

The inheritance of salt exclusion in woody perennial fruit species

S.R. SYKES

CSIRO, Division of Horticulture, Merbein, Victoria, 3505, Australia

Key words: citrus, Cl-ion exclusion, grapevines, hybrids, inheritance, Na-ion exclusion, rootstocks

Abstract

Citrus and grapevines are salt-sensitive perennial crops. Damage caused by salinity is due mostly to accumulation of excessive concentrations of salt (Na- and Cl ions) in shoot tissues. In both crops, however, some rootstock varieties can restrict the accumulation of salt in scion leaves and stems. Salt-excluding rootstocks, however, are often deficient with regard to other desirable characteristics and as such their use is limited. As a consequence, we have conducted a range of crosses within both crops to select new salt-excluding hybrids which may have potential as new rootstocks and also to investigate the inheritance of salt exclusion in these woody perennials.

In citrus, both Cl-ion and Na-ion exclusion has been observed as a continuous character and progenies segregate widely for their ability to restrict the accumulation of these ions in shoot tissues. The ability to exclude Cl ions appears to be independent of the ability to exclude Na ions. Thus a good Cl-ion excluder is not necessarily a good Na-ion excluder and vice versa. It has been possible, however, to select new salt-excluding citrus hybrids which perform as well as and sometimes better than parent varieties when grafted with a common scion and grown in artificially salinised field plots.

In grapevines, the research has concentrated on the ability for Cl-ion exclusion and depending on the Cl-ion-excluding parent chosen this is inherited as either a polygenic or monogenic trait. In crosses between *Vitis champini* (Cl-ion excluder) and *Vitis vinifera* (Cl-ion accumulator), the ability to restrict Cl-ion accumulation in shoot tissues segregates widely with some offspring transgressing the performance of either parent. In crosses and backcrosses involving *V. berlandieri* and *V. vinifera*, however, hybrids segregate as either Cl-ion excluders or accumulators suggesting the effect of a major dominant gene for Cl-ion exclusion from *V. berlandieri*. This was evident from both field and glasshouse experiments although possible modifying genes from *V. vinifera* may affect the expression of this gene under glasshouse conditions in some crosses.

Introduction

While citrus trees are considered to be salt-sensitive glycophytes (Greenway and Munns, 1980), they exhibit a wide variation for Cl-ion exclusion within species and cultivars (Grieve and Walker, 1983; Sykes, 1985a; Walker and Douglas, 1983). This variation has stimulated breeding programs aimed at producing new salt-tolerant rootstocks (Furr and Ream, 1969; Sykes, 1985b).

High leaf Cl-ion concentrations in citrus scions can lead to physiological disturbances and even-

tually visible leaf damage (Cooper and Shull, 1953). High leaf Na-ion concentrations also have detrimental effects on photosynthesis and transpiration (Behboudian et al., 1986). When grown under conditions of low to moderate root zone salinities (25–50 mM NaCl), nucellar seedlings of *Poncirus trifoliata* Raf. are able to maintain lower leaf Na-ion concentrations than other citrus rootstocks (Grieve and Walker, 1983; Walker, 1986). *Poncirus trifoliata*, sometimes referred to as *Citrus trifoliata* (Bailey and Bailey, 1976), is an important citrus rootstock which is sexually compatible with *Citrus* species. *Pon-*

cirus × *Citrus* crosses produce viable progeny, e.g. Carrizo citrange (*C. sinensis* × *P. trifoliata*). The variation between nucellar seedling populations of *Poncirus* and *Citrus* suggests a heritable basis for Na-ion exclusion, and so screening for this has been a component of CSIRO's salt-tolerant citrus rootstock breeding program.

Grapevines are moderately salt-tolerant if Cl-ion injury can be avoided (Ehlig, 1960). Leaf Cl-ion concentrations have been shown to be associated with symptoms of salt injury and the health of irrigated vines in the Murray Valley (Thomas, 1934; Woodham, 1956). High leaf Cl-ion concentrations in vines have been accompanied by decreased rates of photosynthesis (Downton, 1977a) and reduced yields (Grieve, 1984).

Rootstocks will reduce leaf Cl-ion concentrations in grapevines (Bernstein et al., 1969; Sauer, 1968) and there is considerable variation for Cl-ion exclusion both between (Antcliff et al., 1983; Downton, 1977b) and within (Ehlig, 1960; Groot Obbink and Alexander, 1973) *Vitis* species. This variation has led to a search for new Cl-ion-excluding grapevine rootstocks through breeding and selection (Newman and Antcliff, 1984; Sykes, 1985c, 1987).

During the course of breeding and selecting new salt-tolerant citrus and grapevine rootstocks, observations have been made concerning the mode of inheritance of salt exclusion. Most of the results discussed in this paper have been published (Newman and Antcliff, 1984; Sykes, 1985b; c; 1987; Sykes and Newman, 1987). New data, however, are presented concerning the variation for Na-ion exclusion between and within *Citrus* × *Poncirus* hybrids.

Materials and methods

Citrus

Hybrids between citrus rootstock varieties were produced using techniques described by Soost and Cameron (1975) during 1980, '81 and '82. The combinations produced in 1980 and 1981 have been published (Sykes, 1985b). The hybrids from these crosses were screened initially for leaf

Cl-ion concentrations following a short-term salt test. Since then, leaf materials of eight progenies retained from these tests have been analysed for Na-ion concentrations. Sykes (1985b) described an irrigated pot trial using two hybrids from progeny 80-02, Rangpur lime (*Citrus* × *limonia* Osbeck) × Trifoliolate orange (*Poncirus trifoliata* Raf.). This trial confirmed the Cl-ion-excluding abilities for these hybrids, viz. 80-02-08 and 80-02-38. Another glasshouse trial has since been conducted to assess the Na-ion excluding abilities of these hybrids. An additional hybrid, 80-02-02, which was morphologically similar to 80-02-08 and 80-02-38 but accumulated high leaf Cl-ion concentrations in the original screening experiment, was also included.

Twelve-month-old nucellar seedlings (see Frost and Soost, 1968) of Rangpur lime and Trifoliolate orange and twelve-month-old plants of hybrids 80-02-02, -08 and -38 grown from stem cuttings, were transferred from a standard potting mix to half-strength No. 1 nutrient solutions (Hoagland and Amon, 1950) held in 576-litre fibreglass tanks (1.2 × 0.6 m surface area; 0.8 m deep). Solutions were made with rainwater and were maintained at pH 6.5. Iron (2.5×10^{-5} M Fe as ethylenediametetracetic acid ferric monosodium salt), trace elements (4.6×10^{-5} M B, 9.1×10^{-6} M Mn, 7.6×10^{-6} M Zn, 3.1×10^{-7} M Cu and 1.0×10^{-7} M Mo) and benomyl (4.5×10^{-6} M methyl 1-(butylcarbamoyl)-2-benzimidazole carbamate applied as 'Benalate', a 50:50 wettable powder; Dupont Chemical Company) were added to solutions weekly throughout the experiment. Three plants of each genotype, supported by PVC covers, were randomised within each of four tanks and shoots pruned to 20 cm. One shoot was allowed to develop from the youngest bud. After 30 days solutions were renewed and made up to full strength and the youngest leaf on each plant was labelled with a loosely tied piece of cotton thread. Salt (NaCl) was added to two tanks at a rate of 25 mM per day until the concentration reached 50 mM. The other tanks were salt-free as controls. After 50 days the plants were pruned back to the original stem length of 20 cm. Prunings were divided into stems and leaves above (distal) and below (proximal) labelled leaves. These tissues were dried at 60°C for 120 h,

crushed in a hammermill to pass a 1-mm mesh and retained for ion analyses.

Vitis

Under both vineyard and glasshouse conditions vines of *Vitis champini* and *V. berlandieri* have low Cl-ion concentrations in leaves. Consequently, hybrids involving both species (Newman and Antcliff, 1984; Sykes, 1985c, 1987) crossed with varieties of *V. vinifera* were screened for Cl-ion accumulation as unreplicated vineyard plantings and in replicated glasshouse trials.

Cl-ion exclusion by unreplicated hybrid vines was assessed by measuring Cl-ion concentrations in petioles collected from leaves opposite fruit bunches during January, which is around the time of veraison in the Murray Valley. Petioles were collected from two progenies involving *Vitis champini* (Ramsey), plus an additional progeny from a cross between the other two parents, during 1981 and 1982 (Sykes, 1985c). Petioles were collected from seven progenies from crosses between *V. berlandieri* and *V. vinifera* and four backcross progenies, i.e. (*V. berlandieri* × *V. vinifera*) × *V. vinifera*, during 1983 (Newman and Antcliff, 1984). All petioles were dried at 60°C, crushed in a hammermill to pass a 1-mm mesh and analysed for Cl-ion concentrations.

Replicated glasshouse trials employed nutrient solution cultures containing NaCl (25 mM) similar to those used for citrus screening experiments. The full details have been published and the trials involved all hybrids from the cross between *V. champini* (Ramsey) × *V. vinifera* (Sultana) (Sykes, 1985c) and selected hybrids between *V. berlandieri* × *V. vinifera* and backcrosses (Sykes, 1987).

Ion analysis

All tissues were prepared for ion analysis following the methods described by Walker (1986); Na ions were analysed by atomic absorption spectrophotometry and Cl ions by silver ion titration using a Buchler-Cotlove chloridometer.

Results

Citrus

Leaf Na-ion concentrations varied widely between hybrids within each progeny tested. This variation was continuous over the range (e.g. Fig. 1). In all progenies tested, leaf Cl-ion con-

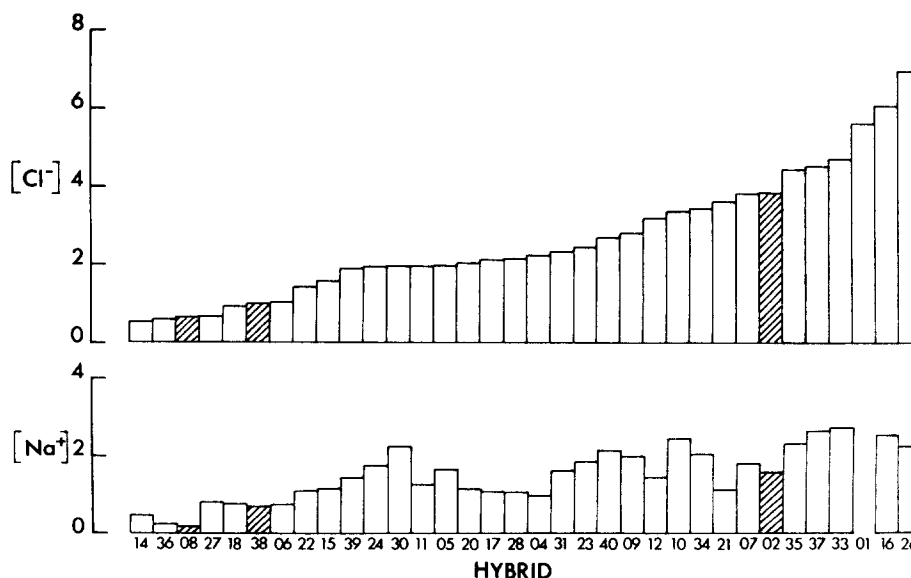


Fig. 1. Leaf Cl-ion and Na-ion concentrations (% of dry weight) for 14-month-old hybrids between Rangpur lime and Trifoliolate orange (80-02) when grown in nutrient solution culture containing NaCl (50 mM) for 56 days. There was insufficient leaf material for Na-ion analysis for hybrid 80-02-01. Hatched bars identify hybrids propagated for a replicated trial (see Table 1).

Table 1. Relationship, expressed as a linear regression, between leaf Na-ion (y axis) and Cl-ion (x axis) concentrations (% dry wt) for hybrids from eight citrus progenies. Leaves were sampled from middle sections of stems of fourteen-month-old seedlings which had grown in nutrient solution cultures containing NaCl (50 mM) for 56 days

Progeny	Parents	n ^a	y = a + bx ^b	b + s.d. ^c	t ^d	r ²
80-02	Rangpur lime × Trifoliolate orange	33	y = 0.575 + 0.359x	0.359 + 0.049	7.395***	0.64
80-04	Clementine mandarin × Trifoliolate orange	39	y = 1.695 + 0.181x	0.181 + 0.080	2.269*	0.12
81-01	Clementine mandarin × Trifoliolate orange	613	y = 0.539 + 0.400x	0.400 + 0.009	45.65***	0.77
81-02	Clementine mandarin × Rangpur lime	444	y = 0.652 + 0.560x	0.560 + 0.014	38.15***	0.77
81-03	Clementine mandarin × Carrizo citrange	77	y = 0.565 + 0.484x	0.484 + 0.059	8.212***	0.47
81-04	Rangpur lime × Trifoliolate orange	18	y = 0.439 + 0.442x	0.442 + 0.185	2.389*	0.26
82-01	Rangpur lime × Trifoliolate orange	33	y = 0.035 + 0.452x	0.452 + 0.048	9.518***	0.74
82-07	Ellendale tangor × Trifoliolate orange	158	y = 0.166 + 0.509x	0.509 + 0.031	16.218***	0.63

^an = number of hybrids in progeny.

^bEquation of linear regression where y = leaf Na⁺ concentration, x = leaf Cl⁻ concentration, a = intercept on y axis and b = slope.

^cs.d. = sample standard deviation of regression coefficient, b.

^dt test for significance of b (*p 0.05, ***p 0.001).

centrations were positively correlated with leaf Na-ion concentrations and linear regressions could be fitted to these data (Table 1). This association, however, was stronger for some progenies than for others. For example progenies 80-04 and 81-01, which were from the same cross, viz. Clementine mandarin × Trifoliolate orange, had r² values of 0.12 and 0.77, respectively. A low leaf Cl-ion concentration did not always correspond to a low Na-ion concentration and vice versa, e.g. hybrids 80-02-04, -21 and -30 (Fig. 1).

With the exception of Na-ion concentrations for leaves and distal stems of hybrid 80-02-08, salt treatment (NaCl 50 mM) increased Cl-ion and Na-ion concentrations of tissues harvested from nucellar seedlings of Rangpur lime and Trifoliolate orange and the vegetatively propagated plants of the three Rangpur lime × Trifoliolate orange hybrids. Analyses of variance of the data gave no significant (p = 0.05) effects due to tanks and so the data were pooled for each genotype and analysed as single classifications (Table 2). For all tissues, there were signifi-

Table 2. Mean (n = 6) leaf Cl-ion and Na-ion concentrations (% of dry weight) for nucellar seedlings of Rangpur lime and Trifoliolate orange and vegetatively propagated plants of three hybrids between these rootstock varieties when grown in nutrient solution cultures containing NaCl (50 mM) for 50 days

Ion	Tissue	Genotype					LSD (p = 0.05)	F ^a	sig ^b	r _i ^c
		Rangpur lime	Trifoliolate orange	80-02-02	80-02-08	80-02-38				
Cl	Proximal leaves	0.32	1.61	2.07	0.34	0.46	0.44	25.7	***	0.80
	Distal leaves	0.27	2.51	2.09	0.30	0.48	0.69	25.0	***	0.80
	Proximal stem	0.59	0.82	1.18	0.39	0.50	0.19	27.4	***	0.81
	Distal stem	0.52	1.08	1.44	0.31	0.47	0.32	21.3	***	0.77
Na	Proximal leaves	0.46	1.01	0.75	0.07	0.49	0.31	10.8	***	0.62
	Distal leaves	0.52	0.68	0.83	0.01	0.61	0.36	6.3	**	0.47
	Proximal stem	0.58	0.75	0.84	0.46	0.52	0.12	14.7	***	0.70
	Distal stem	0.84	0.48	1.34	0.07	0.90	0.24	34.8	***	0.85

a)^aThe variance ratio (F) from analysis of variance comparing the 5 genotypes.

b)^bThe significance of F (**p < 0.01, ***p < 0.001).

c)^cThe intra-class correlation coefficient (Sokal and Rohlf, 1969) was obtained from the Analysis of Variance as follows:

Source	df.	e.m.s
Between genotypes	4	$\sigma_b^2 + 6\sigma_w^2$
Between individuals within genotypes	5(6 - 1)	σ_w^2

$$r_i = \frac{\sigma_b^2}{\sigma_b^2 + \sigma_w^2}$$

cant genotypic differences for both Cl-ion and Na-ion concentrations (Table 2). These differences were larger for Cl ions with Rangpur lime, 80-02-08 and 80-02-38 all having low concentrations. Hybrid 80-02-02 behaved as predicted by the screening test and had Cl-ion concentrations similar to those of Trifoliolate orange. Differences between genotypes for Na-ion concentration were not so large. Nevertheless, all three hybrids accumulated Na ions in the order of ranking as predicted by the screening test. Hybrid 80-02-08 was exceptional in that it only accumulated Na ions in proximal stems. With the exception of Na-ion concentrations for distal leaves, the intra-class correlation coefficient (Table 2) was higher than 0.5 for all ions in all tissues. This indicated that genotypic variation was larger than that between individuals within genotypes.

Vitis

The results from the unreplicated vineyard surveys of hybrid and backcross vines and the replicated glasshouse trials which are pertinent to the following discussion have all been published (Newman and Antcliff, 1984; Sykes, 1985c; 1987).

Discussion

The experience of plant breeders involved with asexually propagated crops is that these species are highly heterozygous and segregate widely upon sexual reproduction (Allard, 1960). While inheritance studies in citrus are scarce, wide segregation has been noted for some characteristics, e.g. root rot resistance (Hutchinson, 1985). An ability for Cl-ion exclusion by citrus hybrids from crosses involving Cl-ion-excluding parents varies widely suggesting it is a polygenic trait (Furr and Ream, 1969; Sykes, 1985b). The results presented here demonstrate this (Fig. 1) and also that the ability to restrict Na ions accumulating in shoots varies widely suggesting that it too is a polygenic trait. The superior nature of hybrid 80-02-08 in excluding Na ions from leaves compared to its parents indicates transgressive segregation.

The data presented in Table 2 support the data provided for Cl-ion exclusion by replicated hybrids by Sykes (1985b) and also support the conclusion that a test period of 56 days using saline nutrient solution cultures is adequate to select new salt-excluding citrus rootstock hybrids. The value of a rapid test to screen young woody perennials in a costly breeding program has been discussed (Sykes, 1985a; b).

In vegetatively propagated crops, the intra-class correlation coefficient (Table 2) provides an estimate of the ratio between the genetic and the phenotypic variance of a particular trait (see Hansche, 1983). This ratio provides a quantitative statement of the relative importance of genetic versus environmental factors affecting observed differences among phenotypic measurements. The intra-class correlation coefficients in Table 2 suggest a strong heritable basis for salt exclusion in Rangpur lime, Trifoliolate orange and their hybrids. These statistics provide an estimate of the maximum value of heritability under the test conditions described. The variance between plants (individuals) within a genotype estimates non-heritable effects while the variance between genotypes estimates heritable and non-heritable effects plus any effects due to a common environment amongst cloned individuals. Two examples of possible sources of variation due to common environment being differences in nutritional reserves of cuttings used to produce individuals within a clone or competition between several nucellar seedlings emerging from one polyembryonic seed. As the data in Table 2 were obtained for nucellar seedlings of parent varieties and for plants grown from cuttings of the hybrids, the effect of a common environment may have inflated the intra-class correlation coefficient. Nevertheless, the relatively high values for this statistic lend further support to the feasibility of breeding new salt-excluding citrus rootstocks.

were positively correlated within citrus progenies, which may suggest the ability to exclude one or both ions could be considered the same characteristic, the strength of this correlation varied. It was possible to identify individuals which were either good Cl-ion excluders but poor Na-ion excluders and vice versa. This supports the data of Walker (1986) who reported

that Cleopatra mandarin is a good Cl-ion excluder but a poor Na-ion excluder. This suggests that the ability to exclude these two ions is due to two different mechanisms although further experiments are needed to show this definitively.

Continuous variation for petiole Cl-ion concentrations in progenies of Ramsey (*V. champini*) × Sultana (*V. vinifera*), Ramsey × Villard blanc (12375-SV, complex hybrid) and Villard blanc × Sultana under vineyard conditions (Sykes, 1985c) suggested that the greater ability for Cl-ion exclusion by Ramsey is a polygenic trait. The variation between replicated hybrids of Ramsey × Sultana under glasshouse conditions supported this. Both vineyard and glasshouse data suggested transgressive segregation. It was therefore possible to identify new genotypes which were better Cl-ion excluders than Ramsey.

Data from the vineyard survey of *V. berlandieri* hybrids and backcrosses (Newman and Antcliff, 1984) suggested that a single dominant gene was the major factor governing the inheritance of Cl-ion exclusion in *V. berlandieri* vines. All hybrids between *V. berlandieri* and *V. vinifera* had low petiole Cl-ion concentrations and backcrosses segregated in a 1:1 ratio for high and low petiole Cl-ion concentrations. Data from glasshouse trials (Sykes, 1987) supported this for two of the four backcrosses. Vines from MF77-13 (*V. berlandieri* × Sultana) × Biancone or Koshu Sanjaku could be identified as either Cl-ion excluders or accumulators when grown in solution cultures containing NaCl (25 mM). The variation in two other backcrosses, however, did not support the vineyard data. This may have been due to the action of modifying genes derived from *vinifera* parents (Sykes, 1987). A similar situation can arise when breeding for disease resistance where the expression of a major gene in interspecific crosses is affected by minor genes from *vinifera* parents (Becker and Zimmerman, 1977).

It has been suggested that there has been a trend towards higher salinities throughout the River Murray in SE Australia and there have been several solutions suggested to overcome the effects of salinity on salt-sensitive irrigated horticultural crops (Blesing and Tuffley, 1977). One proposal has been to breed new salt-tolerant varieties. The results of the research described herein clearly support this philosophy.

Selection in any breeding program can only act effectively on inherited characteristics. The results presented here demonstrate that it is possible to select new salt-excluding citrus and grapevine hybrids and thus salt exclusion must, by inference, be inherited. In citrus, Cl-ion and Na-ion exclusion appears to be inherited polygenically, whereas in grapevines Cl-ion exclusion may be expressed either as a polygenic or monogenic trait depending on parents.

The next stage in breeding new salt-excluding rootstocks is to evaluate hybrids as rootstocks under field conditions. This has almost been completed for some citrus hybrids and the results have been very encouraging; hybrid 80-02-08 is a good salt excluder. However, before new salt-tolerant citrus rootstocks can be released, hybrids have to be assessed for many other characteristics. These include disease and pest resistance, polyembryony, scion compatibility, lime tolerance and horticultural performance. As far as the grapevine hybrids are concerned, the progenies described herein have been screened and selected for ease of rooting and grafting. As a result, selections have been entered as rootstocks grafted to Sultana in trials using salinised field plots to assess their effects on yield and fruit quality. The outcome of this research will hopefully lead to the release of a new salt-tolerant grapevine rootstock.

References

- Allard R W 1960 Principles of Plant Breeding. Wiley, Toppan, NY; London, Tokyo. 485 p.
- Antcliff A J, Newman H P and Barrett H C 1983 Variation in chloride accumulation in some American species of grapevine. *Vitis* 22, 357-362.
- Bailey L H and Bailey E Z 1976 Hortus Third: A Concise Dictionary of Plants Cultivated in the United States and Canada. Macmillan, New York. 1290 p.
- Becker N J and Zimmerman H 1977 Breeding of yield varieties resistant to downy mildew. *In* Génétique et amélioration de la vigne. Proc. 2nd Intern. Symp. on Amelioration of the Vine, pp 209-214. INRA, Paris.
- Behboudian M H, Törökfalvy E and Walker R R 1986 Effects of salinity on ionic content, water relations and gas exchange parameters in some citrus scion-rootstock combinations. *Sci. Hortic.* 28, 105-116.
- Bernstein L, Ehlig C F and Clark R A 1969 Effect of grape rootstock on chloride accumulation in leaves. *J. Am. Soc. Hortic. Sci.* 94, 561-571.
- Blesing N V and Tuffley J R 1977 Study of potential

- economic benefits from reduction in salinity of River Murray water. Amdel Report No. 1179, Adelaide, South Australia.
- Cooper WC and Gorton B S 1952 Toxicity and accumulation of chloride salts in citrus on various rootstocks. *Proc. Am. Soc. Hortic. Sci.* 59, 143–146.
- Cooper W C and Shull A V 1953 Salt tolerance and accumulation of sodium and chloride ions in grapefruit on various rootstocks grown in a naturally saline soil. *Proc. 7th Rio Grande Val. Hortic. Inst.* 7, 107–117.
- Downton W J S 1977a Photosynthesis in salt-stressed grapevines. *Aust. J. Plant Physiol.* 4, 183–192.
- Downton W J S 1977b Chloride accumulation in different species of grapevine. *Sci. Hortic.* 8, 249–253.
- Ehlig E F 1960 Effects of salinity on four varieties of table grapes grown in sand culture. *Proc. Am. Soc. Hort. Sic.* 76, 323–331.
- Frost H B and Soost R K 1968 Seed reproduction: Development of gametes and embryos. *In The Citrus Industry*. Vol. II. Eds. W Reuther, L D Batchelor and H J Webber. University of California, Berkeley.
- Furr J R and Ream C L 1969 Breeding citrus rootstocks for salt tolerance. *Proc. 1st Int. Citrus symposium* Vol. 1, 373–380.
- Grieve A M 1984 The effects of salinity on grapevine productivity. *In Irrigation, Salinity and Grape quality*. Eds. D C Lester and T H Lee. pp 5–13. *Proc. of a seminar*, Loxton, S.A., Nov. 1984.
- Grieve A M and Walker R R 1983 Uptake and distribution of chloride, sodium and potassium ions in salt-treated citrus plants. *Aust. J. Agric. Res.* 34, 133–143.
- Greenway H and Munns R 1980 Mechanisms of salt tolerance in nonhalophytes. *Annu. Rev. Plant Physiol.* 31, 149–190.
- Groot Obbink J and Alexander D McE 1973 Response of six grapevine cultivars to a range of chloride concentrations. *Am. J. Enol. Vitic.* 24, 65–68.
- Hansche P E 1983 Response to selection. *In Methods in Fruit Breeding*. Eds. J N Moore and J Janick. pp 154–171. Purdue University Press, West Lafayette, IN.
- Hoagland D R and Arnon D I 1950 The Water Culture Method for Growing Plants Without Soil. *Circ. Calif. Agric. Exp. Stn. Berkeley, FL*. No. 347.
- Hutchinson D J 1985 Rootstock development screening and selection for disease tolerance and horticultural characteristics. *Fruit Varieties J.* 39(3), 21–25.
- Newman H P and Antcliff A J 1984 Chloride accumulation in some hybrids and backcrosses of *Vitis berlandieri* and *Vitis vinifera*. *Vitis* 23, 106–112.
- Sauer M R 1968 Effects of vine rootstocks on chloride concentration in sultana scions. *Vitis* 7, 223–226.
- Sokal R R and Rohlf F J 1969 *Biometry: The Principles and Practice of Statistics in Biological Research*. Freeman, San Francisco. 776 p.
- Soost R K and Cameron J W 1975 Citrus. *In Advances in Fruit Breeding*. Eds. J Janick and J N Moore. pp 507–540. Purdue University Press, West Lafayette, IN.
- Sykes S R 1985a Effects of seedling age and size on chloride accumulation by juvenile citrus seedlings treated with sodium chloride under glasshouse conditions. *Aust. J. Exp. Agric.* 25, 943–953.
- Sykes S R 1985b A glasshouse screening procedure for identifying citrus hybrids which restrict chloride accumulation in shoot tissues. *Aust. J. Agric. Res.* 36, 779–789.
- Sykes S R 1985c Variation in chloride accumulation by hybrid vines from crosses involving the cultivars Ramsey, Villard blanc and Sultana. *Am. J. Enol. Vitic.* 36, 30–37.
- Sykes S R 1987 Variation in chloride accumulation in hybrids and backcrosses of *Vitis berlandieri* and *Vitis vinifera* under glasshouse conditions. *Am. J. Enol. Vitic.* 38, 313–320.
- Sykes S R and Newman H P 1987 The genetic basis for salt exclusion in grapevines. *Aust. Grapegrower Winemaker*. April 1987, 75–78.
- Thomas J E 1934 The diagnostic value of the chloride content of the vine leaf. *J. Coun. Sci. Indust. Res. Aust.* 7, 29–38.
- Walker R R 1986 Sodium exclusion and potassium-sodium selectivity in salt-treated Trifoliate orange (*Poncirus trifoliata*) and Cleopatra mandarin (*Citrus reticulata*) plants. *Aust. J. Plant Physiol.* 13, 293–303.
- Walker R R and Douglas T J 1983 Effects of salinity level on uptake and distribution of chloride, sodium and potassium ions in citrus plants. *Aust. J. Agric. Res.* 34, 145–153.
- Woodham R C 1956 The chloride status of the irrigated Sultana vine and its relation to vine health. *Aust. J. Agric. Res.* 7, 414–427.