, Ltd.; Ferry Morse Seed Co.; Frazer and Son Ltd.; F. Lagomarsino and Sons; Waller Franklin Seed Co.; William Macdonald Seed Co.).

b) In Britain 1934 - 1969

When rust was reported in Britain, W.H. Simpson and Sons Ltd., was the first seed company to offer rust-resistant varieties in their catalogue. Frank Simpson, then associated with the Company, received seed of rust-resistant antirrhinums from both the Ferry Morse Seed Co., and Waller Franklin Seed Co. (source: correspondence between Simpson and Green, curated at R.H.S. Wisley). These seed companies were among those who held trials for Emsweller and Jones. Table 3.2 shows the date of introduction and the average percentage resistance, (determined by D.E. Green in experimental trials at Wisley) of the American rust-resistant varieties which were offered by W.H. Simpson and Sons Ltd.

From 1935 onwards, Green annually tested new samples of American seed and selections from the original types. He destroyed all plants with the least sign of rust and selfed those which were rust-resistant, with good habit and the best flowers. In 1936 he had two stocks with 100% resistance: a poor flowered magenta one (No.3) and a mixture which was not true in habit. He recorded that the resistant types were inferior to commercial varieties with respect to their flower characteristics.

By 1937, he had three stocks with complete resistance: magenta (No.3) and the American stocks, "Orange Pink" produced by Emsweller and Jones (White, 1943) and "Terra-Cotta Pink", sent by Waller Franklin Seed Co. Green found a resistant yellow sport in "Terra-Cotta Pink" in 1938 which was true breeding. In 1939 he was sent a new American variety, "Brightness"

which increased his resistant stocks to five. These five stocks formed the basis of his breeding programme which started in 1941 (Green, 1937 a and b; 1941). Unfortunately his breeding records for this period have been lost but some of these crosses were undoubtedly the origins of the varieties, "Wisley Golden Fleece", "Wisley Cheerful" and "Wisley Bridesmaid" which received Awards of Merit in the R.H.S. Trial of Rust-Resistant Antirrhinums held in 1949.

Table 3.2 American Rust-Resistant Varieties introduced to Britain by W.H. Simpson & Sons Ltd.

Name of Variety	Average % Resistance	1936	1937	1938	1939	1940	1941	1942	1943
California Supreme	76	X	X	X					
Campfire	75	X	X	X					
Florist Pearl	75	X							
Pinkie	90	X							
Sunset	75	X							
Sierra Snow	75	X	X	X					
Red Boy	82	X	X	X	X	X	X	X	X
Glowing Sunset	75	X							
Franklin D.Rooseveldt	75	X	X	X	X	X	X	X	X
Carmine Rose	78	X	X	X					
Terra Cotta Pink	100		X	X	X	X	X	X	X
Light Salmon Pink	88		X	X	X	X	X	X	
Orange Pink	100		X	X	X	X	X	X	X
Red Beacon	94			X	X	X	X	X	X
Yellow Goliath	68			X	X	X	X	X	X
Feu Ardent	95			0	X	X	X	X	
Rose Precose	-			X					
Yellow Gem	72			0	X	X	X	X	
Pink Dome	93				X	X	X	X	X
White Goliath	74				X	X	X	X	X
Brightness	-				X				
The Sultan	-					X	X	X	X

Presence in Catalogue = X 0 = crop failed

In the same trial, Simpson was awarded an Award of Merit for the "Rust-Resistant Pink" variety which became "Pink Freedom". Since Simpson took the initiative and asked for the American rust-resistant varieties, this variety most likely originated from the American material and probably shares the same genetic factors for resistance with the three Wisley varieties.

The resistance exhibited by the fifth variety to receive an Award in the 1949 Trial may have had an independent origin. The "Rustproof Orange Glow" line was developed from a single plant among the susceptible released variety "Orange Glow" (Ralph Gould - personal communication). The resistance of this variety may thus have had a different genetic basis from the other resistant varieties in the 1949 Trial.

These five varieties formed the basis of a further breeding programme carried out by Green at Wisley from 1949 onwards. Some became the parents of other Wisley varieties which received awards in later trials. The pedigrees of four of these varieties have been reconstructed: "Toreador" (Fig. 3.1), "Polaris (Fig.3.2), Titan (Fig.3.3) and "Aurora" (synonym "Juno") (Fig.3.4). They have been drawn from information extracted from Green's practical notebooks which are curated at Wisley and show only the pathway which leads to the development of the new variety. They demonstrate that the strategy of Green's breeding programme was basically one of an initial hybridization followed by repeated selfing and selecting the most promising lines from each generation. Occasionally he made a second 'cross', usually with another 'breeding line'. It is noteworthy that Green worked with less than ten lines in each generation.

There are no published results of any other breeding work; it was done commercially within seed companies. The number of varieties entered in the Royal Horticultural Society's Trials of Rust-Resistant Antirrhinums, however, is indicative of the commercial effort in developing rust-resistant antirrhinums. The R.H.S. conducted four trials for rust-resistant antirrhinums, in 1949, 1958, 1962 and 1969. In each trial, sixty plants of each 'stock' (genotype) were grown and two rows of "Malmaison" were planted between 'stocks'. "Malmaison" is a particularly susceptible variety and its use in the spreader rows ensured that all 'stocks' were exposed to a high inoculum of rust spores. In addition the plants were sprayed with uredospores of P. antirrhini several times throughout the season. The rust-resistance of all 'stocks' was thus severely tested and only those stocks which were completely free of rust throughout the entire season were considered for an award. In addition the Committee considered the flower character and trueness of each stock.

Table 3.3 Statistics of the Royal Horticultural Society's Trials of Rust-Resistant Antirrhinums

	Year of Trial			
	1949 [1]	1958 [2]	1962 [3]	1969 [4]
Number of Companies sending seed	3	11	8	10
Total Number of Varieties Entered	8	62	59	76
Number of Varieties given an Award of Merit	5	4	5	0
Number of Varieties Highly Commended	0	5	4	0

Report of Trials
1. Anonymous (1950)
2. Anonymous (1959)
3. Anonymous (1963)
4. Brooks (1970)

Figure 3.1 Pedigree of Toreador (original constructed from information in Green's Practical Notebooks)

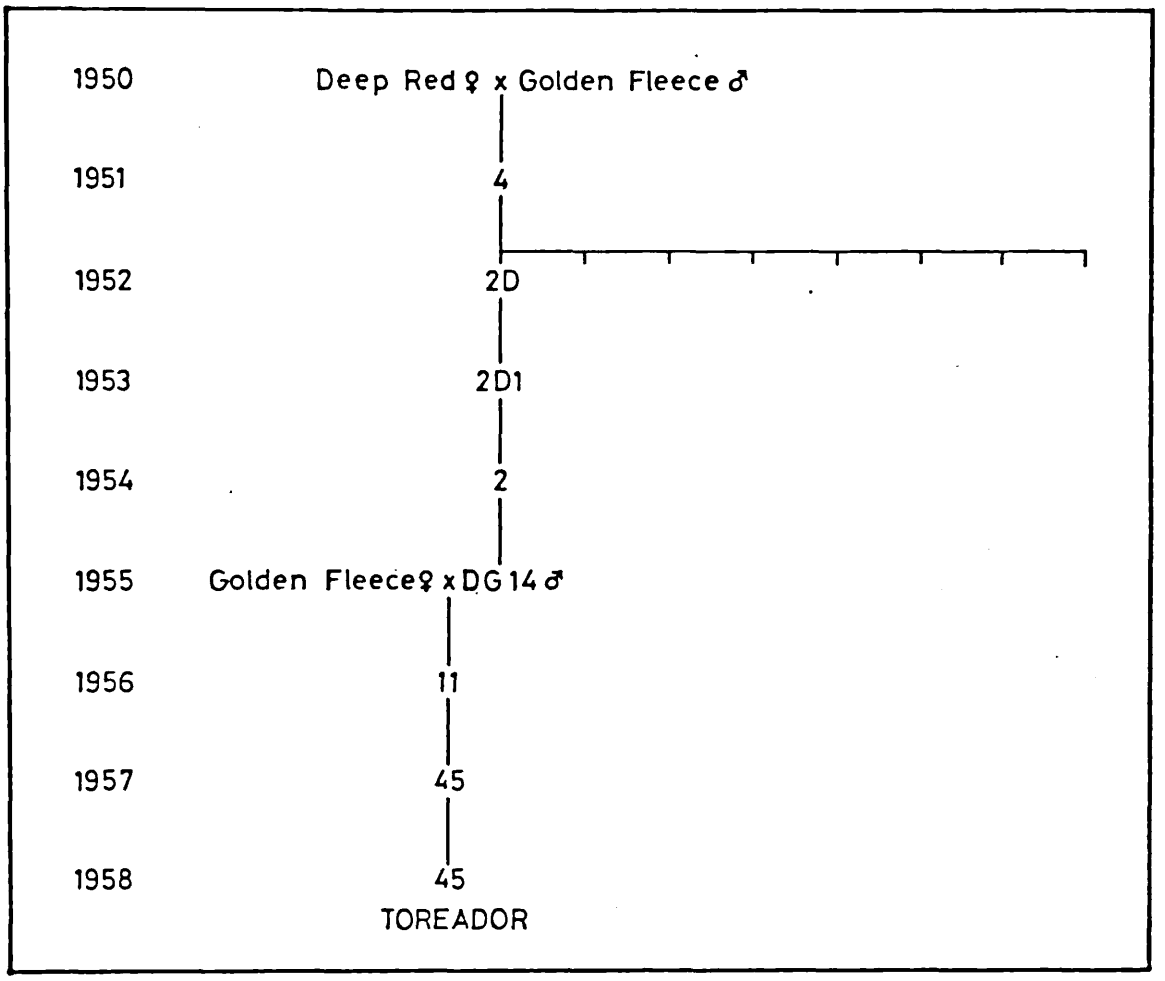


Figure 3.2 Pedigree of Polaris (original constructed from information in Green's Practical Notebooks)

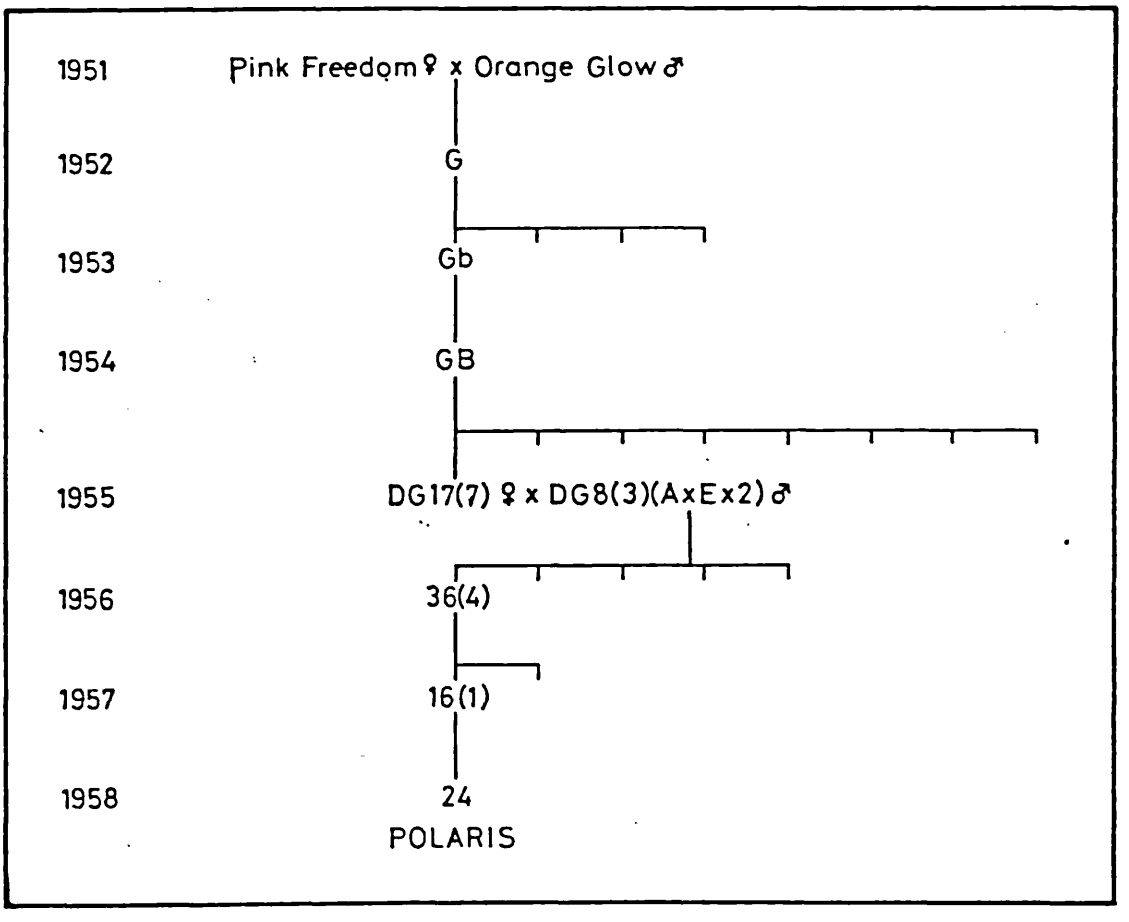


Figure 3.3 Pedigree of Titan
(original constructed from information in Green's Practical Notebooks)

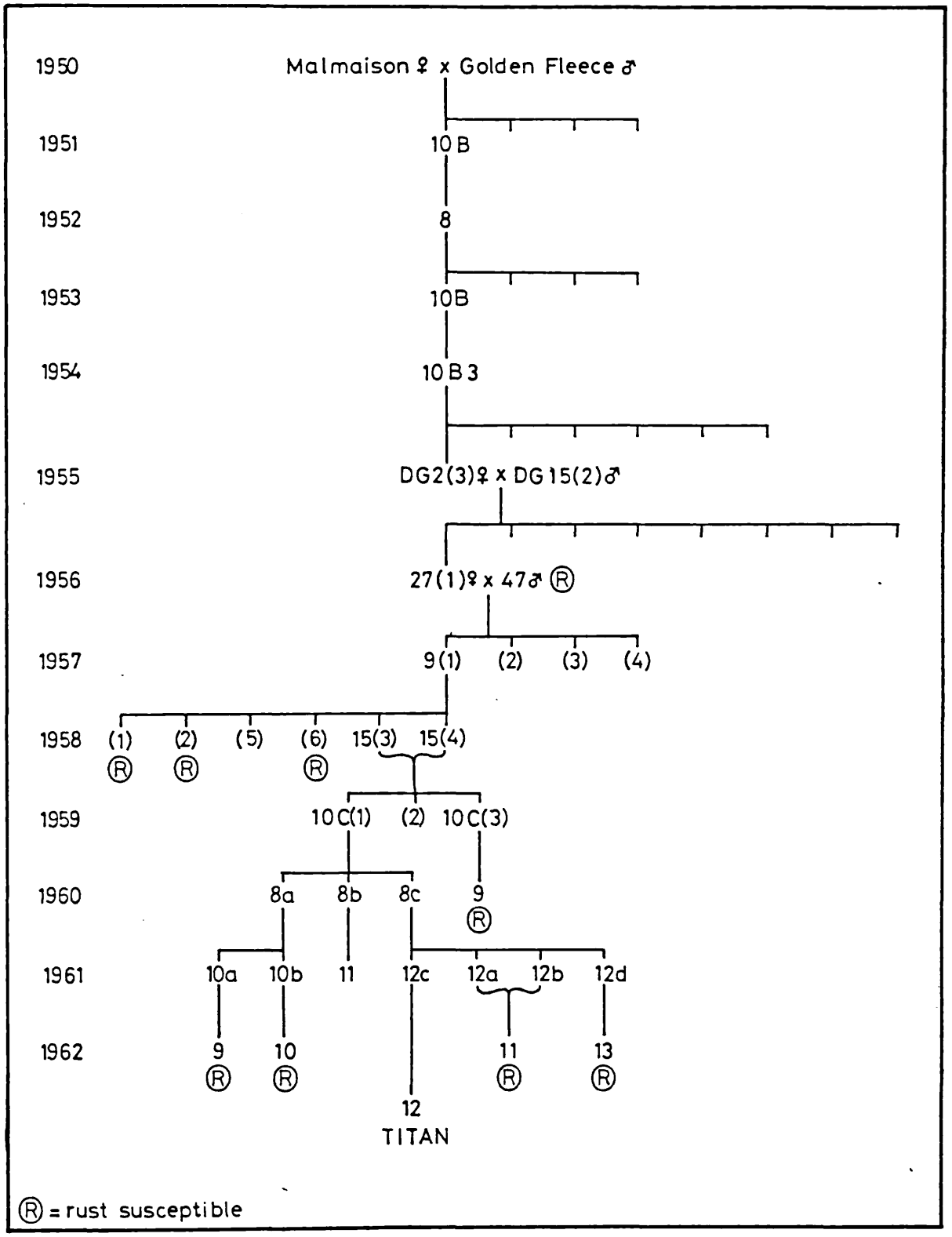


Figure 3.4 Pedigree of Juno
(original constructed from information in Green's Practical Notebooks)

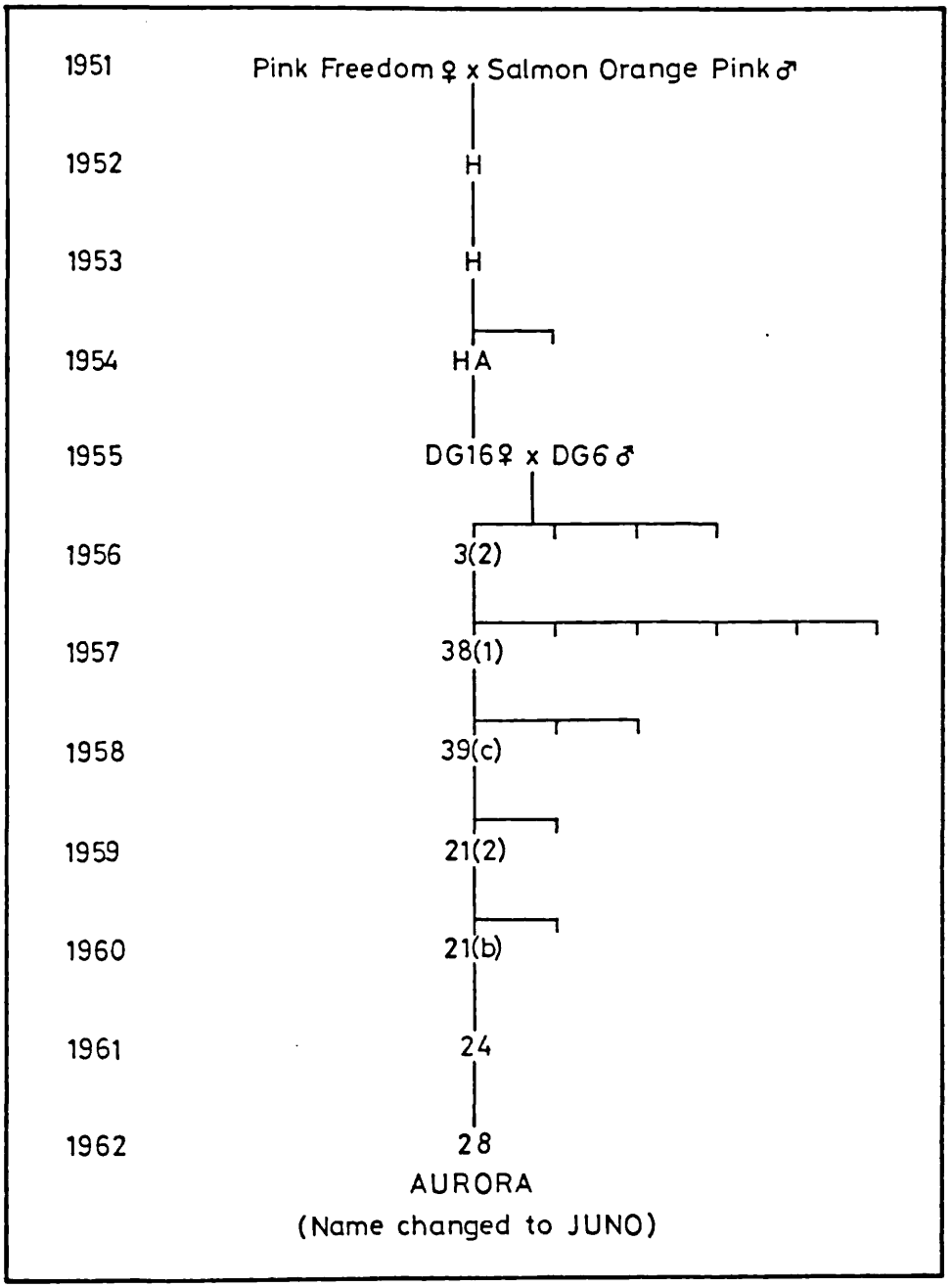
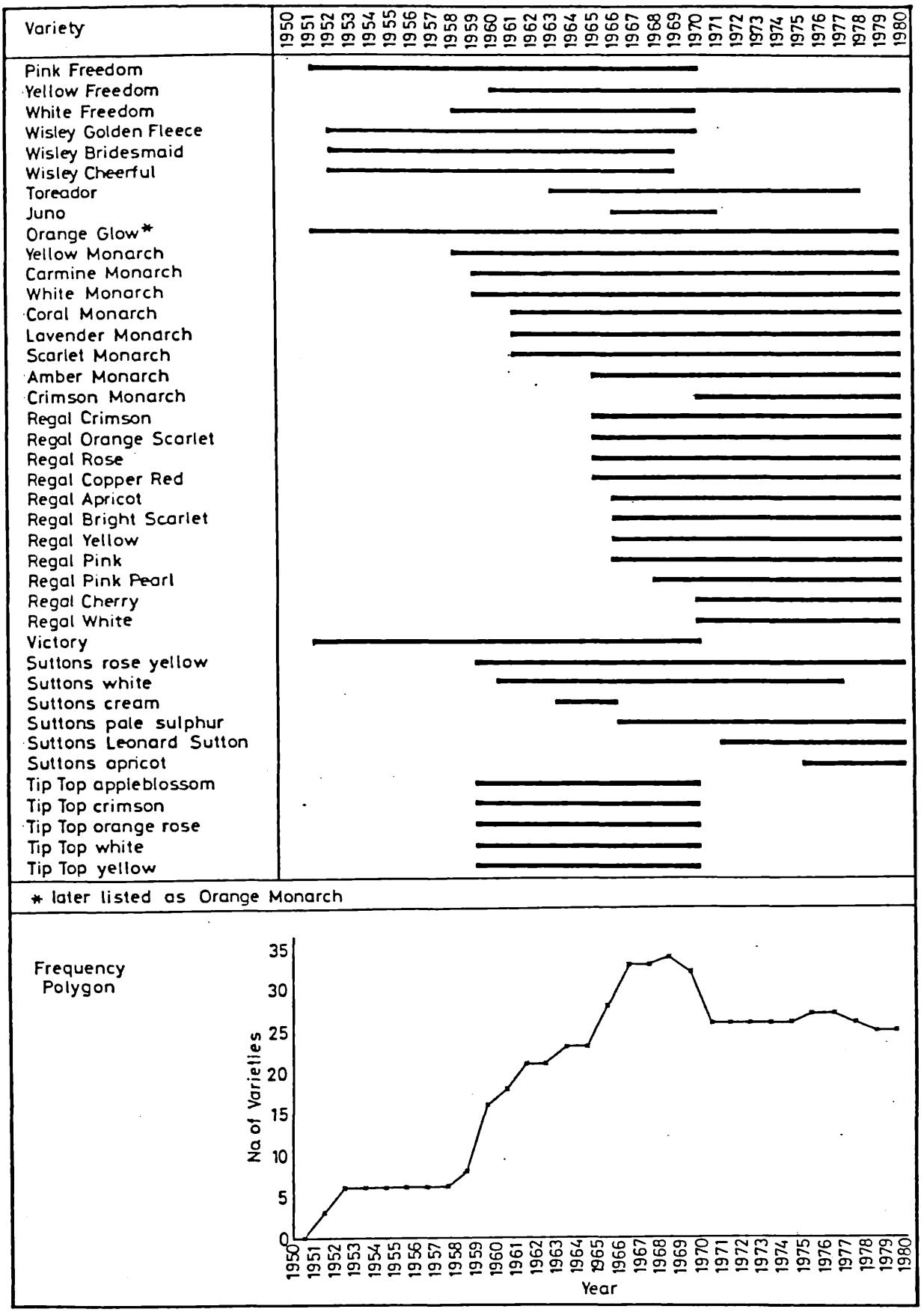


Figure 3.5 The commercial viability of British Rust-Resistant Varieties of Antirrhinum majus.



* information extracted from the following seed catalogues: Hurst, Gunson, Cooper & Taber Ltd., Watkins & Simpson Ltd., - Suttons Seeds Ltd., Thompson & Morgan Ltd.

Table 3.3 summarizes the statistics of the Trials of Rust-Resistant Antirrhinums. The increase in both the number of companies and the total number of varieties entered may reflect the amount of interest in the development of rust-resistant varieties. The proportion of varieties gaining an award in the very small trial of 1949 was unusually high. In the 1958 and 1962 trials, the number of awards given was proportionally lower but constant. There were no awards given in 1969 because no variety was able to satisfy the very stringent conditions of the Committee. According to the conditions laid down for that Trial each plant of the stock had to remain entirely free of rust until the end of the season in order to qualify for an award. Therefore, although a number of varieties exhibited only slight infection even when exposed to a very high level of inoculum, no awards were made that year.

c) In Britain after 1970

After the 1969 trial, there has been confusion among the seed firms about terminology. The term, "rust-resistant" had the connotation of immunity in antirrhinums for such a long time that some firms feel it may no longer be used to describe varieties which may become infected however slight that infection may be. For instance D.R. Colegrave Ltd., in their 1979 catalogue state, "Now that the new strains of Antirrhinum Rust disease have become so widespread we think it would be misleading to continue to offer the original series of varieties that were resistant only to the older races of this fungus." The varieties they have withdrawn, however, are still listed as rust-resistant by other seed firms.

Figure 3.5 shows the changes among the varieties listed as rust-resistant in the seed catalogues. Today the rust-resistant varieties are dominated by the "Monarch" and "Regal" lines developed by Ralph Gould at Hurst, Gunson, Cooper and Taber Ltd. More recently Suttons have released their own rust-resistant types. Nevertheless, the graph at the bottom of Figure 3.5 shows that the number of varieties listed as rust-resistant today is smaller than at any time since the 1969 R.H.S. Trial. The rust epidemic in this trial showed that no variety was immune to the rust and seed companies started to withdraw their varieties previously listed as "rust-resistant" in 1970.

a) Physiologic Race 1.

The genetics of resistance to many diseases is very complex and is not always thoroughly understood. Whilst the success of a breeding programme is not dependent upon a knowledge of the genetics of resistance, the efficiency of such a programme may be increased if the resistance is known to be conferred either by one or a number of genes. Many of the authors who were breeding for rust-resistant antirrhinums reported details of their crosses. It is therefore possible to follow the inheritance of rust-resistance within these varieties. Mains (1935) produced his resistant plants by selfing and selecting the most resistant in each generation. The resistance in these lines was incomplete but the degree of resistance was improved in each generation. It would appear that the resistance within Mains' plants was 'general' or 'field resistance' controlled by the combined action of a number of genes.

It is possible that he may also have found a major gene, although he did not recognise it as such since he says: "While such lines are infected and mycelium developed to a considerable extent, the host cells of-ten die before the rust is able to sporulate." (Mains and Thompson, 1928). This type of resistance is a form of hypersensitive reaction characteristic of a major gene resistance. White (1943) also described an "inhibited or modified form of rust infection", with flecking or chlorosis, instead of the development of a pustule.

Later the presence of a major gene was confirmed by genetical studies. Emsweller and Jones (1934) allowed some of Main's breeding material to open-pollinate in 1930. The progeny included types from a wide range of susceptibility and Emsweller and Jones selected some which were entirely free of rust. They selfed the resistant (immune) plants and found four of these plants were homozygous for resistance and four heterozygous. They interpreted this as evidence for rust-resistance being determined by a single dominant gene. Mains (1935) and White (1933) also found that the gene segregated in the ratio of three resistant to one susceptible in the F_2 generation of a cross between a homozygous resistant and a susceptible variety.

In Europe Lehoczky (1954) also recognised rust-resistance controlled by a single dominant gene in a cross between "Red Emperor" and a homozygous resistant plant. Rajhathy (1957) found a yellow-flowered rust-resistant plant among a population he had treated with colchicine. He assumed that the resistance was due to a mutation from recessive to dominant in the

gene controlling rust-resistance. He showed that this resistance was also inherited by a single dominant gene. Later Sampson (1960) demonstrated that Rajathy's resistant gene in Hungary was the same as the one they were using for studying the linkage of the rust-resistant gene to genes for colour in Canadian material. Unfortunately they were unable to compare their gene with Emsweller and Jones' resistant gene.

Besides the major gene several workers have identified resistance which does not fit a simple Mendelian ratio. Within the large population of open-pollinated resistant plants grown from seed received from Mains, Emsweller and Jones (1934) selected two slightly susceptible plants and crossed these with commercial susceptible types. Each resistant plant in the F 1 was backcrossed to the commercial parent. Emsweller and Jones reported three degrees of resistance in the progeny of this cross: susceptible, slightly susceptible and resistant. As these results did not fit any clear-cut segregation ratio, Emsweller and Jones could only offer the explanation of modifying factors and concluded that each of the slightly susceptible plants selected in 1931 contained modifying genes.

Another form of complex resistance was shown by White (1943) when he reported that susceptible commercial varieties carried hereditary factors for resistance to rust. The initial crosses between nine susceptible varieties were made in a greenhouse and the F 1 progeny tested in a field. All these hybrids were very susceptible but White selfed some that looked as if they would survive until seed had set. In one cross, "Lucky Strike" X "Afterglow", the plants in the F 3 (S 2) generation showed definite differences in their reaction to the rust. White kept seed of those plants with more than 75% resistance and obtained fiftyone plants in the F 4 generation. These fiftyone plants were progeny tested: 8 gave progeny which were all resistant, 25 segregated in the ratio of 3 resistant to 1 susceptible, 12 gave progeny which were less than 75% resistant, 6 gave progeny which were all fully susceptible. White concluded that the hereditary factor for resistance was either recessive or modified dominant. Since he gives no indication of sample size his conclusions about the inheritance of rust-resistance should be interpreted with care. White did show that it is possible to develop lines with rust-resistance from susceptible varieties.

Although it is evident that complex resistance was available, plant breeders in the 1930's preferred the immunity conferred by a single dominant gene. The range of values for average percentage resistance within the American varieties (Table 3.2) shows that the majority of the

American varieties were not homozygous for this gene and some of the varieties may also have possessed some degree of complex resistance. Green, however, selected for his breeding work only those varieties which were homozygous with 100% resistance. He was therefore using the American major gene to confer immunity.

The presence of a dominant gene is evident in the pedigree of Titan (Figure 3.3). In 1956, Green crossed his breeding line with a susceptible variety. The F 1 generation was resistant but in 1958 susceptible plants were present in the F 2 generation indicating the reappearance of the recessive gene in the homozygous state.

Another of the early British rust-resistant varieties, "Victory", has been shown to have a dominant gene for rust-resistance. Miss Rolfe at Worcester College of Higher Education has permitted the use of her results of the segregation, in the F 2, of a cross between the rust-resistant variety, "Victory", and the rust susceptible, "Eclipse" (Rolfe, 1980). The results are shown in Table 3.4. The χ^2 values for each family with 1 degree of freedom are as follows: 1957, χ^2 = 0·341 (p = 0·5 - 0·7); 1958, χ^2 = 0·375 (p = 0·5 - 0·7); 1959, χ^2 = 0·007 (p = 0·9 - 0·95); 1961, χ^2 = 0·401 (p = 0·5 - 0·7). They show that each set of results clearly agrees with the ratio of three resistant to one susceptible. The homogeneity χ^2 value of 1·08 with 3 degrees of freedom (p = 0·7 - 0·9) shows that there is no significant difference between the four families.

Table 3.4 Segregation of resistant and susceptible plants in the F 2 generation of a cross made by Edith Rolfe between the rust-resistant variety, "Victory", and the susceptible, "Eclipse". Unpublished data reproduced with permission of Miss E. Rolfe, Worcester College of Higher Education, Worcester, U.K.

Year	Number of Progeny		Total
	Resistant	Susceptible	
1957	133	40	173
1958	87	33	120
1959	155	51	206
1961	81	31	112
Total	456	155	611

b) Physiologic Race 2.

The inheritance of resistance to the second race of rust in America (Yarwood, 1937) is not so clear cut. Plants with resistance to race 1 may be susceptible, partially resistant or highly resistant to race 2 (Nelson, 1939). Mehlquist and Rahmani (1948) found four commercial varieties which were fairly resistant but not immune to race 2 in 1938. They were not attacked sufficiently for the disease to interfere with normal flowering. True breeding lines which were highly resistant to race 2 were developed from one plant in a line obtained from Nelson. Mehlquist and Rahmani explained the rust-resistance in terms of just two genes and concluded that "the gene controlling resistance to the second form of the rust is not a dominant one, but expressing its effect directly in proportion to dosage." Since a genetic model involving a single locus for resistance to race 2 must have at least three phenotypes which ought to be distinguishable, the report of a dosage-effect by these workers is not consistent with the model they propose, instead it seems to indicate a polygenic system. It was perhaps the complexity of inheritance of resistance to race 2, in comparison to the simplicity of control of race 1, which led Blodgett and Mehlquist (1941) to conclude that "the development of rust-resistant commercial snapdragons does not present a simple problem in plant breeding."

DISCUSSION

This review of the development of rust-resistant antirrhinums has shown that there is a genetical continuity between Green's plants in Britain and those originating in 1922 in Indiana. It is unusual to have such detailed knowledge because the breeding programmes by which most commercial varieties are obtained remain confidential even after those varieties have been withdrawn. A knowledge of the development of previously resistant varieties, however, is extremely useful in deciding upon a strategy for future breeding programmes.

There are several important implications of this review. Though both types of resistance can be identified within Mains' material, only the major gene was used in subsequent breeding programmes. In consequence, virtually all the resistant plants contained the major gene which originated from Mains' material. A possible exception might be the resistant gene which appears to have arisen independently in "Orange Glow". This gene may or may not have been the same as the one in Mains' plants. Such widespread use of the same resistance in all varieties has in effect created a monoculture (Nelson, 1973) and host plant uniformity has been an important cause of many past epidemics (Day, 1978).

In this case, the resistance to race 1 was conferred by a single dominant gene inherited in a Mendelian ratio. This is the simplest case and it has been described for many other plant diseases. None of the varieties tested during this investigation (see next Chapter) possessed a major gene for complete resistance to the prevalent rust strains despite the fact that immunity had been the prime breeding objective of a number of seed companies for over fifty years in America and about twentyfive years in Britain.

CHAPTER FOUR

A QUANTITATIVE ASSESSMENT OF RUST SUSCEPTIBILITY IN VARIETIES OF *ANTIRRHINUM MAJUS*

INTRODUCTION

In many antirrhinum trials (Peltier, 1919; Doran, 1921; Beaumont and Stanland, 1935; Fikry, 1939) the susceptibility of varieties to rust was only assessed once, generally at the end of the season and whilst a number of varietal differences were reported the comparisons were mainly qualitative. Since these early trials there have been many advances in the science of epidemiology. Plant pathologists have recognised four important components of an epidemic (Horsfall and Cowling, 1977):

i a susceptible host
ii a virulent and aggressive pathogen
iii a favourable environment
iv time

Factors i to iii must be near their optimum for a period of time for the epidemic to flourish. Barratt (1945) was the first to recognise the importance of the rate of disease increase and plotted "disease trend curves" for the field performance of fungicides on tomato varieties. Large (1952) used successive disease assessments to depict the progress of blight on various crops. He found the characteristic disease progress curve was sigmoid and this has been confirmed by many other workers. The disease development is initially slow because there is a relatively small amount of inoculum, it then accelerates and slows down again when there is little healthy host tissue left for the pathogen to colonize.

Van der Plank (1963) has recognised three phases of an epidemic based on the sigmoid curve.

(1) The logarithmic phase where the increase of the pathogen is unhindered by the overlapping of lesions and is independent of the amount of disease present. This phase has also been called the exponential phase by Zadoks and Schein (1979) and extends until the amount of disease (X) = 0·05.

(2) The logistic phase extends until X = 0·35 (Van der Plank, 1963) and until X = 0·50 (Zadoks and Schein, 1979).

(3) The terminal phase begins when X is greater than 0·50. It is during this phase that most damage is done to the crop.

It is generally agreed that the disease progress curves need to be transformed for subsequent analysis and in recent years there have been many attempts to fit data of this kind to various mathematical equations. There does not appear to be a single transformation that is satisfactory for all plant diseases, thus semi-log, log-log, probit and logit transformations have all been proposed. The results of all these transformations must be interpreted with care since the rate of disease progress may vary considerably during an epidemic and this may be disguised by a straight line transformation (Kranz, 1977).

Van der Plank (1963) proposed a logistic transformation ($\log_e$ (X/ (1-X)) against time) for "compound interest" disease. This type of disease increase has been called polycyclic by Zadoks and Schein (1979) because the pathogen multiplies through successive generations during the course of an epidemic. The correction factor (1-X) is included to allow for the decreasing proportion of tissue left for infection. The logistic transformation fits a number of fungal epidemics quite well (Simmonds, 1979) and the use of this transformation of the disease progress curve for an epidemic of Puccinia antirrhini on varieties of antirrhinum is discussed in Chapter 6.

An estimate of r, the apparent infection rate (Van der Plank, 1963, 1968, 1975) may be derived from the logistic transformation. The use of r has been critised because it varies with the stage of development of the plant and progress of epidemic (Parlevliet, 1979), the environment (Waggoner, 1965), and it does not provide a test of significance (Kranz, 1974) but despite these disadvantages r has been used for a number of purposes in epidemiological research:

to compare epidemics in a range of cultivars (Fry, 1978);
to assess the effects of fungicide on disease progress (Kannwischer and Mitchell, 1978);
to assess loss of yield (James, Callbeck, Hodgson and Shih, 1971);
to compare sanitation methods (Berger, 1977);
to assess the effect of plant spacing (Strandberg and White, 1978);
to predict the future course of an epidemic (Merrill, 1967).

An epidemic of rust on varieties of antirrhinum was studied to establish whether the susceptibility of previously "rust-resistant" varieties was due to the loss of genetic resistance in Antirrhinum majus. In addition it was thought that some varieties exhibited more "field resistance" to the rust. If these varieties could be identified they may be suitable for a plant breeding project.

MATERIALS AND METHODS

1. Cultivation

During the summers of 1978 and 1979 one hundred and thirty-one varieties of *A. majus* were tested for their susceptibility to the rust fungus at two locations in Surrey, England; Royal Holloway College, Egham and The Royal Horticultural Society's Garden at Wisley. The varieties were listed with the source of seed in Appendix 4.1 and the addresses of contributors given in Appendix 4.2. The very susceptible variety, "Malmaison" (No.67) was used to ensure that there was a uniform high infection over the plots and as a control to compare the degree of rust infection at the two locations.

The varieties number 1 - 67 were included in trials of 1978. The seed was sown on 27th February, seedlings pricked out between the 15th and 30th March and the young plants planted out on the 17th and 18th May at Royal Holloway College and the 30th May at Wisley.

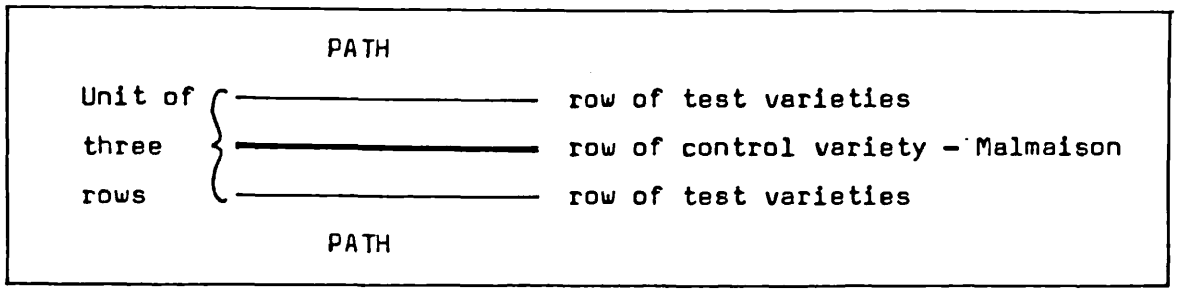
Both the plots were cleared in the late season of 1978 and left for the winter months. In April a general fertilizer "Growmore" was applied at the rate of 4 oz per square yard (160g per square metre) and the plots rotivated to a depth of 4 ins. (10cm).

The trials held during the summer of 1979 included the control variety No. 67, ten varieties repeated from the trial in 1978 - Nos. 1, 15, 18, 29, 37, 39, 45, 52, 56, 62 to assess the seasonal differences and varieties numbered 68 to 131 inclusive. The seed was sown on the 13th March, pricked out between 27th March and 6th April and planted out on 15th and 16th May at Royal Holloway College and on the 4th June at Wisley.

2. Design of Experiment.

At each location a plot measuring 25 metres x 15 metres was used for the trials. The two plots were treated as replicates and were therefore planted in exactly the same arrangement. Basically the varieties were planted in units of three rows (Fig.4.1). A complete row of "Malmaison" was planted in the middle to ensure all areas of the plot were exposed to high inoculum of rust spores. A row of test plants were planted either side of each row of "Malmaison". Each unit of three rows was separated by a path. In addition two guard rows of "Malmaison were planted round the perimeter of the plot.

Figure 4.1 Arrangement of rows of the control and test varieties in the Antirrhinum Trials



In the trial held during the summer of 1978 the varieties were divided into three height categories; dwarf - Nos. 1 - 13, intermediate Nos. 25 - 66 and tall - Nos. 14 - 24. The spacing between the rows were increased from 0·3 metres in the dwarf section, to 0·4 metres in the intermediate section to 0·5 metres in the tall section, whereas the distance between plants within each row was constant at 20cm. Each variety was planted in three blocks (a, b and c) of nine plants in a completely randomized design within each section. In addition, fourteen blocks of the control variety, "Malmaison", were planted within the rows of test plants in a stratified random design in order to determine whether there was uniform rust infection throughout the plot. The resulting arrangement of varieties included in the plot for 1978 is shown in Figure 4.2. The complete rows and guard rows of "Malmaison" are shown by the thicker lines.

Since there was no apparent correlation between the height of the plants and the amount of ground covered it was decided to keep the spacing between the rows constant in 1979. The rows were planted 0·4m apart and the paths were 0·7m wide. This arrangement permitted the use of a randomized block design which is consistently more accurate because the restrictions in the design reduce the experimental errors. (Cochran and Cox, 1968; Fisher, 1948). The plot was divided into three sections (a, b and c) and each variety placed once at random within each section. Thus, each variety was represented by three blocks of nine plants as in 1978. Nine blocks of "Malmaison", three in each section, were planted for the reason given above. In addition two guard rows of "Malmaison" surrounded the plot. The arrangement of varieties in the 1979 plot is shown in Figure 4.3.

3. Disease Assessment

Disease is generally assessed either as;

i disease incidence - expressed by the number of plants infected as a percentage of the total or

Figure 4.2 1978 Trial - Arrangement of varieties on plot

1a	9a	3a	1b	5a		12a	8a	6a	5b	11a	67a	3b
2a	6b	13a	9b	4a	8b	10a	7a	2b	67b	4b	9c	10b
67c	7b	8c	10c	12b	13b	3c	11b	12c	7c	11c	13c	2c
4c	6c	5c	30a	31a	32a	62a	52a	67d	1c	55a	45a	51a
46a	66a	40a	36a	46b	43a	35a	25a	62b	39a	58a	26a	65a
34a	50a		32b	67e	44a	57a	60a	29a	66b		31b	
37a	48a	28a	41a	45b		28b	48b	61a	41b	38a	59a	56a
51b	56b	67f	50b	27a	43b	67g		63a	35b	26b	47a	60b
49a	55b		56c	58b	44b	33a	25b	42a	53a	28c	44c	58c
65b	49b	47b	54a	37b	61b	47c	42b	52b	30b	67h	55c	67i
41c	51c	43c	67j	34b	59b	31c	49c	53b	40b	48c	45c	53c
	25c	59c	64a	32c	38b	33b	57b	29b	39b	52c	34c	42c
38c	60c	27b		33c	36b	50c	27c	26c	63b	66c	54b	65c
61c	37c	54c	40c	39c	62c	46c	57c	36c	64b	63c	29c	64c
30c	35c	22a	20a	24a	18a	19a	67k	23a	22b	19b	21a	20b
18b	24b	15a	18c	19c	14a	17a	24c	15b	16a	23b	16b	14b
20c	67l	16c	17b	14c	67m	21b	23c	22c	21c	15c	17c	67n

Spaces denote blocks that were not filled by test varieties

Figure 4.3 1979 Trial - Arrangement of varieties on plot

95a	37a	112a	99a	124a	115a	84a	97a	127a	86a	131a	69a	125a
87a	75a	129a	107a	101a	91a	67a	71a	83a	72a	121a	105a	120a
111a	126a	85a	39a	117a	93a	123a	88a	68a	89a	114a	52a	104a
74a	1a	98a	67b	102a	119a	15a	128a	62a	78a	76a	113a	118a
82a	116a	29a	108a	77a	79a	100a	81a	73a	96a	109a	130a	110a
80a	94a	122a	18a		106a	92a	45a	90a	67c	56a	103a	70a
71b	124b	84b	37b	95b	89b	112b	87b		88b	104b	86b	1b
105b	102b	110b	67d	100b	76b	130b	62b	97b	92b	74b	82b	122b
29b	131b	70b	111b	125b	73b	67e	113b	78b	93b	101b	45b	68b
77b	85b	69b	120b	56b	52b	18b	80b	103b	107b	99b	81b	15b
83b	123b	91b	90b	121b	117b	106b	108b	126b	127b	98b	128b	72b
67f	114b	79b	118b	115b	75b	39b	119b	94b	116b	109b	129b	96b
121c	88c	15c	113c	29c	74c	131c	93c	95c	84c	76c	67g	116c
109c	86c	96c	72c	99c	97c	62c	80c	71c	18c	110c	106c	75c
94c	127c	52c	122c	68c	37c	82c	104c	67h	56c	111c	92c	100c
115c	125c	90c	1c	78c	69c	79c	77c	124c	98c	112c	70c	102c
128c	67j	105c	87c	101c	39c	120c	85c	81c	117c	89c	123c	118c
119c	130c	107c	114c	103c		129c	73c	45c	91c	83c	108c	126c

Spaces denote blocks that were not filled by test varieties

ii disease severity - where the area of plant tissue affected is expressed as a percentage of the total area (James, 1974).

There is no straightforward assessment that is appropriate for all plant diseases. Large (1966) recommended a general strategy of investigation which concluded in the production of a standard diagram for each disease. Although a photograph and a standard diagram were used in different years of the experiment, the five point scale of 1978 is strictly comparable to the one used in 1979.

The photograph (Figure 4.4) shows leaves selected to illustrate the levels of infection used to assess the disease severity during the summer of 1978. Each leaf was matched against the photograph to determine the level of infection.

Score		Description of infection
1	-	No infection
2	-	Uredia minute to small, distinct and scattered
3	-	Uredia small to medium
4	-	Uredia medium, vigorous but not compound
5	-	Uredia vigorous and compound

This is an arbitary scale and whilst many such indices and rating systems have been used in the past, percentage scales are generally preferred. The latter have the advantage that they standardize assessments and allow comparable assessments to be made by different workers. For this reason the scale used for scoring the rust in 1979 was a modified version of the twelve point logarithmic scale described by Horsfall and Barratt (1945). According to the Weber-Fechner Law visual grading progresses logarithmically, Horsfall and Barratt accounted for this limitation in perception by the human eye in their grading system. They also noted that when assessing percentage disease, the eye assesses the diseased tissue up to 50% and the healthy area above 50%.

The grades in any standard diagram must be clearly distinguishable by eye, therefore the twelve points used by Horsfall and Barratt have been reduced to five in Figure 4.5. No grades are given for greater than 50% disease because this value represents maximum cover. Standard diagrams usually show only the area covered by lesions or pustules, and therefore the grading does not assess the total diseased tissue.

Score	% Cover
1	0
2	1 - 8
3	8 - 25
4	25 - 50
5	>50

In both the 1978 and 1979 plot experiments, the susceptibility of each variety was assessed by scoring five leaves selected at random on each of the test plants. The results were recorded on summary tables; an example for two varieties is shown in Table 4.1. In cases where a plant died the missing data can be estimated by the formula

$$X = \frac{aT + bB - S}{(a-1)(b-1)}$$

where a = number of treatments

b = number of blocks

T = sum of items with same treatment as missing item

B = sum of items in same block as missing item

S = sum of all observed items

where only one item is missing, a reduction in the number of degrees of freedom gives an approximate analysis of variance (Snedecor, 1956, Pg.310).

An index figure for the susceptibility of each variety may be derived from these grades. There are two types of mean value commonly used. The arithmetic mean, obtained by multiplying the number of leaves in each category by the mean percentage of that category, adding the products and dividing by the number of leaves; this mean value, however, is distortedby extreme individual scores consequently a better index figure is the geometric mean obtained by adding all the individual scores and dividing by the total number of leaves. This second mean value is the one used in the subsequent analysis of results.

Figure 4.4 Photograph showing leaves selected to illustrate the five levels of infection in 1978.

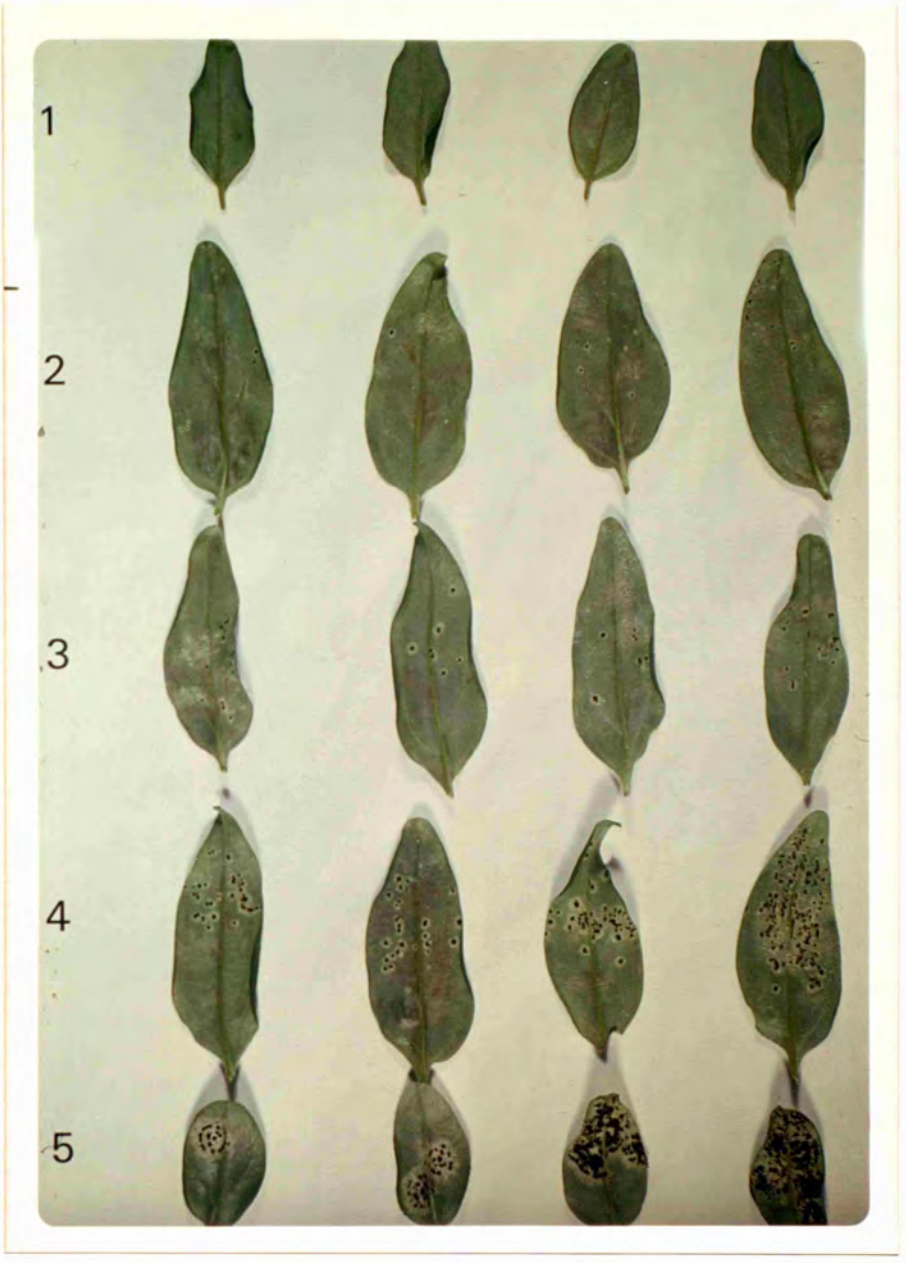


Figure 4.5 Standard diagram for scoring rust infection on antirrhinum leaves in 1979.

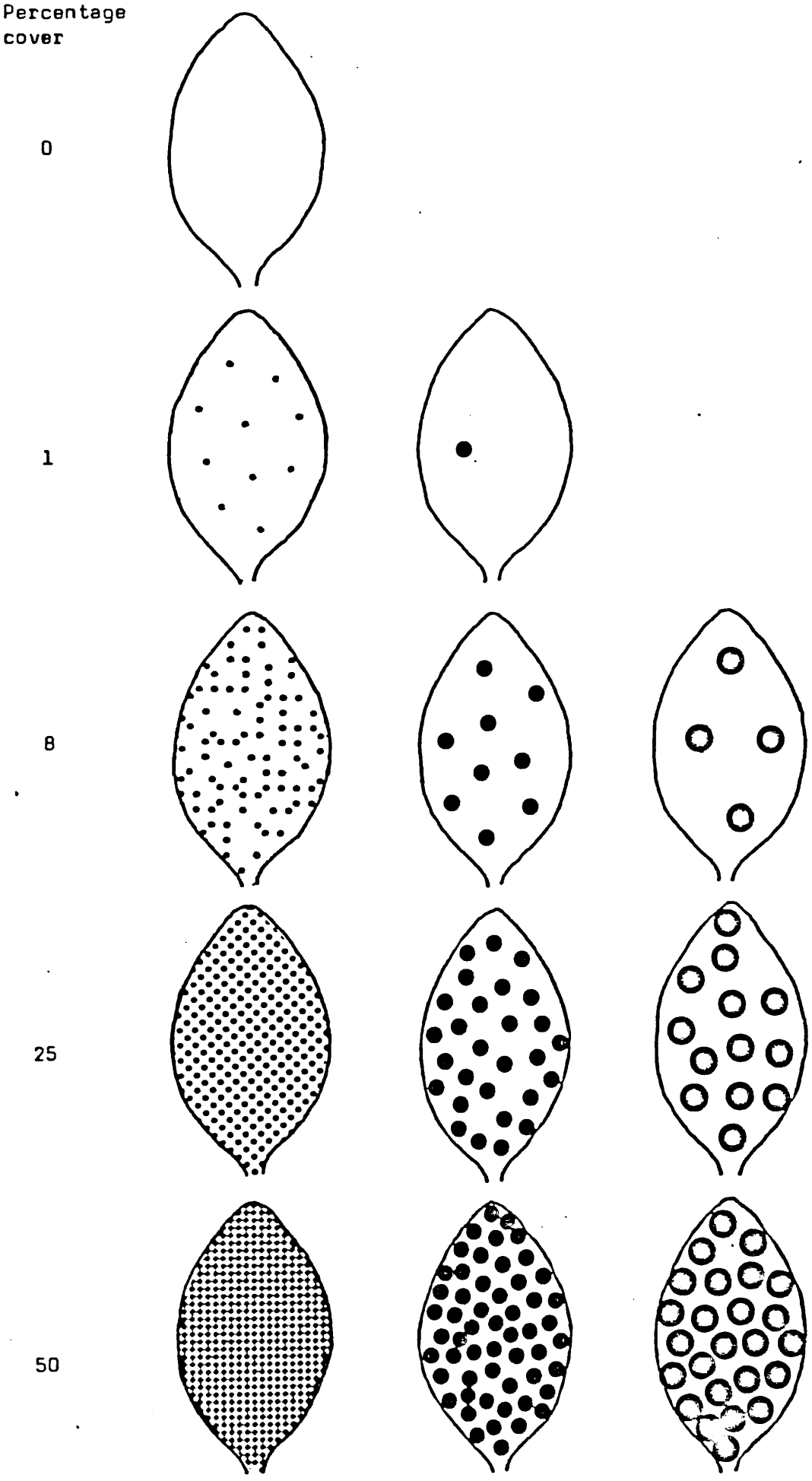


Table 4.1 Sample of one page of results showing values for disease assessment for two varieties.

Variety No 90 - Rocket Red

	leaf letter	a									b									c									d									e								
	plant number	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Replicate I (RHC)	block A	3	3	1	1	1	1	1	1	1	3	2	2	1	2	1	1	1	1	2	1	2	2	2	2	2	1	2	2	1	2	1	1	2	1	1	1	2	2	2	2	2	1	1	1	1
	B	1	2	2	3	1	1	1	1	1	1	2	1	2	1	2	1	2	2	2	1	2	2	2	2	1	2	2	1	2	1	1	1	1	2	1	2	2	2	2	2	2	1	1	1	1
	C	2	1	1	2	2	1	1	1	1	3	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1
Replicate II (Wisley)	block A	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	3	3	2	2	1	2	2	2	1	3	3	2	2	2	2	2	2	1	3	3	2	2	2	2	2	2
	B	2	2	2	2	2	2	2	2	2	2	2	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	2	2	2	2	2	2	2	1	2	2	2	2
	C	2	1	1	2	3	2	2	2	2	2	1	1	2	3	2	2	1	2	1	2	2	2	3	3	2	1	2	1	2	2	2	3	3	3	1	2	2	2	2	2	4	3	3	1	3

Variety No. 91 - Rocket Orange

	leaf letter	a									b									c									d									e								
	plant number	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Replicate I (RHC)	block A	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	2	2	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	B	1	1	1	4	1	1	2	4	2	2	1	2	3	2	2	1	4	2	1	2	1	4	1	1	2	2	2	1	1	1	4	2	2	2	3	1	1	2	1	3	1	1	2	1	1
	C	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Replicate II (Wisley)	block A	3	2	2	2	2	1	2	2	1	3	3	3	3	3	2	2	2	3	4	4	2	3	2	2	2	1	2	3	2	2	2	2	2	2	1	2	3	3	3	3	2	2	2	1	2
	B	2	2	2	2	2	2	2	2	2	2	2	3	2	2	2	2	2	2	2	2	2	2	2	3	2	2	2	2	2	2	2	2	2	2	2	3	1	2	2	2	3	2	2	2	2
	C	2	2	2	2	2	1	2	3	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	2	2

4. Quantitative Techniques

a) Design of the experiment

i The variation and interaction of variables within each variety.

The statistical analysis of both the completely randomized and randomized block designs is straightforward with an analysis of variance. The BMD02V computer programme (1977) was used to compute an analysis of variance for factorial designs. The output of this programme includes an analysis of variance table and a grand mean. Tables 4.2 a and b and Tables 4.3 a and b show samples of the output for variety number 90 - "Rocket Red" and number 91 - "Rocket Orange" in the first scoring at both plots in 1979. The values for F were calculated for a three factor analysis of variance with variables 1 and 2 (plants and leaves) fixed and variable 3(blocks) random (Zar, 1974). The significance of the calculated values of F was determined by comparing them with the tabulated critical values given by Rohlf and Sokal (1969). Three significance levels were used as shown;

0·05	*	significant
0°01	**	highly significant
0·001	***	very highly significant

ii Uniform distribution of rust over each plot.

Table 4.4 shows a sample of the output of the BMD02V three factor analysis of variance for the fourteen blocks of the control variety "Malmaison" at the first scoring at Wisley in 1978. In addition, the mean score for rust severity was determined for each block of nine plants. The values for the three blocks of each variety were compared and the highest scores, intermediate scores and lowest scores plotted on a map. The coefficient of variation was used to assess the variation of blocks within one variety. This value, which is generally expressed as a percentage, is obtained by dividing the sample standard deviation by the sample mean.

iii Comparison of the epidemic of both localities.

The starting date and the severity of rust infection at both locations were compared for both years of the experiment.

Table 4.2 Sample of computer output of Analysis of Variance within each variety in the first scoring at Royal Holloway College in 1979

a) Variety Number 90 - Rocket Red

BMD02V - ANALYSIS OF VARIANCE FOR FACTORIAL DESIGN - VERSION OF JULY 22, 1965
HEALTH SCIENCES COMPUTING FACILITY, UCLA

PROBLEM NO. 90

NUMBER OF VARIABLES 3
NUMBER OF REPLICATES 1

VARIABLE	NO. OF LEVELS
1	9
2	5
3	3

(15F5.2)

GRAND MEAN 1.42963

SOURCE OF VARIATION	DEGREES OF FREEDOM	SUMS OF SQUARES	MEAN SQUARES
1	8	8.01481	1.00185
2	4	1.22963	.30741
3	2	2.90370	1.45185
12	32	7.17037	.22407
13	16	6.56296	.41019
23	8	1.83704	.22963
RESIDUAL	64	15.36296	.24005
TOTAL	134	43.08148	

b) Variety Number 91 - Rocket Orange

BMD02V - ANALYSIS OF VARIANCE FOR FACTORIAL DESIGN - VERSION OF JULY 22, 1965
HEALTH SCIENCES COMPUTING FACILITY, UCLA

PROBLEM NO. 91

NUMBER OF VARIABLES 3
NUMBER OF REPLICATES 1

VARIABLE	NO. OF LEVELS
1	9
2	5
3	3

(15F5.2)

GRAND MEAN 1.31852

SOURCE OF VARIATION	DEGREES OF FREEDOM	SUMS OF SQUARES	MEAN SQUARES
1	8	12.10370	1.51296
2	4	1.52593	.38148
3	2	17.30370	8.65185
12	32	4.34074	.13565
13	16	16.69630	1.04352
23	8	1.14074	.14259
RESIDUAL	64	12.19259	.19051
TOTAL	134	65.30370	

Table 4.3 Sample of Computer output of Analysis of Variance within each variety in the first scoring at Wisley in 1979

a) Variety Number 90 - Rocket Red

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BMD02V - ANALYSIS OF VARIANCE FOR FACTORIAL DESIGN - VERSION OF JULY 22, 1965
HEALTH SCIENCES COMPUTING FACILITY, UCLA


PROBLEM NO. 90

NUMBER OF VARIABLES      3
NUMBER OF REPLICATES     1

VARIABLE      NO. OF LEVELS
    1              9
    2              5
    3              3

    (15F5.2)

GRAND MEAN              2.03704
```

SOURCE OF VARIATION	DEGREES OF FREEDOM	SUMS OF SQUARES	MEAN SQUARES
1	8	5.48148	.68519
2	4	.81481	.20370
3	2	.01481	.00741
12	32	5.18519	.16204
13	16	16.11852	1.00741
23	8	1.98519	.24815
RESIDUAL	64	7.21481	.11273
TOTAL	134	36.81481	

b) Variety Number 91 - Rocket Orange

```
BMD02V - ANALYSIS OF VARIANCE FOR FACTORIAL DESIGN - VERSION OF JULY 22, 1965
HEALTH SCIENCES COMPUTING FACILITY, UCLA


PROBLEM NO. 91

NUMBER OF VARIABLES      3
NUMBER OF REPLICATES     1

VARIABLE      NO. OF LEVELS
    1              9
    2              5
    3              3

    (15F5.2)

GRAND MEAN              2.11111
```

SOURCE OF VARIATION	DEGREES OF FREEDOM	SUMS OF SQUARES	MEAN SQUARES
1	8	2.93333	.36667
2	4	1.25926	.31481
3	2	1.73333	.86667
12	32	6.47407	.20231
13	16	10.26667	.64167
23	8	2.78519	.34815
RESIDUAL	64	7.88148	.12315
TOTAL	134	33.33333	

Table 4.4 Sample of Computer output of Analysis of Variance for the fourteen blocks of "Malmaison" in the first scoring at Wisley in 1979

BMD02V - ANALYSIS OF VARIANCE FOR FACTORIAL DESIGN - VERSION OF JULY 22, 1965
HEALTH SCIENCES COMPUTING FACILITY, UCLA

PROBLEM NO. WI

NUMBER OF VARIABLES 3
NUMBER OF REPLICATES 1

VARIABLE	NO. OF LEVELS
1	8
2	5
3	14

(14F5.2)

GRAND MEAN 3.83651

SOURCE OF VARIATION	DEGREES OF FREEDOM	SUMS OF SQUARES	MEAN SQUARES
1	8	.77460	.09683
2	4	.30159	.07540
3	13	158.21587	12.17045
12	32	15.52698	.48522
13	104	54.06984	.51990
23	52	16.72063	.32155
RESIDUAL	416	205.85079	.49483
TOTAL	629	451.46032	

b) Assessment of seasonal variation on rust susceptibility.

Ideally agricultural and horticultural experiments should be performed at a number of places and over a number of years. The effect of the environment on the epidemic may vary considerably from year to year and the purpose of repetition is to determine whether it is possible to make recommendations which are widely applicable.

Yates and Cochran (1938) devised a method to compare trials in different years using the mean square for experimental error. If all the elements of error are essentially the same the errors may be pooled and the mean of the error mean squares is called the true error variance. The error mean squares when divided by the true error variance and multiplied by the number of degrees of freedom will be distributed as χ^2.

Since the antirrhinum trial was only repeated once at two locations, the sample was too small for the method described by Yates and Cochran. Therefore, the ten varieties included in both years of the experiment were

compared with Kendall's Coefficient of Concordance, 'W', (Siegel, 1956) where 'W' measures the extent of association among k sets of rankings of N entities

$$W = \frac{S}{\frac{1}{12} k^2 (N^3 - N)}$$

in which $S = (R_j - R_j)^2$

k = number of sets of rankings

N = number of items ranked

$\frac{1}{12}k^2 (N^3 - N)$ = maximum possible number of squared deviations

The Null Hypothesis (Ho) is that the k sets of rankings are independent. When N is greater than 7 the expression given below is approximately distributed as χ^2

$$\chi^2 = \frac{S}{\frac{1}{12} k N (N + 1)} = k (N - 1) W \text{ with } (N - 1) \text{ degrees of freedom}$$

if the calculated value for χ^2 is greater than the tabulated value, the null hypothesis is rejected.

c) Comparison of Mean Score for each Variety

The BMD02V programme may also be used to compute a four factor analysis of variance for all the varieties in one plot. An example of this output is given in Table 4.5. The values for F were calculated with variables 1, 2 and 3 (variety, plants and leaves) fixed and variable 4 (blocks) random (Zar, 1974).

The four factor analysis of variance table can only show whether there are significant differences between some of the varieties. There are several methods for locating these differences and in this case the method devised by J.W. Tukey and described with some modifications by Snedecor (1956) has been used. This test uses the experiment as a whole for assessing the risk of error and this value may be calculated from the Mean Square of the Residual Error

e.g. Variance $Sx^2 = \frac{\text{Mean Square}}{DF}$

Standard Deviation $Sx = \sqrt{\frac{\text{Mean Square}}{DF}}$

Standard Error $= \frac{Sx}{\sqrt{n}}$

The test may best be explained by an example. The mean scores for each variety was ranked as shown in the left hand column of Table 4.6.

Table 4.5 Sample of computer output of a four factor Analysis of Variance for all the varieties in the second scoring at Royal Holloway College in 1979.

BMD02V - ANALYSIS OF VARIANCE FOR FACTORIAL DESIGN - VERSION OF JULY 22, 1965
HEALTH SCIENCES COMPUTING FACILITY, UCLA

PROBLEM NO. 01

NUMBER OF VARIABLES 4
NUMBER OF REPLICATES 1

VARIABLE	NO. OF LEVELS
1	74
2	8
3	5
4	3

(15F5.2)

GRAND MEAN 1.80931

SOURCE OF VARIATION	DEGREES OF FREEDOM	SUMS OF SQUARES	MEAN SQUARES
1	73	2036.64905	27.89930
2	8	14.08468	1.76059
3	4	44.65606	11.16401
4	2	250.02943	125.01471
12	584	415.10050	.71079
13	292	76.97357	.26361
14	146	1296.57798	8.88067
23	32	7.67908	.23997
24	16	11.32012	.70751
34	8	8.44605	1.05576
123	2336	462.69129	.19807
124	1168	856.07247	.73294
134	584	134.50210	.23031
234	64	13.61882	.21279
RESIDUAL	4672	917.43303	.19637
TOTAL	9989	6545.83423	

Each mean is then subtracted from those above to form the half matrix in Table 4.6. The test is made by computing a difference D which is significant at the 5% level and then comparing this value with the differences between the means

$$D = S\bar{x} \times Q$$

Q is taken from the Studentized Range (Rohlf and Sokal, 1969) In this case D = 0·0482 and if the difference between the means is greater than the value for D the two varieties are significantly different. In Table 4.6 the insignificant differences are underlined.

Table 4.6 Matrix showing significant differences between the first ten varieties in the second scoring at Royal Holloway College in 1979 as distinguished by Tukey's Test

Var.Code No.*	$\bar{x}$	62	131	18	126	122	74	71	128	1
		$\bar{x}$-1·09	$\bar{x}$-1·12	$\bar{x}$-1·21	$\bar{x}$-1·21	$\bar{x}$-1·21	$\bar{x}$-1·33	$\bar{x}$-1·34	$\bar{x}$-1·37	$\bar{x}$-1·37
103	1·38	0·29	0·26	0·17	0·17	0·17	0·05	0·04	0·01	0·01
1	1·37	0·28	0·25	0·16	0·16	0·16	0·04	0·03	0·00	
128	1·37	0·28	0·25	0·16	0·16	0·16	0·04	0·03		
71	1·34	0·25	0·22	0·13	0·13	0·13	0·01			
74	1·33	0·24	0·21	0·12	0·12	0·12				
122	1·21	0·12	0·09	0·00	0·00					
126	1·21	0·12	0·09	0·00		D = 0·0482 insignificent differences are underlined				
18	1·21	0·12	0·09							
131	1·12	0·03								
62	1·09									

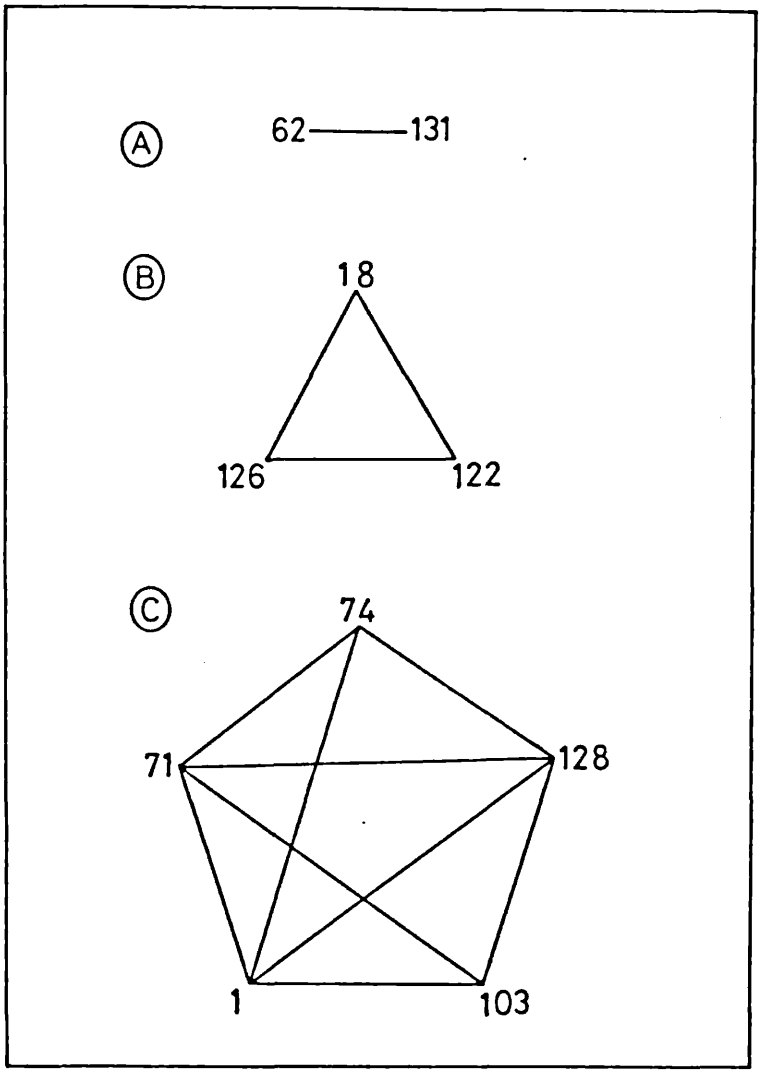
* see Appendix 4.1 for the name and source of each variety or Appendix 4.14 for a fold out list of the variety names.

d) Classification to group varieties with similar resistance.

The insignificant differences shown in the Matrix of Tukey's Test may be used to classify the varieties with respect to their susceptibility to the rust fungus. The classification produces discrete groups (A, B, C etc.) such that similarities within groups are greater than those between groups.

Figure 4.6 shows an example of the classification on the first ten varieties in the second scoring at Royal Holloway College in 1979. Varieties which are insignificantly different from each other as determined by Tukey's Test are joined by a line. The groups are formed when the difference between two adjacent means is greater than the value for D.

Figure 4.6 An example of a classification on the first ten varieties in the second scoring at Royal Holloway College in 1979



Key for the variety numbers is given in Appendix 4.14 which may be folded out for convenience.

e) Calculation of Van der Plank's r.

The epidemic development of Van der Plank's "compound interest" diseases (1963) such as P. entirrhini is determined by the amount of disease present at the start of the epidemic and its multiplication rate and may be described by the apparent infection rate 'r' (Parlevliet, 1979)

$$r = \frac{1}{t_2 - t_1} \left[\log_e \frac{x_2}{1 - x_2} - \log_e \frac{x_1}{1-x_1} \right]$$

where x_1 is the proportion of disease at time t_1

and x_2 is the proportion of disease at time t_2

f) Determination of Percentage fatality

The number of plants killed by rust at the end of the season were counted and expressed as a percentage of the total which were not killed from other causes. In cases where rust had killed the main stem but young shoots had started growing from the base at the end of the season (Figure 4.7) the plant was counted as dead.

Fig. 4.7 Photograph showing plant shooting from the base after rust had killed the main stem

5. Comparison of methods of disease assessment

The average score for disease severity from the combined data of the first and second scorings at both localities in 1979 was used to classify the seventy-five varieties. The varieties were listed in decreasing order of rust resistance and the average disease severity was compared with the overall value of r (section 4e)and the percentage fatality (section 4f) by correlation coefficients.

RESULTS

Quantitative Techniques

a) Design of Experiment

Figures 4.8 and 4.9 show the plot before and after the rust epidemic. By September many of the varieties have prematurely finished flowering and much of the foliage is brown.

Fig.4.8 Photograph of Antirrhinum trial in July before the rust epidemic at Royal Holloway College 1978

Fig. 4.9 Photograph of Antirrhinum trial in September after the rust epidemic at Royal Holloway College in 1978

i The variation and interaction of variables within each variety

The calculated values of F for the three factor analysis of variance within the plants, leaves and blocks in each plot are given in Appendix 4.3 a - h. Inspection of these tables reveals that there are significant differences within the values assigned to some of the varieties. The percentage of significant variations and interactions at three levels of significance of the total 516 sets of values from all eight tables are summarized in Table 4.7.

Table 4.7 The percentage frequency of the significance levels in the variation and interaction of variables from Appendix 4.3 a - h

Significance level		plants	leaves	blocks	plants/lvs.	pl/blocks	lvs/blocks
0·05	*	6·7	8·3	4·7	4·8	11·4	7·9
0·01	**	0·4	2·9	4·8	1·9	15·5	4·8
0·001	***	0·2	0·9	76·9	0·8	41·3	1·7

Table 4.7 shows that there is rarely/significant variation among the plants or leaves of any variety. There is, however, often a highly significant difference between the three blocks of a variety. The interaction between plants and blocks is the only one to have a high percentage of very highly significant values for F.

ii Uniform distribution of rust over each plot.

Tables 4.8 and 4.9 show the calculated values of F for the three factor analysis of variance for the control variety, "Malmaison" in 1978 and 1979 respectively. In the two scorings of both years there was a very highly significant difference between the blocks. In the plots of 1979, there was also a very highly significant interaction between the plants and the blocks

Table 4.8 Values of F from Analysis of variance of control variety "Malmaison" in 1978

Source of variation	RHC I		WIS. I	
	F	signif	F	signif
Between plants	0·15		0·19	
Between leaves	0·71		0·23	
Between blocks	33·93	***	24·59	***
Plants/Leaves	0·72		0·98	
Plants/Blocks	1·50	**	1·05	
Leaves/Blocks	1·30		0·65	

Table 4.9 Values of F from Analysis of Variance of control variety - "Malmaison" - in 1979

Source of Variation	RHC I		RHC II		WIS I		WIS II	
	F	Signif	F	Sign	F	Sign	F	Sign
Between plants	0·93		0·59		0·94		0·99	
Between leaves	2·77	*	2·81	*	6·06	**	0·94	
Between blocks	9·73	***	19·03	***	85·09	***	293·02	***
Plants/leaves	0·89		0·95		0·67		0.66	
Plants/blocks	2·84	***	2·89	***	2·12	***	2·13	***
Leaves/blocks	1·36		1·13		0·93		1·14	

Figures 4.10, 4.11, 4.12 and 4.13 show the plan of the plot with the highest, intermediate and lowest block scores of each variety shaded. All four figures show that some of the highest scores are grouped together similarly there are groups of intermediate scores and of lowest scores.

A coefficient of variation was calculated for each variety in the four plots of the experiment. The distribution of the percentage coefficient of variation is shown in Table 4.10. The table shows that over half the varieties had less than 25% variation in 1978 and less than 20% variation in 1979. In all four plots at least three quarters of the varieties had less than 30% variation

Table 4.10 Distribution of percentage coefficient of variation within the three blocks of each variety

% Coefficient of variation	1978		1979	
	RHC	WIS	RHC	WIS
	n = 66	n = 66	n = 74	n = 74
1 - 5	8	3	7	5
6 - 10	14	15	15	12
11 - 15	9	16	19	19
16 - 20	14	7	23	19
21 - 25	20	12	11	19
26 - 30	14	22	5	9
31 - 35	9	13	11	7
36 - 40	6	9	3	5
41 - 45	1	0	4	4
46 - 50	1	1	1	0
>50	4·5	0	1	1

Figure 4.10 Plan of plot showing areas of highest infection at Royal Holloway College in 1978

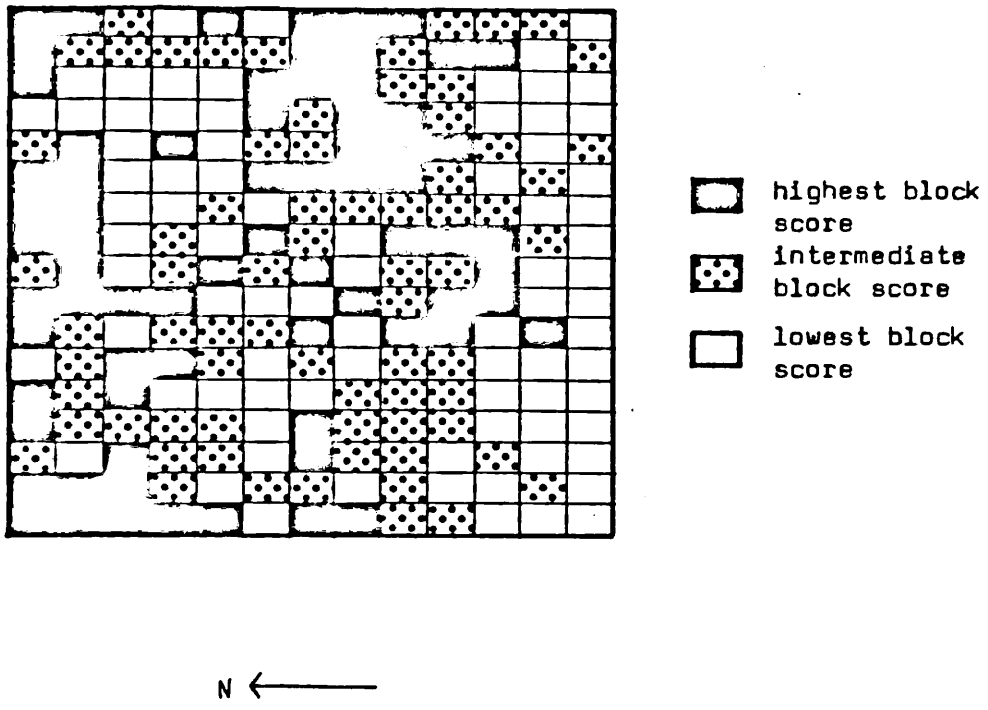
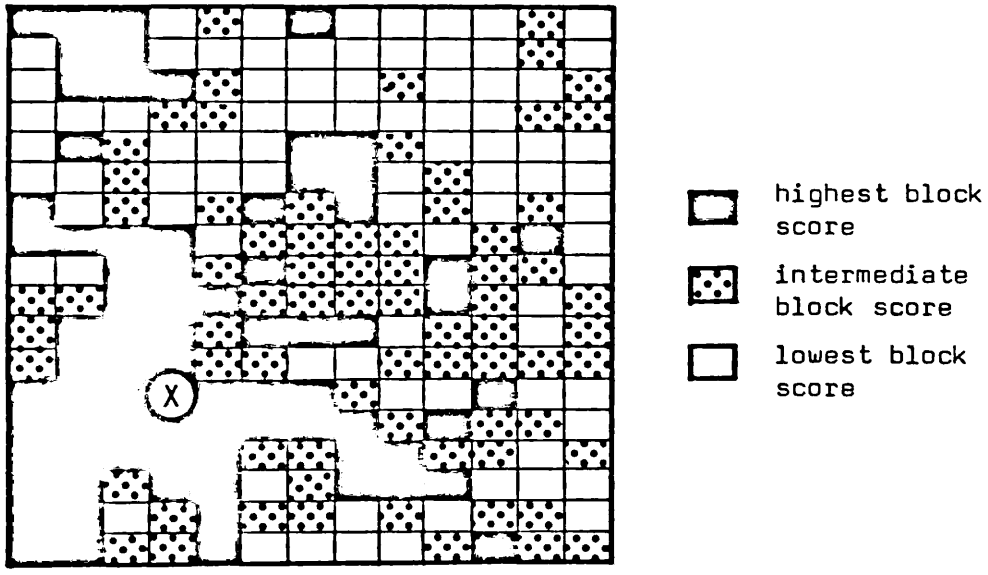


Figure 4.11 Plan of plot showing areas of highest infection at Royal Holloway College in 1979



X shows the block first infected with rust

Figure 4.12 Plan of plot showing areas of highest infection at Wisley 1978

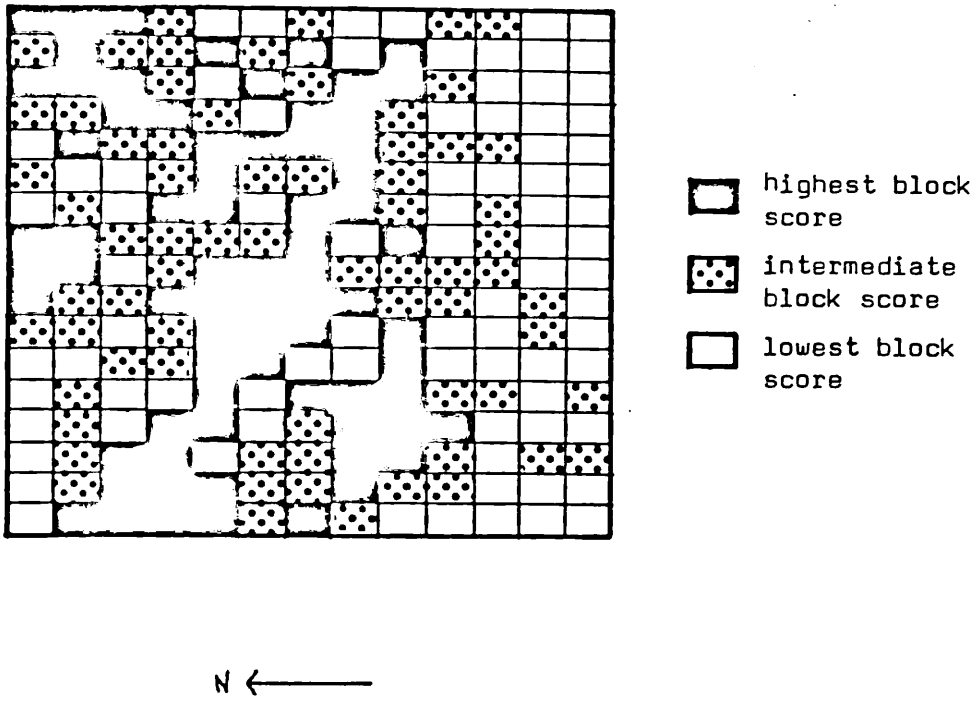
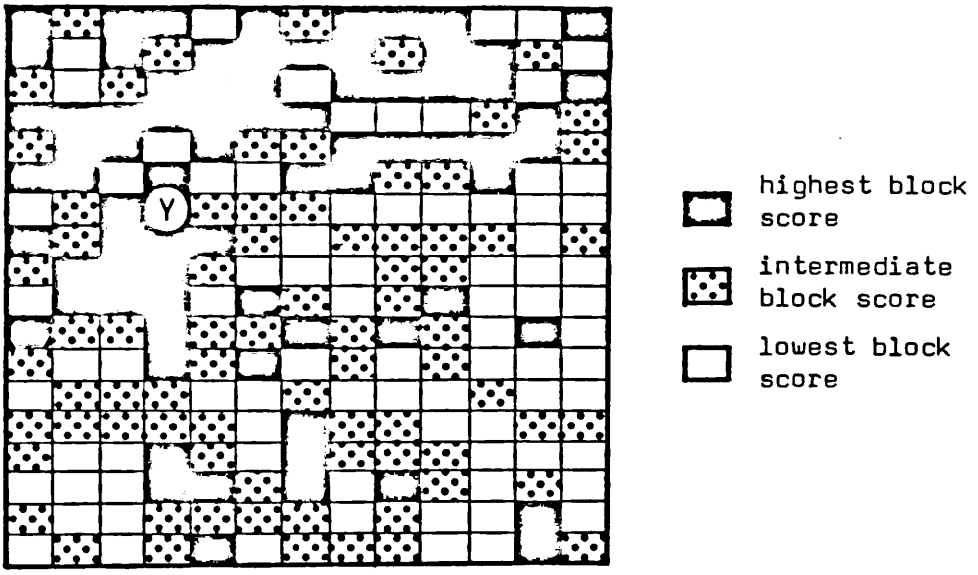


Figure 4.13 Plan of plot showing areas of highest infection at Wisley 1979



Y shows the block first infected by rust

iii Severity of the epidemic at both localities

The rust epidemic was more severe in both plots during 1978 than it was in 1979. At Royal Holloway College in 1978 the rust attacked the test varieties very early but this was due to some spores over-wintering on the rows of "Malmaison". By the 12th September many of the plants had died. At Wisley, although the epidemic did not start until later, many of the varieties scored values of 4 to 5 in early October.

In 1979 the rust started almost simultaneously in both plots. At Royal Holloway College rust was first noticed on 25th July on block C of variety number 74 "Kim Primrose Yellow" (this block is marked by an X on Figure 4.11). The rust was first seen restricted to block B of variety number 16 "Carioca Bright Scarlet" at Wisley (marked Y on Figure 4.13).

b) An assessment of seasonal variation on rust susceptibility

The ten varieties which were repeated in the second year of the experiment were ranked according to their mean score of disease severity. The ranks assigned to the varieties in each scoring are shown in Table 4.11.

In general tied observations depress the value of the Kendall Coefficient of Concordance (W), however, in this case the proportion of ties was very small and the correction was found to be negligible. The calculated value of 'W' was 0·56 and the value of χ^2 = 35·28. The tabulated value for χ^2 with nine degrees of freedom at a probability of 0·001 was 27·88 (Siegel, 1956). The null hypothesis was therefore rejected and there was a very highly significant agreement in the performance of the ten varieties in the two replicates and over the two seasons.

Table 4.11 Rank of the ten varieties repeated in the second year of the experiment using the mean score of disease severity in 1978 and 1979

Code No.	Variety Name	1978				1979			
		1st Score RHC	2nd Score RHC	1st Score Wisley	2nd Score Wisley	1st Score RHC	2nd Score RHC	1st Score Wisley	2nd Score Wisley
1	Pink Pixie	10	- *	5	8·5	2·5	3	6	6
15	Variety B	7	-	8	7	8	6	3	4
18	Variety E	2	-	1	1	1	2	2	2
29	Coronette Pink	9	-	6	6	9	10	9	9
37	Carioca Bright Scarlet	8	-	7	5	10	7	10	10
39	Carioca Yellow	6	-	3	4	6	4	8	8
45	Coronette Scarlet	4	-	2	3	7	8	7	3
52	Regal Yellow	3	-	9	8·5	5	9	5	5
56	Yellow Monarch	5	-	10	10	4	5	4	7
62	Amber Monarch	1	-	4	2	2·5	1	1	1

*since many of the varieties had died before the second scoring at Royal Holloway College in 1978 this scoring was omitted from the calculation.

-Table 4.12 Values for F from 4 factor Analysis of Variance within each score in 1978

A Source of variation	RHC I		RHC II		WIS. I		WIS.II	
	F.	signif.	F.	signif.	F.	signif.	F.	signif.
Between varieties	7·30	***	7·42	***	3·41	***	5·40	***
Between plants	1·35		0·77		2·26		2·88	*
Between leaves	1·10		2·37		4·55	*	489·29	***
Between blocks	210·51	***	50·90	***	163·44	***	11·84	***
Variety/Plants	0·93		0·82		1·06	*	0·88	
Variety/leaves	0·87		1·01	*	1·31	*	2·12	**
Variety/blocks	33·30	***	24·41	***	46·46	***	85·54	***
Plants/leaves	1·16		1·52		2·37	**	1·41	
Plants/blocks	3·38	***	5·34	***	1·55		1·73	
Leaves/blocks	1·63		1·09		1·33		0·29	
Variety/Plants/leaves	0·99		1·19	*	1·05	*	0·99	
Variety/Plants/blocks	2·53	**	4·09	***	2·50	**	5·32	***
Variety/leaves/blocks	1·29	*	1·41	*	1·19	*	1·57	*
Plants/leaves/blocks	0·86		0·91		0·90		0·75	

Table 4.13 Values for F from 4 factor Analysis of Variance within each score in 1979

B Source of variation	RHC I		RHC II		WIS.I		WIS. II	
	F.	signif.	F.	signif.	F.	signif.	F.	signif.
Between varieties	1·14		3·14	***	3·36	***	6·16	***
Between plants	0·45		2·49		0·74		3·09	*
Between leaves	47·34	***	10·57	**	9·38	**	62·23	***
Between blocks	80·43	***	636·63	***	716·52	***	1128·73	***
Variety/Plants	1·03	*	0·97		1·05	*	1·04	*
Variety/leaves	1·23	*	1·14	*	1·14	*	1·14	*
Variety/blocks	48·28	***	45·22	***	59·41	***	67·25	***
Plants/leaves	1·11		1·13		1·50		1·80	*
Plants/blocks	2·74	***	3·60	***	3·75	***	3·84	***
Leaves/blocks	1·55		5·38	***	10·36	***	1·27	
Variety/Plants/leaves	0·96		1·01	*	1·06	*	0·98	
Variety/Plants/blocks	4·08	***	3·73	**	2·91	**	4·11	***
Variety/leaves/blocks	1·09	*	1·17	*	1·35	**	1·07	*
Plants/leaves/blocks	1·09		1·08		1·11		0·78	

These values were compared with tabulated values for F from Rohlf F.J. and Sokal R.R. (1969) Statistical Tables W.H. Freeman & Co.

F 0·05 = * F 0·01 = ** F 0·001 = ***

Table 4.14 The quantitative assessment of susceptibility to rust in varieties of Antirrhinum majus. Royal Holloway College 1978

Code Number	Variety Number	Mean score for disease severity (Max score = 5)		Resistance Group*		Apparent infection rate $r \times 10^{-2}$	Percentage fatality
		1st Score 19th July	2nd Score 12th Sept.	1st Score	2nd Score		12th Sept.
1	Pink Pixie	3.94	-	5	-	>5.96	100
2	Red Pixie	3.62	-	5	-	>6.65	100
3	Rose Pixie	2.90	-	4	-	>7.78	100
4	White Pixie	3.73	-	5	-	>6.36	100
5	Yellow Pixie	4.18	-	5	-	>5.36	100
6	Orange Pixie	4.14	-	5	-	>5.49	100
7	Sweetheart Bronze	4.19	-	5	-	>5.35	100
8	Sweetheart Pink	4.09	-	5	-	>5.62	100
9	Sweetheart Red	3.13	-	5	-	>7.40	100
10	Sweetheart Rose	3.00	-	4	-	>7.62	100
11	Sweetheart White	3.71	-	5	-	>6.45	100
12	Sweetheart Yellow	3.95	-	5	-	>5.96	100
13	Kolibri Formula Mixture	3.32	-	5	-	>7.15	100
14	Variety A	1.38	3.67	1	1	3.56	26
15	Variety B	2.65	-	4	-	>8.15	74
16	Variety C	2.22	-	3	-	>8.78	85
17	Variety D	1.63	4.52	2	2	5.31	17
18	Variety E	1.36	2.65	1	1	2.02	0
19	Variety F	1.29	4.04	1	1	4.55	0
20	Variety G	2.63	-	4	-	>8.16	70
21	Variety H	1.88	-	2	-	>9.27	70
22	Variety I	1.94	-	2	-	>9.18	59
23	Variety J	1.85	-	2	-	>9.33	63
24	Variety K	2.47	-	3	-	>8.42	93
25	Coronette Yellow	2.85	-	4	-	>7.85	48
26	Coronette White	2.31	4.28	3	2	3.58	19
27	Coronette Scarlet	2.16	-	3	-	>8.87	67
28	Coronette Rose	3.30	-	5	-	>7.16	100
29	Coronette Pink	3.57	-	5	-	>6.73	96
30	Coronette Bronze	2.00	4.35	2	2	4.20	15
31	Coronette Cherry	2.28	4.08	3	1	3.05	4
32	Coronette Crimson	1.86	-	2	-	>9.33	67
33	Coronette Orchid	2.35	-	3	-	>8.58	100
34	Variety L	1.16	1.93	1	1	1.35	4
35	Carioca Deep Red	2.45	-	3	-	>8.44	100
36	Carioca Orange	3.30	-	5	-	>7.16	100
37	Carioca Bright Scarlet	2.88	-	4	-	>7.78	59
38	Carioca Peach Bronze	1.77	4.50	2	2	5.11	22
39	Carioca Yellow	2.60	4.65	4	2	4.56	33
40	Carioca Cherry Red	3.02	-	4	-	>7.62	73
41	Carioca Pink	2.82	-	4	-	>7.91	100
42	Carioca White	1.86	4.77	2	2	6.33	15
43	Carioca Appleblossom	3.63	-	5	-	>6.56	93
44	Carioca Rose	3.23	-	5	-	>7.25	85
45	Coronette Scarlet	1.81	-	2	-	>9.40	48
46	Nanum Dazzler	2.95	-	4	-	>7.71	85
47	Nanum Black Prince	1.97	-	2	-	>10.91	96
48	Regal Bright Scarlet	2.07	4.27	3	2	5.60	4
49	Regal Rose	2.42	-	3	-	>8.49	96
50	Regal Orange Scarlet	2.31	-	3	-	>8.65	93
51	Regal White	1.85	-	2	-	>9.33	67
52	Regal Yellow	1.68	-	2	-	>9.60	85
53	Regal Crimson	1.47	4.51	1	2	5.60	26
54	Regal Cherry	1.64	4.57	2	2	5.51	19
55	Regal Apricot	1.69	4.33	2	2	4.67	33
56	Yellow Monarch	2.14	-	3	2	>8.89	33
57	White Monarch	1.28	4.98	1	2	1.93	11
58	Carmine Monarch	1.37	3.93	1	1	4.18	0
59	Lavender Monarch	1.42	4.08	1	1	4.44	19
60	Orange Monarch	2.19	-	3	-	>8.82	67
61	Crimson Monarch	1.78	4.02	2	1	3.60	15
62	Amber Monarch	1.25	1.64	1	1	0.71	4
63	Coral Monarch	1.34	4.19	1	1	4.84	15
64	Scarlet Monarch	1.37	2.98	1	1	2.55	22
65	Cherokee	2.11	-	3	-	>8.95	52
66	Variety M	1.51	2.22	1	1	1.11	11
67	Malmaison	3.18	-	5	-	>7.33	100

* 1 = Resistant, 2 = Fairly Resistant, 3 = Moderate, 4 = Susceptible, 5 = Very Susceptible

Table 4.15 The quantitative assessment of susceptibility to rust in varieties of Antirrhinum majus. Wisley 1978

Code Number	Variety Number	Mean score for disease severity (Max score = 5)		Resistance Groups*		Apparent infection rate $r \times 10^{-2}$	Percentage fatality
		1st Score 5th Sept.	2nd Score 5th Oct.	1st Score	2nd Score		5th Oct.
1	Pink Pixie	2·90	5·00	2	5	14·76	0
2	Red Pixie	2·44	4·95	2	3	16·00	0
3	Rose Pixie	2·19	4·91	1	3	14·24	7
4	White Pixie	2·65	5·00	2	5	15·45	0
5	Yellow Pixie	2·53	4·94	2	3	15·72	4
6	Orange Pixie	3·40	5·00	4	5	13·28	4
7	Sweetheart Bronze	4·00	5·00	5	5	11·10	0
8	Sweetheart Pink	3·99	5·00	5	5	11·10	33
9	Sweetheart Red	3·93	5·00	5	5	11·31	7
10	Sweetheart Rose	3·09	5·00	3	5	14·17	0
11	Sweetheart White	2·83	3·41	2	1	1·62	0
12	Sweetheart Yellow	4·03	5·00	5	5	10·86	11
13	Kolibri Formule Mixture	3·82	4·94	5	3	11·90	26
14	Variety A	1·97	3·51	1	1	4·48	0
15	Variety B	3·37	4·92	4	3	10·97	11
16	Variety C	2·17	4·72	1	2	10·45	0
17	Variety D	2·30	4·64	1	2	9·48	0
18	Variety E	1·57	2·14	1	1	1·79	0
19	Variety F	1·67	3·11	1	1	4·14	7
20	Variety G	3·45	4·41	4	2	4·10	26
21	Variety H	2·92	4·70	2	2	8·38	0
22	Variety I	3·51	4·67	4	2	6·00	15
23	Variety J	3·59	4·66	4	2	5·69	93
24	Variety K	3·22	5·00	3	5	13·86	11
25	Coronette Yellow	2·56	3·92	2	1	4·24	0
26	Coronette White	2·53	4·45	2	2	7·07	0
27	Coronette Scarlet	3·22	4·54	3	2	5·97	7
28	Coronette Rose	3·60	4·77	4	3	6·90	0
29	Coronette Pink	3·11	4·90	3	3	11·72	0
30	Coronette Bronze	2·35	3·36	1	1	2·86	0
31	Coronette Cherry	2·64	4·16	2	1	5·07	0
32	Coronette Crimson	3·21	4·91	3	3	11·41	0
33	Coronette Orchid	4·02	5·00	5	5	11·10	7
34	Variety L	1·13	1·43	1	1	1·07	4
35	Carioca Deep Red	2·84	4·78	2	3	10·00	0
36	Carioca Orange	4·08	5·00	5	5	10·62	22
37	Carioca Bright Scarlet	3·16	4·66	3	2	7·10	0
38	Carioca Peach Bronze	2·27	3·88	1	1	5·07	0
39	Carioca Yellow	2·57	4·08	2	1	5·10	0
40	Carioca Cherry Red	3·89	4·68	5	2	5·10	7
41	Carioca Pink	3·62	5·00	4	5	12·62	0
42	Carioca White	2·08	4·14	1	1	6·59	0
43	Carioca Appleblossom	3·91	5·00	5	5	11·48	0
44	Carioca Rose	3·89	4·97	5	3	11·48	15
45	Coronette Scarlet	2·31	4·05	1	1	5·55	0
46	Nanum Dazzler	3·68	5·00	4	5	12·24	4
47	Nanum Black Prince	2·89	4·86	2	3	10·90	19
48	Regal Bright Scarlet	2·97	4·51	2	2	6·34	0
49	Regal Rose	4·25	5·00	5	5	9·90	30
50	Regal Orange Scarlet	4·29	5·00	5	5	9·59	4
51	Regal White	3·20	4·91	3	3	11·41	4
52	Regal Yellow	3·85	5·00	5	5	11·69	22
53	Regal Crimson	3·81	5·00	5	5	11·90	4
54	Regal Cherry	3·11	4·88	3	3	11·72	11
55	Regal Apricot	3·28	4·83	3	3	9·72	22
56	Yellow Monarch	4·04	-	5	-	>10·86	41
57	White Monarch	3·55	4·96	4	3	12·76	7
58	Carmine Monarch	3·02	4·51	3	2	6·17	0
59	Lavender Monarch	2·56	4·94	2	3	15·72	7
60	Orange Monarch	3·48	4·94	4	3	12·93	4
61	Crimson Monarch	3·22	4·29	3	2	4·28	4
62	Amber Monarch	2·81	3·14	2	1	1·00	4
63	Coral Monarch	2·94	4·85	2	3	10·76	4
64	Scarlet Monarch	2·48	4·40	2	2	6·86	0
65	Cherokee	2·42	4·45	2	2	7·48	15
66	Variety M	1·76	2·85	1	1	3·10	0
67	Malmaison	3·93	5·00	5	5	11·31	43

* 1 = Resistant, 2 = Fairly Resistant, 3 = Moderate, 4 = Susceptible, 5 = Very Susceptible

Table 4.16 The quantitative assessment of susceptibility to rust in varieties of Antirrhinum majus. Royal Holloway College 1979

Code Number	Variety Number	Mean score for disease severity (Max score = 5)		Resistance Group*		Apparent infection rate $r \times 10^{-2}$	Percentage fatality
		1st Score 25th Aug.	2nd Score 21st Sept.	1st Score	2nd Score		19th Nov.
1	Pink Pixie	1·04	1.37	-	1	1·22	73
15	Variety B	1·36	1·95	-	3	2·00	48
18	Variety E	1·01	1·21	-	3	0·89	31
29	Coronette Pink	1·38	2·21	-	2	2·59	4
37	Carioca Bright Scarlet	1·41	2·10	-	4	2·30	30
39	Carioca Yellow	1·13	1·64	-	2	1·85	12
45	Coronette Scarlet	1·34	2·12	-	4	2·48	15
52	Regal Yellow	1·09	2·18	-	2	3·81	38
56	Yellow Monarch	1·07	1·84	-	3	2·93	4
62	Amber Monarch	1·04	1·09	-	1	0·19	0
67	Malmaison	1.36	2·56	-	5	3·81	55
68	Variety N	1·08	1·51	-	1	1·56	4
69	Variety O	1·16	1·77	-	2	2·19	26
70	Variety P	1·07	1·51	-	1	1·74	7
71	Variety Q	1·01	1·34	-	1	1·48	0
72	Variety R	1·22	1·64	-	2	1·63	11
73	Burpee's Super Tetra	1·08	1·83	-	3	2·89	8
74	Tetra Giant Ruffled	1·01	1·33	-	1	1·48	0
75	Kimosy Red	1·10	1·63	-	2	2·07	96
76	Kimosy Delicate Rose	1·10	1·92	-	3	2·89	92
77	Kimosy Primrose Yellow	1·07	2·23	-	2	4·15	100
78	Kimosy Crimson	1·00	1·39	-	1	1·67	81
79	Kimosy White	1·24	2·10	-	4	2·89	100
80	Kimosy Orange	1·01	1·70	-	2	2·70	0
81	Majestic Purple King	1·13	1·91	-	3	2·67	8
82	Majestic Celestial	1·15	2·33	-	5	4·04	58
83	Majestic Snowstorm	1·13	2·04	-	4	3·15	50
84	Majestic Red Chief	1·11	1·97	-	4	3·04	33
85	Majestic Orange King	1·01	1·54	-	1	2·19	4
86	Majestic Forest Fire	1·15	2·05	-	4	3·15	22
87	Majestic Eldorado	1·24	2·04	-	4	2·74	19
88	Rocket Citron Yellow	1·10	2·27	-	2	3·96	27
89	Rocket White	1·30	2·27	-	2	3·15	26
90	Rocket Red	1·43	2·67	-	5	3·48	44
91	Rocket Orange	1.32	2.02	-	4	2·37	26
92	Rocket Orchid	1·14	2·20	-	2	3·59	26
93	Triumph Mauve	1·05	1·67	-	2	2·26	8
94	Triumph Bright Orange	1·46	2·35	-	5	2·89	35
95	Triumph White	1·16	1·99	-	4	2·96	32
96	Triumph Primrose	1·31	2·53	-	5	4·04	36
97	Triumph Scarlet	1·39	3·02	-	5	5·00	56
98	Triumph Orange Salmon	1·19	2·27	-	2	3·52	23
99	Suttons I. White	1·33	2·59	-	5	3·96	58
100	Suttons I. Fire King	1·15	1·53	-	1	4·19	7
101	Suttons I. Bright Crimson	1·08	1·87	-	3	2·74	15
102	Suttons I. Rich Apricot	1·15	1·91	-	3	2·67	15
103	Suttons I. Guardsman	1·02	1·38	-	1	1·67	11
104	Suttons I. Eclipse	1·29	2·44	-	5	3·74	19
105	Suttons I. Yellow	1·13	2·10	-	4	3·30	42
106	Suttons RR Orange Glow	1·21	2·27	-	2	3·52	26
107	Suttons RR Yellow	1·01	1·47	-	1	1·81	11
108	Suttons RR Pale Sulphur	1·01	1·42	-	1	1·67	28
109	Suttons RR Apricot	1·12	1·92	-	3	2·89	23
110	Suttons RR Leonard Sutton	1·09	1·39	-	1	1·22	50
111	Kim White	1·53	2·39	-	5	2·67	100
112	Kim Purple	1·28	1·93	-	3	2·22	96
113	Kim Primrose Yellow	2·09	3·26	-	5	3·48	100
114	Kim Mid Rose	1·26	2·20	-	2	3·19	38
115	Kim Deep Orange	1·67	2·71	-	5	3·22	80
116	Kim Blood Red	1·20	2·10	-	4	3·07	67
117	Frontier White	1·07	1·73	-	2	2·59	4
118	Frontier Flame	1·36	2·23	-	2	2·93	11
119	Frontier Crimson	1·08	1·64	-	2	2·07	15
120	Frontier Yellow	1·36	2·46	-	5	3·52	11
121	Wisley Cheerful	1·21	1·98	-	4	2·74	15
122	Wisley Golden Fleece	1·04	1·21	-	3	0·63	0
123	Toreador	1·06	1·58	-	2	2·11	4
124	Titan	1·03	1·50	-	1	1·74	0
125	Orange Glow	1·67	2·70	-	5	3·22	62
126	Victory	1·03	1·21	-	3	0·63	4
127	Yellow Freedom	1·39	2·04	-	4	2·15	22
128	Yellow Freedom	1·01	1·37	-	1	1·48	7
129	White Freedom	1·06	1·44	-	1	1·56	7
130	Bonfire	1·07	1·50	-	1	1·74	27
131	Variety S (tetraploid)	1·00	1·12	-	1	0·44	20

* 1 = Resistant, 2 = Fairly resistant, 3 = Moderate, 4 = Susceptible, 5 = Very Susceptible

Table 4.17 The quantitative assessment of susceptibility to rust in varieties of Antirrhinum majus. Wisley 1979

Code Number	Variety Number	Mean score for disease severity (Max score = 5)		Resistance Group*		Apparent infection rate $r \times 10^{-2}$	Percentage fatality
		1st Score 13th Sept.	2nd Score 6th Oct.	1st Score	2nd Score		29th Nov.
1	Pink Pixie	1.80	2.94	3	3	4.09	100
15	Variety E	1.69	2.56	2	3	3.04	70
18	Variety E	1.24	1.51	1	1	1.13	96
29	Coronette Pink	2.59	3.67	5	5	3.96	56
37	Carioca Bright Scarlet	2.96	4.01	5	5	4.43	100
39	Carioca Yellow	2.21	3.21	4	4	3.57	56
45	Coronette Scarlet	1.86	2.32	3	2	1.61	44
52	Regal Yellow	1.74	2.72	2	3	3.39	81
56	Yellow Monarch	1.70	3.15	2	4	5.17	100
62	Amber Monarch	1.15	1.39	1	1	1.17	0
67	Malmaison	2.45	3.71	5	5	4.95	100
68	Variety N	1.44	1.82	1	1	1.39	0
69	Variety O	2.00	2.99	3	3	3.57	92
70	Variety P	1.82	2.40	3	2	2.17	37
71	Variety Q	1.58	2.37	2	2	2.74	22
72	Variety R	1.39	2.01	1	2	2.35	11
73	Burpee's Super Tetra	2.03	2.47	3	2	1.43	46
74	Tetra Giant Ruffled	1.45	1.73	1	1	1.22	35
75	Kimosy Red	1.38	2.10	1	2	2.70	92
76	Kimosy Delicate Rose	1.27	2.20	1	2	3.74	100
77	Kimosy Primrose Yellow	2.41	3.53	5	5	4.26	100
78	Kimosy Crimson	1.29	2.01	1	2	2.78	100
79	Kimosy White	2.36	3.06	4	4	2.48	100
80	Kimosy Orange	1.78	2.35	3	2	2.00	58
81	Majestic Purple King	1.61	2.30	2	2	2.57	33
82	Majestic Celestial	2.45	3.73	5	5	4.96	100
83	Majestic Snowstorm	2.64	4.13	5	5	6.39	100
84	Majestic Red Chief	2.94	4.14	5	5	5.35	100
85	Majestic Orange King	2.13	3.19	4	4	3.74	71
86	Majestic Forest Fire	2.03	2.93	3	3	3.13	70
87	Majestic Eldorado	2.12	3.31	4	4	4.26	88
88	Rocket Citron Yellow	2.30	3.60	4	5	4.78	100
89	Rocket White	1.97	2.96	3	3	3.52	85
90	Rocket Red	2.04	3.10	3	4	3.70	85
91	Rocket Orange	2.11	3.42	4	4	4.65	84
92	Rocket Orchid	2.10	3.88	4	5	6.91	96
93	Triumph Mauve	1.89	2.91	3	3	3.52	80
94	Triumph Bright Orange	1.76	2.94	3	3	4.26	52
95	Triumph White	2.00	2.81	3	3	2.83	64
96	Triumph Primrose	2.46	4.10	5	5	6.78	96
97	Triumph Scarlet	2.99	4.53	5	5	8.26	100
98	Triumph Orange Salmon	2.23	3.31	4	4	3.74	83
99	Suttons I.White	2.44	3.73	5	5	4.96	96
100	Suttons I. Fire King	2.42	2.93	5	3	1.91	69
101	Suttons I. Bright Crimson	2.11	3.48	4	4	5.09	84
102	Suttons I. Rich Apricot	2.79	3.61	5	5	3.04	96
103	Suttons I. Guardsman	1.84	2.34	3	2	1.78	27
104	Suttons I. Eclipse	1.97	3.29	3	4	4.83	78
105	Suttons I. Yellow	1.70	2.50	2	3	2.87	100
106	Suttons RR Orange Glow	1.54	2.40	2	2	3.13	50
107	Suttons RR Yellow	1.45	1.65	1	1	0.83	58
108	Suttons RR Pale Sulphur	1.47	1.78	1	1	1.39	48
109	Suttons RR Apricot	1.38	1.86	1	1	1.78	50
110	Suttons RR Leonard Sutton	1.39	1.53	1	1	0.61	38
111	Kim White	2.72	4.10	5	5	5.91	100
112	Kim Purple	2.30	2.69	4	3	1.39	100
113	Kim Primrose Yellow	2.17	3.78	4	5	6.22	100
114	Kim Mid Rose	1.40	1.38	1	1	-	0
115	Kim Deep Orange	2.79	3.04	5	4	0.91	50
116	Kim Blood Red	2.86	3.96	5	5	4.52	100
117	Frontier White	2.13	3.17	4	4	3.52	56
118	Frontier Flame	1.76	3.04	3	4	4.65	74
119	Frontier Crimson	1.61	2.33	2	2	2.74	69
120	Frontier Yellow	2.55	3.98	5	5	5.87	96
121	Wisley Cheerful	1.21	1.81	4	1	2.48	41
122	Wisley Golden Fleece	1.13	1.23	1	1	0.48	0
123	Toreador	1.19	1.61	1	1	1.74	17
124	Titan	1.39	1.71	1	1	1.22	0
125	Orange Glow	2.06	3.09	3	4	3.70	62
126	Victory	1.17	1.21	1	1	0.26	0
127	Yellow Freedom	1.12	1.33	1	1	1.22	0
128	Yellow Freedom	1.09	1.19	1	1	0.52	0
129	White Freedom	1.64	1.90	2	1	0.96	15
130	Bonfire	1.59	1.71	2	1	0.39	27
131	Variety S (tetraploid)	1.24	1.64	1	1	0.17	19

* 1 = Resistant, 2 = Fairly Resistant, 3 = Moderate, 4 = Susceptible, 5 = Very Susceptible

c) Comparison of Mean Score of Each Variety

The calculated values of F for the four factor analysis of variance within each plot are given in Tables 4.12 and 4.13. The first value in each column of both tables is a measure of the variation between varieties. A very highly significant difference was found between the varieties in all scorings except the first scoring at Royal Holloway College in 1979. The insignificance of this latter value of F was probably because the disease was assessed too early in the epidemic.

The mean score for disease severity for each variety in each plot taken from the computer printout are shown in the first two columns of Tables 4.14, 4.15, 4.16, and 4.17. These values were compared using Tukey's Test. The standard error and the critical values of $D_{0.05}$ used to assess the significance of this test are given in Table 4.18. The half matrices showing the insignificant differences in the rust susceptibility of some varieties are given in Appendix 4·4 -·11. The insignificant differences are indicated by a solid circle.

Table 4.18. Critical values for $D_{0.05}$ as used in Tukey's Test

Year	Plot	Scoring	$S\bar{x}$	$D_{0.05}$
1978	RHC	1	0·0130	0·0762
		2	0·0262	0·1348
	WIS	1	0·0126	0·0739
		2	0·0107	0·0604
1979	RHC	1	0·0049	0·0291
		2	0·0081	0·0482
	WIS	1	0·0083	0·0494
		2	0·0121	0·0719

d) The Classifications

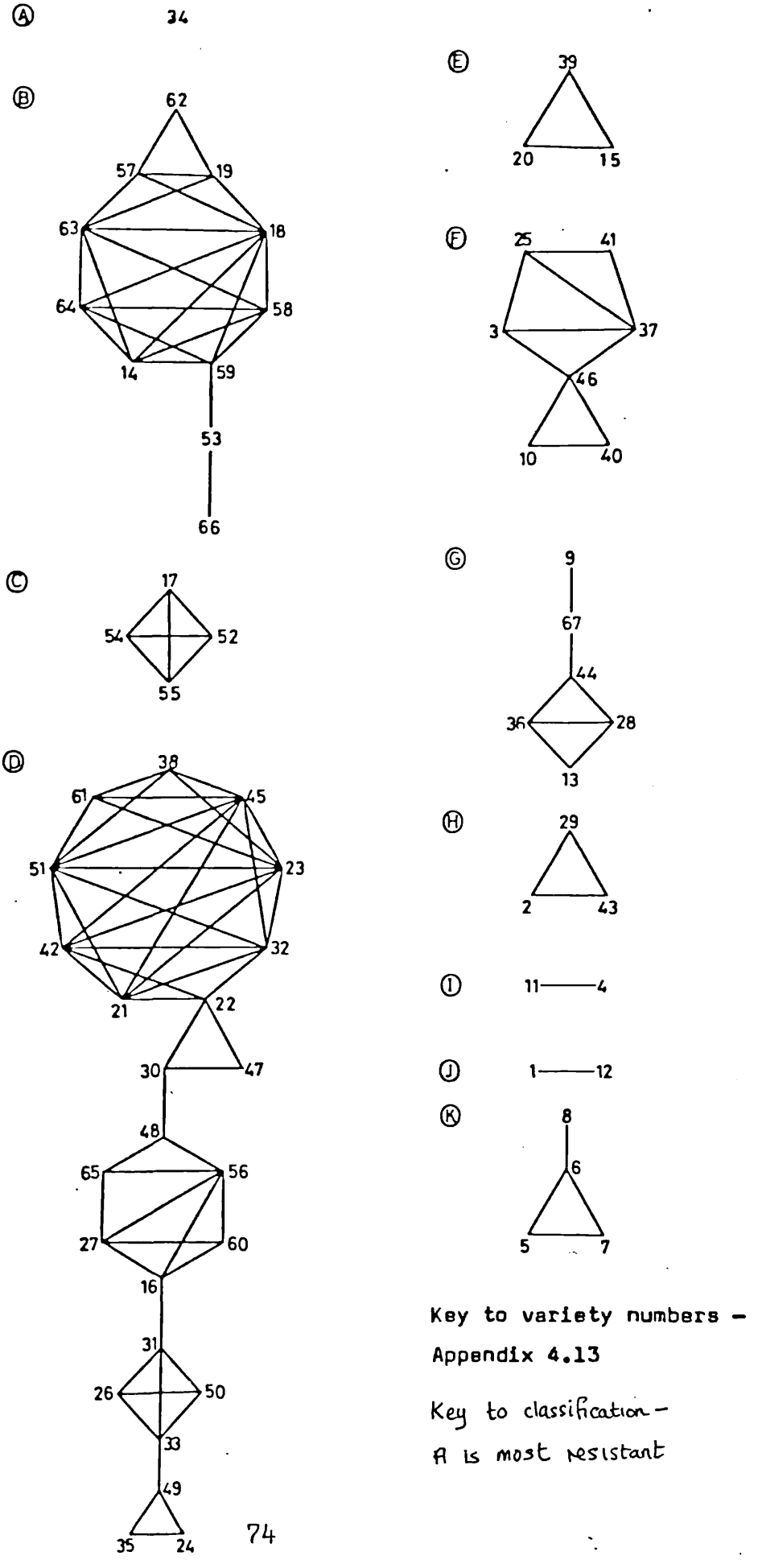
Each matrix in Appendices 4.4-4.11 was used to draw a classification in the form of a constellation diagram. These are shown in Figures 4.14 - 4.21. The key for the variety code numbers is given in Appendices 4.13 and 4.14 which may be folded out for convenience. Although each classification consisted of a different number of groups it is useful to have a visual display of the relationships between varieties. In addition, the classification may be used to group the varieties into five categories of resistance; 1 = Resistant, 2 = Fairly Resistant, 3 = Moderate, 4 = Susceptible, 5 = Very Susceptible. The groups in Figures 4.14 - 4.21 may be used to provide natural boundaries so that varieties with similar rust susceptibility are not separated as they would be if the varieties were just divided into five equal groups. The resistance group of each variety in each plot is shown in columns 3 and 4 of Tables 4.14 - 4.17. Varieties within the resistant or fairly resistant groups at both plots in both scorings were considered as possible sources for resistance for a breeding programme. These varieties are listed in Table 4.19

Table 4.19 Varieties in resistance groups 1 or 2 in all scorings (1 = resistant, 2 = fairly resistant)

Breeders lines	Variety A	Tetraploids - Tetra Giant Ruffled	
	Variety D	Variety S	
	Variety E	Kimosy Red	
	Variety F	" Crimson	
	Variety L	Suttons rust-resistant	Orange Glow
Coronette Bronze			Yellow
Carioca White			Pale Sulphur
Amber Monarch			Leonard Sutton
Scarlet Monarch		Kim Mid Rose	
Old garden strains	Variety M	Old rust-resistant strains	Toreador
	Variety N		Titan
	Variety Q		Yellow Freedom
	Variety R		White Freedom
Frontier Crimson			Bonfire

The classification of varieties into resistance groups also shows that some lines performed well at both plots and are promising with respect to their rust-resistance. Among the more resistant varieties are the breeders lines A, E, F, L, M which were included in group 1 in all four scorings. These varieties are joined exclusively by the "Monarch" line at Royal Holloway College in 1978. The most susceptible

Figure 4.14 Classification of antirrhinum varieties with respect to rust resistance in the first scoring at Royal Holloway College in 1978.



Key to variety numbers - Appendix 4.13

Key to classification - A is most resistant

Figure 4.15 Classification of antirrhinum varieties with respect to rust resistance in the second scoring at Royal Holloway College in 1978.

Ⓐ 62

Ⓑ 34

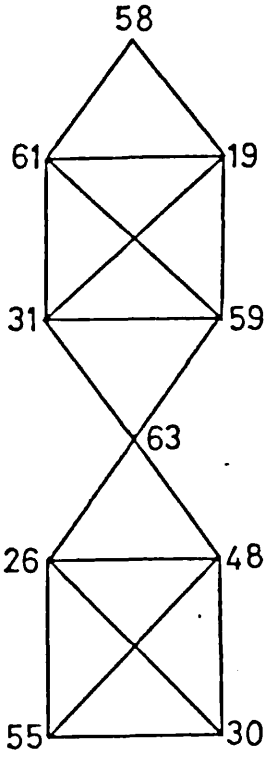
Ⓒ 66

Ⓓ 18

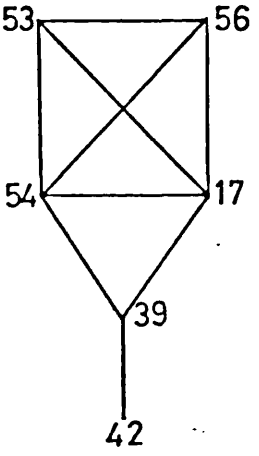
Ⓔ 64

Ⓕ 14

Ⓖ



Ⓗ



Ⓘ 57

Key to variety numbers

Appendix 4.13

Figure 4.16 Classification of antirrhinum varieties with respect to rust resistance in the first scoring at Wisley in 1978

Ⓐ 34

Ⓑ 18

Ⓒ 19

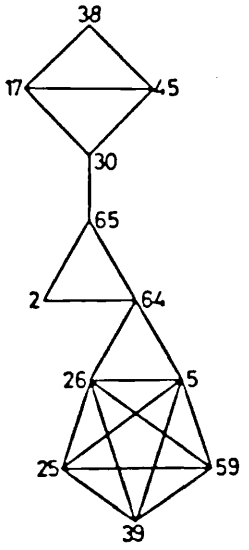
Ⓓ 66

Ⓔ 14

Ⓕ 42

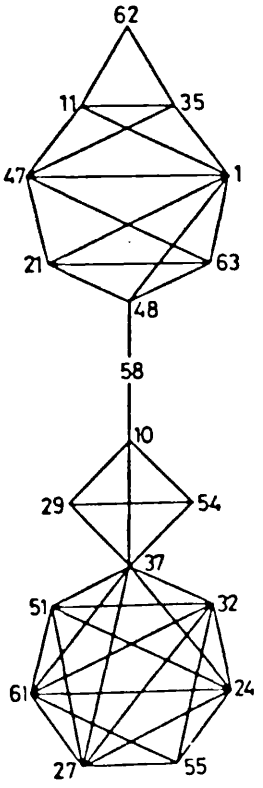
Ⓖ 16———3

Ⓗ

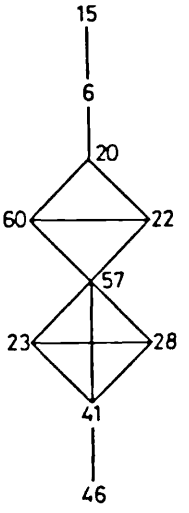


Ⓘ 31———4

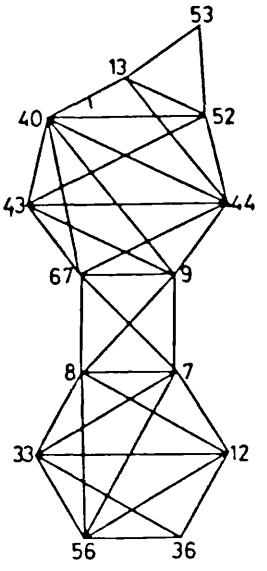
Ⓙ



Ⓚ



Ⓛ



Ⓜ 49———50

Key to variety numbers Appendix 4.13

Figure 4.17 Classification of antirrihum varieties with respect to rust resistance in the second scoring at Wisley in 1978

Key to variety numbers
Appendix 4.13

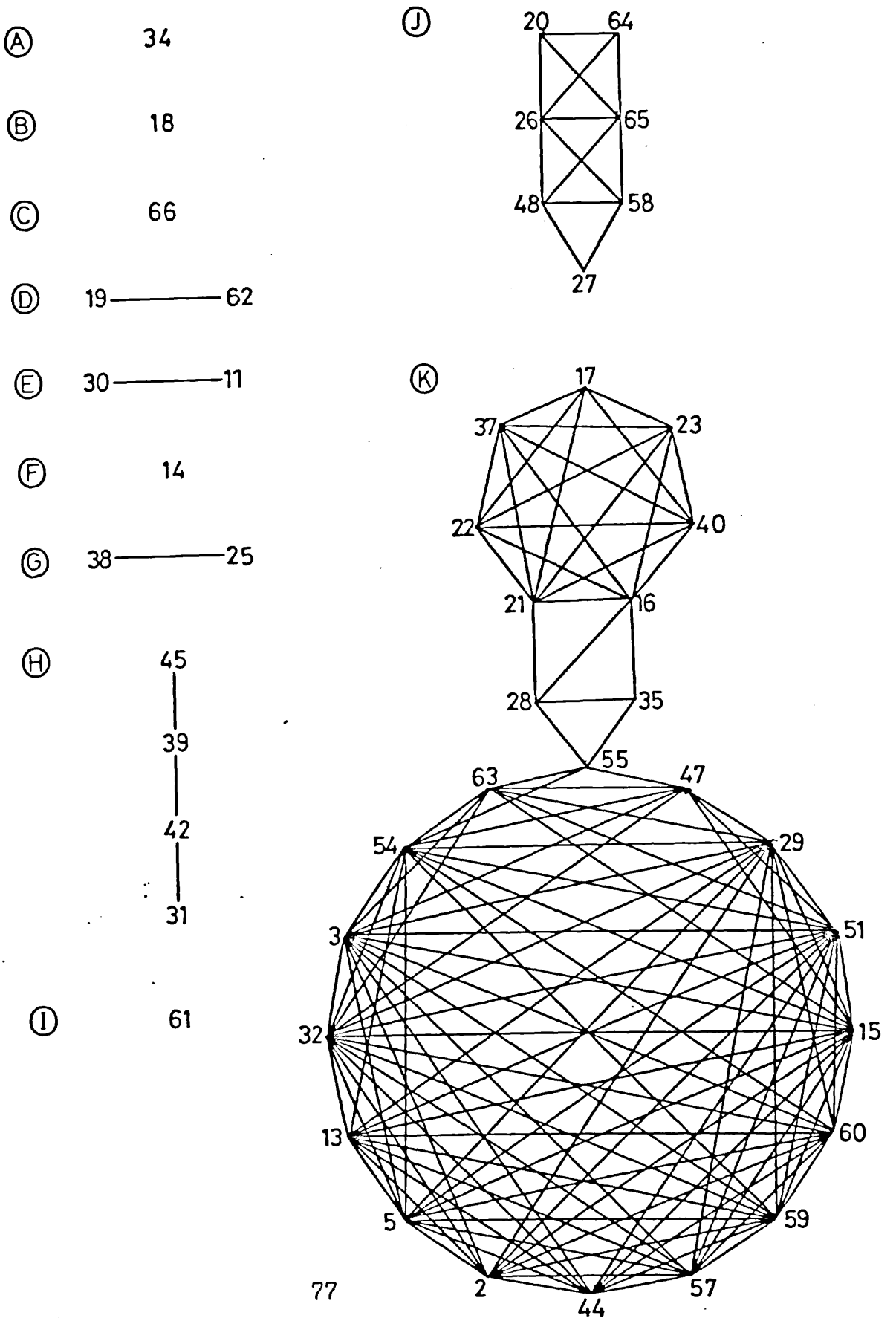


Figure 4.18 Classification of antirrhinum varieties with respect to rust-resistance in the first scoring at Royal Holloway College in 1979

Key to variety numbers - Appendix 4.14

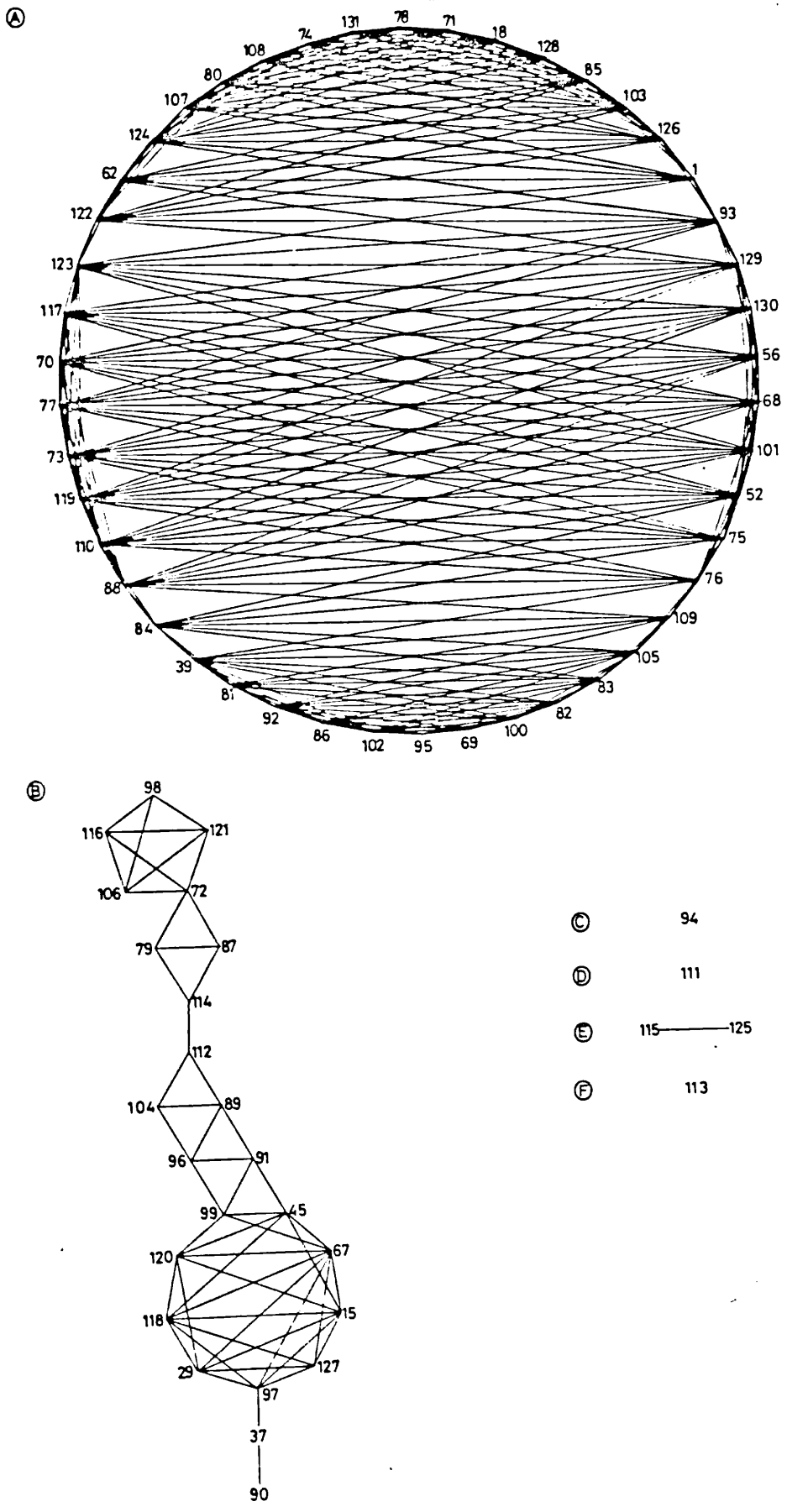


Figure 4.19 Classification of antirrhinum with respect to rust resistance in the second scoring at Royal Holloway College in 1979.

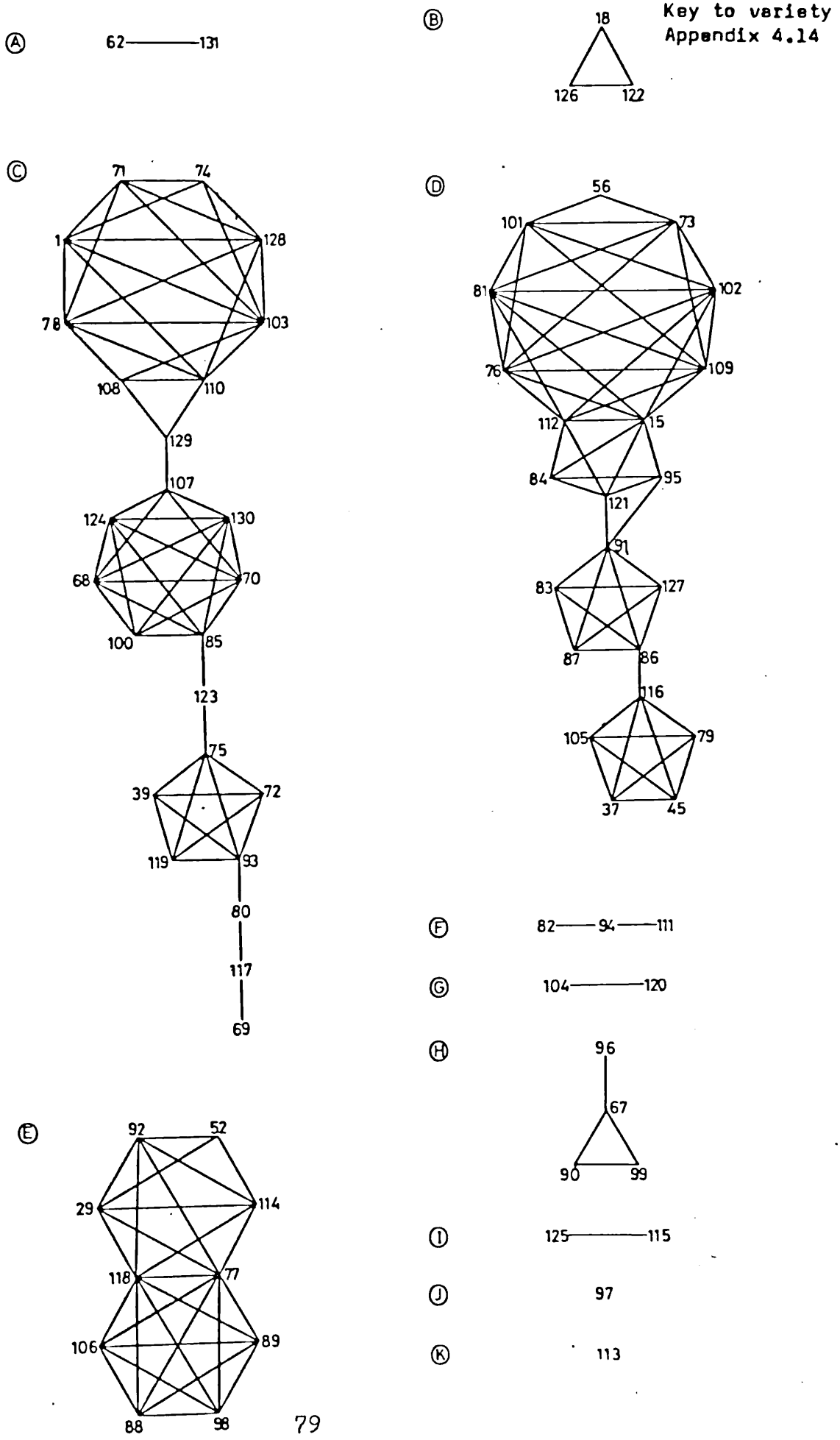


Figure 4.20 Classification of antirrhinum with respect to rust resistance in the first scoring at Wisley in 1979.

Key to variety numbers
Appendix 4.14

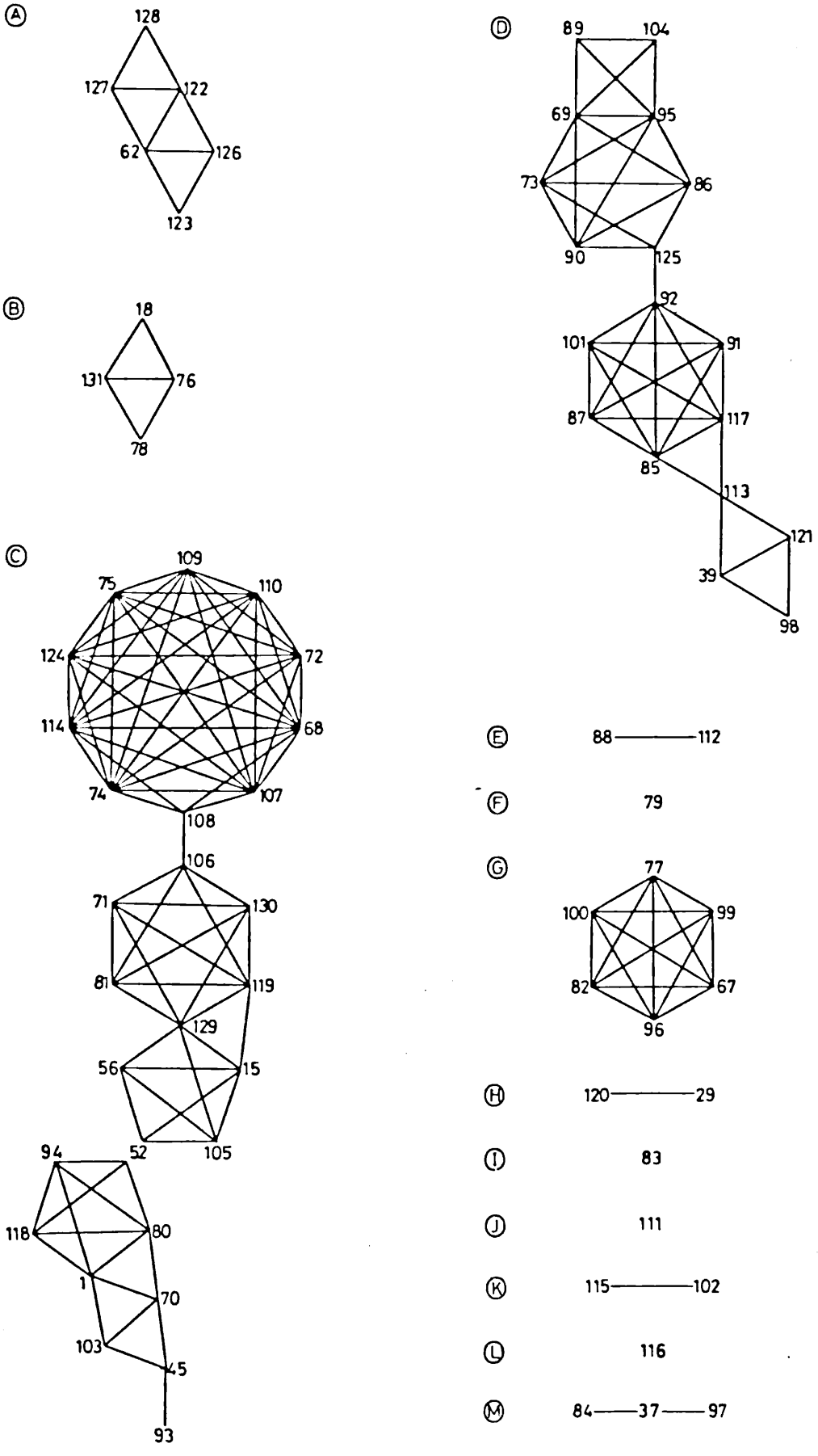
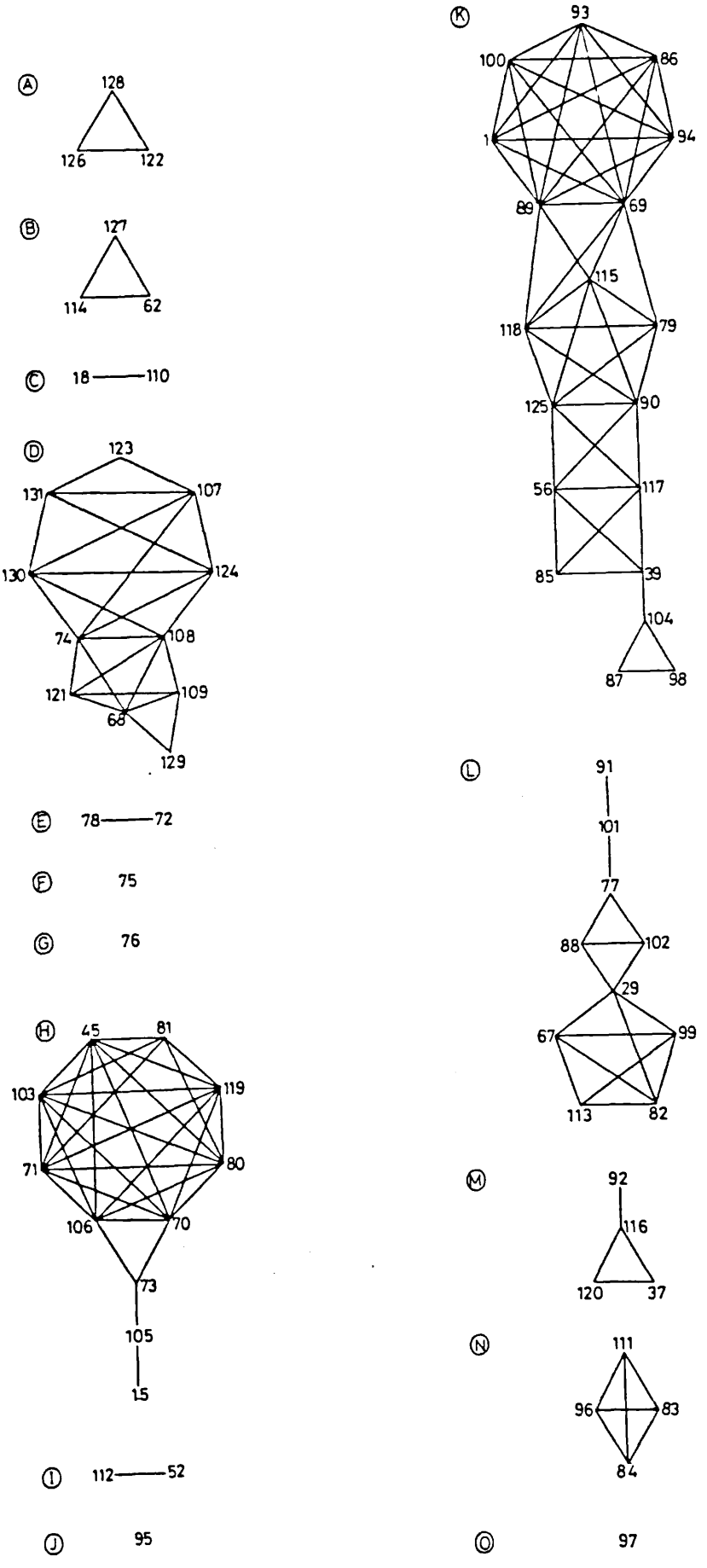


Figure 4.21 Classification of antirrhinum varieties with respect to rust-resistance in the second scoring at Wisley in 1979

Key to variety numbers - Appendix 4.14



varieties in 1979 were the "Majestic" and "Rocket" lines and the most resistant appears to be the "Suttons Rust-Resistant" lines and the old rust-resistant varieties with the exception of "Orange Glow". It is noteworthy that the latter group performed particularly well at Wisley.

Many of the strains showed a range of susceptibility but within each strain there were some varieties which were consistently the most resistant and others which were generally the most susceptible. (Table 4.20)

Table 4.20 The most rust resistant and most susceptible varieties of antirrhinum within each strain

LINE	MOST RESISTANT	MOST SUSCEPTIBLE
Carioca	- White - Peach Bronze - Yellow	- Orange - Pink - Appleblossom
Coronette	- Bronze - Cherry	- Rose - Pink
Frontier	- Crimson	- Yellow
Kim	- Mid Rose	- White - Primrose Yellow - Blood Red
Kimosy	- Crimson	- White - Primrose Yellow
Monarch	- Amber - Scarlet	- Yellow
Regal	- Bright Scarlet	- Rose - Orange Scarlet
Suttons Intermediate	- Guardsman	- White
Suttons Triumph	none	- Primrose - Scarlet

e) Calculation of Van der Plank's r

The rate of epidemic development within each variety was estimated by the apparent infection rate 'r' (Van der Plank,1963). These values are given in Tables 4.14 -4.17. A smaller value of r denotes a slower rate of epidemic development and thus a more resistant variety. In 1978 the rust infection was severe and so the values for r were relatively

higher. Therefore a list of the more resistant varieties (Table 4.21) was composed of varieties with an r value of less than five in both plots in 1978 and less than two in both plots in 1979.

Table 4.21 Varieties considered rust resistant by their low values of 'r', the apparent infection rate

1978 high infection <5 considered resistant	1979 <2 considered resistant
Variety A	Variety N
Variety E	4n Giant Ruffled
Variety F	S.I. Guardsman
Variety L	S. RR Yellow
Coronette Bronze	Pale Sulphur
Coronette Cherry	Leonard Sutton
Carioca Yellow	Wisley Golden Fleece
Crimson Monarch	Titan
Amber Monarch	Victory
Variety M	Yellow Freedom
	White Freedom
	Bonfire
	Variety S

f) Determination of percentage fatality

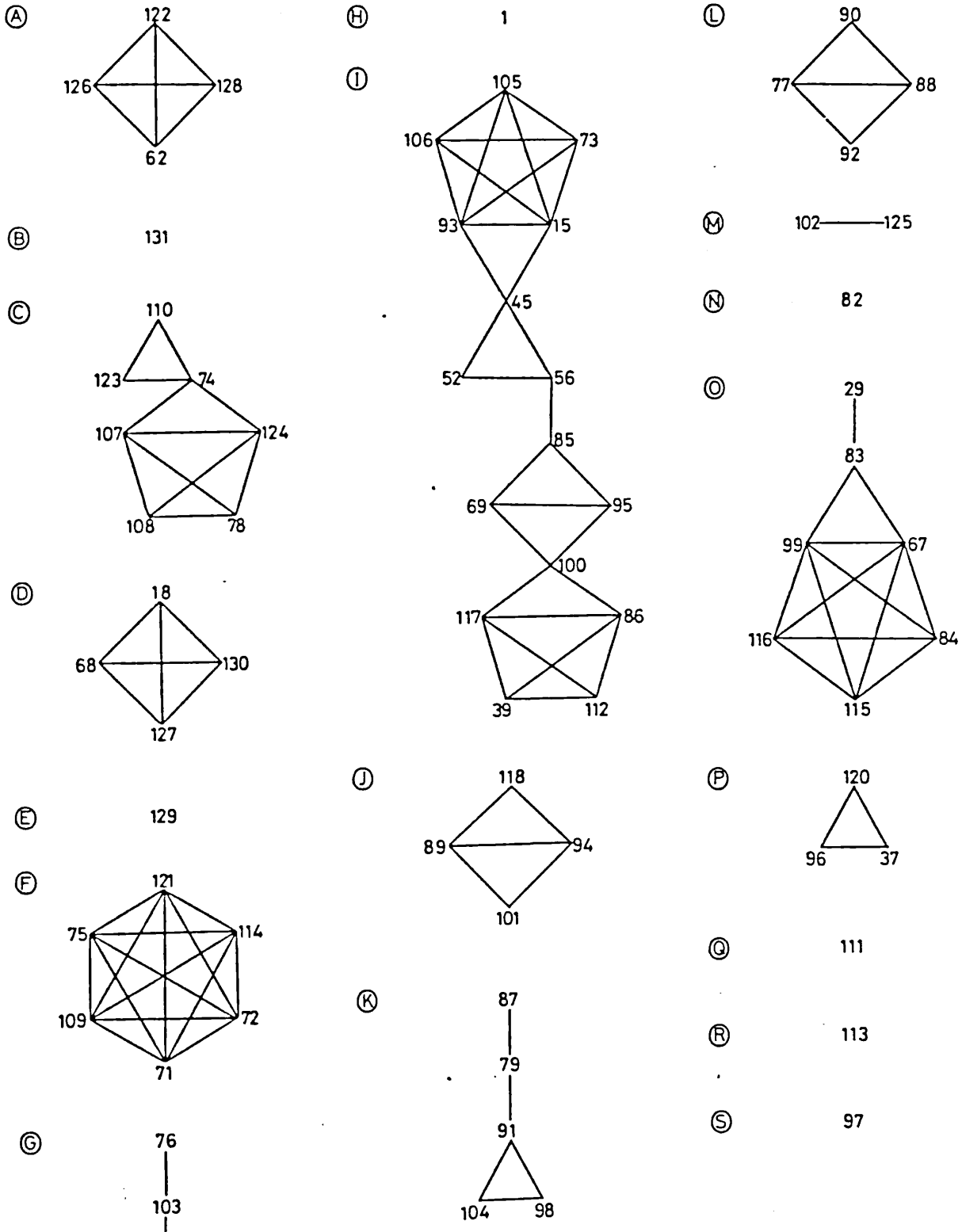
The number of plants killed as a result of rust infection are given as percentage fatality in Tables 4.14 - 4.17. The more resistant varieties were expected to have fewer deaths as a result of rust. A list of the most resistant varieties based on the percentage fatality is given in Table 4.22

Comparison of Methods of Disease Assessment

The mean of all the values for disease severity in 1979 was used to draw a classification from the combined data. The half matrix is given in Appendix 4.12 and the classification in Figure 4.22.

Table 4.23 summarizes the data used to compare methods of disease assessment. The varieties were listed in decreasing order of susceptibility based on the classification of the combined data from both plots and both scorings in 1979. Column 1 gives the classification group (Figure 4.22) thus varieties followed by the same letter are more

Figure 4.22 Classification of antirrhinum varieties with respect to rust resistance using the combined data in 1979.



Key to variety numbers
Appendix 4.14

similar in susceptibility than those followed by other letters. The average rust score in column 2 when compared with the average infection rate 'r' (Van der Plank, 1963) by a correlation coefficient gave a very highly significant result (r = 0·86). The comparison of disease severity with percentage fatality also gave a very highly significant correlation (r = 0·65).

Table 4.22 List of the most resistant varieties based on percentage fatality

% fatality			
	RHC 1978	30%	
	WIS 1978	10%	to give ≏ 30% varieties
	RHC 1979	30%	
	WIS 1979	50%	

Varieties included in both plots in one year

Breeders lines	Variety A	Old garden strains	Variety M
	Variety D		Variety N
	Variety E		Variety P
	Variety F		Variety Q
	Variety L		Variety R
Coronette White		Majestic Purple King	
Coronette Bronze		Suttons Intermediate Guardsman	
Coronette Cherry		Suttons Rust-Resistant Orange Glow	
Coronette Scarlet			Pale Sulphur
Carioca Peach Bronze			Apricot
Carioca White		Old Rust-Resistant varieties	
Regal Bright Scarlet			Wisley Cheerful
Regal Crimson			Wisley Golden Fleece
White Monarch			Toreador
Carmine Monarch			Titan
Lavender Monarch			Victory
Crimson Monarch			Yellow Freedom
Amber Monarch			White Freedom
Coral Monarch			Bonfire
Scarlet Monarch			
Tetraploid Burpee's Super Tetra			
	Tetra Giant Ruffled		
	Variety S		

Table 4.23 Comparison of Methods of Disease Assessment for rust in antirrhinum varieties listed in decreasing order of rust resistance

Code No.	Variety Name	Classification group [a]	Average rust score	Average 'r' x 10^2 [b]	Average % fatality
122	Wisley Golden Fleece	A	1·15	0·56	0
126	Victory	A	1·16	0·45	2
128	Yellow Freedom	A	1·17	1·00	4
62	Amber Monarch	A	1·17	0·68	0
131	Variety S	B	1·25	1·07	20
110	Leonard Sutton	C	1·35	0·92	44
123	Toreador	C	1·36	1·93	11
74	Tetra Giant Ruffled	C	1·38	1·35	18
107	S. Rust Resistant Yellow	C	1·40	1·32	35
124	Titan	C	1·41	1·48	0
108	S. Rust Resistant Pale Sulphur	C	1·42	1·53	38
78	Kimosy Crimson	C	1·42	2·23	90
18	Variety E	D	1·46	1·01	64
68	Variety N	D	1·46	1·48	2
130	Bonfire	D	1·47	1·07	27
127	Yellow Freedom	D	1·47	1·69	11
129	White Freedom	E	1·51	1·26	12
121	Wisley Cheerful	F	1·55	2·61	28
75	Kimosy Red	F	1·55	2·39	94
114	Kim Mid Rose	F	1·56	3·19	21
109	S. Rust Resistant Apricot	F	1·57	2·34	37
72	Variety R	F	1·57	1·99	11
71	Variety Q	F	1·58	2·11	11
76	Kimosy Delicate Rose	G	1·62	3·32	96
103	S. Intermediate Guardsman	G	1·65	1·73	19
119	Frontier Crimson	G	1·67	2·41	42
70	Variety P	G	1·70	1·96	22
80	Kimosy Orange	G	1·71	2·35	29
81	Majestic Purple King	G	1·74	2·62	21
1	Pink Pixie	H	1·79	2·65	87
105	S. Intermediate Yellow	I	1·86	3·09	71
106	S. Rust Resistant Orange Glow	I	1·86	3·33	38
73	Burpee's Super Tetra	I	1·87	2·16	27
93	S. Triumph Mauve	I	1·88	2·89	44
15	Variety B	I	1·89	2·52	59
45	Coronetta Scarlet	I	1·91	2·05	30
52	Regal Yellow	I	1·93	3·60	60
56	Yellow Monarch	I	1·94	4·05	52
85	Majestic orange king	I	1·97	2·97	38
69	Variety O	I	1·98	2·88	59
95	S. Triumph White	I	1·99	2·90	48
100	S. Intermediate Fire King	I	2·01	3·05	38
117	Frontier White	I	2·03	3·06	30
86	Majestic Forest Fire	I	2·04	3·14	46
39	Carioca Yellow	I	2·05	2·71	34
112	Kim Purple	I	2·05	1·81	98
118	Frontier Flame	J	2·10	3·79	43
89	Rocket White	J	2·13	3·34	56
94	S. Triumph Bright Orange	J	2·13	3·58	44
101	S. Intermediate Bright Crimson	J	2·14	3·92	50
87	Majestic Eldorado	K	2·18	3·50	54
79	Kimosy White	K	2·19	2·69	100
91	Rocket Orange	K	2·22	3·51	55
98	S. Triumph Orange Salmon	K	2·25	3·63	53
104	S. Intermediate Eclipse	K	2·25	4·29	49
90	Rocket Red	L	2·29	3·59	65
77	Kimosy Primrose Yellow	L	2·31	4·21	100
88	Rocket Citron Yellow	L	2·32	4·37	64
92	Rocket Orchid	L	2·33	5·25	61
102	S. Intermediate Rich Apricot	M	2·37	2·86	56
125	Orange Glow	M	2·38	3·46	62
82	Majestic Celestial	N	2·42	4·50	79
29	Coronetta Pink	O	2·46	3·27	30
83	Majestic Snowstorm	O	2·49	4·77	75
99	S. Intermediate White	O	2·52	4·46	77
67	Malmaison	O	2·52	3·14	78
116	Kim Blood Red	O	2·53	3·80	84
84	Majestic Red Chief	O	2·54	4·20	67
115	Kim Deep Orange	O	2·55	2·07	65
120	Frontier Yellow	P	2·59	4·70	54
96	S. Triumph Primrose	P	2·60	5·41	66
37	Carioca Bright Scarlet	P	2·62	3·37	65
111	Kim White	Q	2·69	4·29	100
113	Kim Primrose Yellow	R	2·83	4·85	100
97	S. Triumph Scarlet	S	2·98	6·63	78

a. Classification of combined data - Figure. 4.22
b. Units - per infected plant per day.

DISCUSSION

i Design of the Experiment

The randomized block is the most suitable design for a field experiment in which a large number of varieties are to be tested because any differences within the plot are eliminated. In the antirrhinum plot, even with one third of the rows planted with the susceptible variety, "Malmaison", there was not an even distribution of rust over each plot. The centres of high infection were not in the same area of either plot in the two years of the experiment and thus the cause for the high values in any particular area is unlikely to be environmental. In both plots in 1979 it was shown that the greatest density of high values surrounded the block that was first infected. Despite the observed differences in the severity of rust infection over the plot and the very highly significant values of F between the blocks of any one variety, the coefficient of variation in the blocks of any variety was generally under 30%, which is an acceptable level of variation for this type of field experiment (Zadoks, 1977). The variance among the blocks may also be responsible for the very highly significant interactions between the plants and blocks. The randomized block design takes account of the variation and the analysis of variance is robust enough to operate well with considerable heterogeneity of variances provided n_i are equal or nearly equal (Zar, 1974).

The five point scale used to score the disease severity was easy and quick to use. The analysis of results in 1978 should really have been nonparametric because the disease was scored on an ordinal scale, however, there was no suitable nonparametric test which would identify resistant and susceptible varieties and so the Tukey's Test was used in both years. The test was used in preference to other comparisons among means because it is quick to perform and adaptable to different kinds of data (Snedecor, 1956).

The constellation diagrams derived from this test grouped varieties with similar resistance. The groups compared well with the visual impression of the response of the cultivars and were used to divide the varieties into five resistance groups. Thompson and Rees (1979) made a numerical classification of wheat varieties in Australia by pattern analysis. They also found that varieties with similar resistance were grouped together and were therefore able to look for sources of resistance within the upper groups.

ii Cultivar Trials and the selection of varieties

In horticultural and agronomic trials, varieties are generally tested for several consecutive years before any recommendations are made. In this case it was not possible to repeat all the varieties since the purpose of the trials was to screen a large number of varieties and select those which showed promise for rust-resistance. These varieties would be subsequently reassessed at each stage of the breeding programme. Ten varieties were repeated in both plots during the second year of the experiment and although the rust was less severe in 1979 the rankings of these varieties was found to be statistically similar

Figure 4.23 A photograph of the plot in 1978 showing the two extremes of susceptibility to the rust fungus.

Even allowing for some lack of uniformity there was a wide range of resistance to rust exhibited by the varieties. The two extremes are shown in Figure 4.23. All the plants in one block are healthy and still in flower whilst many of the surrounding varieties are completely dead. Inspection of the classification diagrams (Figs. 4.14 - 4.21) shows that the relative position of the varieties is similar in the separate plots. Thus the most susceptible varieties in one plot are generally among the most susceptible in the other plot. Conversely other varieties were among the most resistant in both plots.

In this type of field trial with such a wide range of susceptibility there is an element of cryptic error (Van der Plank, 1963) because the

resistance of varieties with horizontal/non-specific resistance is undervalued. The variety "Amber Monarch" is among the most resistant varieties, nevertheless in the plots it always had slight infection by the end of the season. Sixty plants of this variety were grown isolated from very susceptible varieties in a private garden during the summer of 1979 and all remained completely free of rust. Thus the varieties selected from these trials are likely to perform better when they are not exposed to a high number of spores produced on very susceptible varieties.

iii Comparison of methods of disease assessment

The different methods of disease assessment were compared with the combined classification of varieties in order to find the most suitable method for antirrhinum rust. Opinions on the use of 'r' values to compare epidemics are very varied. Kranz (1968) concludes that apparent infection rates are very sensitive and are therefore suitable for immediate comparisons of effects on epidemic behaviour. Young (1977) concluded the use of 'r' was epidemiologically justified for assessing general resistance to Puccinia striiformis. In the antirrhinum plot, there was a very significant correlation between disease severity and r values. Other authors believe that 'r' is a function of the environment and changes during the season (Waggoner, 1965). In fact Rees, Thompson and Mayer (1979) found that the apparent infection rate (r) was the least valuable of all the methods of disease assessment they used and concluded that this variability may have been due to the uniform application of the logit transformation and the inclusion of zeros and small values in the analysis. Fry (1978) also found that 'r' values were not reliable indicators of general resistance and preferred the use of the area under the disease progress curve. This latter method of disease assessment is probably the most widely used. It has the advantage that it combines the duration and intensity of an epidemic in a single index but this simplification may lead to the disadvantage that undue emphasis may be placed on high values late in the epidemic since similar areas can lie under curves of quite different shapes. In order to calculate the area under a disease progress curve it is necessary to score the disease regularly throughout the season and this may be time consuming in a large plot. A value for 'r', however, may be calculated from a mean score at the beginning and end of the season (Fulton, 1979) provided that the mean is calculated from several independent samples. Fulton concluded that this two point estimation of 'r' is better than an unweighted regression especially where the distribution is assumed to be normal.

In agronomic crops the loss in yield is the most important effect of the disease and this has frequently been used to assess the amount of disease present. Many authors have found a high correlation between loss of yield and intensity of disease (Gill, 1980; James, Callbeck, Hodgson and Shih, 1971). Pennypacker, Knoble, Antle and Madden (1980) used the proportion of diseased plants as a simple measure of disease progress and this value would be more relevant than loss of yield in ornamentals. When the antirrhinum plots were scored, there was rarely a significant difference in the rust infection on the plants of any block but within each variety the ultimate extension of this proportion, the number of dead plants was found to be correlated to disease severity.

Thus it would appear that 'r' values provide a comparison of the resistance of antirrhinum varieties to rust but their use may only be appropriate when different cultivars are being compared within the same plot and thereby reducing environmental variation. The percentage fatality is also a relative measure of disease resistance, although in order to separate resistant varieties it is necessary to have a reasonably early onset of the epidemic. This method has the disadvantage that it is not evident until the end of the season, by which time resistant varieties are clearly visible.

CHAPTER FIVE

EPIDEMIOLOGY

INTRODUCTION

The term epidemiology has been defined by Kranz (1974b) as "the science of populations of pathogens in populations of hosts and the disease resulting therefrom under the influence of the environment, and human interferences". Some aspects of the infection requirements and disease development of Puccinia antirrhini have been described by Doran (1919, 1921), Mains (1935), Hart and Forbes (1935), Kochman (1938), Wahl (1949), Lehoczky (1954), Barbe (1967) and Yap (1969) but only one account (Dimock and Baker, 1951) relates the disease development to the environmental factors.

In Chapter 4, four essential components of an epidemic were discussed: a susceptible host, a favourable environment, an aggressive pathogen and time. It is, however, the reproductive rate of the pathogen which ultimately governs the intensity of the epidemic. There are many factors which may affect the rate: environment; resistance or susceptibility of the host; the virulence of the pathogen; the proportion of spores which germinate; the proportion of germinated spores which enter the host and establish infection; the rate of increase in the size of lesions; the speed at which spores are developed and their number and mobility. A scheme incorporating information on all these variables aids the understanding of the epidemiology of a disease.

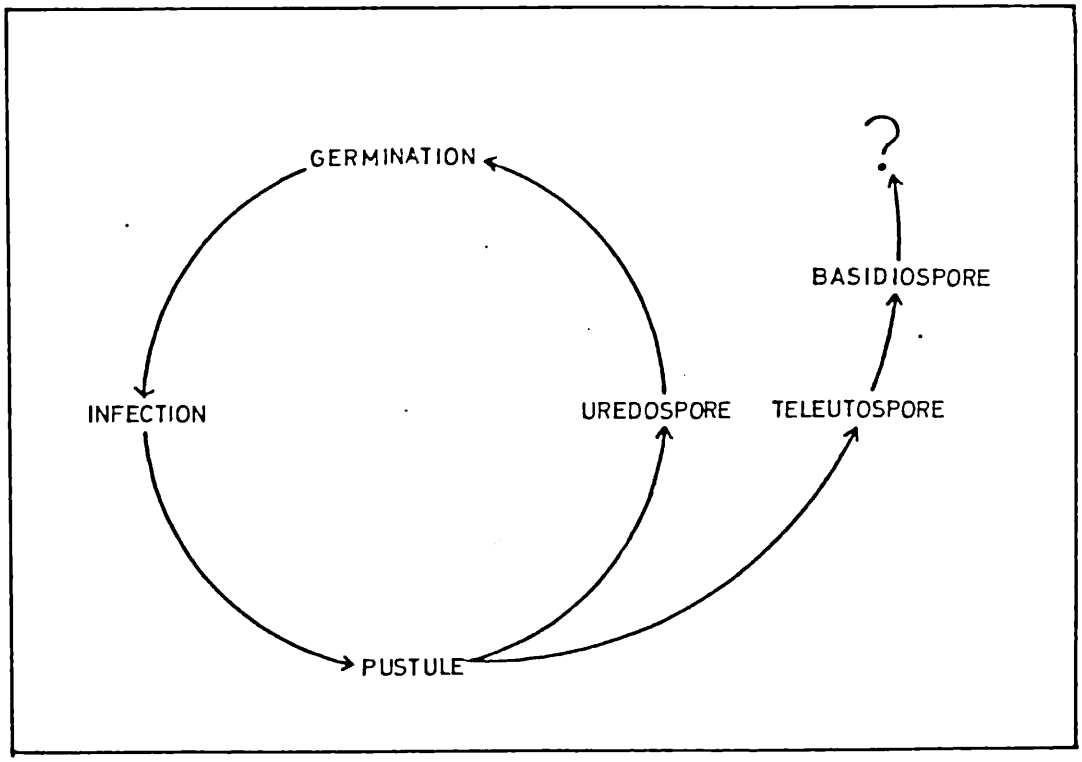
Life cycle of Puccinia antirrhini

The complete sexual life cycle of a rust, which is well documented in P. graminis, involves five spore stages and usually an alternate host, on which the sexual phase occurs. In the case of antirrhinum rust, no alternate host has been found and only two spore stages, the uredospores and teleutospores, are commonly seen. Hockey (1921), Mains (1924), Kochman (1938), Wahl (1949) and Lehoczky (1954) all report the germination of teleutospores and the development of basidiospores but none of these authors have successfully gained infection by basidiospores on A. majus. Truter and Martin (1971) in South Africa reported spermogonial and aecial stages of a rust on A. majus during October of the years 1963-5 and again in 1969. However, their inoculations of A. majus with the aecio-spores failed to produce infection and it was not possible to

decide whether the spermogonia and aecia belonged to Puccinia antirrhini. There is no record of A. majus as an alternate host for any other rust.

Where the alternate host is absent or rare, the longevity of the uredospores is an important factor in the perpetuation of the rust. The longevity of uredospores of P. antirrhini has been found to range from six weeks (Pethybridge, 1934; Yap, 1969; Doran, 1921) to sixteen months (Barbe, 1967). The reason for the discrepancy is probably due to the temperature and humidity under which the spores were kept (Walker, 1954). Barbe (1967) stored spores in glass phials at 4-6° C and found that the percentage germination diminished steadily over the sixteen month period, whereas dried spores at room temperature completely lost their viability in four months. These results suggest that uredospores may not be able to survive the winter; however, Aronescu-Savulescu (1938) and Kochman (1938) both report germination of uredospores which had been over-wintered in harsh but natural conditions. It would appear that the pathogen can over-winter in the uredospore stage. The life cycle of P. antirrhini with the uredospore as the agent of spread throughout the growing season and the probable means of survival in the winter season is shown in Figure 5.1.

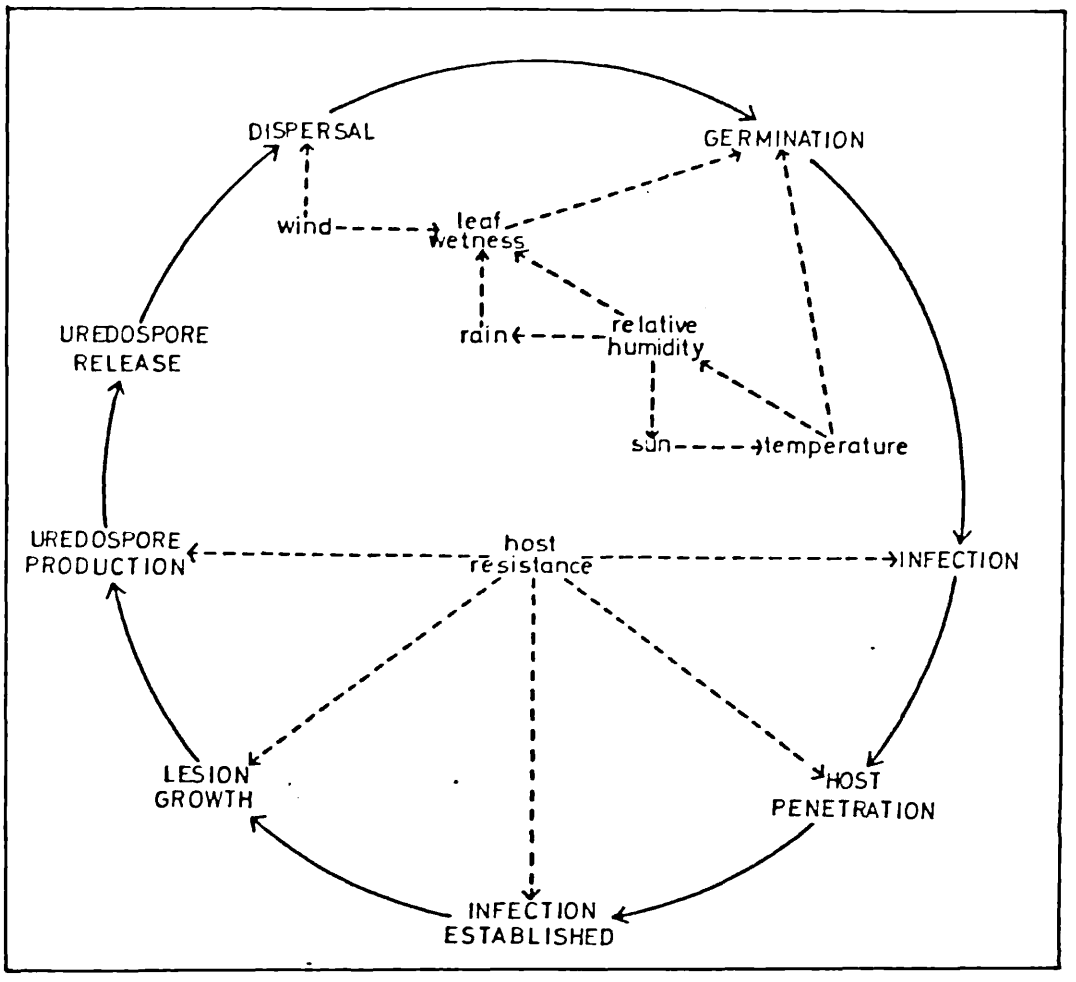
Figure 5.1 The Life Cycle of Puccinia antirrhini



The Disease Cycle

The disease cycle and the factors which may influence it are shown diagramatically in Figure 5.2

Figure 5.2 Factors affecting the rate of reproduction of *Puccinia antirrhini*



The liberation of uredospores of *P. antirrhini* has been studied in a wind tunnel and under field conditions (Yap, 1969; Carter, Yap and Pady, 1970). Carter, Yap and Pady (1970) showed that uredospores were readily liberated at wind speeds greater or equal to 2m/sec. Yap (1969) used spectral analysis to demonstrate that there was a causal relationship between spore release and wind velocity. The increase in uredospore concentration coincided with periods of increasing wind velocity with the peak in the uredospore concentration usually about one hour before the maximum wind velocity. There was a transient increase in uredospore concentration at the onset of rains. Short, intense rain showers caused a large increase but prolonged rainfall caused a rapid decline in concentration. A wind tunnel study revealed no correlation between uredospore release and relative humidity (Yap, 1969).

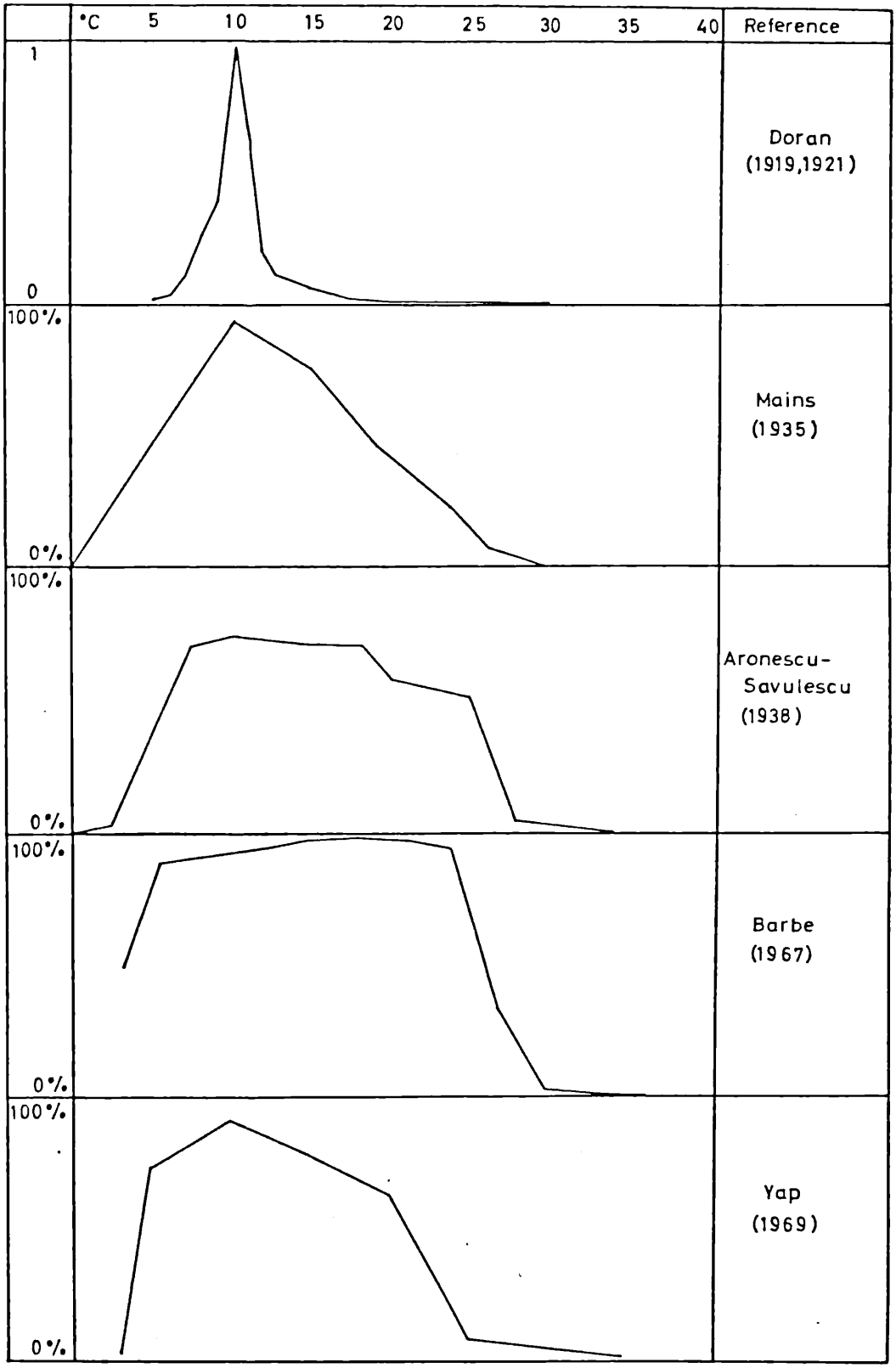
In suitable conditions uredospores germinate rapidly. Kochman (1938) reported germination within two hours at 18° C and within four hours at 10° C. Barbe (1967) found that after two hours the greatest germination was at 18° C but over 50% of the spores had also germinated at 6° C and 12° C. Yap (1969) showed the fastest germination was at 10° C and 15° C where over 50% of the spores had germinated within three hours.

The range of temperatures at which the germination of uredospores has been reported is summarized in Figure 5.3. Doran (1919, 1921) found that the optimum temperature for germination was 10° C and germination fell abruptly either side of the optimum. Mains (1935), Aronescu-Savulescu (1938), Kochman (1938), Barbe (1967) and Yap (1969) all found a much broader range of temperatures were suitable. Doran used a scale of relative numbers instead of the more usual percentage germination, therefore it may not be possible to make a comparison between his work and that of other authors. For instance, the spores may have been stored in conditions which adversely affected the viability. He may have had a low percentage germination even at the optimum temperature and his scale of relative numbers may have accentuated the peak.

Although uredospores do not germinate well above 30° C, it is not clear whether the spores are killed or just inhibited by such temperatures. Aronescu-Savulescu (1938) reported no germination of uredospores at 34° C and 39° C and the spores failed to germinate when they were subsequently incubated at 18° C after one to two hours at the higher temperature. Barbe (1967) found that at least twenty hours at 33° C and two hours at 42° C were required to kill the uredospores. Wahl (1949) found uredospores were killed by exposure to 60° C for six hours but remain viable after five to six hours at 45° C.

Doran (1921) considered 10° C to be the optimum temperature for infection. Later, authors found that the optimum temperature for infection and disease development was higher than that for the germination of uredospores (Yap, 1969; Dimock and Baker, 1951). Dimock and Baker also made the interesting observation that the rust consistently appeared more vigorous and the sporulation more luxuriant in the fluctuating temperature of a greenhouse than in the constant temperature of a growth room. They noted, however, that the light intensity, day length and atmospheric conditions in the greenhouse were different from those in an incubation chamber. Hart and Forbes (1935) showed that

Figure 5.3 Germination of uredospores in response to temperature



uredospores of P. antirrhini germinate and infect A. majus equally well in the light and dark.

A number of authors have reported that free water is necessary for germination and subsequent infection (Barbe, 1967). Yap (1969) showed that the minimum period in a dew chamber necessary for infection was

three hours at 20° C and 8 hours at 5° C and 28° C. No infection was obtained above 30° C.

The growth of germ tubes of P. antirrhini over the surface of A. majus has been studied by Maheshwari (1966). He found the infection hyphae, which frequently showed limited branching, adhered to the surface and formed appressoria on the guard cells. He also observed the formation of appressoria, with the fusion of two or three germ tubes, over a stoma. Lehoczky (1954) also reported that the hyphae of P. antirrhini penetrate through a stoma.

The period after inoculation before the rupture of the epidermis by the developing pustule is called the incubation period. The time generally quoted in the literature for P. antirrhini is eight to fourteen days (Peltier, 1919; and most later authors) although Fikry (1939) concluded it was four to five weeks. The different results may have been due to temperature since Yap (1969) found the optimum temperature for incubation to be between 20° C and 25° C, with the period being greatly extended by temperatures less than 20° C and no pustules developing above 30° C.

Disease development in the field

Although a number of authors included germination tests of uredospores in their investigations, few have studied the epidemiology of the rust. Lehoczky (1954) reported the conditions necessary for an epidemic in Hungary. The air temperature should be between 10° C and 25° C, an average precipitation of 1-5mm with rain every two to three days and a weak breeze. In Hungary these conditions exist at the end of May/beginning of June and again in the autumn; Lehoczky concluded these are the periods when an epidemic is most likely to develop.

There have only been two investigations (Dimock and Baker, 1951; Yap, 1969) in which meterological data has been collected. Dimock and Baker compared the intensity of rust infection with climatic characteristics at five widely separated localities in the U.S.A., (Urbana, Illinois; Beltsville, Maryland; Wooster, Ohio; Ithaca, New York; Los angeles, California). Disease developed at Wooster, Ithaca and Los Angeles but not at Urbana and Beltsville. They found the greatest rust infection at Ithaca where the minimum temperature fell within the range for satisfactory germination on forty of the fifty-two nights studied. Urbana and Beltsville had fewer days of

measurable rainfall and a number of days with a very high maximum temperature and these conditions were not suitable for disease development. The climate of Los Angeles was strikingly different from the eastern stations, with no rainfall for the duration of the experiment. Despite the aridity, the temperature fell to within the range satisfactory for germination on fifty-one of the fifty-two nights. In addition there was probably sufficient difference between the air and leaf temperature for condensation to provide the water necessary for germination. The conditions must have been suitable for the rust since the severity of the disease at Los Angeles was second only to Ithaca. Dimock and Baker concluded that the ratings for disease severity were consistent with the expected ratings on the basis of the known temperature and moisture requirements for snapdragon rust.

The short time necessary for the germination and penetration of most pathogens mean that hourly measurements are more useful than daily mean measurements in epidemiological studies. Yap (1969) measured the hourly uredospore concentration in the atmosphere, wind velocity, temperature, relative humidity and rainfall during 1966 and established a periodicity curve for uredospores of P. antirrhini. He found the maximum uredospore liberation at 1000 hours and a smaller but broader peak during the afternoon and evening and the lowest levels between 0200 and 0700 hours. He also presented a graph showing the relevant meterological data for the season but unfortunately did not relate the disease severity to the climatic information. The interaction of factors which influence an epidemic may be considered in the context of the disease cycle (Figure 5.2). An epidemic will occur when the conditions for each of the links in the cycle are near their optimum and the pathogen multiplies unhindered. The rate of the epidemic is reduced by any factor which slows the cycle, thereby reducing the reproductive rate of the pathogen.

MATERIALS AND METHODS.

1. Disease Progress Curves

The progress of a natural infection of rust within three varieties of A. majus, selected to represent a range of resistance, was studied throughout a growing season in 1979. The source of the seed is given in Appendix 4.1. The varieties were:

A Malmaison - the susceptible control variety
B Amber Monarch - with good field resistance
C Guardsman - with intermediate resistance.

The varieties were planted in three latin squares alongside the large plot at Royal Holloway College (see Chapter 4). The planting plan showing the variety code letter and block number is shown in Figure 5.4. Each block consisted of nine plants. The amount of disease on each plant was assessed six times at ten or eleven day intervals during the course of the epidemic. Ten leaves of each plant were scored using the five point scale of the standard diagram (Figure 4.5).

A disease progress curve was plotted for each variety from the mean score of disease severity at each scoring. In addition a four factor analysis of variance was performed for each scoring. The significance of the calculated values of F was determined by comparing them with tabulated critical values of F given by Rohlf and Sokal (1969). Three significance levels were used:

0.05	*	signifcant
0.01	**	highly significant
0.001	***	very highly significant.

The mean score for disease severity of each variety was compared using Tukey's Test (Zar, 1974)

Figure 5.4 Planting Plan for three latin squares

A 1	B 1	C 1
C 2	A 2	B 2
B 3	C 3	A 3

B 4	C 4	A 4
A 5	B 5	C 5
C 6	A 6	B 6

C 7	A 7	B 7
B 8	C 8	A 8
A 9	B 9	C 9

The rate of disease increase was estimated from Van der Plank's 'r'. A weighted regression analysis (Steel and Torrie, 1960) was used to transform the disease progress curves and obtain a measure of the rate of infection. The regression coefficients of a weighted regression analysis were used in preference to those of a linear

regression analysis because Fulton (1979) found the 'r' values from the former analysis to be closer to the "true" value. The three values of 'r' were compared using a Student Newman Keuls Test (Zar, 1974 p.233). This test is simple to use and suitable when all groups have equal numbers of data. It is slightly more powerful than Tukey's Test.

2. Germination of uredospores

Fresh spores of the "Besancon" isolate were gathered with a cyclone collector from an infected "Malmaison" plant in the greenhouse. The spores were kept at 10° C for up to two hours until required. An Oxoid Nuflow Membrane Filter (grade 0.45μm) was placed on moist filter paper in a petri dish. Six dishes were placed at each incubation temperature (5°C, 10°C, 15°C, 25°C and 36°C) for twelve hours to allow each dish to adjust to the incubation temperature. The uredospores were suspended in water and transferred to the filters with a paint brush; about five hundred spores were spread across the filter. The dishes were wrapped in foil and replaced in the incubation temperature. At the end of three, six, nine, twelve, eighteen and twenty-four hours one dish was removed from each temperature and the filter sprayed with lactophenol cotton blue to prevent further germination and stain the hyphae. The number of spores that had germinated out of a total of three hundred for each dish was counted and expressed as a percentage.

3. Observations on the germination of uredospores and the penetration of hyphae using a scanning electron microscope.

Detached leaves of the susceptible variety "Malmaison", were inoculated with uredospores of the rust in a petri dish (Figure 6.3). After three days, $5mm^2$ sections of the leaf were dehydrated in a graded acetone series (2.5%, 5%, 10%, 15%, 20%, 30%, 50%, 70%, 80%, 85%, 90%, 95%, 100%). The sections were left for fifteen minutes in each solution. The sections were dried with liquid CO_2 in a Polaron critical point dryer, mounted on stubs using "UHU" glue, "sputter" coated using gold palladium and examined using a Jeol JSM 255 scanning electron microscope.

4. Periodicity of Uredospores and Meterological Data

Hourly uredospore counts were recorded above the plot (see Chapter 4) at Royal Holloway College for two twenty-four hour periods. In addition the local rainfall, relative humidity, leaf wetness, windspeed and temperature were measured.

i Hourly uredospore count

The number of uredospores of P. antirrhini in the air three feet above the plot was measured with a rotorod sampler made in the Botany Department, Royal Holloway College from a description from Dr. Perkins, Stanford University, U.S.A. A brass bar (0.159cm or $\frac{1}{16}$" square) was bent into an angular U configuration and rotated about its central point. Each arm of the U was 4cm long and 4cm from the axis of rotation. The sampler was powered by a L.C.P. 13 accumulator. The number of revolutions of the collecting edge per minute was counted using a tachometer and the volume of air sampled was calculated.

The volume of air sampled per hour = area of the two collecting surfaces X circumference of the circular path X speed of rotation

The arms were coated with rubber latex cement thinned with an equal volume of xylene. Barbe (1967) found that rubber latex cement was easy to apply, stable in all weather conditions and easy to mount for microscopic examination. Each collector arm was slowly submerged into the rubber latex cement to prevent air bubbles sticking to the rod and the excess allowed to drip from the tip. A second coat was applied after the first had dried. The coated rods were stored in a large petri dish until required. Barbe says that the coating loses efficiency with age but is satisfactory for four or five days. In this study the prepared rods were used within three hours. After each sampling clear cellotape was pressed onto the leading edge of the rod and pressed with the back of the thumbnail. The cellotape was gently lifted ensuring the cement adhered and the process repeated on the other leading edge. The tape was stuck onto a clean glass slide and labelled. The slides were heated gently to remove air bubbles and the number of uredospores on the latex cement counted.

ii Rainfall

A rain gauge was made with a funnel and a 25ml measuring cylinder. The area sampled was calculated to be 326.85 cm^2. The rainfall was converted into $mm/cm^2/hour$.

iii Relative Humidity

The relative humidity inside the leaf canopy of a dwarf variety (A. height 25cm) and a standard variety (B. height 45cm) was measured hourly using a percentage Relative Humidity Recorder made by Gallenkamp P.O. Box 290, Technico House, Christopher Street, London EC2P 2ER.

iv Leaf Wetness

The leaf wetness was recorded continuously on a Mk.3A Recorder Ref.No. Met. 2001 made by E.F. Collins and Son Ltd., Croydon and borrowed from Imperial College, Silwood Park. The hourly readings were calculated as a percentage of the maximum for the twenty-four hour period.

v Windspeed

The windspeed, 1.5 metres above the ground, was measured hourly using an E.T.A. 3000 anemometer made by Airflow Developments Ltd., High Wycombe, England and borrowed from Mr. Pixton at the Ministry of Agriculture, Fisheries and Food, Slough Laboratory.

vi Temperature

The temperature of the air within the plants at the centre of the plot was measured hourly.

RESULTS

1. Disease Progress Curves

The disease progress curves for three varieties are shown in Figure 5.5. The graphs are the characteristic shape for a disease progress curve. The control variety, "Malmaison", was more severely infected than either "Guardsman" or "Amber Monarch". "Amber Monarch" showed the smallest increase in disease over the period.

The values of F from the analysis of variance (Table 5.1) shows that there was an insignificant difference in the disease scores between the squares, rows, and columns in all six scorings. There was also an insignificant difference between the amount of disease on the three varieties at the first scoring (Day 1) but a highly significant difference from Day 22 to Day 54. Tukey's Test was performed on the mean block score for each variety at each scoring to show the position of the significant difference. The results of Tukey's Test are given in Appendix 5.1 and the significance of the differences are summarized in Table 5.2.

Table 5.1 Values for F from Analysis of Variance for the three Latin Squares

		Source of Variation			
Day No.	Date	Between Squares	Rows within Squares	Columns within Squares	Between Varieties
1	30th Aug. 1979	1.69	1.16	1.04	13.89
11	10th Sept. 1979	2.32	1.77	1.94	32.67 *
22	21st Sept. 1979	5.19	2.84	2.83	151.46 **
33	2nd Oct. 1979	3.76	2.98	3.07	153.05 **
43	12th Oct. 1979	3.81	1.50	1.43	173.69 **
54	23rd Oct. 1979	2.20	1.09	0.95	156.16 **

Table 5.2 Significance of the difference between the amount of disease on three varieties of A. majus (Tukey's Test).

Day No.	Block	B	C
1	A	**	**
	C	NS	
11	A	**	**
	C	NS	
22	A	**	**
	C	*	
33	A	**	**
	C	*	
43	A	**	**
	C	*	
54	A	**	**
	C	**	

Key

A = Malmaison

B = Amber Monarch

C = Guardsman

NS = insignificant difference

* = difference significant at 0.05

** = difference significant at 0.01

Table 5.2 shows that the disease on the susceptible variety "Malmaison" was significantly greater than that on both "Amber Monarch" and "Guardsman" at the 99% level throughout the six scorings. "Amber Monarch" was not significantly different from "Guardsman" on the first and second scoring but by Day 22 the difference was 95% significant and

Figure 5.5 Disease Progress Curves for three commercial varieties of Antirrhinum majus.

A = Malmaison

B = Amber Monarch

C = Guardsman

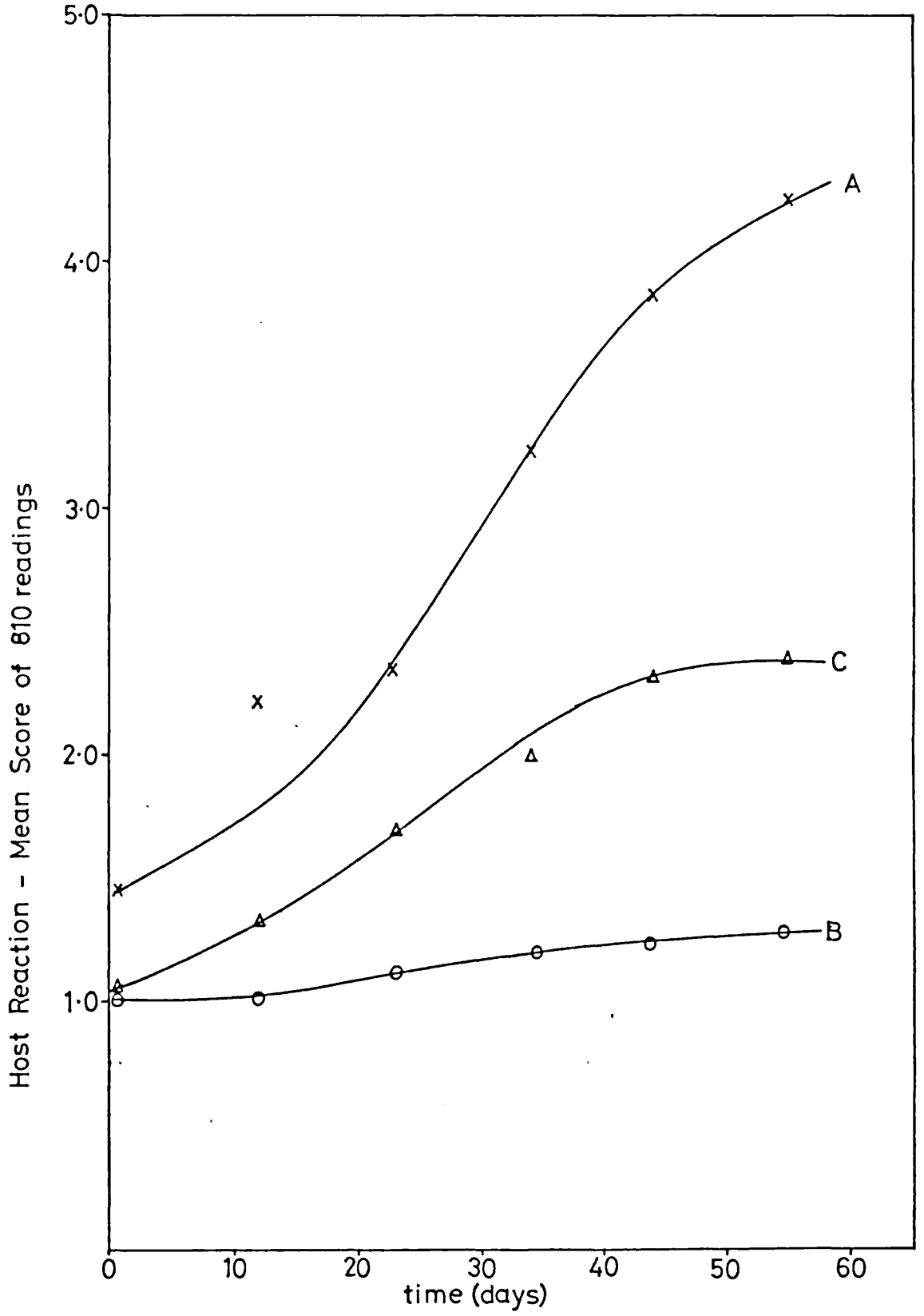
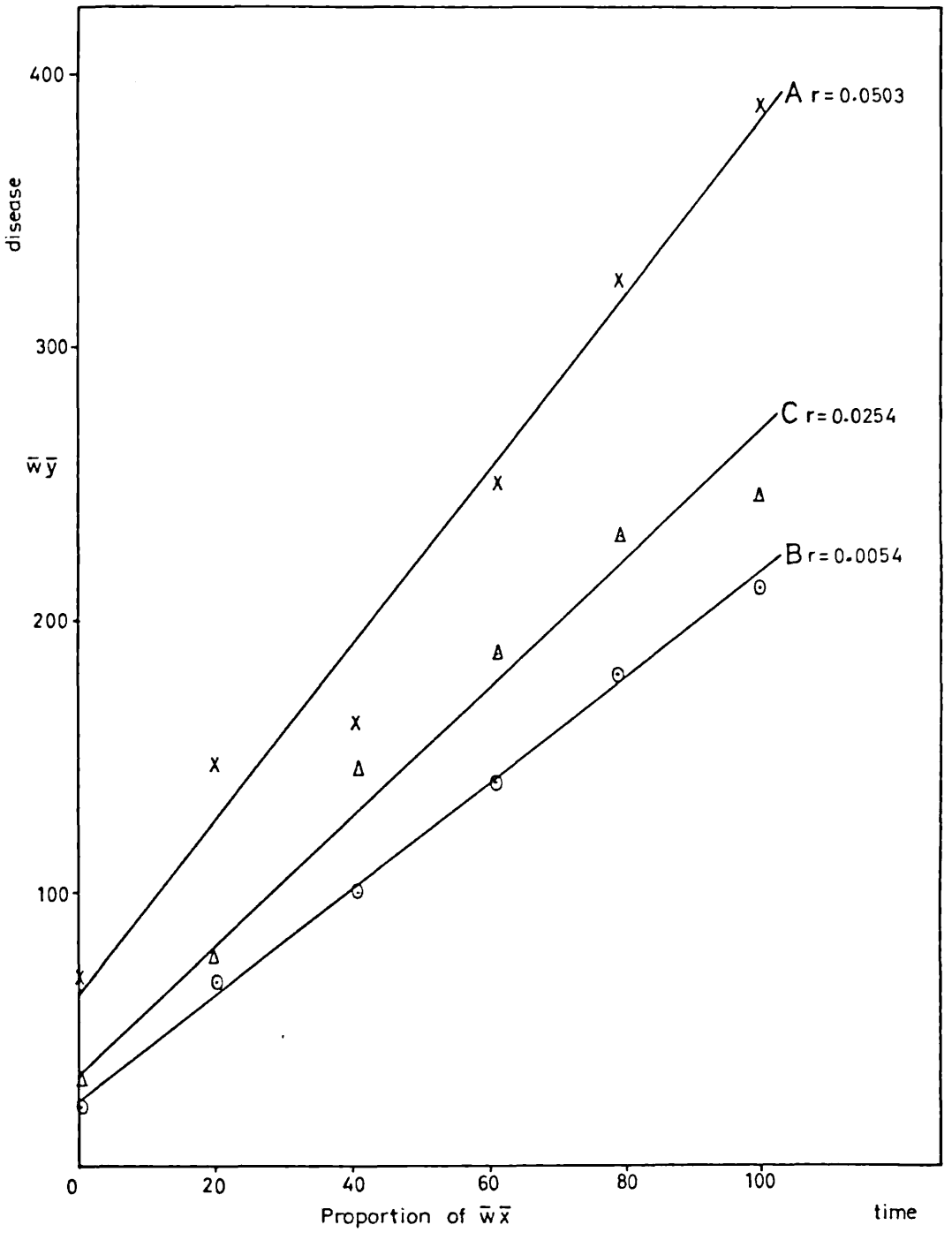


Figure 5.6 Weighted Regression Analysis of three commercial varieties of Antirrhinum majus.



A = Malmaison

B = Amber Monarch

C = Guardsman

the final scoring on Day 54 showed a 99% significant difference.

2. Rate of disease increase

A value for the apparent infection rate 'r' for the three varieties was estimated by the regression coefficient for the weighted regression analysis (Figure 5.6). "Amber Monarch" has the lowest rate of disease increase and exhibits a high level of field resistance. The rate of disease increase in "Guardsman" is five times faster than "Amber Monarch", nevertheless "Guardsman" survived the epidemic well. The disease increased fastest in the susceptible variety "Malmaison". By the end of the experiment many plants of this variety were showing severe symptoms of the disease and a number had died.

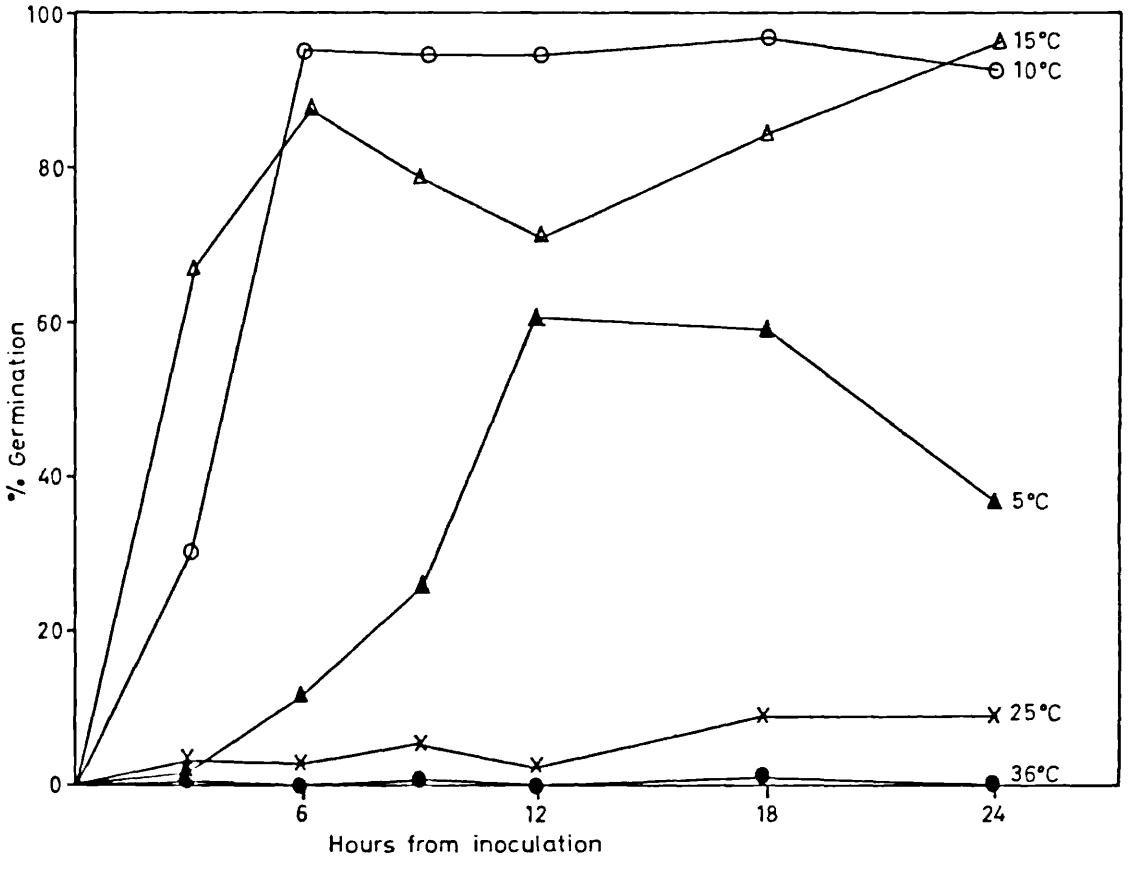
The comparison of the three regression coefficients using the Student Newman Keuls Test is given in Appendix 5.2. The rate of disease increase in all three varieties is significantly different from each other. This confirms the difference in disease severity shown by Tukey's Test.

3. Germination of Uredospores

The graph (Figure 5.7) shows that germination occurred within three hours at 5^{o} C, 10^{o} C, 15^{o} C and 25^{o} C. The germination reached a maximum after six hours at 10^{o} C and 15^{o} C but took longer at lower temperatures. At 25^{o} C there was less than 10% germination after 24 hours and at 36^{o} C only the occasional spore germinated. It was necessary to stain the uredospores with lactophenol cotton blue to count the number that had germinated. Consequently each point on the graph was counted from a separate dish and this may explain the fluctuations on the graph.

Figure 5.8 shows the percentage of spores that had germinated at 5^{o} C, 10^{o} C, 15^{o} C, 20^{o} C, 25^{o} C and 36^{o} C. Germination occurred in the temperature range 4^{o} C where 60% of the spores had germinated after twelve hours, to 36^{o} C, where only the occasional spore germinated. The optimum temperature for germination was between 10^{o} C and 15^{o} C and the percentage germination dropped off rather sharply on either side of these limits.

Figure 5.7 Rate of Germination of uredospores of Puccinia antirrhini at different temperatures (mean of two experiments n = 2 X 300).

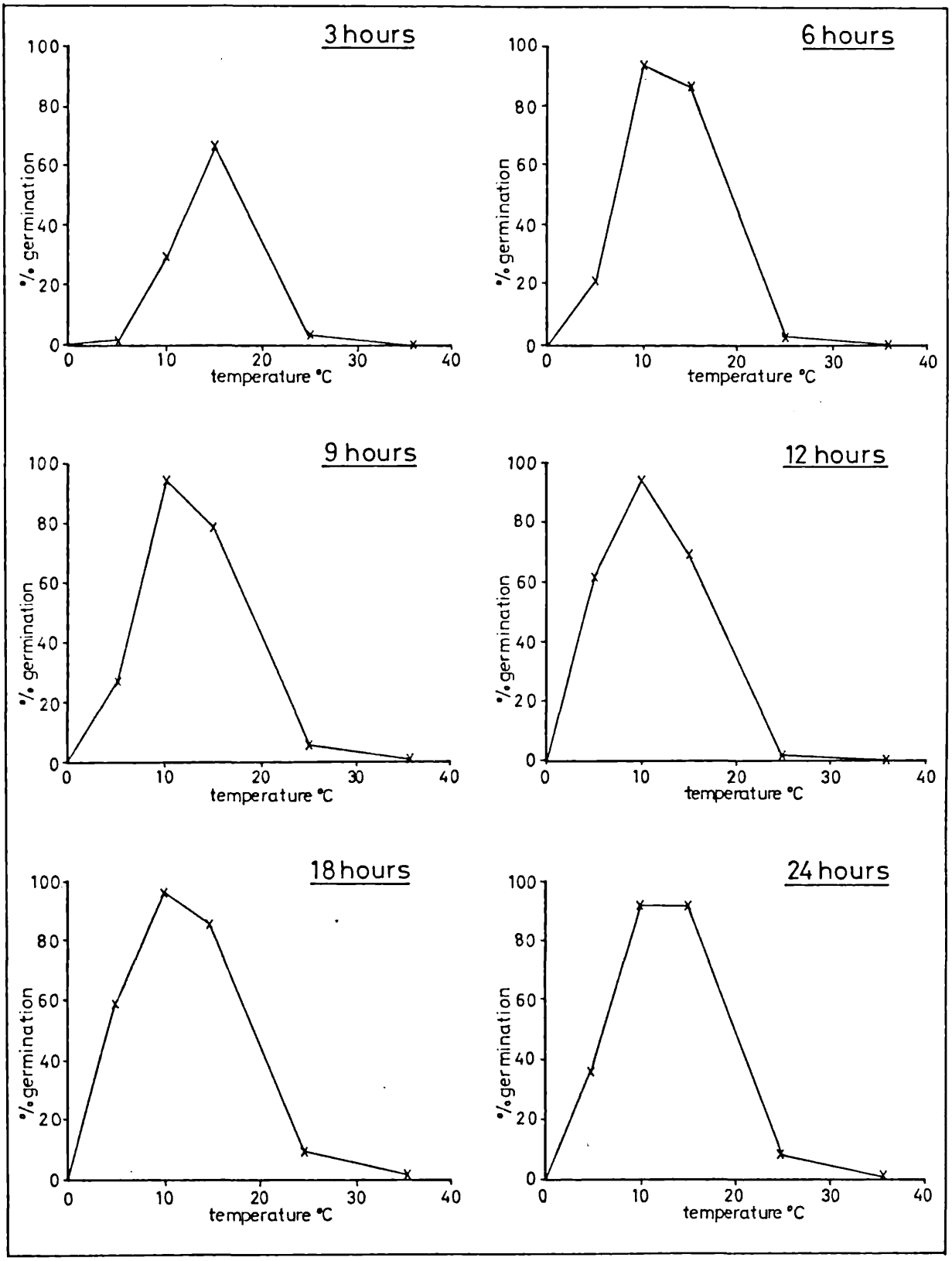


4. Penetration of Hyphae

Figure 5.9 is a scanning electron micrograph showing the germination of the uredospore and the entry of a hypha through a stoma after the formation of an appressorium. The cytoplasm has moved into the leaf leaving the hypha and appressorium collapsed. Figure 5.10 shows the entry through a stoma without the formation of an appressorium. In Figure 5.11, the appressorium has developed beside a stoma and penetration may have occurred through the cuticle. The hyphae from several uredospores appear to have penetrated the cuticle at the base of a glandular hair without appressoria in Figure 5.12. Figure 5.13 shows the fusion of hyphae from two uredospores and the subsequent appressorial formation and penetration through a stoma.

The incubation period of the rust varied from ten days in the summer to four weeks in the winter.

Figure 5.8 Percentage Germination of uredospores over a range of temperatures (mean of two experiments n = 2 X 300).



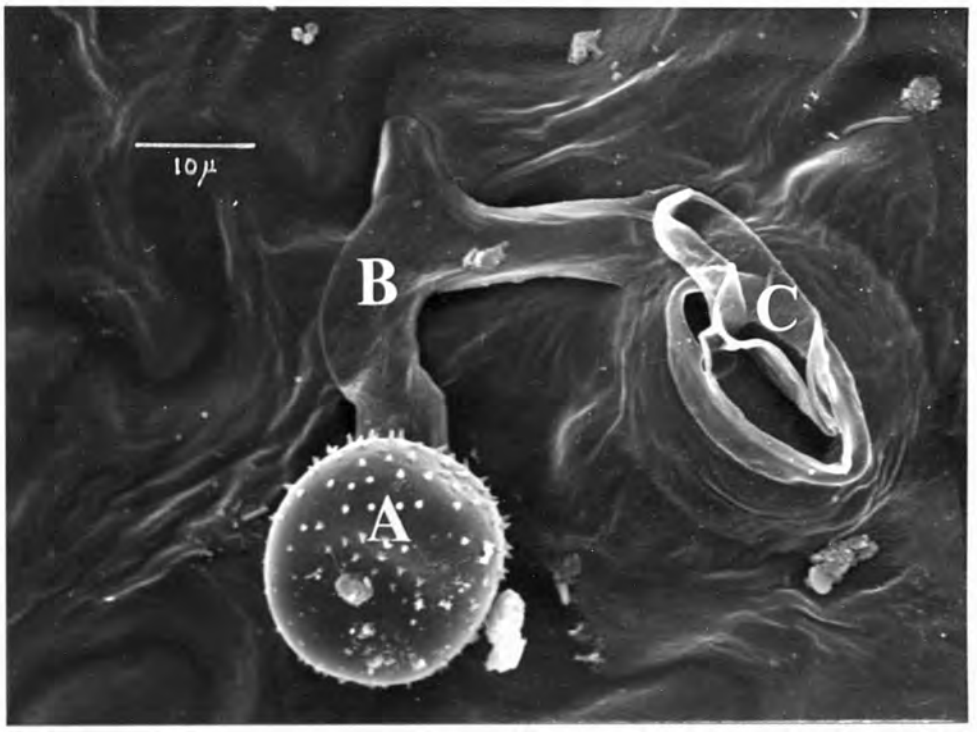


Figure 5.9 S.E.M. showing entry of Puccinia antirrhini through a stoma of Antirrhinum majus. The cytoplasm has moved into the stoma leaving the uredospore (A), the collapsed germ tube (B) and collapsed appressorium (C).

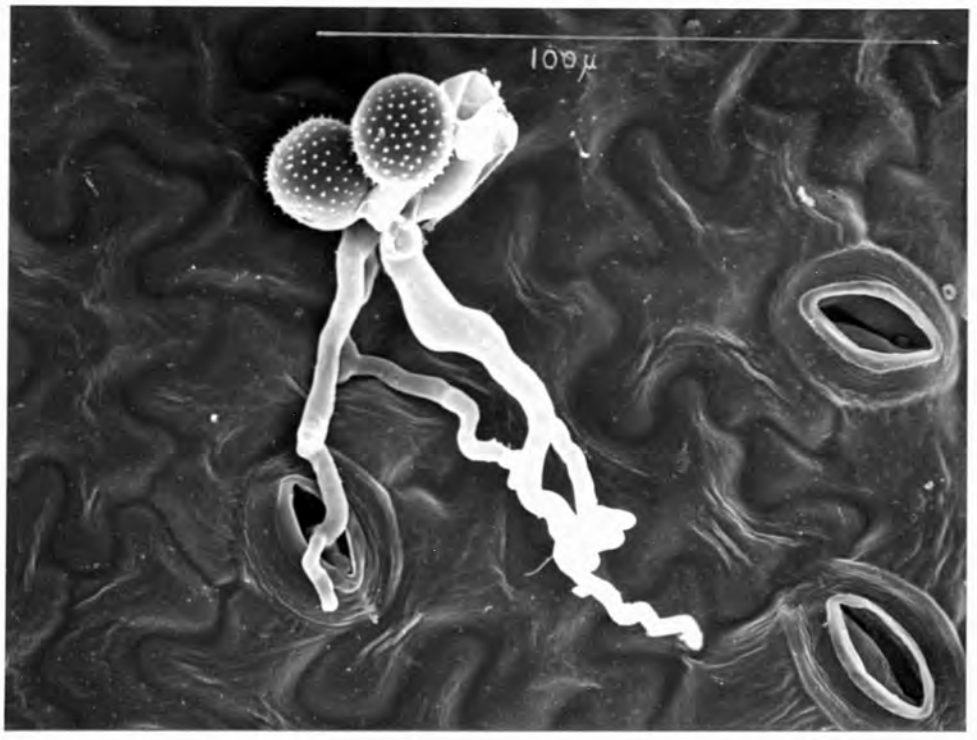


Figure 5.10 S.E.M. showing entry of a hyphae of P. antirrhini through a stoma of A. majus without the formation of an appressorium.

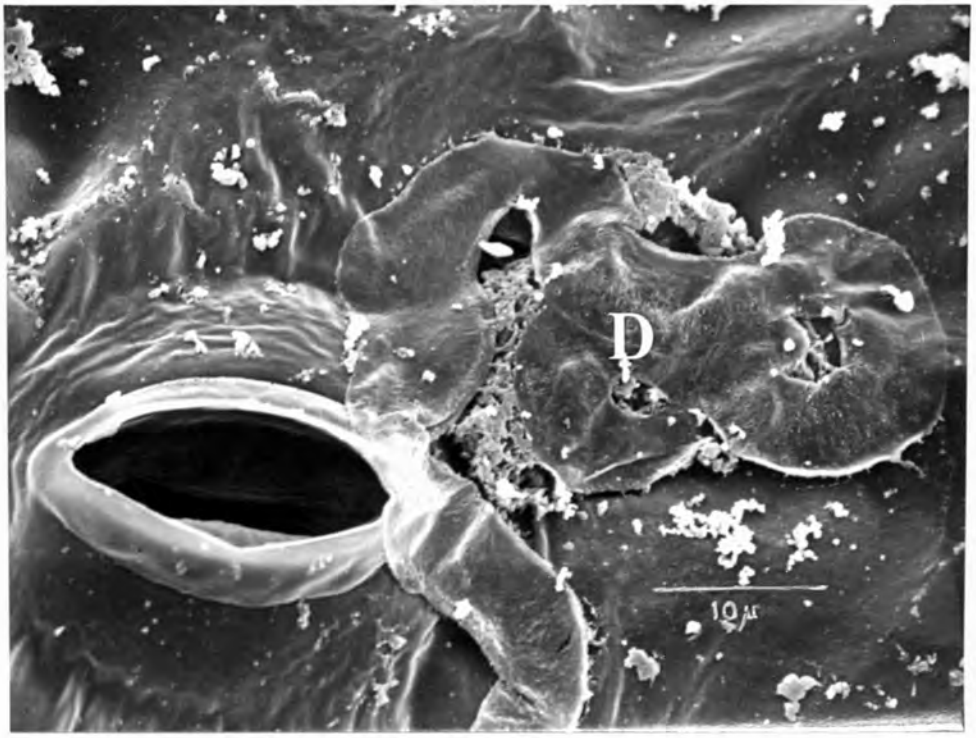


Figure 5.11 S.E.M. showing formation of an appressorium (D) of Puccinia antirrhini beside a stoma of Antirrhinum majus.

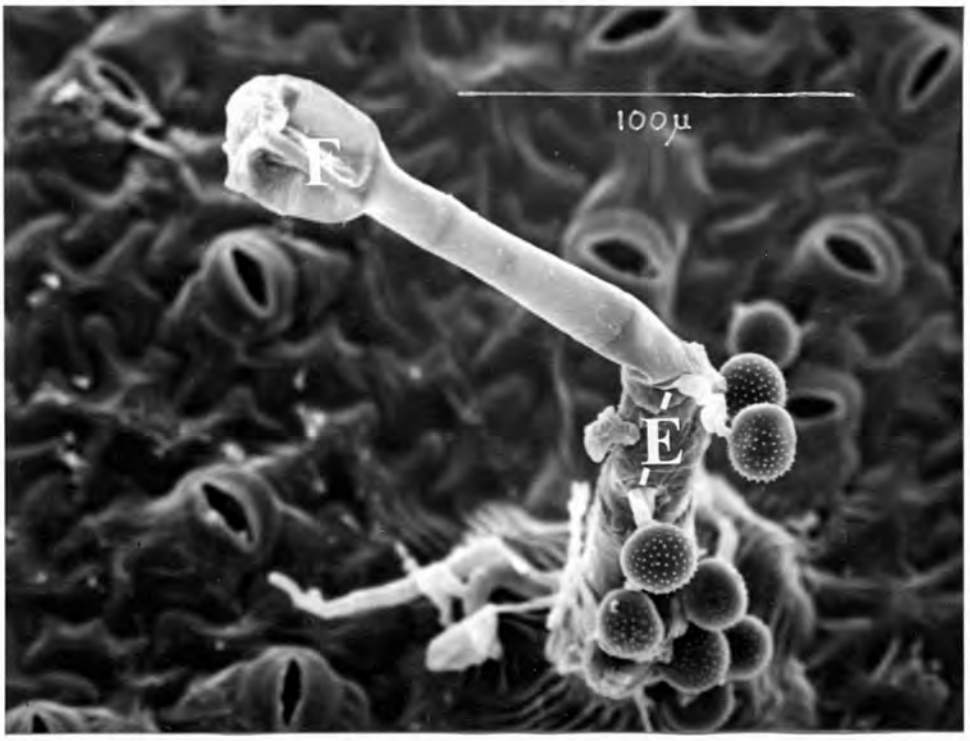


Figure 5.12 S.E.M. showing penetration (E) of hyphae of P. antirrhini through the cuticle at the base of a glandular hair (F).

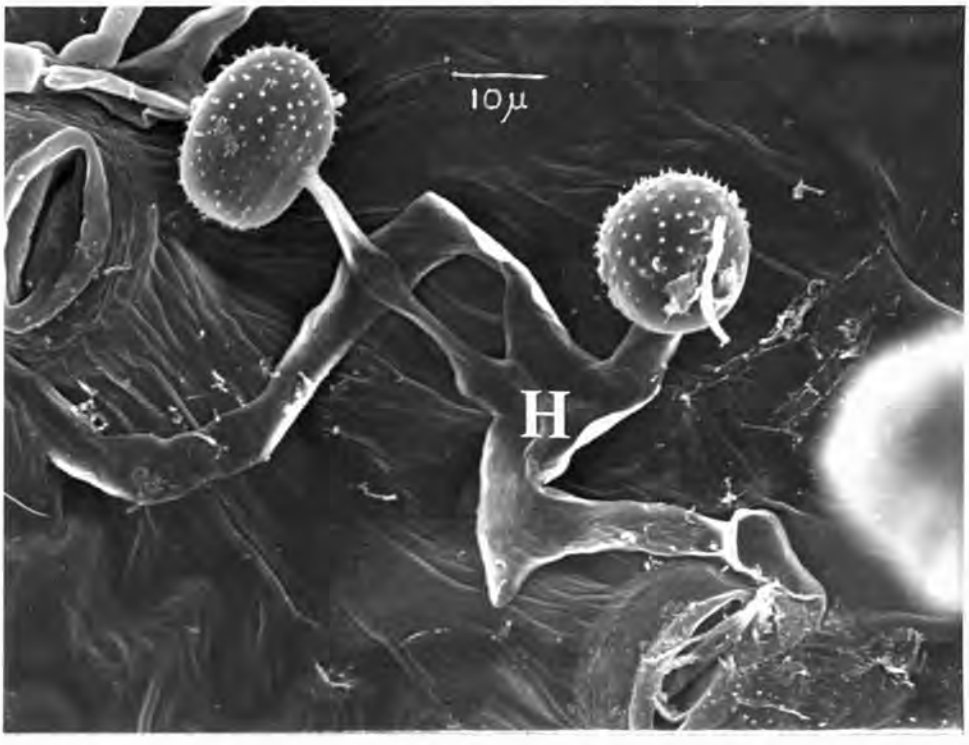


Figure 5.13 Fusion of hyphae (H) from two uredospores of P. antirrhini and subsequent penetration through a stoma of A. majus

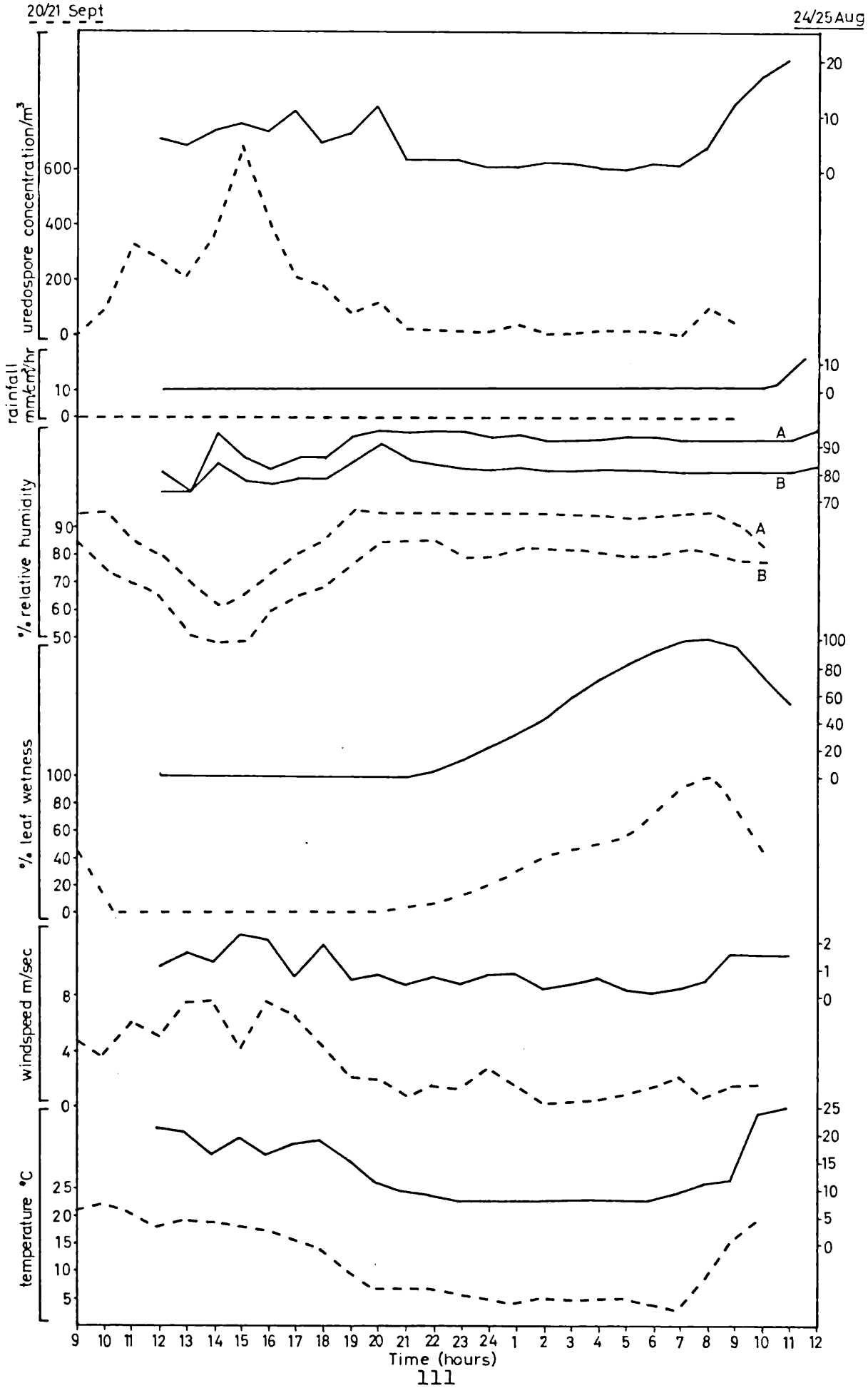
5. Periodicity of Uredospores and Meterological Data

The graphs showing the uredospore count and meterological records for the two twenty-four hour periods are shown in Figure 5.14. The readings for the two periods were not started at the same time of day but the results are comparable and will be discussed together.

i Uredospore count

The number of spores per cubic metre of air on the 24th/25th August was less than the number on the 20th/21st September. The difference was due to the stage of the epidemic. The first recording period on the 24th/25th August was at the start of the epidemic, four days before Day 1 on the disease progress curves (Figure 5.5). By the time of the second recording period on the 20th/21st September the epidemic was well developed (equivalent to Day 22 on the disease progress curves, Figure 5.5). The difference in magnitude affects the size of the peaks but the periodicity of the uredospore liberation is the same in both periods. The lowest score counts were made during the night from 2100 hours to 0700 hours and the greatest number of spores in the air was found during the day.

Figure 5.14 Uredospore count and meterological records for two twenty-four hour periods at Royal Holloway College in 1979.



ii Rainfall

There was only one shower of rain during the two recording periods. The rain started just before 1100 hours on the 25th August and continued steadily until the end of the recording period at 1200 hours.

iii Relative humidity

The relative humidity within the more compact dwarf variety (A) was consistently higher than the relative humidity within the standard variety (B). The humidity never fell to less than 70% during the first recording period whereas it fell to just below 50% during the second period. In the second period, the percentage relative humidity dropped during the morning and early afternoon and began to rise at 1500 hours until 2000 hours where it remained constant during the night.

iv Leaf wetness

The leaf wetness recorder gives a measure of the condensation on the leaves which provides free water for spore germination. During the day the leaves were completely dry. Moisture started to develop on the leaves at 2200 hours, the leaves became wetter during the night to reach a maximum at 0800 hours. The level of moisture then dropped quite sharply: on a dry day the leaves would be completely dry by mid morning.

v Windspeed

During both periods the windspeed reached its highest levels during the afternoon and dropped during the night. The strength of the wind in the two periods was different. In the first the wind only exceeded 2m/sec once whereas in the second period the wind reached nearly 8m/sec on three occasions and exceeded 2m/sec between 0900 hours and 1800 hours.

vi Temperature

The general shape of the two temperature curves was the same. The temperature was lowest during the night but rose sharply in the early morning to reach a peak between 1000 and 1100 hours.

DISCUSSION

Disease progress curves for three selected varieties show that there is a range of susceptibility to the rust fungus within the cultivated varieties of A. majus. In a susceptible variety such as "Malmaison", the rate of disease increase may be as much as ten times faster than the rate in a variety such as "Amber Monarch" with "rate reducing" resistance. "Guardsman" has an intermediate level of "rate reducing" resistance. The rate influences the speed at which the disease cycle revolves and is therefore important in terms of epidemic development. In "Malmaison" a severe epidemic occurs annually whereas in "Amber Monarch" the rate is so much slower that an epidemic is unlikely to reach its climax before the end of the season. The effect of an epidemic on an intermediate variety such as "Guardsman" depends on the susceptibility of surrounding varieties. Its resistance is sufficient to delay an epidemic when planted with varieties of similar or greater "rate reducing" resistance but it may become disfigured by the disease when planted with a more susceptible variety such as "Malmaison".

The development of the epidemic is dependent on favourable environmental conditions. The rate of germination of uredospores in this investigation was consistent with that found by other workers but the percentage germination at the lower temperatures was not as great as that observed by Barbe (1967). The uredospores germinated over a range of temperature similar to those found by Mains (1935), Aronescu Savulescu (1938), Barbe (1967) and Yap (1969). The penetration of hyphae through the stoma of A. majus observed in this study is consistent with the light microscope studies by Maheshwari (1966) and the report by Lehoczky (1954). The formation of an appressorium over epidermal cells and the penetration through the cuticle at the base of a glandular hair which were observed in this study have not previously been reported for P. antirrhini though Maheshwari (1966) reported the formation of an appressorium over a guard cell. Apparently the entry of fungal hyphae is not confined to stoma.

The liberation of uredospores of P. antirrhini is reflected in the hourly collections of uredospores above the plot. The general pattern of uredospore concentration in the air suggested that uredospores are liberated during the day. This is consistent with the results given by Yap (1969). The graphs for the second recording period suggest that higher concentrations of uredospores in the air are associated with higher windspeeds. In the first period, the windspeed only exceeded

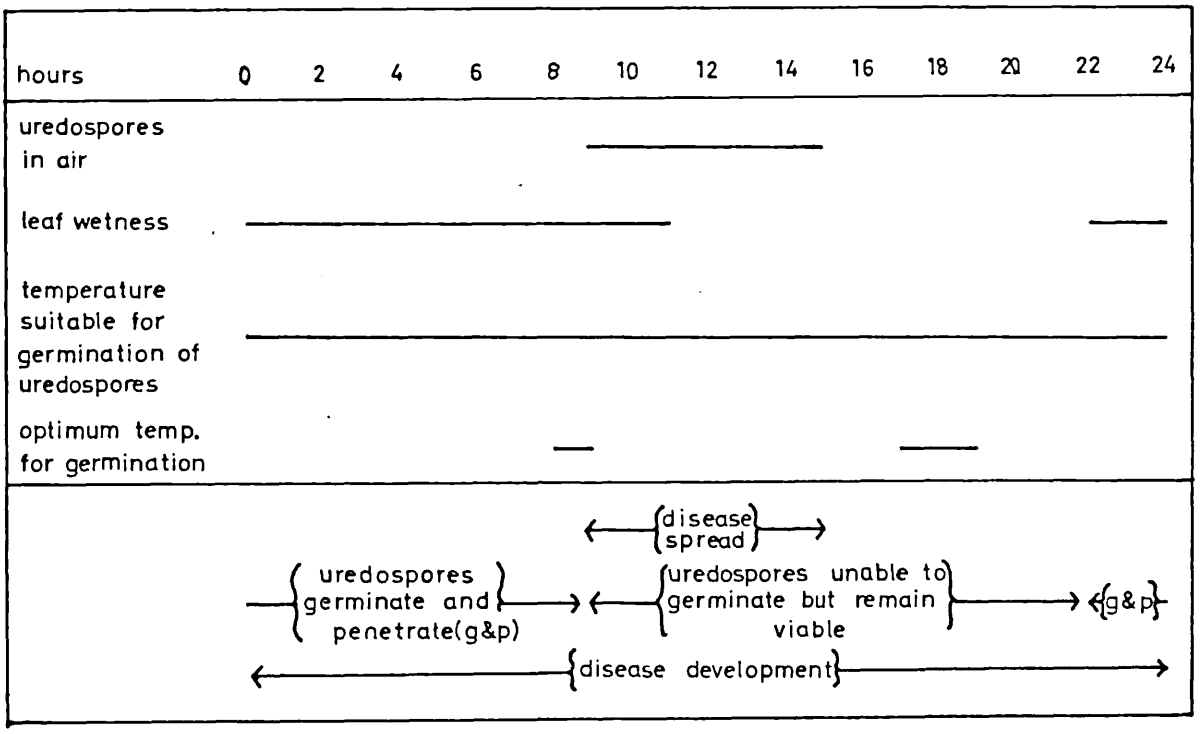
2m/sec (the level below which uredospores are said not to be liberated, (Yap, 1969))once at 1500 hours and yet higher uredospore counts were recorded at 1700 hours and 2000 hours when the recorded windspeed was less than 1m/sec. An hourly reading of the windspeed, 1·5m above the ground, can only give a general pattern and it does not reflect the strength of the wind at plant level but it would appear that uredospores may be liberated at windspeeds of less than 2m/sec.

The increase in the uredospore liberation at the end of the first scoring may be associated with the onset of rain and the increased wind velocity. Yap (1969) found that uredospore liberation increased one hour before short intense showers although he did not find any relationship between uredospore liberation and relative humidity. Dimock and Baker (1951) also noted that the frequency and intensity of rainfall was an important factor in the severity of the disease.

Development of an epidemic.

From the data presented in Figure 5.14 the following scheme (Figure 5.15) can be drawn to illustrate the inter-relationships of the factors which influence the development of an epidemic. The meterological data collected in this investigation was limited because recording equipment was not available. Nevertheless the data may be used to show the conditions necessary for the development of an epidemic.

Figure 5.15 Scheme showing the time when conditions are suitable for each stage of the disease cycle



The following points are important:

i Uredospore liberation occurs during the day and increases just before a period of rain

ii Free water necessary for germination is only present as dew during the night and early morning. Infection should be established within eight hours at 5^{o} C and 8^{o} C, the night temperatures for the two periods and at these temperatures at least 20% of the spores would be expected to germinate.

iii The temperature range of the two twenty-four hour periods never went outside the range satisfactory for germination, therefore germination could occur whenever there was free water. Uredospores can germinate and gain infection in the light and the dark therefore infection could occur during the day or night.

iv Disease development is fastest between 20^{o} C and 25^{o} C but the complete temperature range over the two twenty-four hour periods would be satisfactory for disease development.

These conditions are satisfied by a scheme in which the uredospores are liberated during the day and germinate and establish infection during the night when free water is available. On rainy days, uredospores are liberated just before a shower and the rain may provide free water for long enough for germination and infection. At the higher daytime temperatures infection will be established quicker and may be completed in the hours of daylight.

CHAPTER SIX

VARIATION IN PATHOGENICITY IN *PUCCINIA ANTIRRHINI*

INTRODUCTION

Fungal parasites of crop plants have a considerable capacity for genetic variability: strains often vary in their pathogenicity, that is, their ability to incite disease on a host species. In some plant diseases, variation in the pathogen has resulted in the loss of disease control achieved by previously resistant varieties. This has led to the identification of a number of distinct races within some pathogens.

New races of fungal pathogens can arise by four main methods (Russell, 1978):

i recombination of nuclear genes through sexual reproduction
ii extrachromosomal or cytoplasmic variation
iii mutation in somatic cells
iv reassortment or exchange of genetic material in somatic cells

The production of new physiologic races through sexual reproduction occurs in many plant pathogens and requires little explanation. In *P. antirrhini* the variations in pathogenicity are unlikely to be the result of sexual recombination since the complete sexual life cyle has not been found (see Chapter 5).

Cytoplasmic control of virulence has been described in *Puccinia graminis tritici* by Johnson (1954). He used two races of *Puccinia graminis tritici* which were differentiated by the varieties "Marquis" and "Kota" and showed that the virulence of the progeny of both reciprocal crosses was like that of the maternal parent. This is also an unlikely source of variation in *P. antirrhini*.

The origin of new physiologic races are often attributed to a mutation from avirulence to virulence when it cannot be explained by a known genetic mechanism (Watson, 1970). The rate of mutation may vary considerably from pathogen to pathogen but Day (1974) suggests that the natural mutation rate of genes in most pathogens of economic importance are sufficient to generate mutants which can attack any host variety protected by a single resistance gene. A mutation from avirulence to

virulence is the most likely explanation for the variations in pathogenicity in P. antirrhini although some somatic recombination is also likely since virulence is generally recessive.

Two forms of nuclear exchange are known within the fungi. These are called heterokaryosis and parasexuality. Heterokaryosis produces new phenotypes by the association of unlike nuclei in a single mycelium. The subject has been reviewed by Parmeter, Snyder and Reichle (1963). Most pathogens which are capable of heterokaryosis may also undergo somatic recombination by parasexualism (Day, 1960). This involves the formation of a heterokaryon from two haploid nuclei in the somatic mycelium. Recombination within the diploid nucleus may occur as the result of either "mitotic crossing over" in which linked genes are recombined or "haploidization" where whole chromosomes are recombined. Parasexuality in plant pathogenic fungi has been reviewed by Tinline and MacNeill (1969).

Physiologic races have been identified in other species of rust where no alternate host is known: in P. striiformis for example, they are assumed to arise through mutation, heterokaryosis and the parasexual cycle (Nelson, 1973). Perhaps the origin of races of P. antirrhini may be explained in the same way.

Genetic change within Puccinia antirrhini

When P. antirrhini was first reported on A. majus in California in 1895 (Blasdale, 1903) it was virulent on all the cultivars. This original rust was called "Race 1" when Yarwood (1937) described a second race on the basis of heavy natural infection on varieties resistant to Race 1 in certain coastal areas of California. When the rust was reported in Australia in 1952 it was virulent on varieties with resistance to Race 1 (Walker, 1954). This led Walker to conclude that the Australian rust was similar to Race 2, though he had only shown that it was different from Race 1. In Britain, signs of disease on the previously resistant varieties in the R.H.S. trial of 1969 were considered to be due either to the spread of a virulent race from abroad or a mutation to virulence within the rust population in Britain (Brooks, 1970).

There has been little experimental work on the physiologic races of P. antirrhini. Barbe (1967) infected cultivars of A. majus with two isolates of rust collected from the wild species, A. multiflorum and

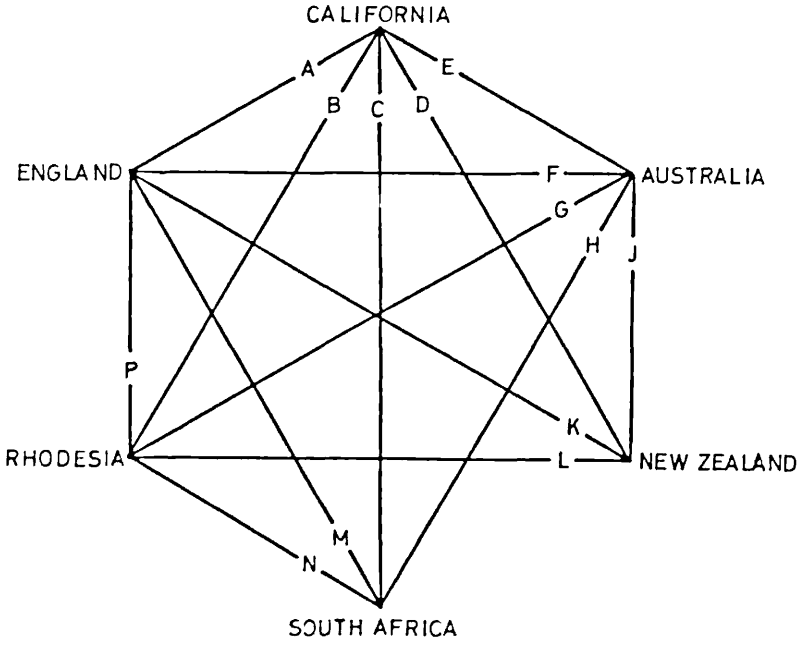
A. virga, and six isolates from cultivars of A. majus in New Zealand, Australia, South Africa, Rhodesia, England and California. He scored the disease on a six-point scale dividing the varieties into the following categories:

i = immune,
0-2 = resistant,
3,4 = susceptible.

He found that the rust isolates from the Californian species of Antirrhinum were distinct since they were avirulent on all the cultivars of A. majus he tested. In addition he found that some of the cultivars differentiated between the isolates of rust. His results are summarized in Figure 6.1 using the three categories above. A line between two rust isolates means that these isolates could be separated by their response to one or more of the varieties of A. majus. It is worth noting that the isolates from South Africa and New Zealand could not be differentiated by the six varieties. The rust from California was the most virulent causing moderate disease on all the varieties. The rust from England caused least disease and all the others were intermediate, each causing moderate disease on a few of the varieties.

There have been no more published reports of virulence. Gawthrop and Jones (in press, Appendix 10), however, have analysed the published results of cultivar trials (Doran, 1921; Mains, 1935; Buchwald, 1936; Korats, 1954 and Walker, 1954) and the unpublished results of the Royal Horticultural Society's Trials of Rust-Resistant Antirrhinums in 1958 and 1962 to determine whether there was evidence for variation in P. antirrhini. They found a strong similarity between the results of trials held in the U.S.A. in 1921 (Doran, 1921) and in Europe in 1936 (Buchwald, 1936), also between the later trials in the U.S.A. in 1935 (Mains, 1935) and in Europe in 1954 (Kovats, 1954). There was, however, a striking difference between the earlier and later trials on each continent. Furthermore, the performance of the varieties in European (Kovats, 1954) and Australian (Walker, 1954) trials held in 1954 was similar while there was an obvious difference between the results of the latest two English trials held in 1958 and 1962. (Anon, 1959 and 1963). Gawthrop and Jones concluded that the differences between the earlier and later trials in the U.S.A., in Europe and in Britain must be attributed to the replacement of previously prevalent races by other more virulent races.

Figure 6.1 Differences between isolates of Puccinia antirrhini found by Barbe (1967) (original).



Differential varieties which separate the pairs of isolates

Differential Varieties	A	B	C	D	E	F	G	H	J	K	L	M	N	P
Colossal Light Rose	+					+				+		+		+
Majus Orange	+	+			+				+	+	+			
Pink Freedom	+		+	+							+		+	+
Orange Glow	+		+		+					+		+		+
Welcome		+	+	+			+	+	+	+		+		+
Crimson Velvet	+	+	+	+	+							+	+	

+ Variety differentiated between the two isolates marked with the code letter

MATERIALS AND METHODS

1. Collection of Isolates

Requests for dried leaves of *A. majus* infected with the rust fungus were sent to botanical gardens and seed companies in various parts of the world. In addition three wild collections of rust were used; one from Dr. G.D. Barbe on *A. multiflorum* and two collected by the author in California (Appendix 7.1) on *A. multiflorum* and *A. virga*. The sources of the rust isolates used in this investigation are shown in Appendix 6.1.

2. Maintenance of Isolates

The isolates were maintained on the susceptible variety "Malmaison" in the greenhouse. The dried infected leaves were placed on moist filter paper in a petri dish for 24 hours. A young healthy plant of the variety "Malmaison", which had been grown in a rust-free environment in a separate greenhouse, was lightly sprayed with water from an atomizer. Uredospores from the rehydrated leaves were transferred to the "Malmaison" plant by gently rubbing the infected leaf along the underside

Figure 6.2 Young Malmaison plant in an incubation tube

leaves of the "Malmaison" plant. The plant was covered with a plastic bag for 48 hours to create a humid atmosphere for the uredospores to germinate. When the plastic bag was removed the plant was covered with an incubation tube (Figure 6.2) to minimize the risk of contamination from other isolates.

The tubes were made from a sheet of plastic purchased from Transatlantic Plastics Ltd. The sheet was joined with "UHU" glue to make a cylinder which fitted tightly over a 3½ins. pot. The top was covered with muslin and two ventilation holes were cut which reduced the condensation within the tube. The ventilation holes were covered with a fine mesh (pore size•25 mm).

The period before new pustules developed varied from two weeks in the summer months to four weeks during the winter. The culture was transferred to another healthy "Malmaison" plant in the same way every eight to ten weeks when the original had become severely infected.

3. Testing for differential plants.

Five lines including some resistant and some susceptible plants were grown from seed donated by a commercial company who wish to remain anonymous. The history of these lines was not known but since each line was understood to possess some resistant and some susceptible plants, each plant was considered individually. The testing started when the plants had eight to twelve leaves. Test plants were placed in a tray with a plant of the susceptible variety "Malmaison" as a control. These plants remained together for the duration of the experiment and were all inoculated with the same isolate at the same time. Two mature, full sized leaves were inoculated with a rust isolate by the method outlined above. The plants were classified as resistant or susceptible after three to four weeks, by then mature pustules had developed on the control variety. If a plant had failed to produce a necrotic area by this time it was considered resistant. The pair of inoculated leaves were removed and the next pair of leaves infected with another isolate of the rust.

The ability shown by some plants to differentiate between rust isolates was then confirmed twice by inoculating detached leaves. In this way it was possible to test all the differential plants with isolates of the rust at the same time. Two healthy leaves of the test plants and the control variety "Malmaison" were removed for each isolate,

placed adaxial surface down on a plastic mesh floating on water in a crystallizing dish (Figure 6.3). The leaves were dusted with uredospores using a brush and then lightly sprayed with water from an atomizer. The dishes were covered with glass plates and left at room temperature until pustules developed.

In all these procedures cleanliness to prevent contamination is essential. The hands were washed and working surface wiped between handling isolates and clean brushes (washed then placed in alcohol), bags and inoculation tubes used for each isolate.

Figure 6.3 Detached leaves of Antirrhinum majus prepared for inoculation.

RESULTS

The isolates from the Californian wild species were avirulent on the susceptible cultivar of A. majus "Malmaison", and the Mediterranean wild species, A. molle and A. meonanthum. Plants of the susceptible Californian wild species on which to culture the rust were not then available. Consequently it was impossible to include the isolates from the Californian wild species in the experiment to find differential plants.

The results of the experiment to find differential plants are shown in Table 6.1. Of the eighty plants used in the tests, the pairs of leaves died in seven but of the remainder 37% were resistant to all isolates tested, 41% were uniformly susceptible and 22% showed a differential reaction.

Figure 6.4 summarizes the differences found between geographical isolates of the rust and lists the differential plant numbers. The rust in parts of Britain appears to be different from that in South Africa, California and France. The rust in South Africa is different from that in California and France and the isolate from France was different from the one in Australia. In addition, there may be differences in the strains or rust within a country. The four collections from Britain appear to fall into two groups. Plant number 45 differentiated between the rusts from Royal Holloway College (R.H.C.) and Herne Bay and plant numbers 11 and 15 differentiated between the rusts from Norwich and Sunbury. A differential plant was not found among either the five used to compare Herne Bay with Norwich or the five used to compare Herne Bay with Sunbury.

Table 6.1 Reaction of Individual Plants of Antirrhinum to rust isolates

Plant Number	Accession No.79-	Tray No.	Sources of isolates								
			BRITAIN Royal Holloway College	BRITAIN Norwich	BRITAIN Sunbury	BRITAIN Herne Bay	SOUTH AFRICA Claremont	CALIFORNIA Ojai	FRANCE Besancon	FRANCE Bretigny	AUSTRALIA Victoria
1	100	I*	✓ ✓				X X		✓ ✓		
2	100	II		✓	✓		✓				
3	100	III		✓		✓			✓		
4	100	IV*			X X		X X	✓ ✓			
5	100	V							X		D
6	100	VI			X				X		
7	100	VII		X	X						
8	100	VIII	X							X	
9	100	XII					X		X		
10	101	I*	✓ ✓				X X		✓ ✓		
11	101	II*		✓ ✓	X X		✓ ✓				
12	101	III		✓		✓			✓		
13	101	IV			✓		✓	✓			
14	102	I	X				X		X		
15	102	II*		✓ ✓	X X		X X				
16	102	III		✓		✓			✓		
17	102	IV*			X X		X X	✓ ✓			
18	102	V							✓		✓
19	102	V*							✓ ✓		X X
20	102	VI			✓				✓		
21	102	VI			✓				✓		
22	102	VII		✓	✓						
23	102	VIII*	✓ ✓							X X	
24	102	VIII	X							X	
25	102	X						X	X		
26	102	X						X	X		
27	102	X						✓	✓		
28	102	XI		X					X		
29	102	XI		✓					✓		
30	102	XII*					✓ ✓		X X		
31	102	XII					X		X		
32	102	XII					✓		✓		
33	102	XII					✓		✓		
34	102	XIV			✓	✓					
35	102	XIV			✓	✓					
36	102	XIV			X	X					
37	102	XV		X				X			
38	102	XV		✓				✓			
39	102	XV		✓				✓			
40	102	XVI						X	X		
41	102	XVI						X	X		
42	102	XVI						X	X		
43	102	XVII	✓			✓					
44	102	XVII	X			X					
45	102	XVII*	X X			✓ ✓					
46	103	I*	✓ ✓				X X		D		
47	103	II		✓	✓		✓				
48	103	III		X		X			X		

Table 6.1 continued

Plant Number	Accession No.	Tray No.	Sources of isolates								
			BRITAIN Royal Holloway College	BRITAIN Norwich	BRITAIN Sunbury	BRITAIN Herne Bay	SOUTH AFRICA Claremont	CALIFORNIA Ojai	FRANCE Besancon	FRANCE Bretigny	AUSTRALIA Victoria
49	103	III				X		X	X		
50	103	IV			X		X	X			
51	103	V							X		X
52	103	VI			✓				✓		
53	103	VII		✓	✓						
54	103	VIII	✓							✓	
55	103	X						✓	✓		
56	103	XI		✓					✓		
57	103	XI		X					X		
58	103	XIII	✓				✓				
59	103	XIII	X				X				
60	103	XIII*	X X				✓ ✓				
61	103	XIV			X	X					
62	103	XV		✓				✓			
63	103	XVI						✓	✓		
64	103	XVII	✓			✓					
65	104	I	X				X		X		
66	104	II		X	X		X				
67	104	III				X		X	X		
68	104	III		✓		✓			D		
69	104	IV			✓		✓	✓			
70	104	V							✓		D
71	104	VI			D				X		
72	104	VII		D	X						
73	104	VIII	✓							D	
74	104	XI*		X X					✓ ✓		
75	104	XIII*	X X				✓ ✓				
76	104	XIII*	X X				✓ ✓				
77	104	XIV			X	X					
78	104	XV		✓				D			
79	104	XVI*						✓ ✓	X X		
80	104	XVII	✓			✓					

78-32 Malmaison was susceptible to isolates tested in all seventeen trials.

Key

✓ = susceptible

X = resistant

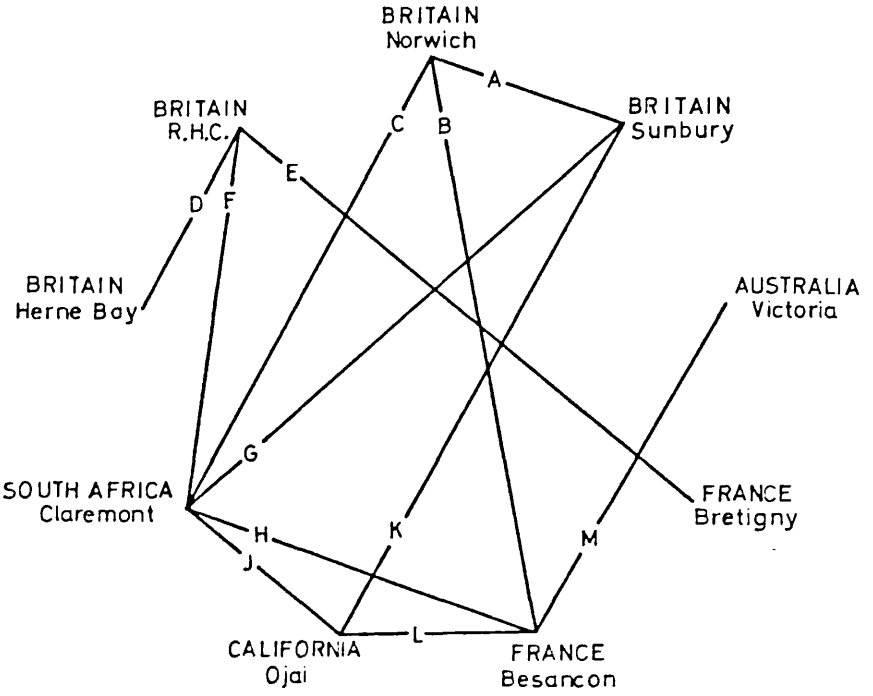
D = leaves died

* = experiment repeated

✓✓ = susceptible in both experiments

X X = resistant in both experiments

Figure 6.4 Differences between isolates of Puccinia antirrhini in present study.



Key	Differential Plant Numbers
A	11, 15
B	74
C	15
D	45
E	23
F	1, 10, 46, 60, 75, 76
G	11
H	1, 10, 30
J	4, 17
K	4, 17
L	79
M	19

DISCUSSION

The results of these experiments show that the prevalent isolates of *P. antirrhini* vary in their pathogenicity. The conclusions which can be drawn about the rust strain on the Californian wild species must be limited, since it was impossible to include these isolates in the tests to find differential species. Their avirulence on cultivars of *A. majus* and two Mediterranean species, *A. molle* and *A. meonanthum*, however, is consistent with Barbe's (1967) findings and support his conclusion that the rust on the wild species is distinct from that found on the cultivated *A. majus*.

The comparison between isolates collected from cultivars of *A. majus* in different parts of the world indicate that there are several different strains (Figure 6.4). Barbe (1967) found similar differences between the rust samples from South Africa and England, California and South Africa and England and California in his studies. Barbe (1967) used a quantitative assessment and found that varieties differentiated between the isolates, whereas this study was based on the response of individual plants and the plants were classified as either immune or susceptible.

Gawthrop and Jones (in press) considered that the origin of the more virulent race in the U.S.A. was likely to have been by mutation since six years elapsed between Main's discovery of resistant plants and their release to other breeders and during that time the resistance was total. Subsequent changes may have occurred as a result of mutation and recombination. Hyphal fusion was observed during this investigation (Figure 5.13). Although in this case it was within one population, fusion may also occur between isolates of *P. antirrhini*.

These experiments were performed with populations of the rust but further experiments using single spore isolates and a clone of each differential plant (Appendix 6.2) may extend the number of races of *P. antirrhini*.

CHAPTER SEVEN

WILD SPECIES

INTRODUCTION

A. Taxonomy

Rothmaler (1956) placed the genus Antirrhinum in the family Scrophulariaceae, the subfamily Antirrhiniodeae, the tribe Antirrhineae and the subtribe Linariinae. The genus has a disjunct and bicentric distribution in the New and Old Worlds correlated with its division into two morphologically distinct sections: Saerorhinum Gray in south west North America with its centre in California and Antirrhinum Rothm. in the Mediterranean area.

1. The American species

The genetics, physiology and ecology of the species within the Saerorhinum section are little understood. Gray (1868) divided the American species described at that time, into three series:

i	axilliflora	A. cornutum
ii	spicata	A. virga
		A. multiflorum
		A. coulterianum
iii	axilliramulosa	A. nuttallianum
		A. breweri
		A. vagans

Jepson (1925) included A. speciosum Gray, A. maurandioides Gray, A. strictum Gray, A. filipes Gray, A. kingii Wats, A. subcordatum Gray and A. ovatum Eastw. Later some of these species were transferred from Antirrhinum to related genera. Munz (1926) in his study of the tribe, recognised eleven species of Antirrhinum within the section Saerorhinum and included a further three "doubtful" species. One of these, A. kelloggii was listed in the genus in his later work (Munz and Keck, 1959). Table 7.1 shows the main synonymies within the Saerorhinum section of the genus Antirrhinum.

Each of the Californian species may be readily distinguished by several characteristics. Thus, they are good Linnaean species within a recognisable section of the genus.

Table 7.1 Synonymies within the section Saerorhinum of the genus Antirrhinum

Accepted Name	Synonym
A. breweri Gray	A. vagans var breweri Jepson
	A. vexillocalyculatum var breweri Munz
A. cornutum var leptaleum (Gray) Munz	A. leptaleum Gray
A. cornutum var typicum Munz	A. emarginatum Eastw.
A. coulterianum Benth.	A. nevinianum Gray
A. coulterianum forma orcuttianum (Gray) Munz	A. orcuttianum Gray
A. cyathiferum Benth.	A. chytrospermum Gray
A. kelloggii Greene	A. hookerianum Penn.
	A. strictum (H & A) Gray non Sibth & Sm.
A. multiflorum Penn.	A. glandulosum Lindl.
A. nuttallianum Benth.	A. pusillum Bdg.
	A. subsessile Gray
A. vexillocalyculatum var typicum Kellogg	A. elmeri Rothm.
	A. vagans Gray
	A. vagans var bolanderi Gray
	A. vagans var rimorum Jepson
Galvesia speciosa (Nutt) Gray	A. speciosum Gray
Howelliella ovatum Rothm.	A. ovatum Eastw.
Neogaerrhinum filipes Rothm.	A. cooperi Gray
	A. filipes Gray

2. The European Species

The European species, on the other hand, are often so close in morphology that they are only in practice distinguished by one or two characters. The taxonomy of this section is much more complicated and the status of a number of species is in dispute.

Baur (1932b) divided the European species into three sections; Antirrhinastrum, Asarina and Orontium. The species within the Asarina and Orontium sections were later transferred to the genera Asarina and Misopates respectively. The last monograph of the genus was written by Rothmaler (1956). He divided the European section, Antirrhinum, into three subsections and nine series: (Table 7.2). This division of the section has been critized by Webb (1971) because "it is too typological in its approach" and does not give sufficient attention to the variants which may bridge the gap between two species. Webb (1971) concluded that

Table 7.2 The division of the genus Antirrhinum section Antirrhinum by Rothmaler (after Stubbe, 1966)

Subsection	Series	Species
1. Kickxiella	i Valentina	A. valentinum
	ii Sempervirentia	A. martenii
		A. sempervirens
		A. pulverulentum
		A. pertegasii
		A. microphyllum
		A. charidemi
	iii Mollia	A. molle
		A. lopesianum
	iv Rupestria	A. mollissimum
		A. caroli-paui
		A. rupestre
	v Glutinosa	A. grosii
		A. hispanicum
2. Streptosepalum	vi Meonantha	A. meonanthum
		A. ambiguum
		A. braun-blanquetii
3. Antirrhinum	vii Sicula	A. siculum
		A. dielsianum
		A. barrelieri
	viii Hispanica	A. boissieri
		A. granticum
		A. australe
	ix Majora	A. majus
		ssp majus
		ssp litigiosum
		ssp tortuosum
		ssp latifolium
		ssp linkianum

taxa such as A. grossii Font Quer, A. hispanicum Chav. and A. braun-blanquetii Rothm. cannot be assigned to any particular subsection. Therefore he reduced the twenty-four species recognised by Rothmaler (1956) to seventeen in his Flora Europaea III account and described two subspecies within A. hispanicum.

The taxonomy of the Antirrhinum section has been studied in Spain and Portugal since the Flora Europaea account. New species, A. bolosii Fdz-Casas and A. saccharatum Fdz-Casas, have been described from the Granada province of Spain (Fernandez-Casas, 1972) and new combinations, A. molle ssp. lopesianum (Lopes, Martins, Rainha, Pinto da Silva, Da Silva, Pinto da Silva and Teles, 1972) A. sempervirens Lapeyr. subsp. pulverulentum (Lazaro) Fdz-Casas, A. sempervirens Lapeyr subsp. micro phyllum (Rothm.) Fdz-Casas, A. molle L. var. oppositifolium Fdz-Casas, A. hispanicum Chav. subsp. hispanicum var. bolosii (Fdz-Casas) Fdz-Casas, A. hispanicum Chav. subsp. mollissimum (Pau) Fdz-Casas, A. hispanicum Chav. subsp. mollissimum var. marianum (Pau) Fdz-Casas, made in the Spanish Flora (Fernandez-Casas, 1974).

Table 7.3 shows the main synonymies within the Antirrhinum section of the genus. The greatest difficulty appears to be within the A. hispanicum - A. mollissimum group. Webb (1971) and Fernandez-Cases (1974) have both assigned A. mollissimum (Pau) Rothm. to A. hispanicum as a subspecies. Whereas, Brooker, Doaigey and Harkiss (1976) compared the histology of A. molle L. and A. mollissimum (Pau) Rothm. and demonstrated that these two species were identical and distinct from A. hispanicum Chav. The taxonomy of the European Antirrhinum species is still under review and further changes may be expected.

Table 7.3 Synonymies within the section Antirrhinum of the genus Antirrhinum

Accepted name	Synonym
A. barrelieri Boreau	A. controversum Pau / A. ibanjezii Pau ined.
	A. majus subsp. litigiosum (Pau) Rothm.
A. braun-blanquetii Rothm.	A. meonanthum auct; non Hoff and Link
A. granticum Rothm.	A. boissieri Rothm.
	A. hispanicum auct; non Chav.
	A. hispanicum var. glabrescens Lange in Willk & Lange
A. hispanicum Chav.	A. caroli-pauí Rothm.
	A. x huteri Rothm.
	A. mollissimum Rothm.
	A. rupestre Boiss et Reut
	A. glutinosum Boiss et Reut non Brot.
A. hispanicum subsp. hispanicum	
A. hispanicum subsp. hispanicum var bolosii (Fdz-Casas) Fdz-Casas	A. bolosii Fdz-Casas
A. hispanicum subsp. mollissimum (Pau) Fdz-Casas	A. hispanicum subsp. mollissimum (Rothm.) Webb.
	A. molle var mollissimum Pau
	A. mollissimum (Pau) Rothm.
A. hispanicum subsp. mollissimum (Rothm.) Webb	A. molle auct., non L.
	A. mollissimum Rothm.
A. hispanicum subsp. mollissimum var marinum (Pau) Fdz-Casas	
	A. caroli-pauí Rothm.
	A. molle var marinum Pau
A. latifolium Miller	A. majus subsp. latifolium (Mill.) Rothm.
A. majus subsp. cirrhigerum (Welw. ex. Fic.) Franco in Webb	
	A. cirrhigerum (Welw. ex. Fic.) Rothm.
	A. latifolium var cirrhigerum Welw. ex. Fic.
	A. major var ramosissimum Willk in Willk & Lange
A. majus subsp. cirrhigerum (Ficalho) Franco	A. latifolium var cirrhigerum Ficalho
A. majus subsp. linkianum (Boiss et Reut.) Rothm.	A. linkianum Boiss. et Reut.
A. majus subsp. tortuosum (Bosc.) Rouy	A. tortuosum Bosc.
A. meonanthum Hoff and Link	A. ambiguum Lange
A. molle var lopesianum Webb	A. lopesianum Rothm.
A. pulverulentum Laz Ibiza	A. sempervirens var densiflorum Lange ex Willk
A. sempervirens Lapeyr subsp. microphyllum (Rothm.) Fdz-Casas	
	A. microphyllum Rothm.
A. sempervirens subsp. pulverulentum (Lazaro) Fdz-Casas	A. pulverulentum Lazaro
	A. sempervirens var densiflorum Lange ex Willk
	A. sempervirens var glabrescens Lange ex Pau
A. siculum Miller	A. cielsianum Rothm.
	A. majus subsp. siculum (Miller) P. Fourn.

3. Morphological Comparison of the two sections.

The following photographs show the flowers of some of the species within the Antirrhinum section of the genus: A. molle (Fig.7.1); A. hispanicum (Fig. 7.2); A. meonanthum (Fig.7.3); A. siculum (Fig.7.4); A. graniticum (Fig.7.5); A. barrelieri (Fig. 7.6) and A. majus subsp. linkianum (Fig. 7.7). The form of the flower in all these species is very similar, in fact a number of the species in this section are only separated by minor characters. Fig. 7.8 shows that the flower of Misopates calycinum from a related genus is also very similar to the European species of Antirrhinum. In habit Misopates spp. appear closer to the Antirrhinum section of the genus Antirrhinum than the American species of Antirrhinum. The American species have smaller flowers and the plants with the exception of A. multiflorum and A. virga are more slender often using tortile branchlets to gain support from surrounding vegetation as shown in A. nuttallianum (Fig. 7.9). Nevertheless the members of the Saerorhinum section are recognisable as a group but they are sufficiently different from the Antirrhinum section for the two sections to receive a higher taxonomic rank.

Figure 7.1 Inflorescence of Antirrhinum molle

Figure 7.2 Inflorescence of Antirrhinum hispanicum

Figure 7.3 Inflorescence of Antirrhinum meonanthum

Figure 7.4 Inflorescence of Antirrhinum siculum

Figure 7.5 Inflorescence of Antirrhinum graniticum

Figure 7.6 Inflorescence of Antirrhinum barrelieri

Figure 7.7 Inflorescence of Antirrhinum majus subsp. linkianum

Figure 7.8 Inflorescence of Misopates calycinum

Figure 7.9 Inflorescence of Antirrhinum nuttallianum

4. Cytology

The chromosome counts, hitherto reported, support the division of the genus into the two sections Saerorhinum and Antirrhinum. The European species; A. sempervirens Lapeyr, A. molle L., A. hispanicum Chav., A. hispanicum subsp. hispanicum (A. glutinosum Boiss.et Reuter), A. meonanthum Hoff.& Link , A. siculum Miller, A. latifolium Miller, A. majus L., A litigiosum Pau listed by Bolkhorskikh, Grif, Matvejeva and Zakharyeva (1969) and A. granticum Rothm., A. majus subsp. majus, A. majus subsp. linkianum (Boiss.et Reuter) Rothm., and A. majus subsp. cirrhigerum (Ficalho) Franco counted by Fernandes, Queiros and Santos (1977) have all been shown to be 2n = 16. Although only a few of the Californian species have been counted, the results show the species to be either tetraploid 2n = 32: A. multiflorum Penn. (Munz, 1968) and A. nuttallianum (Gunther and Rothmaler, 1963) or hypotetraploid 2n = 30: A. coulterianum Benth. and A. elmeri Rothm. (= A. vexillo- calyculatum var typicum Kellogg).

It is worth noting that synthetic tetraploid (autotetraploid) cultivars of A. majus (2n = 32) have been commercially available for some time. They are generally sold as a mixture of colours.

B. Reproductive Biology.

1. Self Compatibility

Baur (1919) distinguished three groups within the section Antirrhinum on the basis of their behaviour when selfed;

i A. siculum and a number of wild Spanish relatives of A. majus are completely self-compatible

ii Species such as A. latifolium and A. tortuosum which are almost completely self-incompatible when they first flower, but become largely self-compatible at the end of the first season and in the second year.

iii Species such as A. barrelieri (as A. ibanjezii), A. molle, A. hispanicum subsp. hispanicum (as A. glutinosum) which are completely self-incompatible. Later it became apparent that the Spanish wild populations of A. majus were generally self-sterile whereas the cultivated races and the Italian wild races were self-fertile (Baur 1924; 1932a). The origin of the Italian races is not certain but they may have arisen by the naturalization of garden races (Baur, 1924).

Thus it appears that a mutation from self-sterility to self-fertility has occurred and that self-fertile individuals have been preferentially selected within cultivated forms of A. majus. The nature of this change has been studied by East (1929), Brieger (1935), Tseng (1938) and Sherman (1939) among others. East (1929) considered that self-sterility was governed by a series of allelomorphic factors which controlled the pollen tubes; interaction between the s allele in the pollen and the style tissue caused the pollen tube to grow slowly but where the alleles differed the tube elongated rapidly. Brieger (1935) described a dominant factor F, which is not an allele of the series of self-sterility genes but destroys the physiological effect of the s alleles, thereby causing self-fertility. Tseng (1938) confirmed the presence of an epistatic fertility factor F in addition to the self-sterility allelomorphs Sm which cause self-sterility in ff homozygotes. Sherman (1939) disagreed with Brieger's explanation for the abnormal segregation in a cross between a plant bearing radially symmetrical self-fertile flowers and self-sterile plants bearing zygomorphic flowers and concluded that the F factor was at the same locus as the allelic series of self-sterility genes.

Gruber and Waldenburg (1937) in their study of the self-sterility alleles in the section Antirrhinum, found fourteen S alleles from fourteen plants of A. glutinosum from Orgiva (collected in Sierra Nevada by Baur (1932a)). They found a further fourteen from ten plants of eight different collections of the same species and fourteen more in different collections of A. molle L., A. valentinum Font Quer, A. charidemi Lange, A. barrelieri Boreau and A. majus L. They note, however, "Drei Allele hatten sie mit A. glutinosum gemeinsam in weiteren drei Allelen stimmten sie trotz erheblicher systematischer und raumlicher Trennung untereinander uberein." Gruber and Waldenburg (1937) claimed to have discovered forty-two S alleles within the species of Antirrhinum they had investigated. Their account implies that each cross which failed to set seed was due to the two parents sharing the same compatibility allele in which case most times the cross would produce abundant seed. Alternatively the failure may have been due to cross-incompatibility in which case most crosses would fail.

2. Interspecific hybrids

Several authors have reported that the two sections of the genus, Saerorhinum and Antirrhinum distinguished by Rothmaler, are genetically distinct. These reports do not indicate the polyploid level of the parent from the Antirrhinum section and consequently it was most likely to have

been diploid. Evidence presented here suggests the species from the Saerorhinum section have basically two genomes and therefore a tetraploid parent from the Antirrhinum section is more likely to result in the formation of a hybrid.

Baur (1932a) found it was impossible to cross species from the Orontium or Asarina sections of the genus with species from the Antirrhinastrum section. Later Harrison and Darby (1955), in their studies of unilateral hybridization obtained viable seed from a cross between Misopates orontium (as A. orontium) and A. meonanthum (from the Antirrhinastrum section). The hybrid was sterile though and this was due to the failure of chromosome pairing at meiosis. Hackbarth, Michaelis and Scheller (1942) obtained F1 hybrids from a cross between Misopates chrysothales (as A. chrysothales) and A. majus. They do not record whether the hybrids were fertile. Nevertheless, it would appear that the barriers between the old Orontium and Antirrhinastrum sections were not absolute.

Within the present Antirrhinum section interspecific hybrids are readily obtainable (Table 7.4). Sixteen of the twentythree species and subspecies listed in Flora Europaea can form a hybrid with at least one other species. It is known that many of the workers had only a few species available to them and therefore a space in the table does not necessarily mean that the cross is impossible. Nevertheless, one may conclude that barriers to gene-exchange between the species in nature are largely geographical.

A. siculum appears to be the most genetically distinct of all the European species. Baur (1924 and 1932a) reports that crosses between A. siculum and the other species of the section succeed only exceptionally Hackbarth et al. (1942) also reported difficulty in crossing A. siculum with other species but when hybrids were produced they were generally fertile. Harrison and Darby (1955) found that species crosses using A. siculum were only successful if A. siculum was the female parent.

The present taxonomic difficulties within the Antirrhinum section of the genus may be partly due to negligible genetic barriers between species. Webb (1971) believes that hybridization and introgression by the expansion of the range of some local endemics and the hybridization between local endemics and such species as A. siculum Miller and A. majus L., (whose natural range has increased over the last five hundred years by cultivation) are responsible for the variation which obscures the distinction between species.

Table 7.4 Summary of interspecific hybrids reported within the genus Antirrhinum section Antirrhinum. The species are listed under the name and in the order given in Flora Europaea

	A. valentinum Font Quer	A.sempervirens Lapeyr	A.charidemi Lange	A.molle L.	A.hispanicum Chav.	A.hispanicum subsp.hispanicum	A.hispanicum subsp.mollissmum Rothm) O.A. Webb	A.meonanthum Hoff. & Link	A.siculum Miller	A.barrelieri Boreau	A.majus subsp. litigiosum (Pau) Rothm.	A.granticum Rothm.	A.latifolium Miller	A.majus L.	A.majus subsp. linkianum (Boiss.et Reut)Rothm.
A. valentinum Font Quer	*			Hackbarth et al.(1942)			Hackbarth et al (1942)			Hackbarth et al.(1942)				Baur (1932)	
A. sempervirens Lapeyr.		*		Hackbarth et al.(1942)						Hackbarth et al.(1942)					
A. charidemi Lange			*				Hackbarth et al (1942)(6)								
A. molle L.				*	Hackbarth et al (1942)	Hackbarth et al.(1942)				Hackbarth et al.(1942)			Hackbarth et al.(1942)		
A. hispanicum Chav.				Hackbarth et al.(1942)	*	Hackbarth et al.(1942) (1)				Hackbarth et al.(1942)	Hackbarth et al.(1942) (8)		Hackbarth et al.(1942)	Brieger (1935) Kuhl (1936) Hackbarth et al.(1942)	Hackbarth et al.(1942) (7)
A. hispanicum subsp. hispanicum	Hackbarth et al.(1942) (1)			Hackbarth et al.(1942) (1)	Baur (1932) (1)	*					Hackbarth et al(1942)(1) (8)		Hackbarth et al.(1942)(1)	Kuhl (1938)(1) Baur (1932)(1) Hackbarth et al.(1942) (1)	Hackbarth et al.(1942)(1) (7)
A. meonanthum Hoff. & Link						Hackbarth et al.(1942)(1)	*			Hackbarth et al.(1942)			Hackbarth et al.(1942)		
A. siculum Miller										Hackbarth et al.(1942)					
A. barrelieri Boreau	Hackbarth et al.(1942)	Hackbarth et al.(1942)		Hackbarth et al.(1942)	Hackbarth et al.(1942)	Hackbarth et al (1942)(1)			Herrmann (1973)	*	Hackbarth et al.(1942)(8)		Baur(1919)(3) Baur (1932) Hackbarth et al.(1942)	Kuhl (1938)(3) Baur (1924)(3) Mehlquist and Rahmani(1948)(3) Herrmann (1973)	Hackbarth et al.(1942) (7)
A. majus subsp. litigiosum (Pau) Rothm.											*			Kuhl (1938)(4)	
A. latifolium Miller				Hackbarth et al.(1942)	Hackbarth et al.(1942)	Hackbarth et al (1942) (1)			Herrmann (1973) Sherman (1939)	Baur (1924)(3) Hackbarth et al.(1942)			*	Kuhl (1938) Baur (1924) Brieger (1935) Herrmann (1971)	Hackbarth et al (1942) (7)
A. majus L.	Hackbarth et al.(1942)	Kuhl (1938) Kuhl (1937) Latsy (1913) Hackbarth et al (1942)	Hackbarth et al (1942)	Baur (1919) Kuhl (1936) Latsy (1913) Hackbarth et al.(1942)	Baur (1919) Hackbarth et al.(1942)	Baur (1932)(1) Baur (1919)(1) Kuhl (1937b)(1) Hackbarth et al.(1942)(1)	Hackbarth et al (1942)(6)	Hackbarth et al.(1942)	Herrmann (1973) Hackbarth et al.(1942)	Herrmann (1973) Baur(1919)(3) Kuhl(1937b)(3) Hackbarth et al.(1942)	Kuhl (1938)(4) Kuhl (1937b)(4) Hackbarth et al.(1942)(8)		Baur (1932) Baur (1924) Kuhl (1937b) Hermann (1973)	*	Kuhl (1938) (5) Kuhl (1937b) (5) Hackbarth et al (1942) (7)
A. majus subsp. linkianum (Boiss. & Reuter)Rothm.												Günther and Rudolph (1970)		Kuhl (1938)(5)	*
A. majus subsp. tortuosum (Bosc) Rouy					Hackbarth et al.(1942)					Baur (1932)(2) Hackbarth et al.(1942)(2)			Baur(1924)(2)	Hackbarth et al.(1942)(2)	Hackbarth et al.(1942) (2) (7)

Key
1. Authors use the name "A.glutinosum", a synonym of A. hispanicum subsp. hispanicum.
2. Authors use the name "A.tortuosum", listed as a subspecies of A. majus in Flora Europaea.
3. Authors use the unpublished name "A.ibanjezii, Pau". An exsiccata of Baur's A.ibanjezii in Kew herbarium has been redetermined by Rothmaler, (who monographed the genus) as A. barrelieri.
4. Author used the name A.litigiosum". Rothmaler (1956) considered it to be a subspecies of A. majus. In Flora Europaea Vol.3, Webb says that A. majus subsp. litigiosum corresponds to A.barrelieri in the northern parts of the latter's range (N.E. Spain).
5. Author used the name "A.linkianum" listed as a subspecies of A.majus in Flora Europaea
5. Author used the name "A.molle mollissimum" which is a synonyn of A. hispanicum subsp. mollissimum.
7. Hackbarth et al.(1942) record A.majus from Cintra to be A.linkianum (P.61)
8. Hackbarth et al.(1942) record A.barrelieri from Chorro to be A. litigiosum (P.50).

spanicum p.mollissmum m) D.A. Webb	A.meonanthum Hoff. & Link	A.siculum Miller	A.barrelieri Boreau	A.majus subsp. litigiosum (Pau) Rothm.	A.granticum Rothm.	A.latifolium Miller	A.majus L.	A.majus subsp. linkianum (Boiss.et Reut)Rothm.	A.majus subsp tortuosum (Bosc,) Rouy
barth l (1942)			Hackbarth et al.(1942)				Baur (1932)		
			Hackbarth et al.(1942)						
barth l (1942)(6)									
			Hackbarth et al.(1942)			Hackbarth et al.(1942)			
			Hackbarth et al.(1942)	Hackbarth et al. (1942) (8)		Hackbarth et al.(1942)	Brieger (1935) Kuhl (1936) Hackbarth et al. (1942)	Hackbarth et al.(1942) (7)	
				Hackbarth et al.(1942)(1) (8)		Hackbarth et al.(1942)(1)	Kuhl (1938)(1) Baur (1932)(1) Hackbarth et al.(1942) (1)	Hackbarth et al.(1942)(1) (7)	
	*		Hackbarth et al.(1942)			Hackbarth et al.(1942)			
			Hackbarth et al.(1942)						
		Herrmann (1973)	*	Hackbarth et al.(1942)(8)		Baur(1919)(3) Baur (1932) Hackbarth et al.(1942)	Kuhl (1938)(3) Baur (1924)(3) Mehlquist and Rahmani(1948)(3) Herrmann (1973)	Hackbarth et al.(1942) (7)	Hackbarth et al.(1942) (2)
				*			Kuhl (1938)(4)		
		Herrmann (1973) Sherman (1939)	Baur (1924)(3) Hackbarth et al.(1942)			*	Kuhl (1938) Baur (1924) Brieger (1935) Herrmann (1973)	Hackbarth et al.(1942) (7)	Baur (1924)(2) Hackbarth et al.(1942) (2)
kbarth al. (1942)(6)	Hackbarth et al.(1942)	Herrmann (1973) Hackbarth et al.(1942)	Herrmann(1973) Baur(1919)(3) Kuhl(1937b)(3) Hackbarth et al.(1942)	Kuhl (1938)(4) Kuhl (1937b)(4) Hackbarth et al.(1942)(8)		Baur (1932) Baur (1924) Kuhl (1937b) Hermann (1973)	*	Kuhl (1938) (5) Kuhl (1937b) (5) Hackbarth et al.(1942) (7)	Kuhl (1936)(2) Hackbarth et al.(1942) (2)
					Günther and Rudolph (1970)		Kuhl (1938)(5)	*	
			Baur (1932)(2) Hackbarth et al.(1942)(2)			Baur(1924)(2)	Hackbarth et al.(1942)(2)	Hackbarth et al.(1942) (2) (7)	*

hmaler (1956) considered it to be a
ea Vol.3, Webb says that A. majus
lieri in the northern parts of the

d as a subspecies of A.majus in

5. Author used the name "A.molle mollissimum" which is a synonyn of A. hispanicum subsp. mollissimum.
7. Hackbarth et al.(1942) record A.majus from Cintra to be A.linkianum (P.61)
8. Hackbarth et al.(1942) record A.barrelieri from Chorro to be A. litigiosum (P.50).

There have been no reports of attempts to cross species within the Saerorhinum section of the genus.

C. Resistance to Rust in the Wild species

During the course of their investigations, a number of workers have examined the wild species for resistance to the rust. Their results are summarized in Table 7.5. In most instances, the resistance observed was complete although Mains (1935) reported a range in response within some of his samples and this is shown on the table.

Table 7.5 shows that many of the species contained races or at least some individuals with resistance to the early genotypes of the rust. Emsweller and Jones (1934) noted with interest that many of the European species showed resistance to the rust; they found this surprising because it seemed most unlikely that these species had been exposed to the disease during their evolution in the light of the Californian origin of the fungus (see Chaper 2).

Some points need consideration in the inspection of the table. Many species were recorded as completely resistant (immune) or susceptible without any indication of the sample size. The failure of some of the authors to check the identification of their material may cause confusion. They simply used the name and locality supplied with the seed by Baur, who had collected the species in Spain. If all authors used the same seed collected by Baur there should be no difficulty and one might expect similar results for the same species collected by Baur from the same locality. This is not the case; for example plants originating from seed of a single population of A. hispanicum Chav. (listed as A. glutinosum from "Orgiva") was reported to be totally susceptible by Emsweller and Jones (1934) and totally resistant by Mains (1935). Blodgett and Mehlquist (1941) also appear to have had problems with identification since they note in the Key to Symbols on their Table 4; "these two strains are quite different things" (referring to two lines of A. barrelieri), "Not A. glutinosum" for plants listed as A. glutinosum and "doubtful identity" for a line listed as A. hispanicum.

Therefore the information summarized in Table 7.5 should be interpretted with care, but it is safe to conclude that at least some individuals of certain species show resistance to the rust.

Table 7.5 Susceptibility of the wild species to the rust fungus *Puccinia antirrhini*

Name (* shows accepted name)	Blesdale (1903)(1919)	Arthur (1934)	Emsweller and Jones(1934)	Mains (1935)	Blodgett and Mehlquist (1941)
*A. valentinum Font. Quer				✓	✓
*A. sempervirens Lapeyr A. sempervirens Lapeyr				0 ✓	
*A. mollе L. 'Leriда' A. mollе L. 'Monsech' A. mollе L. 'Braganza'			✓ 0	 ✓	
*A. hispanicum Chev. 'Celorico' A. hispanicum Chav. A. hispanicum Chav. A. hispanicum Chav. A. hispanicum Chav. A. glutinosum 'Capileira' A. glutinosum 'Orgiva' A. glutinosum 'Lagerfels' A. glutinosum Boiss. et Raut.			✓ 0 ✓	 ✓ ✓ Variable ✓ 0 0 variable	 ✓
*A. meonanthum Hoff. & Link					✓
*A. siculum Miller A. siculum Ucr. A. assurgens	 ✓		0		✓
*A. barrelieri Boreau A. ibanjezii 'Cartagena' A. ibanjezii Rau A. litigiosum			0	✓	✓ ✓ ✓
*A. latifolium Miller A. latifolium Miller A. latifolium 'Mentone' A. latifolium D.C.				✓ ✓ ✓	 ✓
*A. majus L. 'Lucena' A. majus L. Loja A. majus 'Cintra' = linkianum A. linkianum A. tortuosum Bosc. A. tortuosum Bosc. A. tortuosum Bosc.			 ✓	0 variable variable variable variable ✓	✓ ✓ ✓
*A. multiflorum Penn. as A. clandulosum Lindl. as A. clandulosum Lindl.				 ✓ ✓	0
*A. coulterianum Benth.				✓	
*A. vexillocalyculatum Kellogg as A. vagans	 ✓			✓	
*A. nuttallianum Benth.	✓	✓		variable	
*A. virga Gray	✓	✓		0	
*Misopates orontium as A. orontium L.				variable	0
*Asarina procumbens as A. asarina L. A. asarina L.				0 0	
*Maurandia antirrhinifolia as A.maurandioides A Gray				0	

Key ✓ = susceptible, 0 = immune, variable = some individuals susceptible others immune

MATERIALS AND METHODS

1. Sources of Seed

Requests for seed of Antirrhinum species and related genera were sent to selected botanic gardens. A number of European species of Antirrhinum and some related genera were obtained as a result. The Californian species are not frequently grown in botanic gardens and it was much more difficult to find sources of the seed. Eventually two species A. multiflorum and A. virga were received from Dr. G.D. Barbe but these are not representative of the whole group so the author visited California and collected seed of all but one of the wild species. The report of the visit is included in Appendix 7.1

The source of the seed of all the species to which reference is made is given in Appendix 7.2. The identification of the species was checked with the description in Flora Europaea Vol.III for the European species and The California Flora (Munz and Keck, 1959) for the American species. In addition exsiccata of Antirrhinum species were examined at the Kew Herbarium and the British Museum. Exsiccata for all species used in this investigation are curated at the Department of Botany, Royal Holloway College, University of London.

2. Chromosome Preparation

The number of chromosomes in two of the American species, A. multiflorum and A. virga, were counted at metaphase of mitosis in squash preparations of root-tips stained in Feulgen's reagent by the method given in Darlington and La Cour(1969).

3. Self-Compatibility

Two plants of the following species of the Antirrhinum section of the genus were self-pollinated by hand in the greenhouse during the summer of 1978: A. australe, A. graniticum, A. majus subsp. majus, A. majus subsp. linkianum, A. majus subsp. tortuosum, A. meonanthum and A. siculum.

4. Interspecific hybrids

Crosses were made between A. majus cv. "Malmaison" and a number of wild species in order to explore the possibility of transferring genes for rust-resistance from the wild species. Reciprocal crosses were made between "Malmaison" and A. australe, A. barrelieri, A. graniticum,

A. hispanicum subsp. mollissimum, A. majus subsp. majus, A. majus subsp. linkianum, A. majus subsp. tortuosum, A. meonanthum, A. siculum, Asarina procumbens and Galvesia speciosa in a greenhouse during the summer of 1978. The F1 hybrids were grown in the grounds of the Botany Department, Royal Holloway College, Callow Hill, Virginia Water, Surrey during the summer of 1979.

5. Resistance to Rust

Some of the wild species (Appendix 7.2) were assessed for their susceptibility to the rust with

i) natural infection in the field and

ii) artificial infection in the greenhouse.

i) In the 1979 trials, three blocks in each plot were planted with eight species of Antirrhinum and one member of the related American genus, Galvesia. Thus six plants of each of the following species were exposed to natural infection: A. majus subsp. majus (78-7), A. meonanthum (78-10), A. majus subsp. tortuosum (78-159), A. siculum (78-24) A. nuttallianum (78-161), A. graniticum (78-106), A. sempervirens (78-108), A. barrelieri (78-110) and Galvesia speciosa (78-21). Five leaves of each plant were scored for rust infection using the standard diagram (Fig. 4.5).

ii) In the greenhouse plants of each species were sprayed with a suspension of uredospores (of isolate 7) in water. The suspension was either

a) sprayed onto the whole plant. The plant was covered with a plastic bag for 24 hours and then enclosed in an incubation tube (Fig.6.1) until pustules developed or the control variety "Malmaison" showed mature pustules; or

b) sprayed onto detached leaves which were placed on moist filter paper or mesh and suspended above the water in a petri dish (Fig. 6.2) or placed on rubber bands above the water (Fig.7.10). This arrangement was used for pubescent leaves which sank when placed on water.

The number of susceptible plants was counted within each species and expressed as a percentage of the total number of plants.

Figure 7.10 Detached leaves suspended by rubber bands above water in a petri dish.

RESULTS

1. Chromosome Numbers

The somatic number of chromosomes of two plants of each of two Californian species was determined. All plants examined were first generation raised from seed. The number of chromosomes are given in Table 7.6. There have been no previous chromosome counts for Antirrhinum virga.

Table 7.6 Somatic chromosome numbers of two Californian species of Antirrhinum

Species	Accession No. *	2n =
A. multiflorum	78 - 22	32
A. virga	78 - 176	32

* source and locality given in Appendix 7.2

2. Self Compatibility

The following species produced seed abundantly after self pollination:

78 - 7 *A. majus* subsp. *majus*,
78 - 15 *A. majus* subsp. *linkianum*,
78 - 19 *A. majus* subsp. *tortuosum*,
78 - 23 *A. siculum*,
78 - 25 *A. siculum*

These samples of the species are self-compatible. Three species did not set seed when self pollinated:

78 - 134 *A. graniticum*,
78 - 132 *A. meonanthum*,
78 - 133 *A. australe*.

These samples of the species are self-incompatible.

3. Interspecific hybrids

The attempted crosses and interspecific hybrids obtained are listed in Appendix 7.3 and the results summarized in Fig. 7.11. The Figure shows that most crosses between the wild species of *Antirrhinum* and the cultivar of *A. majus*, "Malmaison", are successful. Whereas attempts to produce hybrid seed by crossing "Malmaison" with two species of related genera allied to *Antirrhinum*, *Asarina procumbens* and *Galvesia speciosa* were unsuccessful. Some crosses within the genus *Antirrhinum* did not always produce seed; a hybrid between "Malmaison" and *A. hispanicum* subsp. *mollissimum* was only formed when *A. hispanicum* subsp. *mollissimum* was the pollen donor. When *A. hispanicum* subsp. *mollissimum* was the female parent pods were formed but these were empty. Although apparently viable seed was developed from all crosses between "Malmaison" and *A. meonanthum*, only one batch of seed germinated. The production of hybrids between "Malmaison" and *A. siculum* was the most difficult with only half of the crosses setting seed and only two batches of the produced seed being capable of germination.

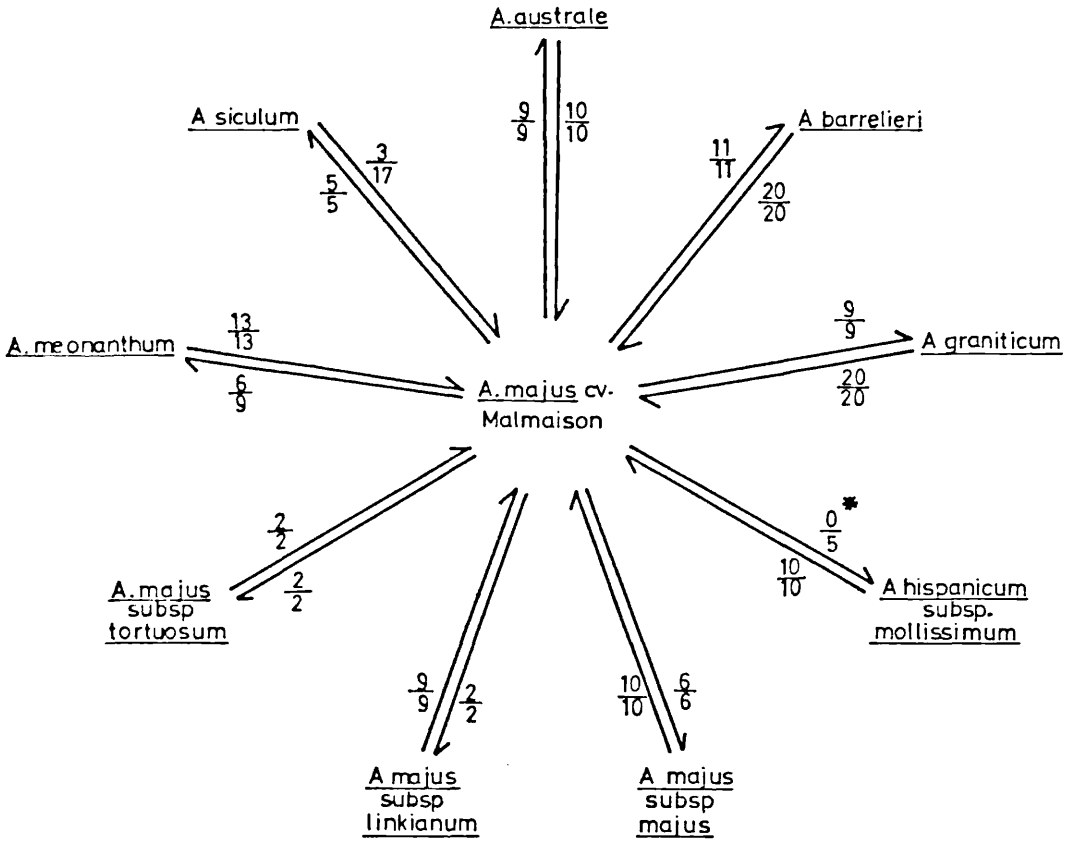
4. Resistance to Rust

i Natural infection

The mean score disease for each plant of the wild species is shown in Table 7.7. There was a greater mortality among the wild species than among the cultivated varieties of *A. majus*. Some plants of the species *A. majus* subsp. *tortuosum*, *A. siculum*, *A. graniticum*, *A. sempervirens* and *Galvesia speciosa* were entirely free of rust at the time of the second scoring, when virtually all the cultivated varieties had some signs of the disease. *A. meonanthum* was the most

susceptible species, some plants being attacked as severely as the susceptible cultivars of A. majus. On the whole, the wild species were less susceptible than the cultivated varieties.

Figure 7.11 Summary of crosses between wild species of the Antirrhinum section and A. majus cv. "Malmaison"



* two seed pods were produced but they were empty.
numerator = number of fruits developed
denominator = number of flowers crossed

ii Artificial inoculations

The results of the artificial inoculations (Table 7.8) shows that most species of Antirrhinum tested included some susceptible and resistant individuals. In five collections, A. barrelieri (78-107), A. graniticum (78-109), A. molle (78-28), A. siculum (78-25) and A. cornutum (79-46), all the plants tested were resistant. Other collections of two of these species, A. barrelieri and A. graniticum included some susceptible plants. It is noteworthy that the related genera did not show a single susceptible plant, an indication of the specificity of P. antirrhini.

Table 7.7 Susceptibility of wild species to natural infection by *Puccinia antirrhini*

Species	Accession Number	Royal Holloway College						Wisley					
		1st Score 25th August			2nd Score 21st September			1st Score 13th September			2nd Score 6th October		
		A	B	C	A	B	C	A	B	C	A	B	C
A. majus subsp. *majus*	78-7	1.0	1.0	1.0	-	1.2	1.6	1.8	-	-	1.4	-	-
A. meonanthum	78-10	-	-	1.0	-	-	2.2	4.6	2.6	2.0	-	2.4	-
A. majus subsp. *tortuosum*	78-159	1.0	1.0	1.0	1.0	1.2	1.2	1.2	-	1.4	1.6	-	1.4
A. siculum	78-24	1.0	1.0	1.0	1.0	-	1.0	2.0	-	1.0	3.2	-	1.0
A. nuttallianum	78-161	-	-	1.0	-	-	-	-	-	-	-	-	-
A. graniticum	78-106	1.0	1.0	1.0	1.0	1.4	1.0	1.6	1.4	1.2	3.0	2.6	1.2
A. sempervirens	78-108	1.0	1.0	1.0	-	1.0	1.0	1.2	1.0	1.0	2.0	1.2	-
A. barrelieri	78-110	1.0	1.0	1.0	1.6	1.4	-	1.8	-	1.0	-	-	-
Galvesia speciosa	78-21	1.0	1.0	1.0	1.0	1.0	1.0	-	-	-	-	-	-

A. B. C. INDICATE RANDOMIZED BLOCK (Fig.4.3, - indicates plant died)

Table 7.8 Susceptibility of Wild Species to artificial infection by *Puccinia antirrhini*

Species	Accession Number	No. of plants inoculated	% plants susceptible
A. European Species			
A. barrelieri	78-31	12	50
	78-107	12	0
A. braun-blanquettii	79-123	3	67
A. graniticum	78-134	12	8
	78-109	12	0
A. latifolium	79-121	12	25
	79-122	12	50
A. majus subsp. *cirrhigerum*	78-148	12	17
A. majus subsp. *linkianum*	78-139	10	40
A. meonanthum	79-120	12	8
	78-132	6	83
	79-98	10	10
A. molle	78-28	12	0
A. siculum	78-25	12	0
B. Californian species			
A. cornutum	79-46	3	0
A. coulterianum	79-50	2	100
A. kelloggii	79-57	6	83
A. nuttallianum	79-72	8	38
A. virga	78-176	7	28
C. Other genera			
Anarrhinum bellidifolium	78-149	5	0
Asarina erubescens	78-2	12	0
Asarina procumbens	78-117	5	0
Maurandia scandens	78-127	5	0
Misopates calycinum	78-146	10	0
Galvesia speciosa	78-21	10	0

DISCUSSION

1. Cytology

The somatic number of chromosomes, 2n = 32, for *A. multiflorum* agrees with other counts for this species (Munz, 1968). There have been no previous reports for the somatic number of chromosomes in *A. virga* but the count, 2n = 32, conforms with the present taxonomic distinction between the European and Californian sections (Rothmaler,1956). The uniformity of the chromosome counts suggests that the Californian species are anciently tetraploid and the two species *A. coulterianum* and *A. elmeri* which are 2n = 30 may be explained by a "polyploid drop". (Gunther and Rothmaler, 1963). None of the wild populations of the European species appear to be tetraploid which supports the hypothesis that the two sections of the genus were isolated a long time ago.

The present taxonomic division of the genus into two sections appears logical. The two sections are sufficiently similar in gross morphology to be considered parts of the same genus, but they are cytogenetically distinct and geographically isolated and the two sections may be worth subgeneric rank. In the Antirrhinum section speciation is largely due to gene mutation rather than chromosomal mutation. (Gunther and Rothmaler, 1963); few physiological barriers have developed and taxa must therefore be maintained either by ecological or geographical isolation. Kuckuck (1934) reports that many colonies of the Spanish species are more-or-less strongly geographically isolated and variation has continued within each local type. *A. siculum* appears to be the most distinct species within the Antirrhinum section and is geographically isolated from the others (Stubbe, 1966).

2. Self Compatibility

The European wild species of *Antirrhinum* may be divided into three distinct groups on account of their behaviour to self-pollination. The first contains *A. siculum*, the only natural self-compatible species (Baur, 1919). In the second are species such as *A. latifolium* and *A. tortuosum*, which are self-incompatible when young but at the end of their first year become self-compatible. The third group includes the majority of species; the wild populations are self-incompatible, although some of the cultivated forms of these species appear to be self-compatible. This mutation to self-compatibility was first reported in *A. majus* but it may also have occurred independently in other species where self-compatible mutants have been selected in cultivation.

Gruber (1932) reported a self-compatible race of A. hispanicum subsp. hispanicum (as A. glutinosum) from "Orgiva" and Lotsy (1913) reported a race of A. sempervirens to be self-fertile. The results of self-pollination in this study confirm that A. siculum is self-compatible, however, the three subspecies of A. majus were also self-compatible. These plants were received from botanic gardens so the self-compatible types may have been preferentially selected.

Despite the change to self-compatibility A. majus cultivars are intolerant of persistent selfing and suffer inbreeding depression. Therefore a programme of sib/sib mating to obtain homozygous lines has been suggested in the breeding strategy (Chapter 9). Perhaps the intolerance of selfing in A. majus cultivars may be circumvented genetically by incorporating self-compatibility genes from the naturally self-compatible species, A. siculum. Alternatively, one of the other species, which has undergone a mutation to self-compatibility, may not suffer the same degree of inbreeding depression if persistently inbred and may also be a useful source of self-compatible genes.

3. Interspecific Hybrids

Many authors have reported successful species crosses within the European section of the genus Antirrhinum (Table 7.4). The purpose of the crosses attempted in this investigation was to explore the possibility of transferring genes for rust-resistance in the wild species to cultivars of A. majus. Therefore crosses were confined to those between A. majus cv."Malmaison" and a selection of the European wild species. Many of the crosses confirmed those previously reported. In addition successful reciprocal crosses were made between "Malmaison" and A. australe and "Malmaison" and A. graniticum. Seed was obtained from the cross "Malmaison" X A. hispanicum subsp. mollissimum but the reciprocal was unsuccessful, although two pods were produced they were empty. Hackbarth et al (1942), however, reported a successful cross A. hispanicum subsp. mollissimum X A. majus. Two further, hitherto unrecorded, crosses were achieved between "Malmaison" and A. siculum and "Malmaison" and A. meonanthum. Harrison and Darby (1955) report that the cross between A. siculum and A. majus is only successful when A. siculum is the female parent. They appear to have used a self-compatible race of A. majus and perhaps the self-compatible cultivars of A. majus permit normal growth of the pollen tube of A. siculum.

These results indicate that there are a number of possible sources of genes for rust-resistance for A. majus. Three of these would be

relatively easy to use because there is a free exchange of genes:

i) between cultivars of A. majus

ii) between the cultivars (as represented by "Malmaison") and wild races of A. majus

iii) between A. majus sensu lato and most of the other Mediterranean species

A further two possible sources would be more difficult to use. Although there is no easy gene exchange between A. majus and related genera such as Asarina and Galvesia, it may be possible to utilize genes from these genera by more sophisticated methods of obtaining hybrids. It would also be interesting to know if barriers exist between A. majus and the Californian species. No systematic investigation has been reported and although some authors have recorded in passing that individual crosses have not been successful, they do not appear to have used the tetraploid A. majus as a parent.

This investigation has shown that genes conferring resistance to P. antirrhini can readily be transferred into cultivars of A. majus from most of the European wild species of Antirrhinum provided that the wild populations have been widely sampled. New techniques would be required to introduce genes from other genera and this would greatly increase the difficulty of the breeding although in view of their immunity this would clearly have potential in a programme for rust-resistance.

4. Resistance to Rust

Artificial inoculations of P. antirrhini on wild species showed that individual plants of some wild species are resistant to the disease. The resistance demonstrated in such tests is complete and may be conferred by one or more genes. The slight natural infection found on many of the European species in the trials of 1979 would suggest that many also possess a complex type of resistance. One might expect to find this type of resistance within some of the Californian species where the host and pathogen coexist in a balanced system but a number of the Californian species showed poor resistance in the artificial inoculations. These results do not conform to the hypothesis of using gene-centres as sources of disease resistance (Leppik,1968). If the two sections of the genus are as distinct as morphology and cytogenetics suggest, it is surprising that any of the European species are susceptible. The resistance of individual plants, however, is more difficult to explain since these species do not appear to have been exposed to the pathogen in the course of their evolution.

CHAPTER EIGHT

HORTICULTURAL ASSESSMENT OF VARIETIES

INTRODUCTION

An efficient plant breeding programme for rust-resistant antirrhinums should not concentrate solely on rust-resistance. The early breeding work in America placed a great emphasis on 100% resistance while disregarding other characters. Consequently the quality of the breeding material deteriorated and the resulting plants, which had small magenta flowers, were not commercially acceptable (White, 1933).

Before commencing on another plant breeding programme it would be advantageous to know if nonspecific resistance is similarly associated with any particular morphological features of antirrhinum. Therefore the height, stage of flowering and the colour of the corolla of the lines grown in the trials were compared with the recorded value for disease severity. In addition the quality of the varieties was assessed since rust-resistant lines must perform as well as susceptible varieties in the absence of the disease if they are to be commercially acceptable.

The dwarf varieties, "Sweetheart" and "Pixie", included many of the most susceptible lines in the 1978 trials and it seemed that rust-resistance might be associated with the height of the plant. The compact habit of the dwarf varieties results in the leaves being very close together, which permits a more efficient transfer of spores, while the greater humidity between the leaves may have increased the proportion of successful infections.

During the course of this investigation several commercial seed producers have mentioned that the disease is never a problem until the varieties are flowering. Some varieties may therefore appear to be more resistant simply because they flowered later.

Many authors have reported rust-resistance to be related to flower colour. Doran (1921) reported more resistance among white-flowered varieties and Zillig (1935) also found that a white-flowered variety remained healthy whilst a "clear red-coloured" variety was susceptible. Buchwald (1936) reported that pink and red-flowered varieties tended to have a higher susceptibility than white and yellow-flowered varieties

Herr Stadtgarnter Albrecht (Blumer, 1935) considered varieties with "clear-flower colours" to be particularly susceptible and Andres (1935) found that rust sometimes attacked red varieties and at other times white-flowered varieties. While breeding for resistance, White (1943) found the flower colour of his resistant lines was restricted to white, yellow and shades of pink; he reported that resistant plants with bronze-foloured flowers were difficult to obtain. Later Sampson (1960) showed that a gene for rust-resistance was linked to two colour genes, Eos and Inc. Eos converts the flower colour from pink to magenta and Inc from ivory to dark magenta.

The uniformity of each variety was assessed as a measure of homozygosity. Emsweller and Jones (1934) found the breeding programme for rust-resistant antirrhinums was quicker if both parents were homozygous. The quality of the habit and the flowering spike is important since a horticulturally acceptable plant must be the aim of a plant-breeding programme.

METHODS

1. Comparison between disease severity and phenotype of the variety.

a) height

The average height of each variety was measured and compared with the average value for disease severity using a correlation coefficient.

b) stage of flowering

The flowering stage of each variety was scored on a five-point scale (Table 8.1) at both plots and the average score was compared with the average value for disease severity using a correlation coefficient.

c) colour

There was no convenient method of quantifying the flower colour of each variety. The varieties were therefore grouped in the three main colours of the pigment pathway; white, yellows including oranges and red including purples. The median value for disease severity was found and the number of varieties in each colour group above and below the median was counted. A χ^2 value was found for the 2 X 3 contingency table.

Table 8.1 The five stages of flowering of Antirrhinum varieties, equivalent horticultural terms in parentheses.

1. bud stage:	even lowest flowers unopened ("in bud")
2. early flowering:	lowest flowers at anthesis but flowers in the middle of the spike unopened ("coming into flower")
3. full flower:	flowers in the middle of the spike at anthesis, with flowers above or below them ("at their best")
4. late flowering:	flowers in the middle of the spike now past anthesis ("past their best")
5. flowering completed:	all flowers withered and the unopened buds aborted ("flowering over")

2. Assessment of quality of varieties of Antirrhinum

A subjective assessment of three horticultural qualities was made for the varieties included in the plots in 1979. The qualities assessed were:

i the uniformity of height, habit and flowering stage of the plants;

ii the habit of the plants (that is its outline shape determined by the position and length of branches and the arrangement of the leaves;

iii the form of the flowering spike (the spike should remain compact and not elongate as it matures, the outline should be a pyramid and the tip should be neither square nor tail off).

An 'ideal' variety:

i is uniform in appearance and height

ii has a compact habit up to about 0·5m tall (many taller varieties require staking)

iii bears a "full-flowering" compact pyramidal spike of large showy flowers held above the leaves.

Each of the three qualities were scored on the three-point scale: 3 = good, 2 = moderate and 1 = poor.

3. Selection of varieties with good habit and an acceptable level of rust-resistance

In order to maintain the quality of the breeding material, the varieties selected as parents in the breeding programme should all be

horticulturally acceptable. The subsequent selection of lines with vigorous growth and a compact habit is just as important as selection for rust-resistance. The five criteria used to select suitable varieties for breeding are given in Table 8.2

Table 8.2 Criteria used to select varieties for the breeding programme

1. low susceptibility to the rust: at least less than three on Fig.4.5*
2. low rate of disease increase = apparent infection rate 'r'*
3. low percentage death as result of disease in September.*
4. vigorous growth = varieties are tolerant of some infection.
5. Horticultural quality: uniformity, habit and flowering spike

* N.B. These values are relative and it is difficult to set an absolute level for accepting varieties because it is dependent on the severity of the disease and the average susceptibility of the varieties.

RESULTS.

1. Comparison between disease severity and phenotype of the variety.

The height, stage of flowering and colour of each variety grown in the 1979 trials are shown in Table 8.3. Despite the range of heights (from 25cm. to 90cm.), the difference in flowering stages (from 1·5 to 4) and the range of colours (all shades found in antirrhinums were present), inspection shows no obvious relationship between any of these factors and susceptibility to rust. This is confirmed by the insignificant correlation between disease severity and height ($r = 0{\cdot}04$) and between disease severity and the stage of flowering ($r = 0{\cdot}09$). (Both these calculated values of r are less than the tabulated value, $r = 0{\cdot}21$, at 5% significance with 73 degrees of freedom). Similarly, the 2 X 3 contingency table used to measure association between disease severity and colour is shown in Table 8·4

Table 8.4 A 2 X 3 contingency table to measure association between disease severity and the colour of the variety.

		White	Yellow	Red
Disease severity	> Median	3	14	17
	< Median	7	12	15

χ^2 value of 1·88 with 2 degrees of freedom is insignificant ($p = 0{\cdot}3 - 0{\cdot}5$)

Table 8.3 Comparison of disease severity and phenotype of varieties of Antirrhinum listed in decreasing order of rust resistance. Combined results of both plots in 1979.

Code No.	Variety Name	Classification group [a]	Average rust score	height cm.	stage of flowering [b]	colour [c]
122	Wisley Golden Fleece	A	1.15	45	2	Y
126	Victory	A	1.16	45	2	R
128	Yellow Freedom	A	1.17	45	3	Y
62	Amber Monarch	A	1.17	40	3	Y
131	Variety S	B	1.25	60	4	M
110	Leonard Sutton	C	1.35	38	3	R
123	Toreador	C	1.36	45	3	R
74	Tetra Giant Ruffled	C	1.38	80	3	M
107	S. Rust Resistant Yellow	C	1.40	38	3·5	Y
124	Titan	C	1.41	45	2·5	R
108	S. Rust Resistant Pale Sulphur	C	1.42	38	3·5	Y
78	Kimosy Crimson	C	1.42	25	3·5	R
18	Variety E	D	1.46	40	2·5	R
68	Variety N	D	1.46	50	2	W
130	Bonfire	D	1.47	50	4	R
127	Yellow Freedom	D	1.47	40	3	Y
129	White Freedom	E	1.51	45	3·5	W
121	Wisley Cheerful	F	1.55	25	1·5	R
75	Kimosy Red	F	1.55	25	3·5	R
114	Kim Mid Rose	F	1.56	28	4	R
109	S. Rust Resistant Apricot	F	1.57	38	3	Y
72	Variety R	F	1.57	50	3·5	M
71	Variety D	F	1.58	60	2·5	M
76	Kimosy Delicate Rose	G	1.62	25	2	R
103	S. Intermediate Guardsman	G	1.65	38	2·5	R
119	Frontier Crimson	G	1.67	55	2	R
70	Variety P	G	1.70	45	3	M
80	Kimosy Orange	G	1.71	25	3·5	Y
81	Majestic Purple King	G	1.74	45	3	R
1	Pink Pixie	H	1.79	20	3·5	R
105	S. Intermediate Yellow	I	1.86	38	3·5	Y
106	S. Rust Resistant Orange Glow	I	1.86	38	2	Y
73	Burpee's Super Tetra	I	1.87	75	3	M
93	S. Triumph Mauve	I	1.88	43	2	R
15	Variety B	I	1.89	45	2·5	Y
45	Coronette Scarlet	I	1.91	40	3	R
52	Regal Yellow	I	1.93	48	4	Y
56	Yellow Monarch	I	1.94	40	3·5	Y
85	Majestic Orange King	I	1.97	45	3	Y
69	Variety O	I	1.98	40	3	M
95	S. Triumph White	I	1.99	43	3·5	W
100	S. Intermediate Fire King	I	2.01	38	2	R
117	Frontier White	I	2.03	55	2·5	W
86	Majestic Forest Fire	I	2.04	45	3·5	R
39	Carioca Yellow	I	2.05	43	3	Y
112	Kim Purple	I	2.05	28	4	R
118	Frontier Flame	I	2.10	55	3	R
89	Rocket White	J	2.13	90	2·5	W
94	S. Triumph Bright Orange	J	2.13	43	2·5	Y
101	S. Intermediate Bright Crimson	J	2.14	38	2	R
87	Majestic Eldorado	K	2.18	45	3·5	Y
79	Kimosy White	K	2.19	25	3	W
91	Rocket Orange	K	2.22	90	3	Y
98	S. Triumph Orange Salmon	K	2.25	43	3	R
104	S. Intermediate Eclipse	K	2.25	38	2·5	R
90	Rocket Red	L	2.29	90	2	R
77	Kimosy Primrose Yellow	L	2.31	25	4	Y
88	Rocket Citron Yellow	L	2.32	90	3·5	Y
92	Rocket Orchid	L	2.33	90	2	R
102	S. Intermediate Rich Apricot	M	2.37	38	3·5	Y
125	Orange Glow	M	2.38	45	2·5	Y
82	Majestic Celestial	N	2.42	45	3·5	W
29	Coronette pink	O	2.46	40	3	R
83	Majestic Snowstorm	O	2.49	45	4	W
99	S. Intermediate white	O	2.52	38	3	W
67	Malmaison	O	2.52	40	3	R
116	Kim Blood Red	O	2.53	28	4	R
84	Majestic Red Chief	O	2.54	45	2·5	R
115	Kim Deep Orange	O	2.55	28	3	Y
120	Frontier Yellow	P	2.59	55	2·5	Y
96	S. Triumph Primrose	P	2.60	43	2·5	Y
37	Carioca Bright Scarlet	P	2.62	43	3	R
111	Kim White	Q	2.69	28	4	W
113	Kim Primrose Yellow	R	2.83	28	4	Y
97	S. Triumph Scarlet	S	2.98	43	2·5	R

a. Classification of combined data (Figure 4.22) varieties followed by the same letter are more similar than those followed by different letters.

b. 1 = in bud, 2 = coming into flower, 3 = at their best, 4 = past their best, 5 = flowering over.

c. W = white, Y = yellow, R = red, M = mixture.

Table 8.5 The horticultural quality of varieties of Antirrhinum

Code No.	Variety Name	Uniformity *	Habit *	Flowering Spike *
1	Pink Pixie	3	3	2
15	Variety B	2	3	3
18	Variety E	1	2	3
29	Coronette Pink	3	3	3
37	Carioca Bright Scarlet	3	3	3
39	Carioca Yellow	2	3	3
45	Coronette Scarlet	2	3	3
52	Regal Yellow	3	3	3
56	Yellow Monarch	3	2	3
62	Amber Monarch	3	3	3
67	Malmaison	3	3	3
68	Variety N	2	2	2
69	Variety O	2	3	2
70	Variety P	2	2	3
71	Variety Q	2	2	2
72	Variety R	2	2	3
73	Burpee's Super Tetra	2	2	3
74	Tetra Giant Ruffled	2	2	3
75	Kimosy Red	3	3	3
76	Kimosy Delicate Rose	3	3	2
77	Kimosy Primrose yellow	2	2	2
78	Kimosy Crimson	3	3	3
79	Kimosy White	3	3	3
80	Kimosy Orange	3	3	3
81	Majestic Purple King	3	3	3
82	Majestic Celestial	3	3	2
83	Majestic Snowstorm	2	2	3
84	Majestic Red Chief	3	3	3
85	Majestic Orange King	2	2	3
86	Majestic Forest Fire	2	3	3
87	Majestic Eldorado	2	2	3
88	Rocket Citron Yellow	2	2	3
89	Rocket White	3	3	3
90	Rocket Red	2	3	3
91	Rocket Orange	3	3	3
92	Rocket Orchid	2	2	3
93	Suttons Triumph Mauve	3	3	3
94	Suttons Triumph Bright Orange	3	3	3
95	Suttons Triumph White	3	3	3
96	Suttons Triumph Primrose	2	2	3
97	Suttons Triumph Scarlet	2	2	3
98	Suttons Triumph Orange Salmon	2	3	3
99	Suttons Intermediate White	2	2	3
100	Suttons Intermediate Fire King	3	3	3
101	Suttons Intermediate Bright Crimson	3	3	3
102	Suttons Intermediate Rich Apricot	2	3	2
103	Suttons Intermediate Guardsman	3	3	3
104	Suttons Intermediate Eclipse	2	3	3
105	Suttons Intermediate Yellow	2	2	2
106	Suttons RR Orange Glow	3	3	3
107	Suttons RR Yellow	3	3	3
108	Suttons RR Pale Sulphur	2	3	2
109	Suttons RR Apricot	2	3	3
110	Suttons RR Leonard Sutton	2	3	3
111	Kim White	3	3	3
112	Kim Purple	3	3	3
113	Kim Primrose Yellow	3	3	3
114	Kim Mid Rose	3	3	3
115	Kim Deep Orange	3	3	3
116	Kim Blood Red	3	3	3
117	Frontier White	2	3	3
118	Frontier Flame	3	3	3
119	Frontier Crimson	3	3	3
120	Frontier Yellow	3	3	3
121	Wisley Cheerful	3	3	3
122	Wisley Golden Fleece	3	3	3
123	Toreador	2	3	3
124	Titan	2	3	3
125	Orange Glow	3	3	3
126	Victory	3	3	3
127	Yellow Freedom	3	3	3
128	Yellow Freedom	3	3	3
129	White Freedom	3	3	2
130	Bonfire	2	3	3
131	Variety S (tetraploid)	2	2	2

* 3 = good, 2= moderate, 1 = poor.

2. Assessment of the quality of varieties of Antirrhinum

The results of the assessment of the quality of varieties included in the plots in 1979 is given in Table 8.5. The majority of the commercial varieties had high scores whereas breeder's lines and old garden varieties were less uniform and generally not such attractive plants.

3. Selection of varieties with good habit and an acceptable level of rust-resistance.

On the basis of the five criteria (Table 8.2), the selection of promising varieties with respect to low susceptibility was given in Table 4.19, the varieties with a low rate of disease increase in Table 4.21, and varieties with low percentage death in Table 4.22. Inspection of these three tables reveals that some varieties notably "Bonfire", "Titan", "Yellow Freedom" (No. 128), "White Freedom", "Amber Monarch", "Coronette Bronze" and "Suttons Rust-Resistant Pale Sulphur" occurred in all three lists. These were the most resistant of all the one hundred and thirty-one varieties tested. Other varieties appeared in two of the lists; "Wisley Golden Fleece", "Victory", "Toreador", "Carioca White", "Carioca Peach Bronze", "Scarlet Monarch", "Crimson Monarch", "Coronette Cherry", "Suttons Rust-Resistant Yellow", "Suttons Rust-Resistant Orange Glow", "Suttons Rust-Resistant Leonard Sutton" and "Suttons Intermediate Guardsman" and all these had an acceptable level of resistance.

The varieties included in just one list were considered individually and some were found to be potentially important for special reasons. "Coronette White", whilst not as resistant as the varieties already mentioned, survived until the second scoring in the severe rust infection at Royal Holloway College in 1978. "Regal Bright Scarlet" also survived until the second scoring at Royal Holloway College in 1978 and although its resistance is not as good as some other red varieties, it is the only commercially available red variety in this height category. The variety, "White Monarch", performed well at Royal Holloway College but did not do so well at Wisley; nevertheless it is still one of the most resistant white varieties. "Carioca Yellow" had reasonably low values for disease severity and borderline 'r' values in both plots. The variety "Frontier Crimson", is the tallest variety with some degree of rust-resistance and "Majestic Purple King" is the best purple flowered variety. The old 'rust-resistant' variety, "Wisley Cheerful" has a rather high mortality but low values for disease severity and reasonably low values for 'r'; it has an attractive dwarf habit but tends to be

rather late flowering. Nevertheless, it has the potential for improvement and it may be possible to develop an earlier-flowering line. The best varieties judged from their rust-resistance and habit at Royal Holloway College and Wisley are listed in Table 8.6.

In addition to these varieties the tetraploid "Tetra Giant Ruffled" satisfied the first three criteria (Table 8.2) and was therefore within the most resistant group but it had lower values for habit and uniformity. Many of the breeders lines would also have been included in Table 8.6 but they have been omitted because they are not commercially available and are not as uniform as many of the varieties.

Table 8.6 Recommended varieties which were acceptably resistant to the rust in the 1978 and 1979 trials held at two plots in Surrey

height cm.	predominant colour					
	white	yellow	orange	pink	red	purple
>50					Bonfire * Frontier Crimson	
45–49	White Freedom*	Yellow Freedom* Wisley Golden Fleece*			Titan* Toreador* Victory* Regal Bright Scarlet	Majestic Purple King
40–44	Carioca White Coronette White White Monarch	Carioca Yellow	Amber Monarch Coronette Bronze Coronette Peach Bronze		Scarlet Monarch Crimson Monarch Coronette Cherry	
35–39		Suttons Rust Resistant – Pale Sulphur – Yellow	Suttons Rust Resistant – Orange Glow	Suttons Rust Resistant Leonard Sutton	Suttons Intermediate Guardsman	
30–34						
25–29				Wisley Cheerful*		

* old rust-resistant varieties released in the 1950's.

DISCUSSION

The results show that, in the varieties tested, rust-resistance is not related to any particular type of antirrhinum. The severe infection on the dwarf lines "Sweetheart" and "Pixie" early in the season in 1978 may have been due to the extreme susceptibility of American lines in Britain. Since the disease does not appear in the field until at least some varieties are in flower it was thought that disease severity may be associated with the stage of flowering. The insignificant correlation coefficient shows that there was no such association within any one variety.

Despite the contradictory report of the association of rust-resistance with flowers of a particular colour, there was no correlation among the varieties tested. The authors who reported a correlation were working with a major gene for resistance and the differences in their results may be explained by the linkage of the gene for rust-resistance to Eos and Inc (Sampson, 1960). The resistance exhibited in the present day varieties does not appear to be controlled by a major gene although some varieties very probably still possess this gene. It is unlikely that a relationship between polygenic resistance and colour will be found among the present-day varieties, at least until something is known about the inheritance of this type of resistance in antirrhinum.

The varieties which are recommended (Table 8.6) do not cover the full height or colour range known in antirrhinum; in particular resistance is lacking among dwarf varieties. However, once an acceptable level or rust-resistance has been demonstrated among the intermediate types, it should be possible to incorporate the genes for resistance into dwarf types.

It is interesting that the table contains so many of the first British 'rust-resistant' (i.e. immune) varieties (marked with an asterisk in Table 8.6). These varieties were released in the 1950's and started to lose their immunity late in 1962 (Green, unpublished); they were then gradually withdrawn from the seed catalogues. The early breeding programmes for rust-resistance were based on a few immune plants and the resistance obtained appears to have been controlled by a major gene (Chapter 3). If this gene was the sole source of their resistance, the plants would have been expected to succumb to severe rust infection soon after 1962. They were, however, only slowly withdrawn and it is surprising that they performed so well in the trials held in 1979.

There appear to be two possible explanations. The first involves the concept of "stabilising selection" (Van der Plank, 1968). Van der Plank believes that vertical genes in the host influence the selection and survival of virulence genes in the pathogen. He suggests that simple races of the pathogen become more complex by acquiring virulence genes to match the vertical resistance in the host. As the rust-resistant antirrhinums become more widely grown, virulent races in the pathogen population would have a selective advantage because they would be able to attack the 'rust-resistant' antirrhinums. Therefore the proportion of virulent races (g_2) in the pathogen population would increase. The "boom and bust" cycle appears; the scarcity of virulence allows the "boom" and the adaption of this virulence causes the "bust". Once the 'rust-resistant' varieties were withdrawn the selective advantage disappears, stabilizing selection operates and unnecessary virulence genes are lost. Therefore when old rust-resistant varieties are grown again in 1979 they appear to be resistant because virulent races of the rust are now an insignificant proportion of the pathogen population. This sequence of events is summarized in Figure 8.1.

Figure 8.1 A speculation on the effect of stabilizing selection on the relative proportions of races g_1 and g_2 in the population of Puccinia antirrhini following Van der Plank's concept of 'stablizing selection'.

Year	Relative proportions of rust genotypes g_1 and g_2	Van der Plank's Model	Explanation in Antirrhinum
<1962		g_1 is predominant race and varieties with major gene R_1 are resistant	Immunity operative
1963		Major gene resistance R_1 is broken as proportion of g_2 increases	"Immune" varieties now susceptible
1969		Proportion of g_2 increases further	RHS Trial of Rust resistant Antirrhinums abandoned - all stocks infected with rust.
1974		Proportion of g^2 decreases as selective advantage disappears.	Varieties with major gene resistance R_1 withdrawn
1979		Proportion of g^2 decreases further	Varieties with major gene R_1 only slightly susceptible

This concept has met with mixed reaction. It has been evaluated by Nelson (1973, pp 58-65). The principal objections appear to surround

the statement that complex races revert to simple races. Van der Plank (1975) has qualified his earlier concept by the statement that stabilizing selection operates "if virulence reduces [the rust's] fitness to survive when it [the virulence] is unnecessary" (page 184). Presumably if the virulent race is also aggressive it may not be affected by stabilizing selection and will remain in the population. There are a number of cases reported where unnecessary virulence genes have not been lost (see Nelson, 1973). For example, one of the most prevalent strains of Puccinia recondita in Australia contains virulence genes which are not needed to attack the commonly grown wheats (Watson, 1970). Thus, there is data both to support and refute the concept of stabilizing selection. It is by no means universal and further tests would be required to see if this sequence of events may have occurred within antirrhinum varieties.

The second and alternative explanation is based on a comment in the report of the Royal Horticultural Society's Trial of Rust-Resistant Antirrhinums in 1969 (RHS unpublished). No awards were made at that trial because no stocks were entirely free of rust, but a number of the varieties had only slight infection: that is some plants of the stock had light infection and others remained free of disease. Therefore the loss of resistance in these varieties was not as dramatic as was generally believed; immunity was lost but they still possessed some resistance. A long breeding programme for specific resistance often reduces the amount of non-specific resistance because the major gene masks the cumulative effect of the minor genes and there is no selection for the latter (Parlevliet and Kuiper, 1977). This is known as the Vertifolia effect (Van der Plank, 1968). Minor gene resistance, however, does not always seem to be lost in the absence of positive selection. In the case of antirrhinums, the polygenic resistance present in Mains' breeding material may have been retained unconsciously, especially since the majority of generations were selfed. The degree of resistance found in the old rust-resistant varieties in 1979 may have been the same as it was in 1962 when immunity was lost. Perhaps there were other reasons for the withdrawal of these varieties. Ralph Gould (personal communication) suggested that the plants were inferior on account of their smaller flowers and later flowering period. In addition the plants were shy seeders (this may have been due to the prolonged inbreeding in a naturally outbreeding species) and there was also a drop in demand as other bedding plants became available. Thus it would seem that the loss of immunity to the rust was only one factor in the withdrawal of these varieties.

CHAPTER NINE

STRATEGY FOR IMPROVEMENT OF ANTIRRHINUMS

A. OBJECTIVES

Van der Plank (1963) describes two main objectives of a plant breeding programme; to achieve the highest yield and the highest quality. Disease reduces both the yield and quality and therefore breeding for resistance is necessary. Breeding for resistance, however, may conflict with the primary aims and often results in limiting genetic diversity and thus increasing genetic vulnerability (Cowling, 1978). In the past, the quality and seed yield of rust-resistant antirrhinums have been ignored in the attempt to obtain lines with immunity; indeed, the early British rust-resistant varieties appear to have been withdrawn mainly because they were inferior to other commercially available varieties. Thus the objectives of a new breeding programme should be a stable and durable type of resistance in lines which would compare favourably with the quality of susceptible varieties in the absence of disease.

B. BREEDING SYSTEM

The majority of wild populations of Antirrhinum species are self-incompatible (S.I.) but the garden races of A. majus are self-compatible (S.C.) (Baur 1924 and 1932). In S.I. cultivated plants, S.C. arises by mutation; S.C. types are subsequently favoured in horticulture because they breed true and usually have a high yield of seed.

Lewis and Crowe (1958) studied unilateral incompatibility in flowering plants and considered A. majus to occupy an intermediate position between S.C. and S.I. on account of the behaviour of its pollen on styles of other species of Antirrhinum. They found that the pollen of S.C. A. majus was similar to other S.I. species and grew uninhibited on both S.C. and S.I. species. They concluded that the garden A. majus had only recently become S.C. by mutation and selection.

Baur (1924) believes that the garden races are generally outbred in spite of their self-fertility. This self-fertility has been utilized in breeding, after hybridization and selection, to obtain homozygous lines by persistent self-pollination. Many breeders reported decreased vigour and increased sterility within the progeny as inbreeding progressed

(Emsweller and Jones, 1934; Mains, 1935). "Inbreeding depression" occurs in some facultatively outbred species after prolonged inbreeding: perhaps this occurs in A. majus. Certainly the practice of developing true-breeding varieties by selfing may have inherent defects. An alternative and improved method would be to treat the plant as S.I. and obtain lines homozygous for horticultural qualities by sib/sib mating. During multiplication by the trade, open pollinations prevail and this would preserve the genetic diversity of the varieties for characteristics other than horticultural qualities.

C. INHERITANCE OF COLOUR

Antirrhinum majus is noted for a wide range of corolla colours; the distinguishing feature of many varieties. Accordingly the colour of the corolla cannot be ignored in the objectives of a breeding programme. The colour is due to the presence of flavonoids which have been thoroughly investigated (Harborne, 1967). In cultivars of A. majus there are five classes of flavonoids (aglycones) each with a different pattern of glysosylation. Thus anthocyanins typically occur as - 3 rutinosides, flavonols as -3 glucosides, flananones as -7 rutinosides, flavones as 7 glucuronides and aurones as -6 glucosides (Harborne, 1967). The pigments found in each class of flavonoid in A. majus are listed in Table 9.1

The range of colours found in the corolla of the cultivated forms of A. majus are the result of various combinations of these pigments. Thus magenta flowers contain pure cyanidin; scarlet - cyanidin and aurones; pink - pure pelargonidin; apricot - pelargonidin and aurones; yellow - aurones and ivory - apigenin and luteolin. The pure white occasionally found in antirrhinum is completely lacking in flavonoids. Although these are the main pigments that are responsible for flower colour, there are some minor flavonoids which accompany the more important pigments. The pigment constitution of the main colour types has been analysed by chromatography (Dayton,(1956)and Sherratt (1958))and chemical analyses (Jorgensen and Geissman (1955); Geissman and Harborne (1955) and Seikel (1955)). The pigments found in different colour types by Dayton (1956) and Harborne (1967) are compared in Table 9.2. The important features include the presence of Apigenin 7 glucuronide in all except the pure white and the association between each anthocyanidin and a different flavonol.

The basic pathway of flavonoid synthesis is common to all higher plants and the many steps are frequently controlled by single independent genes. The naming of these genes in antirrhinum is confused because people in England, Germany and America have all worked on the inheritance of colour and used different symbols for the same pigment genes. Table 9.3 gives a comparison of the more important pigment genes.

Table 9.1 Corolla pigments of Antirrhinum majus

Flavonoid Class	Pigments	Reference
Cinnamic Acid	p Coumarylglucose	Harborne & Corner (1961)
	Caffeylglucose	Harborne & Corner (1961)
	Ferulylglucose	Harborne & Corner (1961)
Flavanone	Naringenin 7 glucoside	Seikel (1955)
	Naringerin 7 rhamnosylglucoside	Seikel (1955)
Flavones	Apigenin 7 glucuronide	Seikel (1955)
	Apigenin 7, 4' diglucuronide	Harborne (1963)
	Luteolin 7 glucuronide	Harborne (1963)
	Chrysoeriol 7 glucuronide	Harborne (1963)
Chalcones	Chalcononaringenin 4 gluco	Gilbert (1973)
	3, 4, 2', 4', 6' pentahydroxy chalcone 4' glucoside	Gilbert (1973)
	C_3 - unidentified	Gilbert (1973)
Aurones	Aureusidin 6 glucoside	Geissman & Harborne (1955)
	Bractaatin 6 glucoside	Harborne (1963)
Flavonol	Quercetin 3 glucoside	Jorgensen & Geissman (1955b)
	Quercetin 3 rhamnoglucoside	Fincham (1962)
	Kaempferol 3 glucoside	Harborne (1963)
	Kaempferol 3, 7, diglucoside	Harborne (1963)
Anthocyanins	Cyanidin 3 rutinoside	Scott Moncrieff (1930)
	Cyanidin 3 glucoside	Gilbert (1971)
	Pelargonidin 3 rutinoside	Harborne & Sherratt (1951)

The inheritance of anthocyanins in A. majus has been determined by Strickland and Harrison (1974) and by Harrison and Strickland (1974). They found that the gene nivea (niv) blocked all flavonoid synthesis; the gene incolorata (inc) blocked flavanonol synthesis; the gene eosinea (eos) controlled the production of pelargonidin and cyanidin and the gene pallida (pal) acted as a late block after flavanonol synthesis. Pal has a series of recessive alleles which reduce the quantity of anthocyanin: thus pallida rubra (pal rub) is pale red, pallida carnea (pal car) is flesh coloured, pallida rhode (pal rhod) is pale flesh coloured, pallida tincta (pal tin) and pallida recurrens (pal rec) are ivory (Stubbe 1966). The position of the four genes in the biosynthetic pathway of flavonoids as described by Strickland and Harrison (1974) is shown in Figure 9.1. Thus a plant homozygous for niv is pure white with no flavonoid production. The recessive inc/inc produces flavones and

Table 9.2 Pigments of *Antirrhinum majus* colour types

Corolla Colour †	ANTHOCYANIDINS: Cyanidin	ANTHOCYANIDINS: Pelargonidin	FLAVANOLS: Quercetin	FLAVANOLS: Kaempferol	FLAVONES: Luteolin	FLAVONES: Chrysoeriol	FLAVONES: Apigenin	FLAVANONE: Naringenin	AURONES: Aureuridin	AURONES: Bracteatin
Magenta (1)	+	–	+	–	+	+	+	–	T	T
Magenta (2)	+	–	+	–	+	*	+	*	–	–
Crimson (2)	+	–	+	–	–	*	+	*	+	+
Crimson (2)	+	–	+	–	+	*	+	*	+	+
Orange Red (1)	+	–	+	–	+	+	+	–	+	+
Scarlet (2)	–	+	–	+	–	*	+	*	+	+
Pink (1)	–	+	–	+	–	–	+	+	T	T
Apricot/Pink (2)	–	+	–	+	–	*	+	*	–	–
Orange Yellow (1)	–	+	–	+	–	–	+	+	+	+
Yellow (1)	–	–	–	–	+	+	+	X	T	T
Yellow (1)	–	–	–	–	–	–	+	+	+	+
Yellow (2)	–	–	–	–	–	*	+	*	+	+
Yellow (2)	–	–	+	–	–	*	+	*	+	+
Yellow (2)	–	–	+	–	+	*	+	*	+	+
Ivory (1)	–	–	–	–	+	+	+	X	T	T
Ivory (1)	–	–	–	–	–	–	+	+	T	T
Ivory (2)	–	–	–	–	–	*	+	*	–	–
Ivory (2)	–	–	+	–	–	*	+	*	–	–
Ivory (2)	–	–	+	–	+	*	+	*	–	–
White (1)	–	–	–	–	–	–	–	–	–	–
White (2)	–	–	–	–	–	*	–	*	–	–

† (1) = Harborne (1967)

(2) = Dayton (1956) NB. Sherratt (1958) named some of Dayton's unidentified pigments:- Pigments 6 and 7 as kaempferol derivatives. Pigment 5 as Apigenin 7 gluc-uronide Pigment 4 was inferred to be a quercetin derivative but it appears that it could also have been chrysoeriol.

+ = present

– = absent

* = not described by Dayton

T = Trace

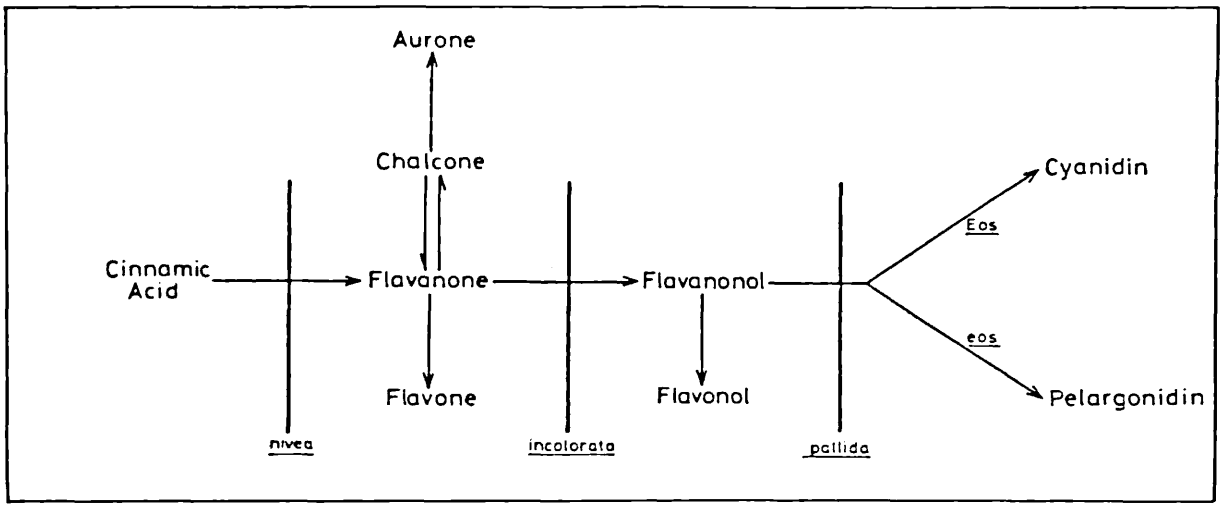
X = symbol not included in key by Harborne (1967) Page 255

Table 9.3 Comparison of the set of symbols used by different workers for the pigment genes in Antirrhinum majus

Action of gene / Principle Users	ENGLAND	GERMANY	AMERICA		PRESENT
	Wheldale (1907) Wheldale (1914) Wheldale & Bassett (1914) Dayton (1956) Sherratt (1958)	Baur (1910) Baur (1912) Baur (1924)	Haney (1954)	Seikel (1955) Harborne (1963) Harborne (1967)	Baur (1932) Sampson (1960) Strickland & Harrison (1974) Harrison & Strickland (1974)
Basic flavonoid production (recessive plants contain no flavonoids)	y	b	w	n	niv
Basic anthocyanin production	l	f	iv	p	inc
Modification of anthocyanin (dominant = cyanidin recessive = pelargonidin)	b	a	dil	m	eos
Suppression of aurone	i	c	y	y	sulf

aurones but no flavonols or anthocyanidins. Therefore each gene acts as a block in the biosynthetic pathway and anthocyanidins are only naturally produced when at least one allele of both niv and inc is in the dominant (wild type) condition

Figure 9.1 Gene control in the biosynthetic pathway of flavonoids (after Strickland and Harrison, 1974)



By comparison with the knowledge of the inheritance of the pink and purple pigments, the genes controlling the yellow pigments are not so thoroughly understood. Baur (1932) described a gene sulfurea (sulf) which is responsible for the yellow corolla in plants homozygous for inc (i.e. when there is no red pigment). Sulf$^+$ is incompletely dominant over sulf and sulf$^+$/sulf$^+$ corollas are always ivory. The intensity of the yellow is modified by the gene eburnea (ebu) such that sulf/sulf, ebu/ebu produces medium yellow and sulf/sulf, ebu$^+$/ebu$^+$, dark yellow.

The genotype of the main corolla colours found in A. majus can be deduced from the pigments responsible for the colour (Table 9.2) and the pigment pathway (Fig. 9.1) and the two ends of the range of these genotypes are given in Table 9.4. Each colour is determined by the condition of relatively few genes: thus all pure white flowers are niv/niv; all ivory are inc/inc and sulf$^+$/sulf$^+$; all yellow are inc/inc and sulf/sulf; crimson are inc$^+$/inc, sulf/sulf, eos$^+$/eos and magenta inc$^+$/inc, sulf$^+$/sulf$^+$, eos$^+$/eos. Both orange and scarlet varieties are inc$^+$/inc, sulf/sulf, and eos/eos but the actual hue depends upon the state of the yellow modifying gene ebu and the recessive allele of the pallida series.

Our present knowledge of the inheritance of colour enables us to predict the segregation for colour in the F_2 generation of a cross between

Table 9.4 Genotype of Corolla colours found in A. majus

White	niv	niv	inc	inc	sulf	sulf	ebu	ebu	pal	pal	eos	eos
	niv	niv	inc$^+$	inc$^+$	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
Ivory	niv$^+$	niv	inc	inc	sulf$^+$	sulf$^+$	ebu	ebu	pal	pal	eos	eos
	niv$^+$	niv$^+$	inc	inc	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
Pale Yellow	niv$^+$	niv	inc	inc	sulf$^+$	sulf	ebu$^+$	ebu	pal	pal	eos	eos
	niv$^+$	niv$^+$	inc	inc	sulf$^+$	sulf	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
Mid Yellow	niv$^+$	niv	inc	inc	sulf	sulf	ebu	ebu	pal	pal	eos	eos
	niv$^+$	niv$^+$	inc	inc	sulf	sulf	ebu	ebu	pal$^+$	pal$^+$	eos$^+$	eos$^+$
Dark Yellow	niv$^+$	niv	inc	inc	sulf	sulf	ebu$^+$	ebu$^+$	pal	pal	eos	eos
	niv$^+$	niv$^+$	inc	inc	sulf	sulf	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
Orange	niv$^+$	niv	inc$^+$	inc	sulf	sulf	ebu$^+$	ebu$^+$	pal$^+$	pal	eos	eos
	niv$^+$	niv$^+$	inc$^+$	inc$^+$	sulf	sulf	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos	eos
Scarlet	niv$^+$	niv	inc$^+$	inc	sulf	sulf	ebu	ebu	pal$^+$	pal	eos	eos
	niv$^+$	niv$^+$	inc$^+$	inc$^+$	sulf	sulf	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos	eos
Crimson	niv$^+$	niv	inc$^+$	inc	sulf	sulf	ebu	ebu	pal$^+$	pal	eos$^+$	eos
	niv$^+$	niv$^+$	inc$^+$	inc$^+$	sulf	sulf	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
Magenta	niv$^+$	niv	inc$^+$	inc	sulf$^+$	sulf$^+$	ebu	ebu	pal$^+$	pal	eos$^+$	eos
	niv$^+$	niv$^+$	inc$^+$	inc$^+$	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
Pink	niv$^+$	niv	inc$^+$	inc	sulf$^+$	sulf$^+$	ebu	ebu	pal$^+$	pal	eos	eos
	niv$^+$	niv$^+$	inc$^+$	inc$^+$	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos	eos

two different coloured plants. The expected results of crosses between ivory and each of the main colours is shown in Table 9.5. For simplicity the genes in both parents are in their homozygous state and all genes, which are not expressed in the phenotype, are in their "wild type" condition. Consequently all the F_2 ratios show the maximum proportion of plants with the dominant magenta pigmentation. If some of the genes were in the heterozygous condition, the proportion of magenta flowered plants would be decreased and the proportion of other shades correspondingly increased. Table 9.6 shows an example of the theoretical results of a cross between an ivory and a pink-flowered plant with just three genes in the heterozygous condition. The proportion of magenta progeny was decreased from 56% to 25% while the percentages of pink progeny increased from 19% to 25% and ivory from 25% to 50%.

The predominance of magenta progeny in previous breeding programmes may have been because the genes in at least one parent were in the "wild

type" condition. Since the proportion of magenta progeny is rarely more than 60%, one can only presume that the breeders were working with a small number of plants and selection for rust-resistance was so strong in the early stages that selection for colour was ignored.

Table 9.5 Theoretical segregation for colour in crosses between an ivory-flowered plant and each of the other main colour types

Ivory	niv$^+$	niv$^+$	inc	inc	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$	
X													
Magenta	niv$^+$	niv$^+$	inc$^+$	inc$^+$	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$	
F_1	niv$^+$	niv$^+$	inc$^+$	inc	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$	
F_2	Magenta 75%												
	Ivory 25%												
Ivory	niv$^+$	niv$^+$	inc	inc	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$	
X													
Crimson	niv$^+$	niv$^+$	inc$^+$	inc$^+$	sulf	sulf	ebu	ebu	pal$^+$	pal$^+$	eos$^+$	eos$^+$	
F_1	niv$^+$	niv$^+$	inc$^+$	inc$^+$	sulf$^+$	sulf	ebu$^+$	ebu	pal$^+$	pal$^+$	eos$^+$	eos$^+$	
F_2	Magenta 55%												
	Crimson 20%												
	Ivory 19%												
	Yellow 6%												
Ivory	niv$^+$	niv$^+$	inc	inc	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$	
X													
Scarlet	niv$^+$	niv$^+$	inc$^+$	inc$^+$	sulf	sulf	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos	eos	
F_1	niv$^+$	niv$^+$	inc$^+$	inc	sulf$^+$	sulf	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos	
F_2	Magenta 39%												
	Crimson 14%												
	Pink 16%												
	Scarlet 6%												
	Ivory 19%												
	Yellow 6%												
Ivory	niv$^+$	niv$^+$	inc	inc	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$	
X													
Pink	niv$^+$	niv$^+$	inc$^+$	inc$^+$	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos	eos	
F_1	niv$^+$	niv$^+$	inc$^+$	inc	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos	
F_2	Magenta 56%												
	Pink 19%												
	Ivory 25%												

Table 9.5 continued

Ivory	niv$^+$	niv$^+$	inc	inc	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
X												
Orange	niv$^+$	niv$^+$	inc$^+$	inc$^+$	sulf	sulf	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos	eos
F_1	niv$^+$	niv$^+$	inc$^+$	inc	sulf$^+$	sulf	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos
F_2	Magenta 39% Crimson 14% Pink 16% Orange 6% Ivory 19% Yellow 6%											
Ivory	niv$^+$	niv$^+$	inc	inc	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
X												
Yellow	niv$^+$	niv$^+$	inc	inc	sulf	sulf	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
F_1	niv$^+$	niv$^+$	inc	inc	sulf$^+$	sulf	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
F_2	Ivory 75% Yellow 25%											
Ivory	niv$^+$	niv$^+$	inc	inc	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
X												
White	niv	niv	inc$^+$	inc$^+$	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
F_1	niv$^+$	niv	inc$^+$	inc	sulf$^+$	sulf$^+$	ebu$^+$	ebu$^+$	pal$^+$	pal$^+$	eos$^+$	eos$^+$
F_2	Magenta 56% Ivory 19% White 25%											

Table 9.6 Theoretical segregation for colour in F_1 and F_2 generations of a cross between an ivory and pink-flowered parent

Parents: ivory	niv+ niv+	inc inc	sulf+ sulf+	ebu+ ebu+	pal+ pal	eos+ eos
pink	niv+ niv+	inc+ inc	sulf+ sulf+	ebu+ ebu+	pal+ pal+	eos eos

Genotypes within the F_1 Generation	Phenotype	Segregation for colour in the F_2 generation within each class.			
		Magenta	Pink	Ivory	Rose Shades*
(1) niv+ niv+ inc+ inc sulf+ sulf+ ebu+ ebu+ pal+ pal+ eos+ eos	Magenta	56	19	25	-
(2) niv+ niv+ inc+ inc sulf+ sulf+ ebu+ ebu+ pal+ pal eos+ eos	Magenta	41	16	25	19
(3) niv+ niv+ inc+ inc sulf+ sulf+ ebu+ ebu+ pal+ pal+ eos eos	Pink	-	75	25	-
(4) niv+ niv+ inc+ inc sulf+ sulf+ ebu+ ebu+ pal+ pal eos eos	Pink	-	56	25	19
(5) niv+ niv+ inc inc sulf+ sulf+ ebu+ ebu+ pal+ pal+ eos+ eos	Ivory	-	-	100	-
(6) niv+ niv+ inc inc sulf+ sulf+ ebu+ ebu+ pal+ pal eos+ eos	Ivory	-	-	100	-
(7) niv+ niv+ inc inc sulf+ sulf+ ebu+ ebu+ pal+ pal+ eos eos	Ivory	-	-	100	-
(8) niv+ niv+ inc inc sulf+ sulf+ ebu+ ebu+ pal+ pal eos eos	Ivory	-	-	100	-

* actual colour depends on the recessive allele of the pallida series

OTHER SOURCES OF RUST RESISTANCE

Besides the rust-resistance in cultivars of *A. majus*, demonstrated in Chapter 4, there are two other sources of resistance: wild species and among susceptible varieties.

1) Wild Species

Wild species, as a source of genes for resistance have usually been regarded as a last resort (Watson, 1970) and yet a reservoir of valuable resistant material may be found in them. A number of the wild species of *Antirrhinum* possess individual plants with some resistance to the rust (Tables 7.6, 7.7, and 7.8). Furthermore many of the species of the section Antirrhinastrum hybridize with *A.majus* and produce fertile hybrids (Table 7.5). It would therefore appear relatively easy to incorporate resistance from the wild species into the cultivars of *A. majus*.

There are a few reports of experiments with resistance in the wild species. Main (1935) crossed *A. hispanicum* Chav. (as *A. glutinosum*) with one of his resistant lines of "Giant White". He also showed that the resistance in *A.barrelieri* Bor. (as *A.ibanjezii*) was inherited by a single dominant gene, by crossing resistant plants of *A. barrelieri* with a susceptible variety of *A. majus*. Another European species has been used in commercial breeding (personal confidential communication). Although only the presence of major resistance genes have been demonstrated, it is likely that many species may also possess some degree of non-specific resistance. It may be more difficult to transfer minor genes from wild species to *A. majus* because much of the resistance will be lost in the many backcross generations required to eliminate undesirable characters (Russell, 1978).

2) Commercially acceptable varieties

In recent years it has been realised that it is not necessary to breed varieties that they are so highly resistant that they appear immune. Russell (1978) believes that the breeding of varieties with an intermediate level of durable resistance, which gives an adequate level of disease control should be the main objective of breeding programmes. Other authors have also advocated the increased use of polygenic resistance (Hooker, 1967; Simmonds, 1979). Proof that it can give adequate protection against plant diseases is demonstrated by the classic examples of the control of *Puccinia sorghi* in Maize (Hooker 1967) and *Puccinia striiformis* in wheat (Lupton and Johnson, 1970).

It is evident that even susceptible varieties possess some factors for resistance. Sharp, Sally and Taylor (1976) and Krupinsky (1977) identified progeny with greater resistance to P. striiformis than that of either parent. Thus it is clear that some minor genes may have an additive effect on the control of plant disease. The presence of complex resistance has even been shown within A. majus: White (1943) crossed susceptible varieties and from one cross, "After Glow" X "Lucky Strike" obtained plants with a good degree of resistance. The development of resistance by the recombination of minor genes from susceptible varieties is a relatively unexplored area of applied Antirrhinum genetics.

CHOICE OF BREEDING STRATEGY

There is no correct breeding strategy which is suitable for all crops and when breeding for resistance, it is necessary to decide whether to breed for vertical or horizontal resistance. The value of each within any particular crop needs to be assessed (Robinson, 1971) and the available genes for resistance used wisely to ensure an adequate and long-lasting resistance to the disease.

There are many advantages in using monogenic resistance to pathogens and when available it has nearly always been used. It is easy to manage in a plant-breeding programme. The resistant and susceptible plants in the progeny are clearly distinguishable and are segregated in a simple Mendelian ratio. It is dramatically effective against one or more races of the pathogen though there is always the potential disadvantage that it may become ineffective against other races. Since the resistance is usually inherited by a single gene, the pathogen only requires one genetic change to overcome the resistance: thus vertical resistance is likely to be unstable. Johnson (1961) suggests that plant breeders may have been unconsciously responsible for epidemics by exerting a selective force on the pathogen which has favoured virulent genotypes.

Simmonds(1979) suggests five ways in which genes for vertical resistance might be deployed to reduce the danger of loss of control;

i temporally
ii geographically
iii spatially
iv mixtures
v multilines

They all require the co-operation of the grower and the first three would only work if each farmer agreed to grow a suggested variety. A mixture

is defined as a mixture of distinct varieties having complementary vertical resistance genes in which the components must be homogeneous for the time of maturity but may otherwise be quite diverse (Simmonds, 1979, p.273). The last, 'multilines', is generally regarded as the most efficient use of genes for vertical resistance. Day (1978) defines a multiline cultivar as one which consists of a set of 8-16 lines that are as near as possible isogenic except that they carry different genes for resistance to a given pathogen. Multilines effectively use stabilizing selection to maintain simple races of the pathogen but they have the disadvantage that varietal improvement is more laborious. Theoretically this appears to be a good use of genes for vertical resistance but it is not yet known whether they actually prolong the useful life of a vertical resistance gene.

The use of polygenic resistance as a means of disease control is becoming increasingly popular. It tends to be more stable because several simultaneous changes are necessary in the pathogen to overcome the resistance in the host. The loss of polygenic resistance is usually gradual and seldom complete. Polygenic resistance is less dramatic than monogenic resistance, having a quantitative rather than qualitative effect and acts by slowing the rate of epidemic development, thus reducing the value of Van der Plank's 'apparent infection rate' (Van der Plank, 1963). The advantages of polygenic resistance are evident and as its use in breeding programmes has increased it has been realised that it is not as difficult to handle in a plant breeding programme as was at first thought (Krupinsky (1977); Lupton and Johnson (1970)).

It has usually been the differences between the two types of resistance and the mechanism of their genetic control that have been emphasized and this has caused them to appear as alternative methods of disease control. Van der Plank (1968) suggests that there would be considerable advantage in synthesizing cultivars which incorporate genes for both specific and non-specific resistance; the combined resistance should decrease the probability of loss of control. Unfortunately, it is more difficult to test for the presence of minor genes in the presence of masking major genes though there are a number of examples where the expression of resistance controlled by major genes is often increased by the presence of minor modifying genes. Allston, Watkins and Wertz (1974) showed resistance to apples to collar rot and powdery mildew are conditioned by major genes which may be modified by minor genes. Volin and Sharp (1969) and Sharp and Volin (1970) identified lines of wheat

with major genes for resistance to specific isolates of Puccinia striiformis and minor genes conditioning reaction to other isolates.

In their antirrhinum breeding programmes, plant breeders have been looking for a dominant gene giving immunity to 'the second race' of P. antirrhini since 1933 in America and since 1963 in Britain. It would now appear that there are a number of physiological races (Brooks, 1970; Gawthrop and Jones, in press; personal communications from various seed companies) which may explain why, despite much work, there is still no commercial variety with complete resistance. In other crops, where genes for immunity have been easier to find, they have usually only provided resistance for a few years. It is difficult to develop a variety which is resistant to all known races of a pathogen using specific resistance alone. There are examples in the literature which demonstrate that such varieties have given good rust protection when first released, but when extensively grown they have succumbed to a virulent physiological race of the pathogen (see review by Hooker, 1967).

Perhaps the time has come to change the strategy for breeding rust-resistant antirrhinums from absolute resistance to an adequate level of general resistance. This may help to restore the genetic equilibrium between the antirrhinum and its rust to that found in natural populations of host and parasites (Nelson, 1978).

STRATEGY

The change from breeding for immunity to rust to breeding for an acceptable level of resistance, involves a reconsideration of the breeding strategy. Donald (1968) proposed three basic breeding strategies: the first eliminates defects; the second selects for yield through inbreeding and selection; the third selects for model plants or ideotypes. The first two strategies have been used for a very long time but it is now recognised that plant breeders need to have some sort of ideotype (Simmonds, 1979). Each plant breeder will have a slightly different concept of the ideal plant but the important principle remains: clear objectives are necessary to ensure that each new variety is an improvement on existing varieties, not only with respect to rust-resistance but also in general horticultural features.

In the past, plant breeding has tended to improve the adaption of a species at the expense of its variability and hence its long term adaptability (Simmonds, 1962). It is now realised that the time has come to reverse the trend and to enlarge the genetic base of crop plants. Parlevliet and Zadoks (1977) believe that our crops should be sufficiently diverse to imitate the genetic homeostasis found in natural populations. Genetic homeostasis operates so strongly in wild species that virtually all resistance genes remain effective although corresponding virulence genes are present: the host and pathogen coexist in a balanced system. The pressures on the pathogen in cultivation are different but it is still possible to make the resistance in the crop diverse either by multilines or by polygenic control.

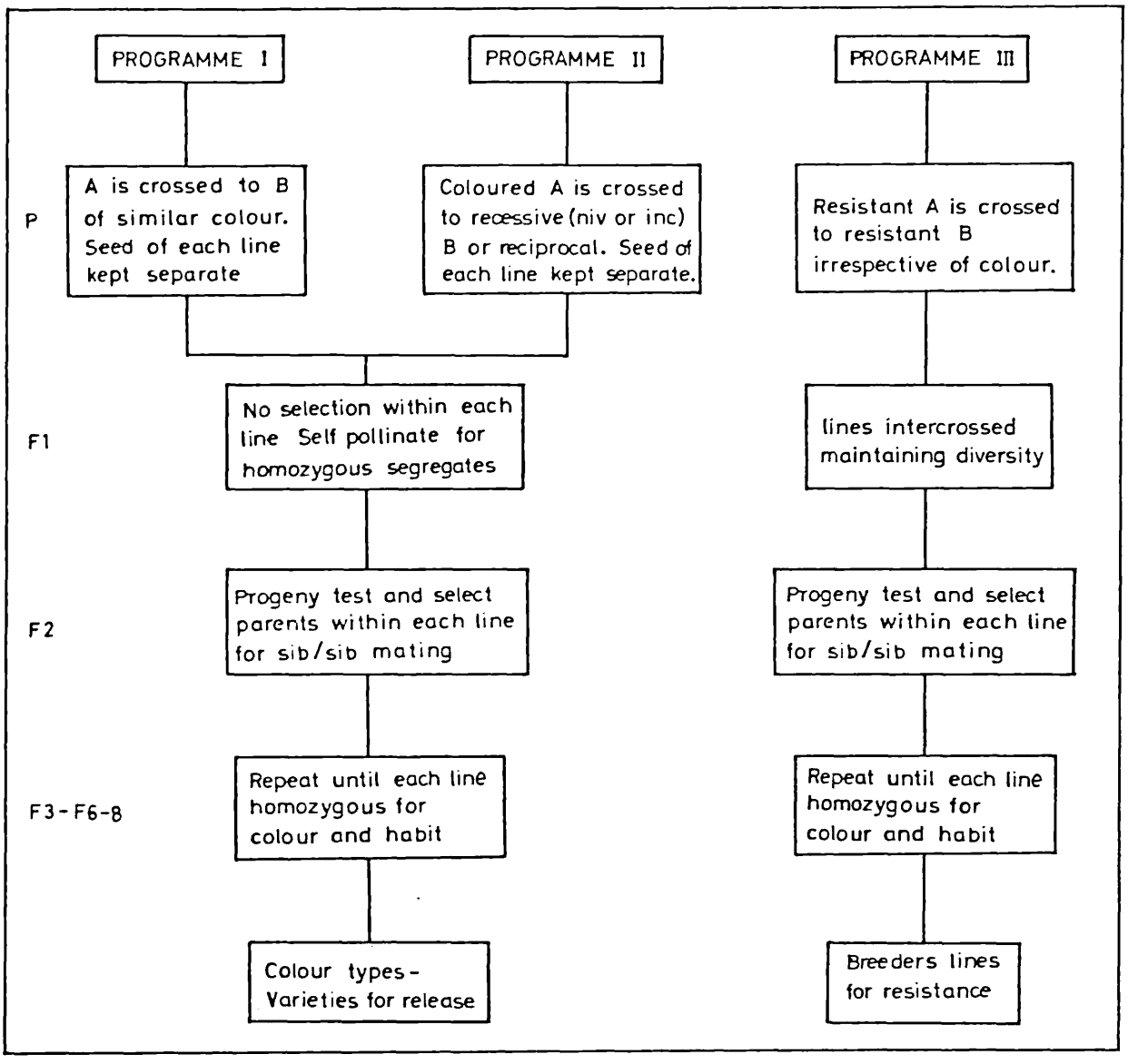
The most effective way of controlling P. antirrhini appears to be through the development of varieties in which genes of relatively small effects are accumulated. Ideally the genes should be derived from different sources therefore parents should be selected from at least different lines and preferably those developed by different breeders. There are three ways in which new varieties with polygenic resistance may be created; these are summarized in Figure 9.2. All three programmes use the pedigree method and require a quantitative assessment of rust-resistance in each generation.

Programme I involves a series of crosses between parents of similar colour. Both parents should have an acceptable level of general resistance and come from different sources (A and B) so that the polygenes are unlikely to be the same. This programme is only suitable where there are two parents of similar colour with acceptable resistance and therefore it may only produce a limited range of colours. It would be rapid and should produce lines uniform in habit and colour in 4-5 generations.

Programme II involves crossing a coloured-flowered parent with a white or ivory-flowered parent. The genes controlling the flower colour of white (homozygous for niv) and ivory (homozygous for inc) are at the beginning of the pigment pathway (Figure 9.1). Other corolla colours are dominant over white and ivory because they contribute the wild type niv^+ and inc^+ alleles which complete the pigment pathway with the production of anthocyanin. Therefore Programme II is suitable for extending the range of colours developed through Programme I but it may take longer (six generations) to produce lines homozygous for colour and habit.

The third programme is designed to preserve the best resistance genes for future exploitation in breeding work. This programme relies upon

Figure 9.2 Summary of breeding programmes



intercrossing without strong selection for colour in the early stages. The development of varieties is not the prime intention of this programme but the resistance from Programme III may be transferred to either Programme I or II in case of difficulties. Hence it has a supportive role in the strategy because it is likely to have the greatest accumulation of minor genes for resistance.

Cultivars of A. majus fall somewhere between the categories ofcross-pollinated and self-pollinated crops; they are self-compatible but suffer inbreeding depression if persistently inbred. Nevertheless, the F_1 generation of programmes I and II is self-pollinated because this will reveal the recombinants but homozygous lines are produced in all subsequent generations by sib/sib mating.

Testing and Assessment of Resistance

Any breeding programme for polygenic resistance to P. antirrhini must involve a quantitative evaluation of the progeny for rust-resistance in each generation. At each stage the epidemic should be of suitable intensity and duration for effective screening and there are two factors which need consideration:

i) each plant should be exposed to the same level of inoculum;
ii) there is a gradual build-up of inoculum during the season.

i) The first criterion can be satisfied by the design of the plot. A 'spreader row' of the susceptible variety "Malmaison" planted between two test rows (Fig.4.1) will spread the disease over the plot and ensure that each plant has an equal chance of becoming infected.

ii) The level of horizontal resistance within a plant tends to accumulate with the age of the plant therefore an artificially induced epidemic which is severe at the start of the season might eliminate useful resistance (Robinson, 1973). This situation places the plant breeder in a predicament because some plant diseases do not occur naturally every year. Antirrhinum rust generally occurs every year although the attack is not always severe. In both years of this antirrhinum trial, a natural epidemic had started by mid August. If there is no widespread rust infection by the last week in August, however, it should be possible to inoculate the "spreader rows" with the local rust by spraying with a suspension of uredospores.

The assessment of resistance is easy where vertical genes are operating and there is a clear distinction between resistant and susceptible plants. In horizontal resistance, the variation in response is continuous and differences are quantitative. The five-point standard diagram (Fig.4.5) may be useful to score the disease severity, but it should be possible for the experienced eye to select plants corresponding to an average score of less than two. These plants should be tolerant to the disease and should neither be disgifured on the leaves nor have a reduced flowering period. The importance of selection for good habit and florifery cannot be over emphasized. Thus Russell (1978) suggested that the avoidance of extreme susceptibility may be a better policy since breeding for a high level of resistance involves special selection programmes where only the most resistant are retained.

Production of Rust-Resistant Varieties

Some of the varieties with an acceptable resistance to rust and a good habit selected from this investigation have been used as parents in the initial crosses of the three breeding programmes (Fig.9.2); the details of which are included in Appendix 9.1. The breeding work will be continued at the Botany Department, Royal Holloway College and the Royal Horticultural Society's (R.H.S.) Garden at Wisley. Once the breeder's selection is completed, the potential new cultivars may be submitted for comparison with standard cultivars in a R.H.S. trial. If the breeder's line shows promise, the stock seed may be multiplied commercially. In the breeding programme the lines of A. majus will have been cross-pollinated and the commercial seed production should maintain the degree of heterozygosity to prevent inbreeding depression. Bees, the natural pollinators of antirrhinums, will maintain the heterozygosity within each variety but to ensure there is no cross-pollination with foreign pollen, each variety must be isolated from other varieties of A. majus. The minimum isolation distance for antirrhinums required by the Dutch Seed Association is 100m-400m (North 1979, p.131). As with all seed production of cross-pollinated crops, it is essential that a balance is achieved and frequent reselection is necessary to prevent excessive heterozygosity or a shift in the gene balance. Perhaps the Royal Horticultural Society will ultimately take responsibility for the genetic integrity of the variety especially in the maintenance of rust-resistance.

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Appendix 4.1 Varieties assessed for their resistance to rust in the plot experiments of 1978 and 1979

1978	Code No.	Accession No.	Variety Name	Source *
Dwarf Varieties	1	78-42	Pink Pixie	D.R. Colegrave Seeds Ltd.
	2	78-43	Red Pixie	"
	3	78-44	Rose Pixie	"
	4	78-45	White Pixie	"
	5	78-46	Yellow Pixie	"
	6	78-47	Orange Pixie	"
	7	78-48	Sweetheart Bronze	"
	8	78-49	Sweetheart Pink	"
	9	78-50	Sweetheart Red	"
	10	78-51	Sweetheart Rose	"
	11	78-52	Sweetheart White	"
	12	78-53	Sweetheart Yellow	"
	13	78-71	Kolibri Formula Mixture	Sluis & Groot B.V.
Tall Varieties	14	78-91	Variety A	
	15	78-92	Variety B	
	16	78-93	Variety C	
	17	78-94	Variety D	
	18	78-95	Variety E	
	19	78-96	Variety F	
	20	78-97	Variety G	
	21	78-98	Variety H	
	22	78-99	Variety I	
	23	78-100	Variety J	
	24	78-101	Variety K	
Medium Varieties	25	78-33	Coronette Yellow	D.R. Colegrave Seeds Ltd.
	26	78-34	Coronette White	"
	27	78-35	Coronette Scarlet	"
	28	78-36	Coronette Rose	"
	29	78-37	Coronette Pink	"
	30	78-38	Coronette Bronze	"
	31	78-39	Coronette Cherry	"
	32	78-40	Coronette Crimson	"
	33	78-41	Coronette Orchid	"
	34	78-58	Variety L	
	35	78-59	Carioca Deep Red	Sluis & Groot B.V.
	36	78-60	Carioca Orange	"
	37	78-61	Carioca Bright Scarlet	"
	38	78-62	Carioca Peach Bronze	"
	39	78-63	Carioca Yellow	"
	40	78-64	Carioca Cherry Red	"
	41	78-65	Carioca Pink	"
	42	78-66	Carioca White	"
	43	78-67	Carioca Appleblossom	"
	44	78-68	Carioca Rose	"
	45	78-70	Coronette Scarlet	"
	46	78-72	Nanum Dazzler	Hurst Gunson Cooper Taber Ltd.
	47	78-73	Nanum Black Prince	"
	48	78-74	Regal Bright Scarlet	"
	49	78-75	Regal Rose	"
	50	78-76	Regal Orange Scarlet	"
	51	78-77	Regal White	"
	52	78-78	Regal Yellow	"
	53	78-79	Regal Crimson	"
	54	78-80	Regal Cherry	"
	55	78-81	Regal Apricot	"
	56	78-82	Yellow Monarch	"
	57	78-83	White Monarch	"
	58	78-84	Carmine Monarch	"
	59	78-85	Lavender Monarch	"
	60	78-86	Orange Monarch	"
	61	78-87	Crimson Monarch	"
	62	78-88	Amber Monarch	"
	63	78-89	Coral Monarch	"
	64	78-90	Scarlet Monarch	"
Old Varieties	65	78-55	Cherokee	Mrs. E.L. Rolfe, Worcester
	66	78-103	Variety M	Ms. Swithin
	67	78-32	Malmaison	Hurst Gunson Cooper Tabler Ltd.

Appendix 4.1 continued

1979	68	78-111	Variety A	Mrs. Adams
	69	78-154	Variety C	Mr. M. Tavassoli
	70	78-166	Variety P	Mrs. Keefe, Egham, Surrey
	71	78-188	Variety Q	Ms. M. Hodgman, Oxford
	72	79-2	Variety R	Mrs. Jones, Herne Bay
	73	79-26	Burpee's Super Tetra	W. Atlee Burpee Company
	74	78-201	Tetra Giant Ruffled	Royston Petrie Seeds Pty Ltd.
	75	79-16	Kimosy Red	L. Clause
	76	79-17	Kimosy Delicate Rose	"
	77	79-19	Kimosy Primrose Yellow	"
	78	79-20	Kimosy Crimson	"
	79	79-21	Kimosy White	"
	80	79-23	Kimosy Orange	"
	81	79-4	Majestic Purple King	"
	82	79-5	Majestic Celestial	"
	83	79-7	Majestic Snowstorm	"
	84	79-8	Majestic Red Chief	"
	85	79-9	Majestic Orange King	"
	86	79-11	Majestic Forest Fire	"
	87	79-12	Majestic Eldorado	"
	88	79-25	Rocket Citron Yellow	"
	89	78-189	Rocket White	Joseph Harris Company Inc.
	90	78-191	Rocket Red	"
	91	78-193	Rocket Orange	"
	92	78-194	Rocket Orchid	"
	93	78-244	Suttons Triumph Mauve	Suttons Seeds Ltd.
	94	78-245	Suttons Triumph Bright Orange	"
	95	78-246	Suttons Triumph White	"
	96	78-247	Suttons Triumph Primrose	"
	97	78-225	Suttons Triumph Scarlet	Suttons Seeds (Market Growers) Ltd.
	98	78-227	Suttons Triumph Orange Salmon	"
	99	78-222	Suttons Intermediate White	"
	100	78-223	Suttons Intermediate Fire King	"
	101	78-230	Suttons Intermediate Bright Crimson	Suttons Seeds Ltd.
	102	78-231	Suttons Intermediate Rich Apricot	"
	103	78-232	Suttons Intermediate Guardsman	"
	104	78-233	Suttons Intermediate Eclipse	"
	105	78-234	Suttons Intermediate Yellow	"
	106	78-237	Suttons Rust Resistant Orange Glow	"
	107	78-239	Suttons Rust Resistant Yellow	"
	108	78-240	Suttons Rust Resistant Pale Sulphur	"
	109	78-241	Suttons Rust Resistant Apricot	"
	110	78-164	Suttons Rust Resistant Leonard Sutton	Suttons Seeds (Market Growers) Ltd.
	111	78-213	Kim White	"
	112	78-216	Kim Purple	"
	113	78-217	Kim Primrose Yellow	"
	114	78-218	Kim Mid Rose	"
	115	78-220	Kim Deep Orange	"
	116	78-173	Kim Blood Red	L. Clause
	117	78-195	Frontier White	Joseph Harris Company Inc.
	118	78-198	Frontier Flame	"
	119	78-199	Frontier Crimson	"
	120	78-200	Frontier Yellow	"
Old Rust	121	78-177	Wisley Cheerful	Asmer Seeds Ltd.
Resistant	122	78-178	Wisley Golden Fleece	"
Varieties	123	78-179	Toreador	"
	124	78-180	Titan	"
	125	78-181	Orange Glow	"
	126	78-182	Victory	"
	127	78-183	Yellow Freedom	"
	128	78-184	Yellow Freedom	"
	129	78-185	White Freedom	"
	130	78-187	Bonfire	"
	131	79-38	Variety S (tetraploid)	Botanical Supply Unit, Royal Holloway College

* Addresses given in Appendix 4.2

APPENDIX 4.2 Addresses of senders of seeds to 1978 and 1979 plot experiments.

A. Companies

(1) Asmer Seeds Ltd.,
Asmer House,
Ash Street,
Leicester, LE 5 ODD

(2) L. Clause (Seed growers and breeders)
91220 Bretigny-sur-Orge,
France.

(3) D.R. Colegrave Seeds Ltd.,
West Adderbury,
Banbury, Oxon. OX17 3EY.

(4) Hurst Gunson Cooper Taber Ltd.,
Great Domsey Farm,
Feering,
Colchester, Essex CO5 9ES.

(5) Joseph Harris Company Inc.,
Moreton Farm,
Rochester,
New York 14624, U.S.A.

(6) Royston Petrie Seeds Pty Ltd.,
P.O. Box 77,
Dural 2158
Australia

(7) Sluis & Groot B.V.,
P.O. Box 13, 1600 AA,
Enkhuizen,
Holland.

(8) Suttons Seeds (Market Growers Ltd)
Charvil Farm,
New Bath Road,
Charvil, Reading RG10 9RU.

(9) Suttons Seeds Ltd.,
Hele Road,
Torquay,
Devon TQ2 7Q7

(10) W. Atlee Burpee Company,
300 Park Avenue,
Warminster,
Pennsylvania 18974, U.S.A.

B. Private senders

(11) Mrs. N. Adams,
6, Austen Road,
Guildford, Surrey GU1 3NP

(12) Ms. M Hodgman,
Little Garth,
Bletchingdon, Oxford.

(13) Mrs. Jones,
55 Tyndale Park,
Herne Bay, Kent.

(14) Mrs. Keefe,
6, Chestnut Drive,
Egham,
Surrey

(15) Miss E. Rolfe,
Worcester College of Higher Education,
Henwick Grove, Worcester WR2 6AJ

(16) Ms. J. Swithin,
14 Slades Gardens,
Enfield, Middx.

(17) Mrs. M. Tavassoli,
C/o Physics Department,
Tehran University,
Tehran, Iran.

APPENDIX 4.3 Values of F for three factor analysis of variance
a) 1978 - first scoring at Royal Holloway College

	Variation			Interaction		
Variety Number	between plants	between leaves	between blocks	plants/ leaves	plants/ blocks	leaves/ blocks
1	1.29	0.34	7.04 **	0.73	5.85 ***	1.49
2	1.05	2.14	135.48 ***	1.69 *	3.59 ***	1.22
3	0.39	2.23	21.19 ***	0.95	1.59	0.76
4	0.88	0.40	59.51 ***	0.98	1.78	1.26
5	1.42	0.39	37.01 ***	0.57	4.11 ***	1.89
6	1.06	1.43	8.74 ***	1.36	3.91 ***	0.86
7	0.37	0.60	19.23 ***	1.68 *	2.07 *	2.19 *
8	3.29 *	0.82	49.75 ***	1.17	1.74	1.57
9	0.63	0.07	1.98	0.78	2.32 *	1.48
10	0.53	1.26	46.90 ***	0.89	2.41 **	1.37
11	4.69 **	0.55	6.44 **	1.17	1.22	2.09
12	1.30	0.81	21.36 ***	1.12	2.13 *	1.66
13	0.62	1.40	50.85 ***	0.81	4.16 ***	1.17
14	1.23	0.72	2.96	1.48	1.92 *	1.71
15	0.88	1.41	133.70 ***	1.33	2.16 *	0.83
16	1.04	1.58	27.85 ***	1.16	1.37	1.20
17	3.56 *	0.42	23.23 ***	0.73	0.67	1.85
18	0.36	0.16	30.49 ***	1.30	2.31 *	1.03
19	1.07	0.51	0.79	1.08	2.73 **	1.42
20	1.29	0.36	90.03 ***	1.25	2.07 *	2.17 *
21	1.54	0.21	0.83	1.52	2.29 *	2.15 *
22	0.52	2.05	17.95 ***	1.44	2.92 **	1.19
23	1.00	1.30	10.31 ***	2.03 **	1.24	1.32
24	2.20	0.42	35.53 ***	0.46	0.87	1.88
25	1.44	0.46	28.40 ***	0.85	1.73	0.72
26	0.25	1.08	15.97 ***	0.89	1.55	1.02
27	1.23	0.57	22.59 ***	1.65	2.82 **	1.08
28	1.15	0.18	67.28 ***	0.64	1.82	1.13
29	1.27	1.04	184.28 ***	0.91	0.88	2.28 *
30	1.02	1.10	25.37 ***	0.76	3.00 **	1.19
31	0.41	1.22	3.35 *	0.79	0.98	0.65
32	0.78	1.18	2.37	0.63	1.61	0.66
33	0.90	1.76	24.67 ***	0.59	1.84 *	1.28
34	1.12	2.62	3.65 *	0.95	3.81 ***	0.84
35	0.99	0.76	7.29 **	1.06	2.51 **	1.11
36	1.28	2.55	8.91 ***	1.14	2.72 **	0.63
37	0.63	0.17	2.01	0.90	2.35 **	3.41 **
38	0.86	0.54	6.20 **	0.61	1.27	0.76
39	0.43	0.35	25.86 ***	0.95	4.41 ***	1.91
40	1.02	3.43	6.05 **	0.70	1.10	0.95
41	0.36	0.81	19.68 ***	0.49	2.41 **	1.72
42	0.42	0.20	9.17 ***	0.72	2.13 *	0.83
43	1.14	0.39	10.03 ***	0.84	4.11 ***	1.85
44	0.59	0.53	47.62 ***	0.72	2.81 **	2.57 *
45	1.28	3.34	6.15 **	1.13	1.08	0.85
46	1.06	0.17	1.00	0.95	5.22 ***	1.48
47	1.32	0.33	1.08	0.56	2.88 **	0.41
48	0.54	2.42	28.27 ***	1.11	4.05 ***	1.45
49	0.33	0.29	15.07 ***	1.21	2.72 **	0.77
50	0.82	0.24	107.09 ***	1.71 *	2.13 *	1.54
51	1.17	0.84	104.16 ***	1.38	1.39	1.47
52	0.26	6.65 *	23.88 ***	1.11	5.19 ***	0.27
53	3.23 *	0.29	50.46 ***	0.94	1.07	0.88
54	2.46	2.73	40.53 ***	0.70	0.56	0.79
55	0.68	1.38	168.64 ***	1.22	2.90 **	0.89
56	1.06	1.07	372.18 ***	0.98	3.36 ***	1.16
57	0.75	0.86	24.38 ***	1.16	5.05 ***	0.91
58	0.33	1.05	10.44 ***	0.88	1.85 *	0.52
59	0.53	0.55	9.97 ***	0.87	1.38	1.19
60	0.88	0.35	314.51 ***	1.55	6.30 ***	2.06
61	2.63 *	1.68	10.63 ***	1.37	2.10 *	0.66
62	0.95	1.76	20.12 ***	1.29	4.15 ***	0.70
63	0.54	2.29	10.20 ***	0.74	3.00 **	0.49
64	0.56	3.58	25.09 ***	1.93 *	8.74 ***	1.08
65	1.10	0.69	71.32 ***	1.08	2.34 *	1.32
66	0.90	0.78	38.12 ***	1.08	17.29 ***	1.66

APPENDIX 4.3 Values of F for three factor analysis of variance
b) 1978 - second scoring at Royal Holloway College

Variety Number	Variation			Interaction		
	between plants	between leaves	between blocks	plants/ leaves	plants/ blocks	leaves/ blocks
14	1.04	0.96	66.52 ***	3.48 ***	4.74 ***	5.15 ***
17	0.46	0.56	46.11 ***	1.15	6.51 ***	2.24 *
18	1.27	0.26	10.27 ***	1.03	2.68 **	1.13
19	0.77	1.35	31.12 ***	1.34	4.79 ***	1.14
26	0.98	1.61	156.64 ***	1.48	9.36 ***	1.89
30	0.49	0.56	37.99 ***	1.33	14.17 ***	1.91
31	0.31	2.57	108.62 ***	1.16	9.83 ***	0.90
34	1.20	0.41	20.64 ***	1.11	21.38 ***	1.66
38	1.12	0.70	6.25 **	1.54	29.73 ***	3.59 **
39	2.21	0.55	64.19 ***	1.76 *	4.21 ***	2.18 *
42	1.13	1.85	64.57 ***	0.96	3.28 ***	1.60
48	0.17	2.25	47.76 ***	1.45	10.26 ***	1.55
53	0.83	1.21	124.70 ***	1.36	2.55 **	0.49
54	2.91 *	2.12	74.13 ***	1.62	1.15	0.58
55	9.12 ***	5.84 *	11.10 ***	2.38 **	1.30	0.70
57	1.00	1.00	1.94	1.00	0.85	0.73
58	1.75	1.09	78.81 ***	1.22	4.14 ***	1.09
59	1.40	2.34	134.97 ***	1.16	3.41 ***	0.82
61	0.79	2.16	20.63 ***	1.96 *	15.57 ***	2.18 *
62	1.17	1.30	64.22 ***	1.40	8.51 ***	4.38 ***
63	2.39	1.89	69.01 ***	2.25 **	2.19 *	1.32
64	0.75	0.90	342.92 ***	2.62 **	13.25 ***	5.41 ***
66	0.66	0.51	37.20 ***	1.09	18.54 ***	1.13

APPENDIX 4.3 Values of F for three factor analysis of variance
c) 1978 - first scoring at Wisley

Variety Number	Variation			Interaction		
	between plants	between leaves	between blocks	plants/ leaves	plants/ blocks	leaves/ blocks
1	0.63	2.47	110.74 ***	1.49	2.34 *	0.93
2	2.26	8.12 **	48.94 ***	0.98	2.59 **	0.51
3	1.65	0.40	50.56 ***	0.73	0.80	1.20
4	0.91	0.94	61.26 ***	2.81 ***	6.94 ***	1.14
5	3.60 *	0.70	70.47 ***	1.90 *	2.13 *	3.14 **
6	0.98	0.49	18.57 ***	0.35	1.99 *	1.35
7	0.48	0.78	28.43 ***	0.90	3.03 **	1.88
8	1.10	3.09	34.30 ***	0.81	3.61 ***	1.13
9	0.95	0.25	6.44 **	0.81	3.79 ***	1.09
10	3.32 *	0.46	64.60 ***	1.03	1.09	0.80
11	0.93	0.15	56.76 ***	1.20	2.09 *	2.91 **
12	3.02 *	5.48 *	15.73 ***	1.10	2.06 *	0.41
13	1.18	0.31	63.46 ***	0.89	3.80 ***	0.67
14	0.72	0.97	48.47 ***	0.77	2.28 *	0.63
15	0.89	0.65	111.81 ***	1.13	1.80	0.57
16	1.00	0.56	14.82 ***	0.80	1.53	0.59
17	0.24	0.92	23.21 ***	1.06	2.46 **	0.77
18	3.15 *	0.30	31.96 ***	1.12	0.74	1.76
19	0.49	1.11	20.42 ***	0.91	3.55 ***	0.75
20	1.27	1.24	116.41 ***	0.99	1.29	0.49
21	0.50	1.80	22.32 ***	1.44	4.55 ***	0.68
22	0.29	3.33	35.81 ***	0.61	4.93 ***	0.22
23	1.41	1.53	139.24 ***	1.16	1.63	1.57
24	0.38	3.85 *	3.54 *	1.02	5.29 ***	1.04
25	2.71 *	1.77	67.01 ***	0.71	1.84 *	1.01
26	1.88	0.62	56.30 ***	1.29	4.63 ***	3.07 **
27	1.67	0.72	1.81	0.97	1.70	1.98
28	0.37	0.33	27.11 ***	0.98	4.83 ***	0.50
29	0.56	1.27	21.21 ***	1.72 *	5.89 ***	1.57
30	1.17	1.56	30.45 ***	1.00	1.83	1.13
31	0.73	0.90	30.54 ***	0.64	2.24 *	1.06
32	0.92	0.96	10.69 ***	0.89	1.00	1.37
33	0.55	0.63	8.38 ***	0.78	4.30 ***	3.16 **
34	2.19	0.52	8.48 ***	1.18	3.14 ***	1.41
35	0.40	2.67	50.13 ***	1.58	2.47 **	1.77
36	0.39	1.33	32.99 ***	0.90	3.75 ***	1.10
37	2.69 *	1.65	47.99 ***	1.02	1.93 *	0.69
38	0.90	2.84	34.15 ***	1.32	1.81	0.67
39	0.73	1.80	54.97 ***	1.64	3.79 ***	1.21
40	1.42	1.73	96.84 ***	1.14	1.43	0.45
41	0.38	5.21 *	25.32 ***	0.99	1.88 *	0.53
42	3.40 *	2.72	34.98 ***	1.39	0.89	1.18
43	1.54	0.33	18.19 ***	1.69 *	2.09 *	4.59 ***
44	0.89	1.39	8.98 ***	1.42	1.77	1.55
45	0.90	2.06	60.29 ***	0.71	1.54	1.12
46	1.65	0.27	7.79 ***	1.07	1.56	3.69 **
47	1.45	3.40	51.00 ***	0.89	2.44 **	0.54
48	0.70	0.91	76.78 ***	1.24	2.68 **	2.17 *
49	0.93	1.36	10.77 ***	1.07	1.11	0.87
50	3.09 *	1.52	11.13 ***	1.10	0.83	0.93
51	1.09	4.18 *	107.42 ***	1.58	1.38	0.72
52	2.18	0.78	102.85 ***	0.86	1.05	0.89
53	0.25	7.08 **	27.82 ***	0.75	1.38	0.24
54	2.61 *	0.15	179.87 ***	1.51	2.71 **	1.85
55	1.46	1.21	81.01 ***	0.89	1.71	1.94
56	0.93	1.89	35.37 ***	1.10	6.61 ***	1.02
57	2.76 *	0.78	9.99 ***	0.85	1.33	1.12
58	1.10	4.46 *	100.69 ***	1.01	1.60	1.11
59	0.71	10.78 **	25.26 ***	0.66	1.81	0.31
60	0.94	2.68	30.67 ***	1.25	2.26 *	0.59
61	1.08	1.27	14.14 ***	0.55	3.67 ***	1.32
62	2.93 *	0.42	77.83 ***	1.17	1.39	1.24
63	0.65	0.19	67.46 ***	1.42	3.58 ***	1.31
64	0.34	1.10	100.40 ***	1.54	3.32 ***	2.70 *
65	0.54	0.55	147.95 ***	1.43	5.43 ***	0.68
66	1.61	0.81	16.89 ***	1.39	2.25 *	2.12 *

APPENDIX 4.3. Values of F for three factor analysis of variance
d) 1978 - second scoring at Wisley

Variety Number	Variation			Interaction		
	between plants	between leaves	between blocks	plants/ leaves	plants/ blocks	leaves/ blocks
1	0.00	0.00	0.00	0.00	0.00	0.00
2	1.00	1.00	12.26 ***	1.00	5.36 ***	1.19
3	1.00	1.00	13.71 ***	1.00	1.71	0.14
4	0.00	0.00	0.00	0.00	0.00	0.00
5	1.00	1.00	10.18 ***	1.00	2.23 *	1.35
6	0.00	0.00	0.00	0.00	0.00	0.00
7	0.00	0.00	0.00	0.00	0.00	0.00
8	0.00	0.00	0.00	0.00	0.00	0.00
9	0.00	0.00	0.00	0.00	0.00	0.00
10	0.00	0.00	0.00	0.00	0.00	0.00
11	1.05	1.13	1847.48 ***	0.99	3.04 **	3.82 **
12	0.00	0.00	0.00	0.00	0.00	0.00
13	1.00	1.00	14.84 ***	1.00	4.41 ***	0.35
14	0.69	5.05 *	46.67 ***	1.18	4.50 ***	1.38
15	1.00	1.00	15.69 ***	1.00	4.04 ***	1.18
16	1.75	2.15	21.18 ***	0.91	1.64	0.82
17	1.66	2.11	7.09 **	1.33	2.61 **	1.64
18	1.57	2.53	55.22 ***	0.73	1.71	1.70
19	1.24	2.01	115.05 ***	1.89 *	6.37 ***	1.53
20	1.32	2.31	27.38 ***	1.81 *	5.41 ***	2.79 *
21	1.85	0.77	2.02	0.96	4.35 ***	6.61 ***
22	1.50	2.72	9.27 ***	0.69	2.19 *	1.34
23	0.73	1.72	70.16 ***	0.88	3.69 ***	0.58
24	0.00	0.00	0.00	0.00	0.00	0.00
25	1.21	20.63 ***	95.92 ***	1.22	2.68 **	0.29
26	1.91	3.73	50.89 ***	1.59	2.69 **	4.20 ***
27	1.15	2.75	57.78 ***	0.75	3.03 **	0.53
28	1.32	3.07	14.85 ***	1.17	2.67 **	2.85 **
29	0.79	0.88	16.48 ***	1.03	6.40 ***	2.08
30	0.47	3.93 *	127.82 ***	0.94	4.15 ***	1.47
31	0.58	2.73	94.71 ***	0.53	9.86 ***	2.53 *
32	1.00	1.00	20.38 ***	1.00	2.95 **	1.85
33	0.00	0.00	0.00	0.00	0.00	0.00
34	0.79	4.10 *	37.81 ***	1.09	23.53 ***	0.83
35	0.79	1.19	32.52 ***	1.01	2.84 **	3.49 **
36	0.00	0.00	0.00	0.00	0.00	0.00
37	0.49	1.48	22.96 ***	0.74	4.05 ***	3.25 **
38	0.84	12.55 **	38.16 ***	0.56	3.82 ***	1.41
39	1.13	7.71 **	26.95 ***	0.87	4.03 ***	0.84
40	0.54	3.05	16.15 ***	0.48	2.11 *	1.33
41	0.00	0.00	0.00	0.00	0.00	0.00
42	1.09	6.04 *	44.53 ***	1.31	4.67 ***	0.36
43	0.00	0.00	0.00	0.00	0.00	0.00
44	1.00	1.00	3.99 *	1.00	1.00	3.99 **
45	1.24	3.59	50.41 ***	1.27	6.64 ***	1.89
46	0.00	0.00	0.00	0.00	0.00	0.00
47	0.62	0.92	11.22 ***	1.01	11.06 ***	1.35
48	0.59	5.57 *	16.89 ***	0.65	4.53 ***	0.57
49	0.00	0.00	0.00	0.00	0.00	0.00
50	0.00	0.00	0.00	0.00	0.00	0.00
51	1.00	1.00	28.79 ***	1.00	4.50 ***	2.80 *
52	0.00	0.00	0.00	0.00	0.00	0.00
53	0.00	0.00	0.00	0.00	0.00	0.00
54	1.09	0.94	22.96 ***	1.81 *	11.53 ***	22.48 ***
55	1.47	0.74	10.99 ***	1.31	2.32 *	2.57 *
57	1.97	0.00	1.66	0.53	1.93	1.07
58	0.43	2.11	44.58 ***	1.26	3.64 ***	0.86
59	2.26	2.45	5.38 **	2.04 **	2.19 *	2.19 *
60	1.00	1.00	8.08 ***	1.00	1.77	3.13 **
61	0.94	1.53	22.05 ***	0.90	4.38 ***	1.25
62	0.15	4.72 *	233.62 ***	1.25	7.06 ***	0.42
63	0.16	0.90	1.92	0.94	5.54 ***	1.15
64	1.13	8.80 **	64.32 ***	0.99	3.51 ***	0.94
65	0.38	1.16	32.23 ***	0.81	13.72 ***	2.99 **
66	0.94	30.59 ***	49.94 ***	0.71	19.54 ***	0.30

APPENDIX 4.3 Values of F for three factor analysis of variance
a) 1979 - first scoring at Royal Holloway College

Variety Number	Variation			Interaction		
	between plants	between leaves	between blocks	plants/ leaves	plants/ blocks	leaves/ blocks
1	1.00	1.00	7.55 **	1.00	2.79 **	1.51
15	1.18	2.00	24.42 ***	1.14	1.40	1.06
18	1.00	1.00	1.00	1.00	1.00	1.00
29	0.67	4.11 *	20.63 ***	1.02	7.24 ***	0.63
37	0.12	4.55 *	22.47 ***	0.75	5.88 ***	0.49
39	0.61	1.35	13.36 ***	0.95	9.39 ***	1.25
45	0.65	5.12 *	33.31 ***	1.09	11.79 ***	0.43
52	0.41	4.92 *	3.02	0.50	1.28	0.89
56	1.18	2.30	4.28 *	0.82	1.17	2.55 *
62	0.68	0.53	1.05	1.08	1.05	1.42
68	0.77	4.55 *	7.41 **	0.77	7.39 ***	0.52
69	1.39	1.83	5.12 **	1.21	2.97 **	1.11
70	1.10	1.77	3.96 *	1.03	1.58	2.19 *
71	1.00	1.00	1.00	1.00	1.00	1.00
72	1.62	0.96	48.33 ***	1.12	4.21 ***	1.20
73	0.81	3.38	4.82 *	1.18	3.77 ***	0.74
74	1.00	1.00	1.00	1.00	1.00	1.00
75	0.80	0.88	13.81 ***	1.02	2.36 **	1.35
76	0.73	2.55	9.40 ***	0.83	6.89 ***	0.90
77	0.77	0.93	3.19 *	1.01	2.90 **	0.93
78	0.00	0.00	0.00	0.00	0.00	0.00
79	0.93	1.33	44.67 ***	1.13	7.67 ***	3.00 **
80	0.83	0.67	0.51	1.05	1.08	1.14
81	0.53	1.83	11.73 ***	0.68	2.03 *	1.16
82	0.58	5.00 *	11.10 ***	0.90	13.47 ***	0.21
83	0.88	3.84 *	5.99 **	0.82	5.41 ***	1.00
84	2.62 *	5.23 *	3.36 *	1.32	1.36	1.03
85	0.82	4.00 *	0.47	0.82	1.00	0.47
86	1.16	0.91	11.09 ***	1.01	1.47	0.58
87	1.45	1.36	27.47 ***	1.28	6.77 ***	3.13 **
88	0.66	1.21	4.96 *	1.20	2.46 **	1.80
89	1.01	12.04 **	4.42 *	0.37	3.02 **	0.50
90	2.44	1.34	6.05 **	0.93	1.71	0.96
91	1.45	2.68	45.42 ***	0.71	5.48 ***	0.75
92	1.15	2.15	14.89 ***	1.47	3.55 ***	3.60 **
93	1.52	2.43	1.11	0.97	2.53 **	0.91
94	1.55	1.23	196.42 ***	1.11	8.02 ***	1.97
95	0.77	3.25	4.52 *	0.66	3.38 ***	0.81
96	1.38	0.49	24.74 ***	1.12	2.29 *	0.89
97	0.30	2.21	5.08 **	0.77	3.01 **	0.83
98	0.27	13.01 **	2.41	0.63	3.25 ***	0.56
99	1.94	0.36	69.84 ***	1.50	3.98 ***	0.43
100	0.60	2.50	8.49 ***	0.90	3.63 ***	0.53
101	1.56	1.76	1.87	0.74	1.48	1.72
102	2.77 *	1.36	3.58 *	1.19	1.11	1.21
103	3.00 *	2.29	1.71	2.29 **	1.71	1.00
104	1.11	1.69	58.01 ***	0.99	4.25 ***	1.85
105	3.52 *	1.66	8.69 ***	1.50	2.39 **	2.44 *
106	0.74	3.22	16.33 ***	1.33	13.45 ***	0.54
107	3.99 **	0.67	0.44	0.67	0.44	1.00
108	1.00	1.00	1.00	1.00	1.00	1.00
109	1.09	1.41	25.97 ***	1.14	1.46	3.35 **
110	1.20	3.74	2.43	0.82	1.01	0.52
111	1.37	1.09	100.09 ***	0.81	5.63 ***	0.87
112	0.91	0.73	88.14 ***	0.89	2.95 **	0.39
113	1.51	1.00	1229.26 ***	1.47	8.24 ***	1.52
114	1.30	1.04	45.77 ***	0.88	5.36 ***	1.28
115	1.96	3.40	78.69 ***	1.10	4.03 ***	0.94
116	0.95	1.35	44.32 ***	0.86	4.34 ***	0.58
117	0.77	1.91	4.10 *	0.90	4.44 ***	0.87
118	0.73	0.09	64.69 ***	0.88	2.34 *	1.57
119	1.98	0.79	4.08 *	0.94	1.10	1.19
120	0.71	1.89	97.82 ***	0.49	0.87	1.22
121	1.06	2.25	9.27 ***	0.55	0.83	1.12
122	2.43	5.00 *	0.87	1.39	0.63	0.33
123	0.75	1.24	6.98 **	0.95	1.69	1.50
124	1.65	0.67	1.10	0.87	0.79	2.47 *
125	0.80	2.11	93.93 ***	1.22	8.58 ***	0.80
126	1.00	1.00	5.02 **	1.00	1.49	1.88
127	1.01	1.69	217.70 ***	1.22	8.69 ***	0.83
128	1.00	1.00	1.00	1.00	1.00	1.00
129	1.33	4.60 *	12.94 ***	5.65 ***	8.26 ***	1.29
130	0.84	2.62	9.86 ***	0.89	3.25 ***	0.56
131	0.00	0.00	0.00	0.00	0.00	0.00

APPENDIX 4.3 Values of F for three factor analysis of variance
f) 1979 - second scoring at Royal Holloway College

Variety Number	Variation			Interaction		
	between plants	between leaves	between blocks	plants/ leaves	plants/ blocks	leaves/ blocks
1	0.52	1.12	8.79 ***	0.66	0.80	0.74
15	0.43	6.93 *	103.75 ***	0.97	3.94 ***	0.75
18	1.78	0.67	12.29 ***	1.00	2.56 **	1.48
29	0.53	6.44 *	17.31 ***	1.02	9.90 ***	0.26
37	0.45	1.72	3.67 *	1.67 *	4.07 ***	1.65
39	0.67	0.12	17.64 ***	2.07 **	3.79 ***	1.45
45	0.67	2.78	40.45 ***	1.41	13.05 ***	0.88
52	1.33	1.27	57.06 ***	0.70	1.95 *	0.89
56	0.53	0.77	77.79 ***	0.78	1.00	2.42 *
62	0.56	1.24	0.40	0.85	4.26 ***	1.22
68	0.72	17.62 ***	26.91 ***	1.01	4.36 ***	0.15
69	0.47	0.69	18.13 ***	0.74	3.80 ***	3.19 **
70	1.12	2.14	26.02 ***	1.57	5.10 ***	1.70
71	0.74	4.04 *	1.77	1.00	1.54	1.46
72	0.91	0.98	271.30 ***	1.11	22.32 ***	2.07
73	1.28	0.46	15.66 ***	2.06 **	7.99 ***	2.01
74	1.35	5.79 *	11.74 ***	1.39	1.73	0.61
75	2.89 *	0.94	28.79 ***	0.96	2.20 *	0.64
76	0.40	0.64	37.47 ***	0.98	9.30 ***	2.21 *
77	2.18	0.10	5.26 **	0.57	3.38 ***	1.17
78	0.55	0.89	11.00 ***	1.45	2.56 **	2.43 *
79	0.38	1.29	49.85 ***	0.80	4.78 ***	0.29
80	1.65	6.63 *	2.94	0.88	1.20	0.52
81	0.30	1.58	3.26 *	0.87	3.18 ***	0.59
82	1.04	5.21 *	9.60 ***	1.08	7.10 ***	0.68
83	1.35	1.15	14.51 ***	1.52	8.59 ***	1.09
84	1.15	3.17	1.80	1.19	1.80	0.33
85	2.78 *	0.80	3.69 *	1.16	1.68	2.69 *
86	0.83	0.60	104.27 ***	1.26	10.40 ***	3.94 ***
87	2.03	1.25	2.51	1.07	3.01 **	1.07
88	1.24	1.99	18.57 ***	1.11	2.27 *	1.72
89	0.91	9.89 **	11.56 ***	1.05	4.29 ***	0.58
90	1.04	3.36	10.94 ***	0.55	1.08	0.66
91	1.94	5.43 *	52.24 ***	1.45	2.20 **	0.69
92	1.52	0.96	13.48 ***	0.54	1.44	0.53
93	1.17	5.41 *	16.81 ***	0.87	1.89 *	0.95
94	0.55	0.80	123.36 ***	0.93	9.69 ***	1.67
95	1.98	0.26	6.75 **	0.96	3.04 **	1.26
96	1.02	2.51	56.85 ***	0.84	3.19 **	1.44
97	0.45	0.98	54.09 ***	0.62	7.44 ***	0.97
98	1.27	0.52	4.36 *	0.72	3.37 ***	1.46
99	1.43	1.34	179.79 ***	0.85	5.87 ***	1.79
100	1.65	1.81	17.29 ***	1.03	4.18 ***	1.03
101	1.55	1.89	34.49 ***	0.67	2.90 **	1.18
102	1.64	1.45	20.59 ***	0.98	1.18	0.83
103	2.78 *	1.35	21.01 ***	1.25	0.98	2.83 **
104	0.60	0.89	215.48 ***	0.95	7.84 ***	1.94
105	0.94	2.10	13.48 ***	1.09	3.73 ***	1.17
106	1.38	4.92 *	21.60 ***	1.44	4.86 ***	1.26
107	1.44	1.79	2.29	0.95	1.79	1.69
108	1.74	1.08	19.34 ***	0.67	1.50	1.44
109	1.04	1.85	106.35 ***	0.98	3.70 ***	1.27
110	1.28	1.82	1.30	1.74 *	2.81 **	1.18
111	2.74 *	2.12	96.65 ***	0.92	2.33 *	0.54
112	1.01	0.43	17.20 ***	0.95	1.17	0.87
113	2.69 *	1.43	1001.23 ***	1.43	3.21 ***	1.97
114	1.09	2.69	240.79 ***	1.05	3.76 ***	0.74
115	1.85	0.68	140.90 ***	0.88	1.46	1.16
116	0.26	1.12	21.77 ***	1.35	7.79 ***	1.65
117	0.33	3.18	14.39 ***	1.91 *	2.63 **	0.96
118	0.76	1.05	110.82 ***	0.92	4.48 ***	0.99
119	1.74	2.42	6.06 **	0.65	1.65	0.71
120	0.79	2.02	98.45 ***	1.72 *	3.78 ***	1.03
121	0.70	3.59	87.91 ***	0.76	2.01 *	0.64
122	1.25	4.28 *	20.90 ***	1.01	0.54	0.29
123	0.96	1.37	19.11 ***	0.73	1.12	1.05
124	1.30	0.50	12.32 ***	1.68 *	2.40 **	1.58
125	0.46	1.42	114.79 ***	0.78	3.34 ***	1.17
126	0.98	1.81	27.84 ***	2.05 **	5.78 ***	2.14 *
127	1.57	0.17	191.87 ***	0.89	1.97 *	2.04
128	0.18	1.10	21.00 ***	1.01	3.61 ***	3.55 **
129	2.66 *	3.04	8.40 ***	0.38	1.43	1.26
130	1.10	3.00	31.46 ***	0.88	2.41 **	0.81
131	0.87	1.00	1.32	1.14	1.88 *	0.91

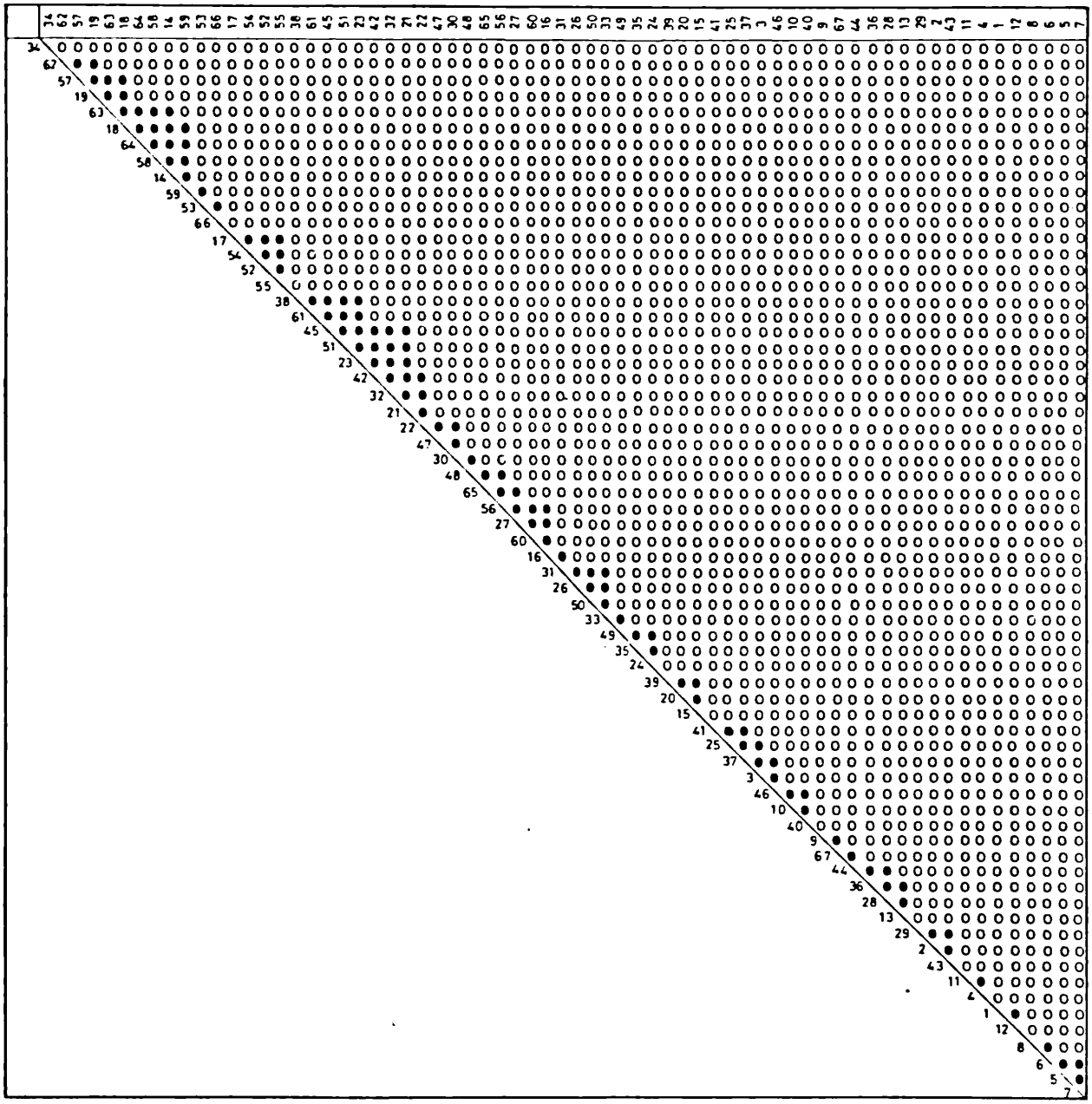
APPENDIX 4.3 Values of F for three factor analysis of variance
g) 1979 - first scoring at Wisley

Variety Number	Variation			Interaction		
	between plants	between leaves	between blocks	plants/ leaves	plants/ blocks	leaves/ blocks
1	1.32	1.06	110.89 ***	0.82	4.81 ***	1.56
15	0.54	2.57	42.11 ***	1.42	2.24 *	0.85
18	0.89	1.13	97.86 ***	0.86	2.69 **	2.73 *
29	1.07	0.59	108.97 ***	0.91	1.91 *	2.23 *
37	0.71	3.32	154.97 ***	1.72 *	2.61 **	2.29 *
39	1.75	3.09	164.48 ***	1.17	0.71	0.70
45	0.73	2.61	18.92 ***	1.04	3.89 ***	1.12
52	1.15	0.16	3.61 *	0.71	3.53 ***	1.54
56	1.08	0.96	18.05 ***	1.27	3.28 ***	2.56 *
62	0.94	3.57	7.38 **	0.73	0.68	0.83
68	1.85	1.39	53.51 ***	0.91	2.37 **	1.79
69	1.94	1.26	49.62 ***	1.27	1.21	1.17
70	0.49	1.14	48.72 ***	1.18	4.79 ***	1.70
71	2.82 *	1.26	1.67	1.17	2.39 **	1.24
72	1.15	9.57 **	14.67 ***	0.58	3.10 ***	0.54
73	1.42	3.34	82.71 ***	1.14	5.39 ***	1.78
74	0.49	0.39	10.88 ***	0.82	5.86 ***	2.13 *
75	2.05	1.35	18.21 ***	2.05 **	0.65	1.55
76	1.71	3.09	3.08	0.55	0.91	0.84
77	1.16	3.68	131.96 ***	1.09	4.09 ***	1.87
78	1.01	1.48	15.53 ***	0.61	0.76	1.26
79	1.49	3.10	72.65 ***	0.79	2.53 **	1.95
80	0.75	2.37	72.86 ***	1.26	0.86	2.05
81	0.38	0.85	50.45 ***	1.10	1.83	0.88
82	0.57	3.72	96.69 ***	0.76	2.88 **	1.19
83	0.61	0.78	51.61 ***	1.80 *	7.10 ***	3.39 **
84	0.67	2.07	242.94 ***	0.76	4.48 ***	1.58
85	0.55	2.77	67.45 ***	1.06	6.84 ***	1.00
86	1.59	1.54	67.88 ***	0.98	3.18 ***	1.18
87	0.79	0.62	65.99 ***	1.11	2.56 **	1.83
88	1.79	1.74	64.94 ***	1.07	1.09	0.89
89	1.45	0.20	13.06 ***	1.38	1.39	1.43
90	0.68	0.82	0.07	1.44	8.94 ***	2.20 *
91	0.57	0.90	7.04 **	1.64	5.21 ***	2.83 **
92	2.92 *	1.81	2.66	0.64	0.85	1.40
93	1.21	1.72	134.00 ***	1.26	1.80	1.35
94	0.33	2.78	16.12 ***	1.26	6.30 ***	2.23 *
95	0.70	2.26	68.68 ***	1.15	7.67 ***	0.67
96	0.71	2.27	89.76 ***	0.67	2.82 **	1.18
97	2.99 *	2.18	24.80 ***	1.79 *	2.91 **	2.12 *
98	1.67	7.39 **	175.40 ***	1.59	4.48 ***	1.12
99	1.59	2.50	181.16 ***	0.79	2.94 **	1.16
100	1.12	9.37 **	163.87 ***	0.74	2.01 *	0.33
101	1.01	2.38	247.81 ***	0.85	1.41	2.25 *
102	0.67	2.25	90.13 ***	1.23	4.31 ***	2.25 *
103	0.79	1.95	99.41 ***	1.92 *	5.20 ***	1.75
104	1.75	3.80	27.44 ***	0.84	2.71 **	1.39
105	1.77	1.67	13.29 ***	0.89	1.76	0.99
106	0.81	0.54	0.61	1.77 *	1.20	2.21 *
107	1.44	3.08	40.12 ***	1.07	1.63	1.02
108	1.43	3.33	9.75 ***	0.85	2.15 *	1.14
109	1.48	1.29	94.82 ***	1.27	1.68	1.44
110	1.26	1.48	11.27 ***	0.58	7.63 ***	1.45
111	0.66	4.81 *	112.11 ***	0.65	3.12 ***	0.55
112	2.29	2.39	64.63 ***	1.23	2.31 *	0.90
113	1.04	3.91	5.83 **	1.51	4.84 ***	1.55
114	1.33	3.80	6.17 **	0.95	0.97	1.03
115	2.43	1.46	41.15 ***	0.86	1.19	0.67
116	1.23	0.27	34.36 ***	1.16	1.88 *	2.85 **
117	0.43	1.44	244.36 ***	1.46	2.00 *	1.03
118	0.55	2.14	72.04 ***	0.77	2.76 **	1.65
119	1.40	2.79	31.96 ***	0.57	1.58	1.57
120	3.03 *	0.05	238.90 ***	0.74	1.42	0.75
121	0.25	4.09 *	2.26	1.70 *	0.84	0.94
122	3.87 *	0.85	4.01 *	0.61	0.34	1.58
123	0.88	1.69	9.46 ***	0.88	1.07	0.88
124	0.37	0.36	34.66 ***	1.28	2.66 **	2.98 **
125	0.65	2.88	69.01 ***	1.31	4.06 ***	2.09
126	1.19	1.66	4.26 *	1.26	1.98 *	1.12
127	1.07	0.53	21.49 ***	0.92	1.67	1.62
128	1.25	2.75	2.73	1.27	2.59 **	0.78
129	0.81	2.08	174.70 ***	1.14	2.52 **	3.19 **
130	0.97	0.71	45.96 ***	0.86	2.82 **	1.45
131	0.92	1.27	16.72 ***	0.96	4.81 ***	1.19

APPENDIX 4.3 Values of F for three factor analysis of variance
h) 1979 - second scoring at Wisley

Variety Number	Variation			Interaction		
	between plants	between leaves	between blocks	plants/ leaves	plants/ blocks	leaves/ blocks
1	0.37	2.02	242.70 ***	0.55	3.53 ***	0.62
15	0.73	0.33	61.18 ***	0.84	3.13 ***	1.41
18	0.43	2.38	137.25 ***	1.34	1.47	0.68
29	1.19	0.69	70.24 ***	0.86	3.24 ***	1.73
37	1.17	1.82	197.36 ***	0.86	3.72 ***	2.49 *
39	2.53	1.59	212.02 ***	1.55	4.28 ***	1.55
45	0.94	1.53	36.27 ***	1.25	3.86 ***	1.57
52	0.32	0.40	22.78 ***	1.42	6.81 ***	4.54 ***
56	1.54	0.50	9.18 ***	0.83	6.10 ***	1.24
62	2.87 *	4.41 *	15.18 ***	1.18	0.88	0.54
68	0.88	3.57	48.36 ***	0.97	6.99 ***	1.30
69	0.38	11.27 **	119.35 ***	0.75	2.72 **	0.30
70	1.94	0.62	29.83 ***	0.69	2.46 **	0.44
71	2.07	2.38	1.57	1.16	9.55 ***	1.46
72	1.38	1.84	12.88 ***	1.33	6.19 ***	1.47
73	1.37	1.71	7.86 ***	0.91	6.85 ***	1.44
74	0.85	0.60	5.19 **	1.58	8.87 ***	2.36 *
75	0.95	0.79	40.93 ***	0.78	2.74 **	1.77
76	1.41	2.20	0.00	1.36	4.33 ***	1.15
77	0.92	1.21	364.26 ***	0.47	4.63 ***	1.19
78	2.43	0.90	11.81 ***	1.35	1.26	0.98
79	0.37	2.34	26.14 ***	1.36	5.08 ***	0.40
80	2.96 *	3.32	62.29 ***	1.25	2.07 *	0.37
81	1.41	1.56	17.45 ***	0.88	4.65 ***	0.53
82	0.19	0.46	91.44 ***	1.21	9.83 ***	1.34
83	1.52	1.21	11.13 ***	1.15	6.09 ***	0.66
84	1.72	2.13	352.88 ***	0.94	8.21 ***	2.63 *
85	1.20	1.02	17.03 ***	1.54	13.37 ***	2.24 *
86	0.68	1.16	53.50 ***	0.85	4.28 ***	0.65
87	0.29	1.14	123.81 ***	0.77	9.57 ***	2.36 *
88	1.65	23.12 ***	106.42 ***	1.08	1.63	0.28
89	1.72	1.20	26.78 ***	0.82	1.60	0.96
90	3.01 *	1.25	24.34 ***	0.98	2.33 *	0.38
91	1.14	1.82	170.83 ***	1.10	2.92 **	0.79
92	0.15	1.00	78.16 ***	1.11	1.95 *	1.30
93	1.05	3.42	169.41 ***	0.55	3.67 ***	0.44
94	0.34	4.73 *	56.26 ***	0.84	9.96 ***	0.60
95	0.57	2.75	56.35 ***	0.96	16.55 ***	0.54
96	0.52	6.72 *	78.60 ***	0.68	8.18 ***	0.47
97	2.00	1.85	17.60 ***	1.06	2.30 *	0.65
98	0.97	1.62	427.21 ***	0.78	3.12 ***	2.49 *
99	1.29	2.16	379.82 ***	1.98 *	7.65 ***	0.57
100	2.33	3.30	58.71 ***	1.32	2.63 **	0.94
101	1.43	1.85	367.44 ***	1.22	4.70 ***	1.47
102	2.06	1.07	121.73 ***	0.95	0.96	1.00
103	1.36	6.39 *	12.05 ***	0.70	5.84 ***	0.78
104	1.86	3.07	10.15 ***	1.09	3.74 ***	1.14
105	1.23	1.99	15.04 ***	0.86	2.53 **	0.83
106	1.20	7.61 **	41.77 ***	0.61	2.55 **	0.79
107	0.94	4.16 *	12.24 ***	0.90	1.87 *	0.68
108	0.91	1.11	15.56 ***	1.16	2.42 **	1.47
109	0.25	0.66	41.95 ***	0.77	1.72	0.54
110	1.38	0.80	11.72 ***	1.79 *	7.53 ***	1.17
111	0.46	2.38	490.87 ***	0.67	10.39 ***	0.63
112	0.94	4.30 *	46.93 ***	0.95	3.18 ***	0.90
113	0.65	2.16	86.76 ***	1.97 *	5.69 ***	1.31
114	0.72	4.70 *	1.45	0.69	0.56	1.01
115	0.91	3.37	20.22 ***	1.02	2.55 **	1.17
116	1.03	2.57	179.78 ***	0.69	2.61 **	1.05
117	0.65	2.65	200.49 ***	0.47	2.34 *	0.80
118	2.21	3.00	171.94 ***	1.28	2.66 **	0.58
119	1.11	3.01	244.67 ***	1.10	5.70 ***	1.08
120	0.36	0.97	180.46 ***	1.36	5.76 ***	1.26
121	1.93	3.51	9.98 ***	1.58	1.46	1.72
122	0.79	9.74 **	3.00	1.20	0.60	0.23
123	0.60	1.48	48.03 ***	0.66	1.66	1.01
124	1.09	14.78 ***	21.50 ***	0.96	2.23 *	0.35
125	0.70	1.44	235.80 ***	1.32	2.49 **	1.51
126	1.05	1.99	1.88	0.92	0.83	2.32 *
127	1.02	0.75	2.27	0.78	0.67	1.38
128	1.22	2.38	8.62 ***	1.10	0.83	0.69
129	1.41	1.11	18.56 ***	0.65	2.26 *	0.66
130	1.09	1.67	22.91 ***	0.65	6.22 ***	0.83
131	2.62 *	1.79	16.12 ***	0.63	1.31	1.37

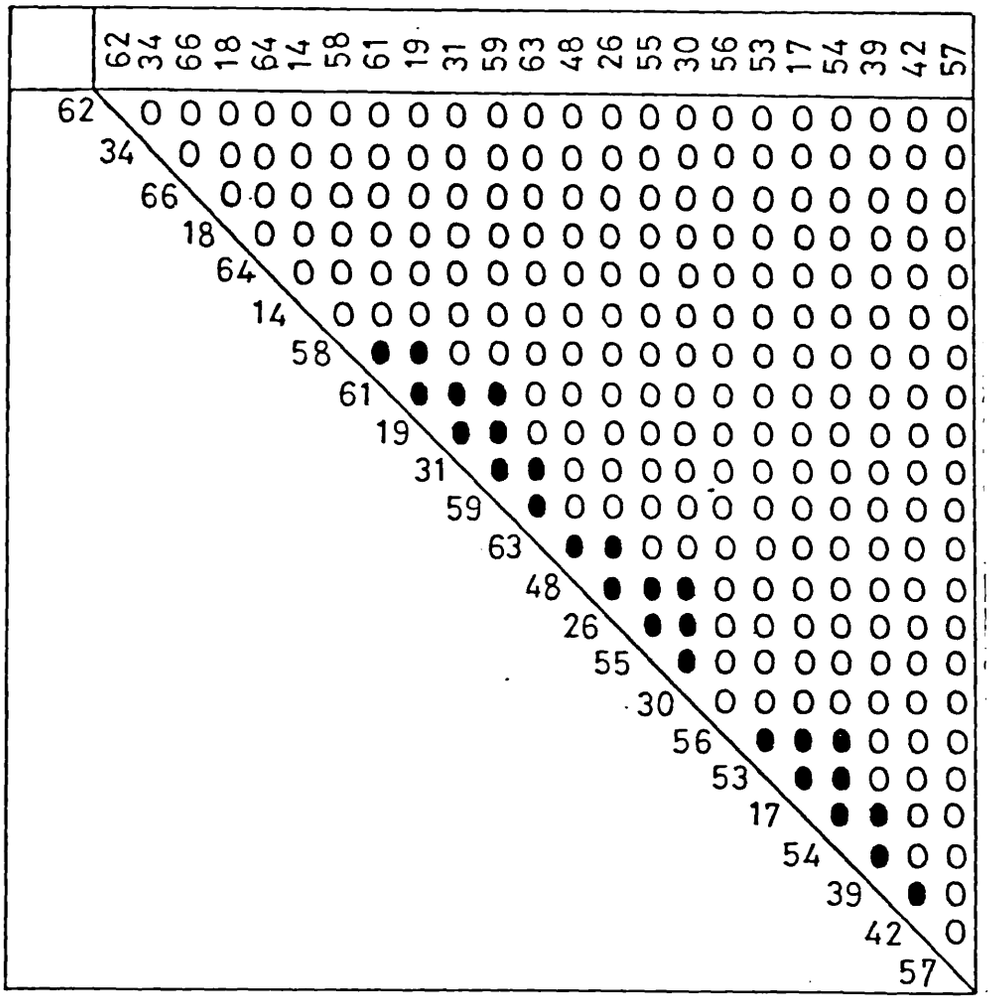
APPENDIX 4.4 Matrix showing significant and insignificant differences in the rust susceptibility of Antirrhinum varieties in first scoring at Royal Holloway College in 1978



Solid circle = insignificant difference

Key to varieties code numbers - Appendix 4.13

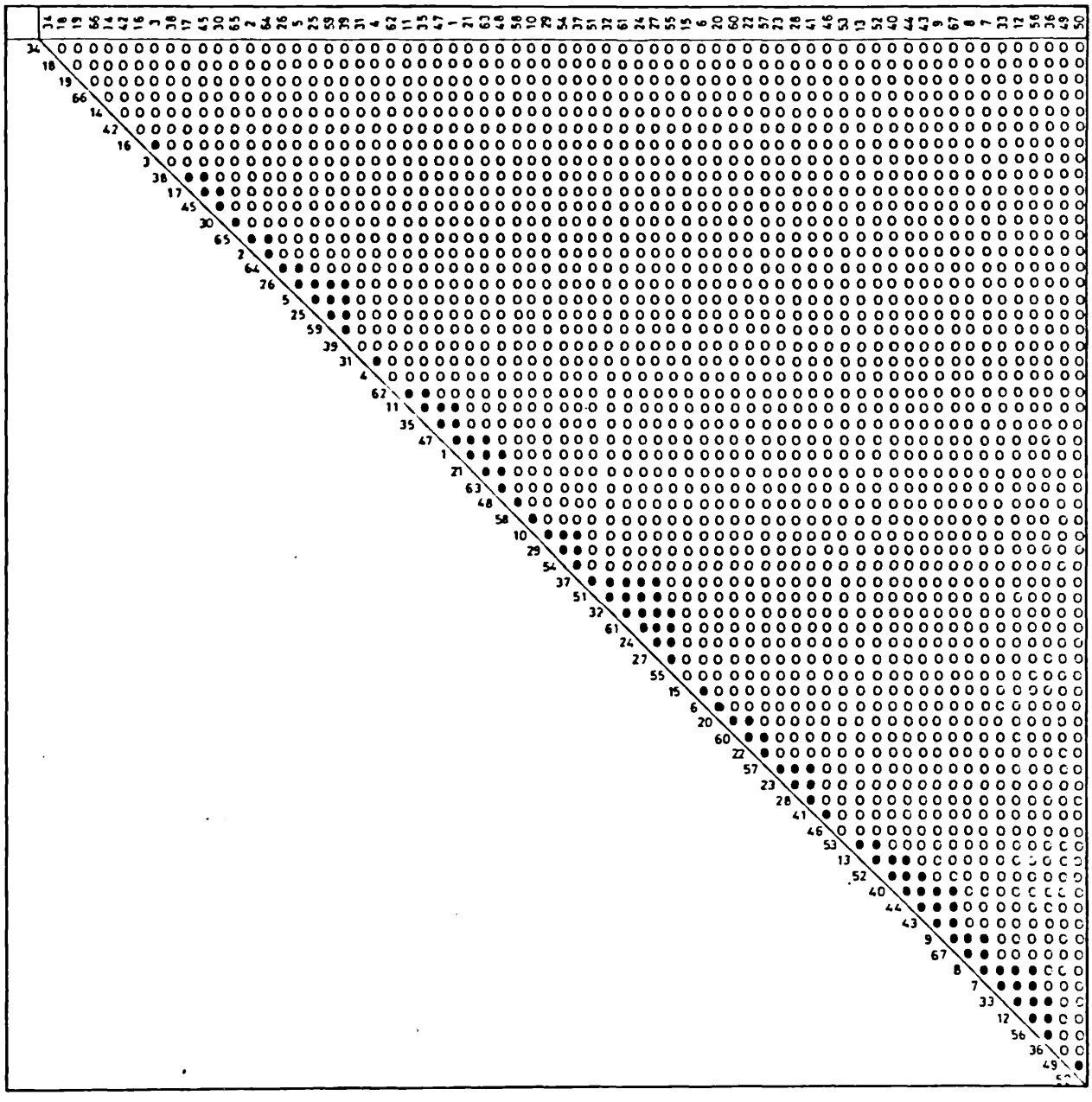
APPENDIX 4.5 Matrix showing significant and insignificant differences in the rust susceptibility of Antirrhinum varieties in second scoring at Royal Holloway College in 1978



Solid circle = insignificant difference

Key to varieties code numbers - Appendix 4.13

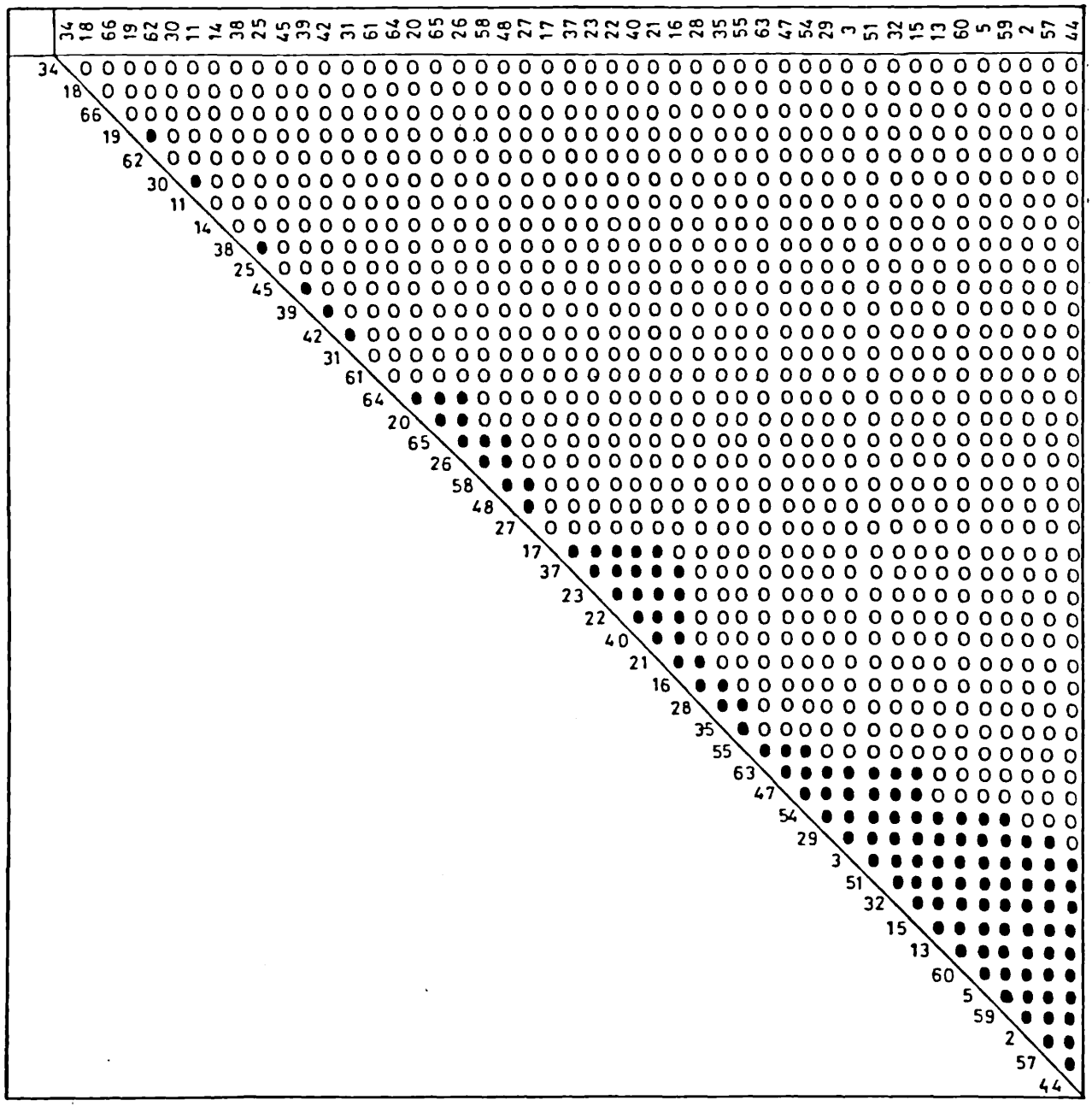
APPENDIX 4.6 Matrix showing significant and insignificant differences in the rust susceptibility of Antirrhinum varieties in first scoring at Wisley in 1978.



Solid circle = insignificant difference

Key to varieties code numbers - Appendix 4.13

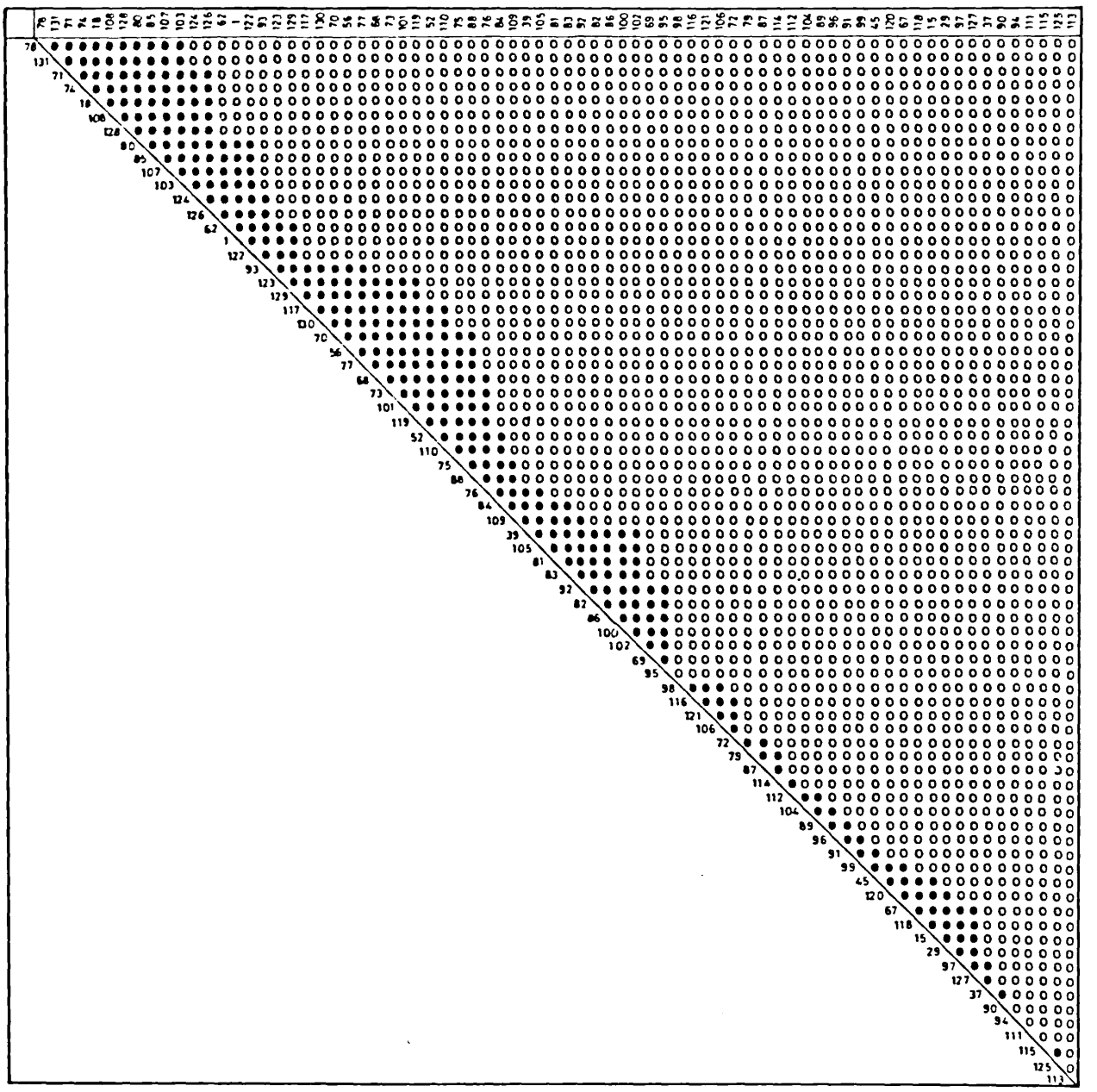
APPENDIX 4.7 Matrix showing significant and insignificant differences in the rust susceptibility of Antirrhinum varieties in the second scoring at Wisley in 1978.



Solid circle = insignificant difference

Key to varieties code numbers - Appendix 4.13

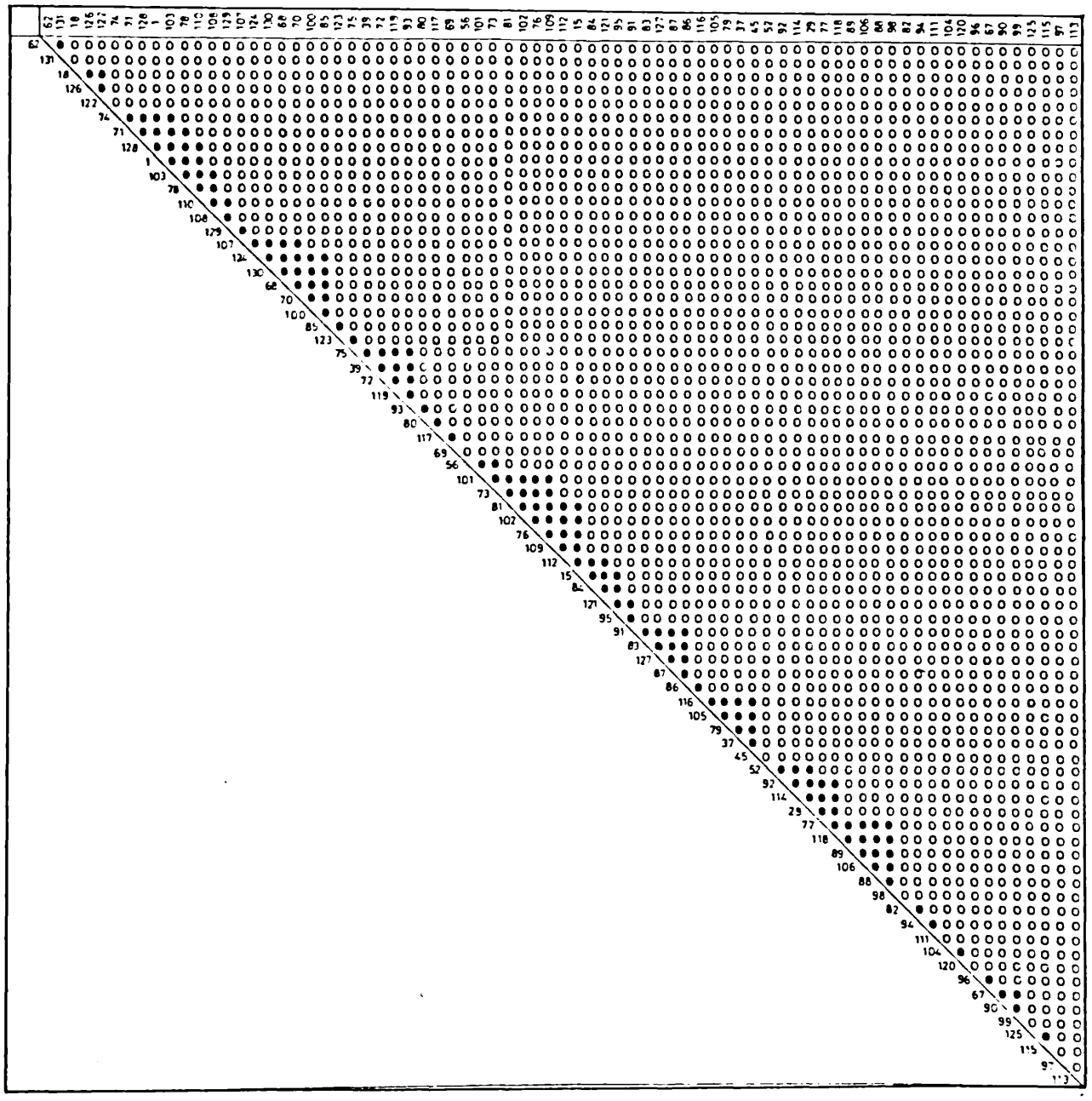
APPENDIX 4.8 Matrix showing significant and insignificant differences in the rust susceptibility of Antirrhinum varieties in the first scoring at Royal Holloway College in 1979



Solid circle = insignificant difference

Key to varieties code numbers - Appendix 4.14

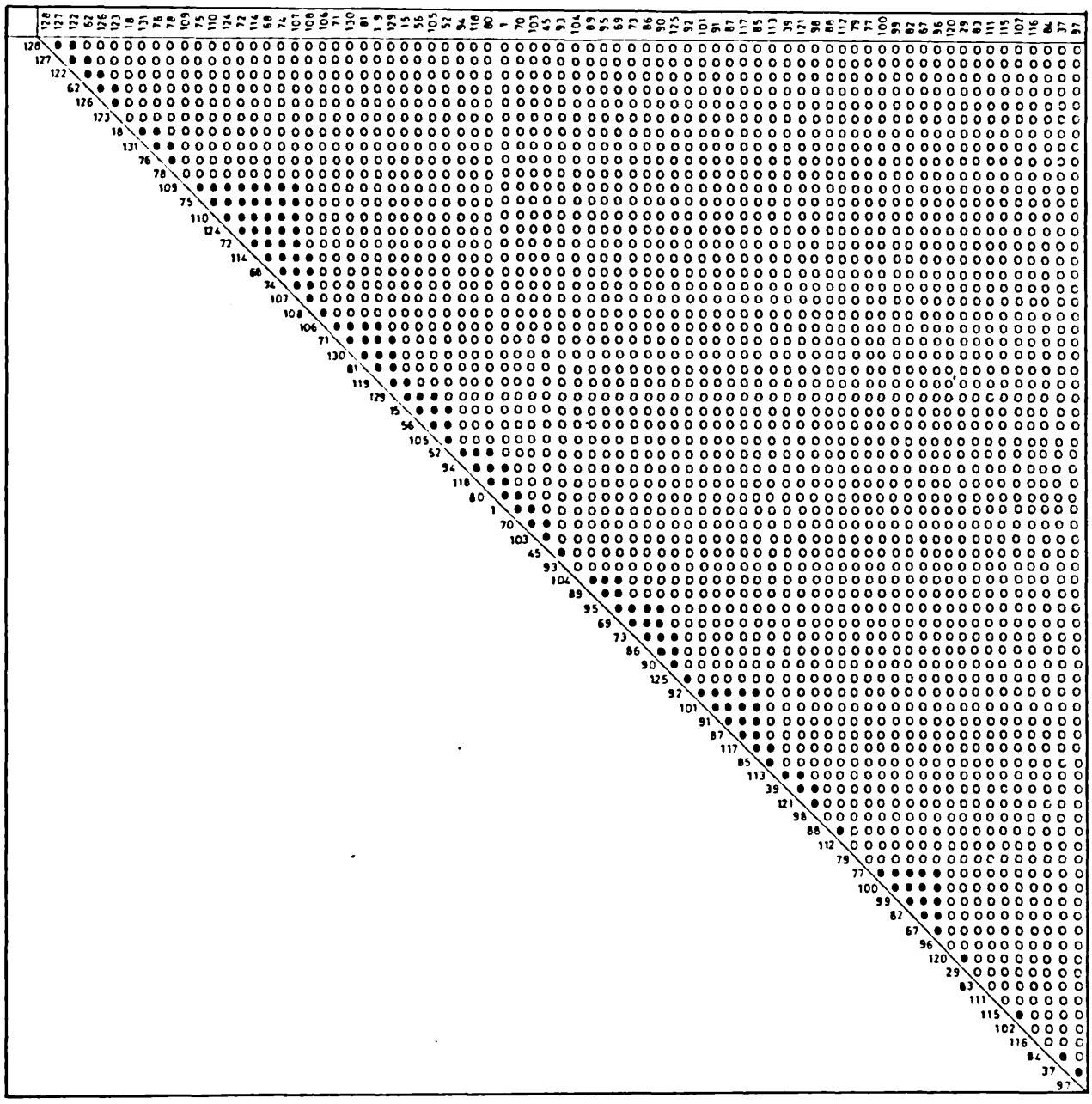
APPENDIX 4.9 Matrix showing significant and insignificant difference in the rust susceptibility of Antirrhinum varieties in the second scoring at Royal Holloway College in 1979



Solid circle = insignificant difference

Key to varieties code numbers - Appendix 4.14

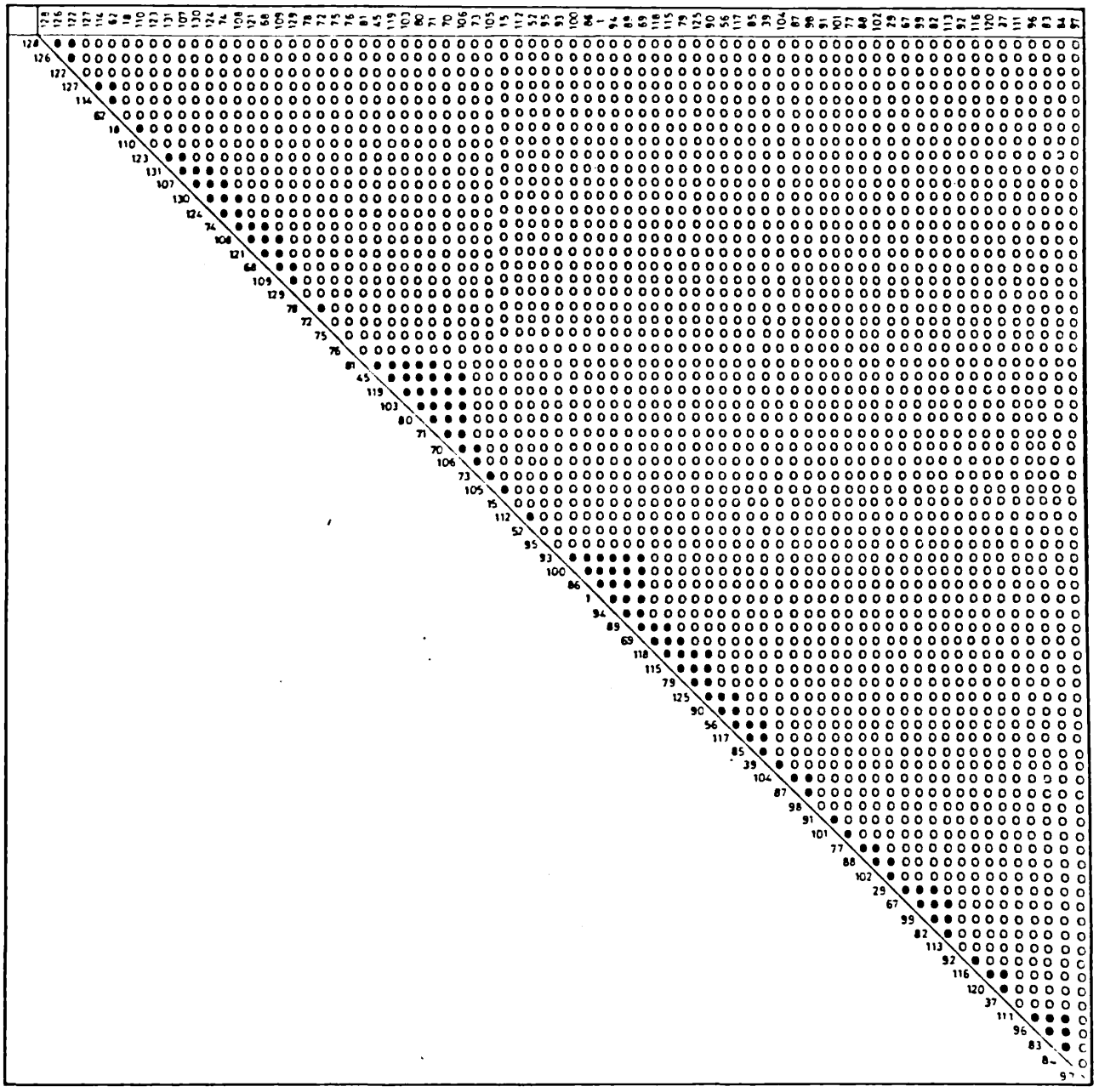
APPENDIX 4.10 Matrix showing significant and insignificant difference in the rust susceptibility of Antirrhinum varieties in the first scoring at Wisley in 1979



Solid circle = insignificant difference

Key to varieties code numbers – Appendix 4.14

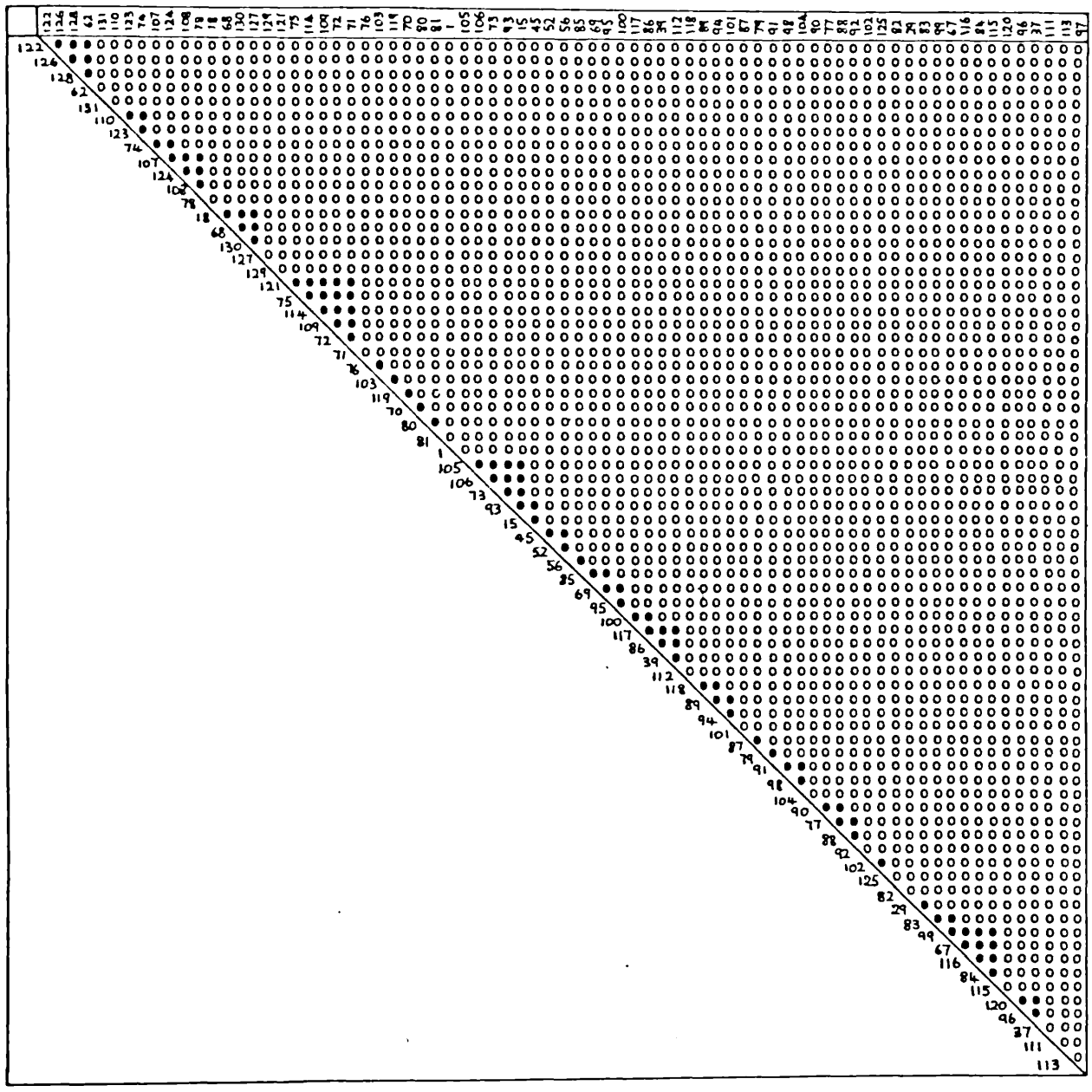
APPENDIX 4.11 Matrix showing significant and insignificant difference in the rust susceptibility of Antirrhinum varieties in the second scoring at Wisley in 1979



Solid circle = insignificant difference

Key to varieties code numbers – Appendix 4.14

APPENDIX 4.12 Matrix showing significant and insignificant differences in the rust susceptibility of Antirrhinum varieties using combined data of Royal Holloway College and Wisley in 1979



Solid circle = insignificant difference

Key to varieties code numbers – Appendix 4.14

Appendix 4.13

Key for the Varieties included in the Plot Experiment - 1978

Code No.	Variety Name	Code No.	Variety Name
1	Pink Pixie	35	Carioca Deep Red
2	Red Pixie	36	Carioca Orange
3	Rose Pixie	37	Carioca Bright Scarlet
4	White Pixie	38	Carioca Peach Bronze
5	Yellow Pixie	39	Carioca Yellow
6	Orange Pixie	40	Carioca Cherry Red
7	Sweetheart Bronze	41	Carioca Pink
8	Sweetheart Pink	42	Carioca White
9	Sweetheart Red	43	Carioca Appleblossom
10	Sweetheart Rose	44	Carioca Rose
11	Sweetheart White	45	Coronette Scarlet
12	Sweetheart Yellow	46	Nanum Dazzler
13	Kolibri Formula Mixture	47	Nanum Black Prince
14	Variety A	48	Regal Bright Scarlet
15	Variety B	49	Regal Rose
16	Variety C	50	Regal Orange Scarlet
17	Variety D	51	Regal White
18	Variety E	52	Regal Yellow
19	Variety F	53	Regal Crimson
20	Variety G	54	Regal Cherry
21	Variety H	55	Regal Apricot
22	Variety I	56	Yellow Monarch
23	Variety J	57	White Monarch
24	Variety K	58	Carmine Monarch
25	Coronette Yellow	59	Lavender Monarch
26	Coronette White	60	Orange Monarch
27	Coronette Scarlet	61	Crimson Monarch
28	Coronette Rose	62	Amber Monarch
29	Coronette Pink	63	Coral Monarch
30	Coronette Bronze	64	Scarlet Monarch
31	Coronette Cherry	65	Cherokee
32	Coronette Crimson	66	Variety M
33	Coronette Orchid	67	Malmaison
34	Variety L		

Appendix 4.14

Key for the Varieties included in the Plot Experiment - 1979

Code No.	Variety Name
1	Pink Pixie
15	Variety B
18	Variety E
29	Coronette Pink
37	Carioca Bright Scarlet
39	Carioca Yellow
45	Coronette Scarlet
52	Regal Yellow
56	Yellow Monarch
62	Amber Monarch
67	Malmaison
68	Variety N
69	Variety O
70	Variety P
71	Variety Q
72	Variety R
73	Burpee's Super Tetra
74	Tetra Giant Ruffled
75	Kimosy Red
76	Kimosy Delicate Rose
77	Kimosy Primrose Yellow
78	Kimosy Crimson
79	Kimosy White
80	Kimosy Orange
81	Majestic Purple King
82	Majestic Celestial
83	Majestic Snowstorm
84	Majestic Red Chief
85	Majestic Orange King
86	Majestic Forest Fire
87	Majestic Eldorado
88	Rocket Citron Yellow
89	Rocket White
90	Rocket Red
91	Rocket Orange
92	Rocket Orchid
	Suttons Triumph-
93	-Mauve
94	-Bright Orange
95	-White
96	-Primrose
	Suttons Triumph cont.
97	-Scarlet
98	-Orange Salmon
	Suttons Intermediate-
99	-White
100	-Fire King
101	-Bright Crimson
102	-Rich Apricot
103	-Guardsman
104	-Eclipse
105	-Yellow
	Suttons Rust Resistant-
106	-Orange Glow
107	-Yellow
108	-Pale Sulphur
109	-Apricot
110	-Leonard Sutton
111	Kim White
112	Kim Purple
113	Kim Primrose Yellow
114	Kim Mid Rose
115	Kim Deep Orange
116	Kim Blood Red
117	Frontier White
118	Frontier Flame
119	Frontier Crimson
120	Frontier Yellow
121	Wisley Cheerful
122	Wisley Golden Fleece
123	Toreador
124	Titan
125	Orange Glow
126	Victory
127	Yellow Freedom
128	Yellow Freedom
129	White Freedom
130	Bonfire
131	Variety S (tetraploid)

Appendix 5.1 Comparison of Means of three Varieties by Tukey's Method

Day No.	$S_{\bar{x}}$	$D_{0.05}$	$D_{0.01}$	Var	Mean Block Score $\bar{x}$	Significance of Difference	
						$\bar{x}$-90.33	$\bar{x}$-95.77
1	5.14	19.94	27.09	A	132.55	42.22 **	36.78 **
				C	95.77	5.44	
				B	90.33		
						$\bar{x}$-93.33	$\bar{x}$-119.11
11	11.02	42.76	58.08	A	198.88	105.55 **	79.77 **
				C	119.11	25.78	
				B	93.33		
						$\bar{x}$-100.88	$\bar{x}$-151.88
22	9.74	37.79	51.33	A	212.77	111.89 **	60.89 **
				C	151.88	51.00 *	
				B	100.88		
						$\bar{x}$-107.22	$\bar{x}$-179.55
33	16.04	62.24	84.55	A	290.66	183.44 **	111.11 **
				C	179.55	72.33 *	
				B	107.22		
						$\bar{x}$-111.11	$\bar{x}$-208.66
43	20.05	77.82	105.69	A	348.55	237.44 **	139.89 **
				C	208.66	97.55 *	
				B	111.11		
						$\bar{x}$-114.55	$\bar{x}$-215.11
54	22.63	87.80	119.26	A	383.11	268.56 **	168.00 **
				C	215.11	100.56 **	
				B	114.55		

A = Malmaison

B = Amber Monarch

C = Guardsman

APPENDIX 5.2 Comparison of the weighted regression coefficients for "Malmaison", "Amber Monarch" and "Guardsman" using the Student Newman Keuls Test.

Rank of Regression Coefficient	1	2	3
Variety Code Letter	B	C	A
Weighted Regression Coefficient (b)	0.0054	0.0254	0.0503
Size of Sample	6	6	6

Comparison	Differenc in b	S.E.[1]	q^2	p	$q_{0.05,12,p}$[3]	Conclusion
A vs B	0.045	0.0029	15.30	3	3.773	Reject Ho $b_A = b_B$
A vs C	0.025	0.0033	7.70	2	3.082	Reject Ho $b_A = b_C$
B vs C	0.020	0.0011	17.9	2	3.082	Reject Ho $b_B = b_C$

1. Standard error (S.E.)

$$= \sqrt{\frac{(s^2_{y.x.})_p}{2} \left[\frac{1}{(\Sigma x^2)_A} + \frac{1}{(\Sigma x^2)_B} \right]}$$

where $(s^2_{y\,x})_p = \left(\frac{\text{residual S.S.}_1 + \text{residual S.S.}_2}{\text{residual D.F.}_1 + \text{residual D.F.}_2} \right)$

2. $q = \dfrac{\bar{x}_B - \bar{x}_A}{S.E.}$

3. critical value of q read from Table D.12 (Zar, 1974)

APPENDIX 6.1 Sources of isolates of *Puccinia antirrhini* used in this investigation

A. Collections from *Antirrhinum majus*

1. Britain - Royal Holloway College (R.H.C.)

   collected from natural infection on Malmaison by F.M. Gawthrop

2. Britain - Norwich

   collected by Mr. B. Harrison, John Innes Institute, Colney Lane, Norwich.

3. Britain - Sunbury

   collected by Miss J. Jenkins, Botany Department, Royal Holloway College.

4. Britain - Herne Bay

   collected by Dr. B.M.G. Jones, Botany Department, Royal Holloway College.

5. Australia - Victoria (Welshpool)

   collected by Mr. D.E. Harrison, Plant Research Institute, Department of Agriculture, Victoria, Australia 3121

6. South Africa - Claremont

   received from The Director, National Botanic Gardens of South Africa, Kirstenbosch Botanic Garden, Claremont 7735, South Africa.

7. France - Besancon

   received from The Director, Jardin Botanique de la ville et de l'Universite, Place Marechal Lederc, 25042 Besancon - Cedex France.

8. France - Bretigny sur Orge

   collected by Madame H. Wache, L. Clause, Seed Growers and Breeders 91220 Bretigny sur Orge France.

9. California - Ojai

   collected by Mrs. F.M. Gawthrop from private garden in Ojai.

B. Collections from wild species of *Antirrhinum* in California

10. On *A. multiflorum* in Purissima Hills, North of Lompoc, Santa Barbara County - collected by Mr. G.D. Barbe, Plant Taxonomy Laboratory, Department of Food and Agriculture, 1200 N.Street, Room 340 Sacramento CA 95814 U.S.A.

11. On *A. multiflorum* in the Purissima Hills, North of Lompoc. On a steep slope of a S.E. facing canyon 6.4 miles North of Bridge over Santa Ynez, Lompoc on State Highway 1 collected by F.M. Gawthrop.

12. On *A. virga* in Lake County. In chaparral above small road cutting on both sides of Highway 53 between Lower Lake and Highway 20, 0.5 miles N. of Cache Creek Bridge (S.E. end of Clear Lake).

APPENDIX 6.2 Clonal propagation of *Antirrhinum majus* from leaf cuttings.

Leaves of many species are capable of producing roots and some have the further power of developing buds after rooting. Plants belonging to the Crassulaceae, Gesneriaceae and Melastomataceae are commonly propagated by this method. The author has found no report of any member of the Scrophulariaceae producing buds from leaf cuttings.

However, this phenomenon was first noticed in *A. majus* (Scrophulariaceae) when detached leaves were floated on water in a crystallizing dish and the dish covered with a glass plate. Roots were produced from the cut petiole of the majority of leaves within two or three weeks and a young plant developed in some of these after two to three months (Figure 1). The young plant may be carefully transplanted into soil. Although it was not attempted to raise plants of other species of *Antirrhinum* by this method, roots were observed on a number of species after two weeks.

This technique produces more plants from a single parent than the conventional stem cuttings and could be a useful method of increasing a limited amount of parental material.

Figure 1. Young plant developing from a leaf cutting of *Antirrhinum majus*.

APPENDIX 7.1 Report made to the S.R.C. and Central Research Fund of the University of London on return from visit 13th July, 1979 (reproduced unedited)

Report of a visit to California to collect samples of the rust fungus, Puccinia antirrhini, and seed specimens of the native species of Antirrhinum.

Two grants, one from the Central Research Fund and the other from the Science Research Council were used to finance the visit to California. The duration of the visit was four weeks and was within the period of study for a PhD. degree of the University of London. The isolates of P. antirrhini and the wild species of Antirrhinum collected in California will be used in the research work for the PhD. degree.

Wild species of the genus Antirrhinum are relatively uncommon in California. Consequently before going to California recent locations of the species were sought in the herbaria of the Royal Botanic Gardens, Kew and the British Museum of Natural History. In California three other herbaria were visited; the Jepson Herbarium, Berkeley, the University of California Herbarium at Berkeley, the herbarium at the Santa Barbara Botanic Gardens. Advice was also sought from field botanists and plant collectors in California on the types of habitat where Antirrhinums might be found. Help was found in particular from Mr. L.R. Heckard, Mr. S. Junak and Mr. G.D. Barbe.

In the five herbaria 723 specimens of Antirrhinums were found but there were precise locations for only 197 of these (Table 1). An attempt was made to visit the majority of the locations, the route taken is shown on the map. A number of the sites were found to be inaccessible as a result of road closures or the location being in private property. In several cases the habitat had been destroyed by the development of mountain roads or the building of private houses along the canyon roads. A total of nine species including the introduced A. majus were found from twentythree sites. The one species which was not found was A. subcordatum. This is a rare plant as reflected by the small number of specimens located in the herbaria (Table 1). It has been collected only from a restricted area of the Inner Coast Range in Glenn and Colusa Counties. Mr. Heckard, curator of the Jepson Herbarium, expects that he will shortly be in this area and will look for the species again.

Table 1 Summary of the number of Antirrhinum species found in the five herbaria and the number of these with precise locations.

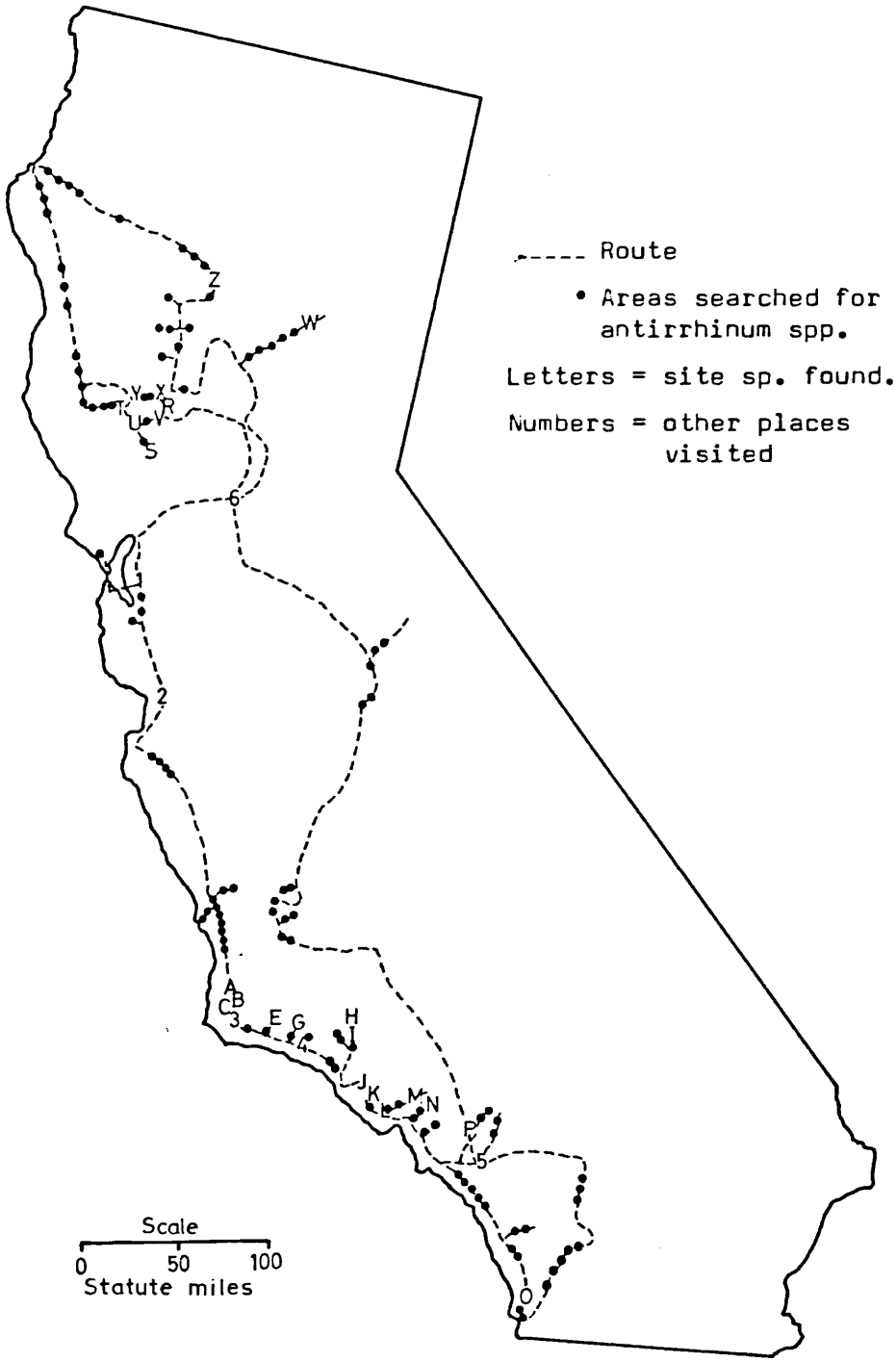
Species	Total No. of specimens	No. with precise locations
A. breweri	83	29
A. cornutum	60	15
A. coulterianum	119	27
A. kelloggii	53	16
A. multiflorum	104	44
A. nuttallianum	155	18
A. subcordatum	6	4
A. vexillocalyculatum	113	28
A. virga	30	16
	723	197

A sample of all species found will be offered to the Royal Botanic Gardens, Kew and the British Museum for inclusion in their herbaria and a complete collection will be curated at the herbarium at the Department of Botany, Royal Holloway College, University of London. The seed collected will be grown in the greenhouses at Royal Holloway College, Department of Botany and the plants used in subsequent experiments to test for different strains of the fungus. At the end of this study the seed will be offered to a seed bank.

All rust diseases show variation in timing and severity from year to year and P. antirrhini is no exception. Although several herbarium specimens which had been collected in June and July showed severe rust infection, the disease was not prevalent in June and July in California this year. The rust was collected from three locations on the susceptible wild species A. multiflorum and A. virga and four collections were made on the cultivated A. majus. Where antirrhinums were seen growing in private gardens the owners were approached and all allowed their antirrhinums to be inspected for rust disease. Addressed envelopes were left with these people who all agreed to send a sample of the rust if the disease appeared later in the year. In addition the field botanists have agreed to look for the disease later at the sites where uninfected susceptible wild species were collected during this visit. Although fewer rust isolates were found than had been hoped, it is very probable that more samples will arrive later in the season from personal contacts made.

The financial assistance of the Central Research Fund and the Science Research Council is gratefully acknowledged. This very worthwhile and interesting visit could not have been made without their help.

Frances Gawthrop



Key to the sites where Antirrhinum species were found

Antirrhinum breweri Gray — Site W
Plumas Co. - occasional isolated plants beside road on Hwy 70. 1 - 4 miles east of bridge over N fork of Feather River and junction of road to Caribou. Between Belder and Virgilia.

Antirrhinum cornutum Benth. — Site Z
Tehama Co. - About 6 miles S. of Red Bluff. On disturbed soil on S side of Coyote Creek, about 50 metres W of bridge over Rawson Road, 0.6 miles N of Flores Ave. (NB Rawson Road runs parallel and about 1 mile to the W of Interstate 5 and Flores Av. crosses Interstate 5 at the exit for Proberta and Gerber).

Antirrhinum coulterianum Benth. — Site M
Los Angeles Co. - Santa Monica Mts. Along S side and W end of layby on S side of Mulholland Hwy, 1.9 miles W of junction with Las Virgenes Road. N of Hwy 1 between Malibu and Point Dume.

Antirrhinum coulterianum Benth. — Site P
Los Angeles Co. - On dry NW facing slope on N side of Pico Canyon Road, 2.0 miles W of Interstate 5 (from central reservation).
NB Pico Canyon Road crosses Interstate 5 at the Valencia and Newhall exit, N of Los Angeles.

Antirrhinum kelloggii Greene — Site L
Los Angeles Co. - Santa Monica Mts. 1.9 miles along Encinal Canyon Road north of Pacific Coast Hwy 1 between Santa Monica and Point Hueneme. On a dry bank N of a development road. The area had been burned in the fall of 1978.

Antirrhinum majus L — Site I
Ventura Co. - Naturalised in front garden of Mrs. Sims, 985 Fordyce Road, Ojai.

Antirrhinum majus L — Site V
Lake Co. - Old variety which had been in the garden since before 1961. Mr. Dittmar, 1710 Lower Lake.

Antirrhinum multiflorum Penn. — Site A
Santa Barbara Co. - In the Purissima Hills, N of Lompoc. On steep slope of a SE facing canyon 6.4 miles N of bridge over Santa Ynez River, Lompoc on state Hwy 1. Locally abundant in chaparral vegetation with occasional Quercus agrifolia.

Antirrhinum multiflorum Penn. — Site B
Santa Barbara Co. - In the Purissima Hills, N of Lompoc. Annual and perennial plants growing on both sides of road by a limestone road cutting, 5.7 miles N of Santa Ynez River, Lompoc on State Hwy 1.

Antirrhinum multiflorum Penn. — Site C
Santa Barbara Co. - In the Purissima Hills, N of Lompoc. A mixed population of pink and white flowered plants growing in short chaparral vegetation below (lower than) the road and beside a layby, 4.9 miles N of Santa Ynez River, Lompoc on state Hwy 1.

Antirrhinum multiflorum Penn. — Site G
Santa Barbara Co. - Santa Ynez Hills, N of Sheffield Reservoir. Along both sides of Gibraltar Road, 2.25 miles N of junction with Mountain Drive, N of Santa Barbara. At base of sandstone roadcutting.

Key to the sites where Antirrhinum species were found contd.

Antirrhinum multiflorum Penn. Site H
Ventura Co. - A single plant beside the footpath to Grindley springs camp, 150-200 metres from Grindley Road. The footpath starts from the west side of Grindley Road, 1.1-1.2 miles N of Grand Ave.,Ojai. NB plant growing 5 ft from the edge of a burn.

Antirrhinum multiflorum Penn. Site J
Los Angeles Co. - 4.9 miles along Little Sycamore Canyon Road from Yerba Buena Road. NB Little Sycamore Canyon Road is the right fork of Yerba Buena Road, 2.2 miles N of Pacific Coast Hwy 1 between Point Hueneme and Santa Monica. Perennial plants growing on loose shale beside road.

Antirrhinum multiflorum Penn. Site K
Los Angeles Co. - Santa Monica Mts. 5.3 miles along Little Sycamore Canyon Road from Yerba Buena Road. NB Little Sycamore Canyon Road is the right fork of Yerba Buena Road, 2.2 miles N of Pacific Coast Hwy 1 between Point Hueneme and Santa Monica. Annual and perennial plants on rock outcrop beside road.

Antirrhinum multiflorum Penn. Site N
Los Angeles Co. - Santa Monica Mts. On an E facing rock outcrop on N side of Mulholland Hwy, 1.2 miles W of junction with Las Virgenes Road. N of Pacific Coast Hwy 1 between Malibu and Point Dume.

Antirrhinum nuttallianum Benth. Site L
see location for Site L under A. kelloggii on previous page.

Antirrhinum nuttallianum Benth. Site O
San Diego Co. - On an area of coastal sage scrub NNE of Torrey Pines State Park. 1.1 miles up Carmel Valley Road from Business Route 5 between Del Mar and La Jolla. Locally abundant 200 metres N of Carmel Valley Road and about 20 metres E of Portofino Road. Variable population in habit and colour.

Antirrhinum vexillocalyculatum Kell. Site S
Napa Co. - 13.0 miles along Butts Canyon Road from Hwy 53 (just N of Middletown) to Aetna Springs. (also 3.15 miles SE of Lake/Napa Co. line growing on loose shale on a SE facing slope below the road and above the creek.

Antirrhinum vexillocalyculatum Kell. Site U
On bank above road cutting on N side of Hwy 29 between Kelseyville and Lower Lake, 4.85 miles W of Lower Lake. Plants supported by their tortile branchlets entwined with grass.

Antirrhinum vexillocalyculatum Kell. Site X
A single plant growing in loose shale on the South side of the road up Indian Valley. 7.65 miles W of Junction with road from Leesville and Wilbur Springs. E of Hough Springs.

Antirrhinum virga Gray Site R
Lake Co. - In chaparral above small road cutting on both sides of Hwy 53 between Lower Lake and Hwy 20, 0.5 miles N of Cache Creek Bridge (SE end of Clear Lake)

Key to the sites where Antirrhinum species were found contd.

Antirrhinum virga Gray — Site T
Lake Co. - South of Clear Lake. South of Hwy 29, 3.2 miles E of bridge over Kelsey Creek on road from Lakeport to Lower Lake. A single plant (about 2m tall) on road bank.

Antirrhinum virga Gray — Site U
Lake Co. - On bank above road cutting on N side of Hwy 29 between Kelseyville and Lower Lake, 4.85 miles W of Lower Lake.

Antirrhinum virga Gray — Site Y
Lake Co. - Locally abundant perennial in chaparral N of Clear Lake between Bartlett Springs and Hough Springs, 20.0 miles along Bartlett Springs Road from junction with Hwy 20 at Lucerne.

Key to the numbered points where visits were made

1. University of California at Berkeley
2. Goldsmiths Seed Company, Gilroy.
3. Bodgers Seed Company, Lompoc.
4. Santa Barbara Botanic Garden, Santa Barbara.
5. Rancho Santa Ana Botanic Garden, Claremont, Low. Angeles.
6. Dept of Food and Agriculture, Sacramento.

APPENDIX 7.2 Sources of wild species used in this study

Species Name	Accession Number	Source	Photograph	Cytology	Self Compatibility	Interspecific Hybrid	Resistance to rust in field	Resistance to rust in greenhouse
A. European Species								
A. australe	78-133	Hortus Botanicus, Coimbra Portugal			+	+		
A. barrelieri	78-31	Botanische Garten, Berlin Dahlem Germany						+
	78-107	Tala vera de la Reina Toledo (Segura Zubizarreta)				+		+
	78-110	Encisa (Logrono) (Segura Zubizarreta)	+			+	+	
A. braun-blanquetii	79-123	University of Bristol, Botany Department						+
A. granticum	78-13	Hortus Botanicus, Coimbra Portugal				+		
	78-106	Argecilla, Guadala Jara (Segura Zubizarreta)					+	
	78-109	Guadalupe (Segura Zubizarreta)	+					+
	78-134	Hortus Botanicus Coimbra Portugal			+	+		+
A. hispanicum	78-206	Kew Gardens	+					
A. hispanicum subsp.mollissimum	78-116	Universitat 4056 Basel Schweiz Schonkein str 6				+		
A. latifolium	79-121	Hanbury, Genova, Italy						+
	79-122	Hanbury, Genova, Italy						+
A. majus subsp. majus	78-7	Hortus Botanicus, Coimbra Portugal			+	+	+	
A. majus subsp. cirrhigerum	78-148	Hortus Botanicus, Coimbra, Portugal						+
A. majus subsp. linkianum	78-15	Hortus Botanicus, Nijmegen Netherlands	+		+	+		
A. majus subsp. tortuosum	78-19	Instituto ed Orto Botanico Catania Italy			+	+		
	78-159	Instituto ed Orto Botanico di Roma Italy					+	
A. meonanthum	78-10	Hortus Botanicus, Coimbra Portugal				+	+	
	78-132	Hortus Botanicus, Coimbra Portugal			+	+		
	78-140	Hortus Botanicus, Coimbra Portugal	+					
	79-98							+
	79-120	Chelsea Physic Garden						+
A. molle	78-28	Botanical Supply Unit, University of London (Rockery)	+					+

APPENDIX 7.2 Sources of wild species used in this study contd.

Species Name	Accession Number	Source	Photograph	Cytology	Self Compatibility	Interspecific Hybrid	Resistance to rust in field	Resistance to rust in greenhouse
A. sempervirens	78-108	Peregrina, Guada lagara Segura Zubizurreta					+	
A. siculum	78-23	Giardino Botanico, Coloniale di Palerno	+		+	+		
	78-24	Giardino Botanico Coloniale di Palerno					+	
	78-25	Botanical Supply Unit, University of London (Rockery)			+	+		+
B. Californian Species								
A. cornutum	79-46	Site Z (see Appendix 7.1)						+
A. coulterianum	79-50	Site P (see Appendix 7.1)						+
A. kelloggii	79-57	Rancho Santa Ana Botanic Garden, Claremont, California						+
A. multiflorum	78-22	Santa Barbara Botanic Garden California		+				
A. nuttallianum	78-161	Rancho Santa Ana Botanic Garden, Claremont,	+				+	
	79-72	Site O (see Appendix 7.1) / California						+
A. virga	78-176	Lake County, California (Douglas Barbe)		+				+
C. Other genera								
Anarrhinum bellidifolium	78-149	Hortus Botanicus, Coimbra Portugal						+
Asarina erubescens	78-2	Jardin Botanico, Gerona Spain						+
Asarina procumbens	78-117	Universitat 4056 Basel (Schweiz)Schonbein str 6				+		+
Galvesia speciosa	78-21	Santa Barbara Botanic Garden, California				+	+	+
Maurandia scandens	78-127	Botanic Garden, University of Hull						+
Misopates calycinum	78-146	Hortus Botanicus, Coimbra, Portugal						+
	78-204	Kew Gardens	+					

APPENDIX 7.3 Results of crosses between wild species of the Antirrhinum section and A. majus cv. "Malmaison"

Species	Accession Number	Plant No.	Cross	No. of flowers crossed	Fruits developed	Germination
A. australe	78-133	1	A. australe x Malmaison	3	3	✓
		2A	A. australe x Malmaison	3	3	✓
		2B	A. australe x Malmaison	3	3	✓
		25	Malmaison x A. australe	5	5	✓
		26	Malmaison x A. australe	5	5	✓
A. barrelieri	78-107	1A	A. barrelieri x Malmaison	5	5	✓
		1B	A. barrelieri x Malmaison	3	3	✓
		21	Malmaison x A. barrelieri	5	5	✓
		22	Malmaison x A. barrelieri	5	5	✓
	78-110	1	A. barrelieri x Malmaison	3	3	✓
		19	Malmaison x A. barrelieri	5	5	✓
		20	Malmaison x A. barrelieri	5	5	✓
A. graniticum	78-13	1	A. graniticum x Malmaison	2	2	✓
		15	Malmaison x A. graniticum	5	5	✓
		16	Malmaison x A. graniticum	5	5	✓
	78-134	1	A. graniticum x Malmaison	4	4	✓
		31	Malmaison x A.graniticum	5	5	✓
		32	Malmaison x A.graniticum	5	5	✓
A. hispanicum subsp. mollissimum	78-116	1	A. hispanicum subsp.mollissimum x Malmaison	3	0	
		2	A. hispanicum subsp.mollissimum x Malmaison	2	0	
		23	Malmaison x A. hispanicum subsp. mollissimum	5	5	✓
		24	Malmaison x A. hispanicum subsp. mollissimum	5	5	✓
A. majus subsp. majus	78-7	1	A.majus subsp. majus x Malmaison	3	3	✓
		2	A.majus subsp. majus x Malmaison	3	3	✓
		17	Malmaison x A.majus subsp. majus	5	5	✓
		18	Malmaison x A.majus subsp. majus	5	5	✓

APPENDIX 7.3 Results of crosses between wild species of the Antirrhinum section and *A. majus* cv. "Malmaison" contd.

Species	Accession Number	Plant No.	Cross	No. of flowers crossed	Fruits developed	Germination
A. majus subsp. *linkianum*	78-15	1	*A. majus* subsp. *linkianum* x Malmaison	2	2	✓
		3	Malmaison x *A. majus* subsp. *linkianum*	5	5	✓
		4	Malmaison x *A. majus* subsp. *linkianum*	4	4	✓
A. majus subsp. *tortuosum*	78-19	2A	*A. majus* subsp. *tortuosum* x Malmaison	2	2	✓
		2B	*A. majus* subsp. *tortuosum* x Malmaison	2	2	✓
A. meonanthum	78-10	1A	*A. meonanthum* x Malmaison	3	0	
		9	Malmaison x *A. meonanthum*	5	5	lost
		10	Malmaison x *A. meonanthum*	3	3	X
	78-132	1	*A. meonanthum* x Malmaison	6	6	✓
		30	Malmaison x *A. meonanthum*	5	5	*
A. siculum	78-25	1	*A. siculum* x Malmaison	3	3	✓
		11	Malmaison x *A. siculum*	4	0	
		12	Malmaison x *A. siculum*	3	3	✓
	78-23	1A	*A. siculum* x Malmaison	2	2	X
		27	Malmaison x *A. siculum*	5	0	
		28	Malmaison x *A. siculum*	5	0	
Asarina procumbens	78-117	1	*Asarina procumbens* x Malmaison	4	0	
		35	Malmaison x *Asarina procumbens*	5	0	
Galvesia speciosa	78-21	1B	*Galvesia speciosa* x Malmaison	3	0	
		36	Malmaison x *Galvesia speciosa*	5	0	

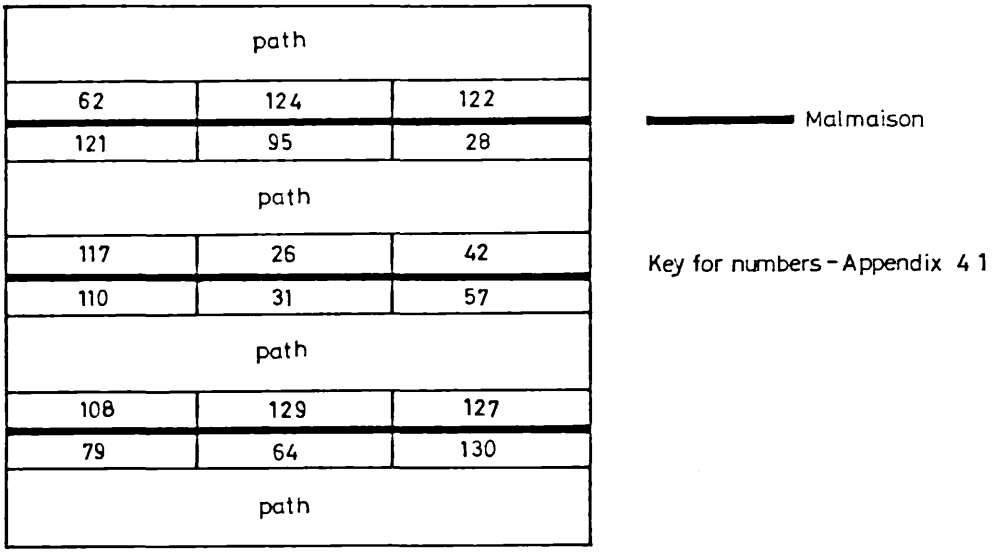
* Two seed pods were produced but they were empty.

APPENDIX 9.1. BREEDING PROGRAMME 1980

A small selection of varieties with an acceptable level or resistance and reasonable horticultural features were grown in the plot at Royal Holloway College in 1980 and used to make the initial crosses of the breeding programme for varieties with improved resistance.

The seed was sown on the 28th March, pricked out between the 14th and 18th April and thirty plants of each variety were planted out on the 29th May in the design shown in Figure 1. As the varieties were only going to be cross-pollinated it was not necessary to use the randomized block design and thirty plants of one variety were planted in a straight line to one side of a 'spreader row' of Malmaison.

Figure 9.1 Arrangement of varieties in 1980



Five plants of each parent variety were selected for the cross. All open flowers and developing seed pods were removed from the spike with scissors. The lowest bud was left in tact as a pollen donor and the next two buds were emasculated using forceps. The flowers of A. majus are big and easy to manipulate and it is possible to open the mouth of the corolla and remove the anthers without cutting the corolla. Four more buds were left untouched in case the weather deteriorated and the top of the inflorescence was pinched out leaving the seven buds. The inflorescence was covered with a bag and tied securely to a stake. The pollen donor was covered to ensure that the pollen had not been contaminated by pollen from other varieties and brought by bees. The majority of the emasculations were performed on August 2nd 1980.

The pollinations were made on August 4th and are summarized on Table 1. Pollen from a dehisced anther from the lowest flower of the bagged inflorescence of the male donor was placed on the receptive stigmas of the two emasculated flowers of the female parent. The remaining four buds were removed and the inflorescence rebagged and labelled. The bags were removed on August 6th and the seeds left to mature on the plant. The seed pods were collected just before they were fully ripe.

Table 1 Crosses between varieties of A. majus for selections with improved resistance and acceptable horticultural features

Programme *	Objective	Code No.	Female Parent	Male Parent
I	White	80-32	95 Suttons Triumph White	57 White Monarch
I	White	80-33	117 Frontier White	57 White Monarch
I	White	80-48	129 White Freedom	26 Corone tte White
I	Yellow	80-40	122 Wisley Golden Fleece	127 Yellow Freedom
I	Orange	80-35	130 Bonfire ("off type")	62 Amber Monarch
I	Flame	80-38	130 Bonfire	62 Amber Monarch
I	Scarlet	80-37	64 Scarlet Monarch	124 Titan
I	Pink	80-34	28 Coronette Rose	110 Leonard Sutton
I	Pink	80-36	31 Coronette Cherry	110 Leonard Sutton
II	Pale Yellow	80-39	108 Suttons R.R. Pale Sulphur	95 Suttons Triumph White
II	Yellow	80-31	127 Yellow Freedom	26 Coronette White
II	Pale orange	80-46	57 White Monarch	130 Bonfire ("off type")
II	Orange	80-44	42 Carioca White	62 Amber Monarch
II	Flame	80-45	57 White Monarch	130 Bonfire
II	Red	80-50	28 Coronette White	64 Scarlet Monarch
II	Pale Pink	80-49	110 Leonard Sutton	117 Frontier White
II	Deep Pink	80-47	129 White Freedom	31 Coronette Cherry
III	Breeders line I	80-41	62 Amber Monarch	127 Yellow Freedom
III	Breeders line 2	80-42	122 Wisley Golden Fleece	108 Suttons R.R. Pale Sulphur
III	Breeders line 3	80-43	130 Bonfire	110 Leonard Sutton

* see Chapter 9, Figure 9.2

APPENDIX 10

EVIDENCE FOR GENETIC CHANGE IN THE ANTIRRHINUM RUST (*Puccinia antirrhini*)

F.M. GAWTHROP
and
B.M.G. JONES

Botany Department, Royal Holloway College,
(University of London), Egham, Surrey, U.K.

ABSTRACT

The available data on the resistance of *Antirrhinum majus* L. to rust, *Puccinia antirrhini* Dietel & Holway, is reviewed. There is evidence for one or more genetic changes in the pathogen. In one instance it can be demonstrated that this change is likely to have been by mutation. The chronology of the changes is: in the U.S.A., east of the Rockies between 1921 and 1935 and in California during 1936; in Europe between 1936 and 1954 and in Britain between 1958 and 1962. A virulent race was present in Australia by 1954.

Key Words: *Puccinia antirrhini* Dietel and Holway, rust, *Antirrhinum majus* L., mutation, virulence.

INTRODUCTION

Antirrhinum rust (*Puccinia antirrhini* Dietel and Holway) is the most serious disease affecting the garden antirrhinum. The disease was first reported in California in 1895 (Blasdale, 1903) on the cultivated forms of *Antirrhinum majus* L. It has now spread throughout the world and attacks antirrhinums wherever they are grown. The disease caused severe losses in the seed trade and this prompted breeders to develop inherited resistance. Varieties of antirrhinum resistant to the rust were available in the U.S.A. in the early 1930's. The first report that their resistance was 'broken' was by Yarwood (1937), who noticed

extensive infection on previously resistant varieties of antirrhinum in California in the summer of 1936. This virulent race of P. antirrhini (which he called "race 2") was apparently restricted to the coastal region of California until at least 1937-38 (Blodgett and Mehlquist, 1941). A virulent race of the pathogen has also been reported from Australia (Walker, 1954). Other references to virulence are mostly restricted to trade journals.

In this paper we review the published results of trials of antirrhinums, confirm the presence of one or more virulent races of P. antirrhini, show that a virulent race of P. antirrhini occurred in the eastern U.S.A. before the Californian outbreak in 1936 and give dates by which virulent types has reached Europe, the U.K. and Australia.

MATERIALS AND METHODS

Between 1921 and 1954 the results of five trials for rust-resistance in antirrhinums was published (Doran, 1921; Mains, 1935; Buchwald, 1936; Kovats, 1954 and Walker, 1954). The Royal Horticultural Society (R.H.S.) held trials of Rust-Resistant Antirrhinums at Wisley, Surrey in 1958 and 1962 and we have been given access to their unpublished records. We have made a comparison between varieties with definitive names which were tested by at least two authors. The assessment of rust tended to be rather subjective and ranged from the six-point scale used by Kovats (1954) to the purely descriptive assessment of Walker (1954). Nevertheless, the criteria given by each author have allowed us to make a direct comparison of their results (Table 1).

The degree of rust infection may be conveniently divided into four categories, from 0 where all individuals are immune, to 3 where all the plants are eventually killed. Table 1 shows that Kovats was the only author to find all the categories of rust infection. Doran (1921) used a "scale of relative numbers",0-100, but these are not percentages. They are difficult to interpret since they were apparently subjective and insufficient information was given to indicate how they were obtained. Even "0" does not mean "immune" since Doran says (p.62) "None of these (highly resistant varieties) is really resistant" and he suggests that "resistant varieties, if any appear" should be selectively propagated. For this reason the varieties given the scale number of "0" by Doran are assigned to the category 1.

The nonparametric sign test is suitable for assessing difference between two related samples (Siegel, 1956). Each pair of trials was compared using this test. The performances of the varieties were ranked with respect to each other and the direction of the difference used as the basis for the sign test. Under the null hypothesis one would expect half of the differences to be negative and the other half to be positive. If too few differences of one sign appear the null hypothesis is rejected and the trials are significantly different. Pairs of trials having less than five varieties in common are too small for the sign test to be used; these were compared subjectively by inspection.

RESULTS

The results for thirty-seven varieties included in the trials, transformed according to the system given in Table 1, are given in Table 2. The significance of the difference between trials, calculated by the sign test, is given in Table 3.

There is a strong similarity between the results of the trials held in the U.S.A. in 1921 and in Europe in 1936, also between the later trials in the U.S.A. in 1935 and in Europe in 1954. There is, however, a striking difference between the earlier and later trials on each continent. The performance of varieties in the European and Australian trials held in 1954 is also similar. There is an obvious difference between the results of the two English trials in 1958 and 1962. It is noteworthy that more varieties exhibited low susceptibility in the earlier trials. Doran (1921) and Buchwald (1936) both found the white-flowered varieties more resistant than other shades.

DISCUSSION

Despite the differences in distance and time, there are similarities between four pairs of trials held on different continents. We therefore believe that the climatic and seasonal influences are not particularly important in determining the response of the plant to the fungus.

The significant differences between the earlier and later trials in the U.S.A. (Doran, 1921 and Mains, 1935), between those in Europe (Buchwald, 1936 and Kovats, 1954) and between those in Britain (R.H.S., 1958 and 1962) must be attributed to the replacement of previously

prevalent races by other more virulent races. The same applies to the difference between the trials in Britain in 1958 and in Australia in 1954.

The change in the rust occurred before 1935 east of the Rockies, since Table 3 indicates a significant difference between the results of Doran and Mains. This preceeded the report of a second race for California in 1936 (Yarwood, 1937). Mains was the first breeder to select resistant plants of antirrhinum and to create new resistant lines which were used by others in breeding resistant commercial varieties. There are two possible explanations for the origin of a virulent race of rust. It may be selected from existing variation in populations of the rust when only a virulent type can infect a "resistant" plant. Alternatively, the virulent race arose by mutation. We favour the latter explanation because six years elapsed between Mains' discovery of resistant plants and their release to other breeders and during that time the resistance was total (Mains, 1935).

The results obtained by Buchwald in his Danish trials are very similar to those obtained by Doran in Massachusetts. Only the original race of the rust was present in Dorans' trials and therefore that race must also have been present in Denmark fifteen years later. By 1954, however, the rust in Europe appears to have become virulent as seen in Kovats' trials. The rust in Britain changed from the original race to a more virulent race between 1958 and 1962, the dates of two trials organised by the Royal Horticultural Society.

It is interesting that when Walker held his trials in Australia, he found heavy infection on four varieties of antirrhinums which were still immune four years later when they were tested in Britain (Walker, 1954). Walker also received a resistant line (No.61) from Dr. K. Baker, who worked in California, and found it to be severely infected in his Australian trials. These results indicate that the Australian race of rust was genetically distinct from both that in California and in Britain during the 1950's.

There is thus sufficient evidence to indicate that the rust fungus, P. antirrhini has undergone one or more genetic changes during the last fifty years, one or more new and virulent races having replaced those previously prevalent. In order to determine whether the apparent changes in virulence are due to more than one mutation it will be necessary to test rust isolates from widely separated localities against a range of hosts. This work is now in progress.

Acknowledgement. We thank the Director of the Royal Horticultural Society at Wisley for permission to examine the records of their trials of antirrhinums.

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Table 1. Comparison of the assessments of susceptibility used in trials of rust-resistance in Antirrhinum majus

Author	Type of Comparison	Degree of Susceptibility			
Present Paper	4 point scale	0 immune	1 slight infection	2 moderate infection	3 severe infection
Doran (1921)	0-100	(see text)	20	20-80	80
Mains (1935)	description	not observed	not observed	rust developed more slowly and plants usually survived	majority of varieties killed by rust
Buchwald (1936)	3 point scale	not observed	+ slight infection	++ moderate infection	+++ severe infection
Kovats (1954)	6 point scale	6	5	4-3	2-1
Walker (1954)	description	not observed	not observed	susceptible, chlorosis visible, uredosori smaller	fully susceptible, no chlorosis visible, profuse uredosorus development
R.H.S. (1958) and (1962)	qualitative	no rust	slight infection	moderate infection	severe infection

Table 2 Susceptibility to rust in *Antirrhinum* varieties included in more than one trial

Location	U.S.A. (Massachusetts)	U.S.A. (Michigan)	Denmark (Vangede)	Hungary (Nemetboly)	Australia (N.S.W.)	Britain (Wisley)	Britain (Wisley)
Year	1921	1935	1936	1954	1954	1958	1962
Author	Doran	Mains	Buchwald	Kovats	Walker	R.H.S.	R.H.S.
Variety							
Appleblossom	-	3	2	3	-	-	-
Black Prince	2	-	3	-	-	-	-
Bridesmaid	1	-	1	3	-	-	-
Canary Bird	-	2	3	3	-	-	-
Carter's Pink	3	-	3	-	-	-	-
Coral Red	3	-	3	-	-	-	-
Crimson Queen Victoria	3	-	3	-	-	-	-
Defiance	2	-	3	2-3	3	-	-
Fiery Belt	3	-	3	-	-	-	-
Firebrand	1	3	1	-	-	-	-
Giant Blood Red	1	-	1	-	-	-	-
Giant Pink	3	-	1	-	-	-	-
Giant Scarlet	1	-	1	-	-	-	-
Giant White	1	2	1	-	-	-	-
Giant Yellow	1	-	1	0-2	-	-	-
Golden Queen	3	2	3	2	-	-	-
Goteling	-	3	3	3	-	-	-
Hephaestos	1	-	1	2	-	-	-
Luteum	-	-	3	3	2	-	-
Mont Blanc	1	3	1	3	-	-	-
Melrose	2	3	2	3	-	-	-
Orange King	2	-	2	3	-	-	-
Phelp's White	1	3	1	-	-	-	-
Pink Freedom	-	-	-	-	3	0	-
Pure White	1	-	1	-	-	-	-
Purity	-	3	-	3	-	-	-
Queen of the North	1	3	1	3	-	-	-
Queen Victoria	1	3	1	3	3	-	-
Rose Dore	1	3	1	-	-	-	-
Rose Marie	-	-	-	2-3	2	-	-
Ross Queen	3	-	3	3	-	-	-
Silver Pink	2	3	2	-	-	-	-
The Rose	2	-	3	-	2	-	-
Venus	3	-	3	-	-	-	-
Wisley Bridesmaid	-	-	-	-	3	0	2
Wisley Cheerful	-	-	-	-	3	0	2
Wisley Golden Fleece	-	-	-	-	3	0	1

Table 3. Matrix of results of the sign test to compare the pairs of trials

Ho: the positive differences equal the negative differences at = 0.05 level of significance

		Britain R.H.S. (1962)	Britain R.H.S. (1958)	Australia Walker (1954)	Hungary Kovats (1954)	Denmark Buchwald (1936)	U.S.A. Mains (1935)
U.S.A.	Doran (1921)	-	-	-	X	✓ †	X
U.S.A.	Mains (1935)	-	-	-	✓	X	
Denmark	Buchwald (1936)	-	-	✓	X		
Hungary	Kovats (1954)	-	-	✓			
Australia	Walker (1954)	-	X †				
Britain	R.H.S. (1958)	X †					

Key:- ✓ = Ho accepted; trials not significantly different.
X = Ho rejected; trials significantly different
† = Comparison made by inspection
- = No comparison possible