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Phalaris improvement in Australia

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Abstract The genetic improvement of *Phalaris aquatica* L. and its scientific basis are reviewed. The few accessions made in the 1890s gave rise to cv. Australian. Trumble selected 'Gb81' within 'Australian'. Major collections in 1951 and 1954 gave cultivars Sirocco and El Golea through selection within Moroccan ecotypes, and cultivars Sirosa, Sirolan, and Holdfast by hybridisation with 'Australian', followed by recurrent selection for various traits. Selection within the seed-retaining Argentinian cultivar El Gaucho, gave 'Seedmaster', and a single mutant seed-retaining plant within 'Australian' gave 'Uneta'. Future cultivars are previewed and alternative selection methods, such as widespread testing of synthetics, are discussed.

Keywords *Phalaris aquatica* L.; phalaris; breeding; review; prospects; biology

THE ROLE OF PLANT INTRODUCTION

Plant exploration and introduction have provided the basic breeding material for present-day cultivars of phalaris (*Phalaris aquatica* L.), but only the original cultivar, Australian, was put into commercial use without any form of selection. Selection for higher herbage productivity was practised within cv. Australian by Trumble (1952), at the Waite Agricultural Research Institute, Adelaide, and gave the population 'Gb81'. However, there was no effective procedure for producing certified seed of this population after its release, so it was re-absorbed into 'Australian'. At least one other accession of phalaris was brought into Australia at about the same time that 'Australian' was brought into the Toowoomba Botanic Gardens, viz. the one recorded at the Adelaide Botanic Gardens (D. E. Symon pers. comm.). McWilliam et al. (1971) found no evidence of ecotypic differentiation within 'Australian', nor of introgression of genes from any other contrasting naturalised accession. There is limited turnover of plants within established phalaris swards, because the seedlings are too weak to become established under grazed, competitive conditions (Hume & Barker 1991; McCallum et al. 1991). Thus, in contrast to the perennial/annual ryegrass coenospecies, there has been much less opportunity for genetic shift or ecotypic differentiation within 'Australian'. Some genetic shift might have occurred in cultivars sensitive to free aluminium (Al) in acid soils (all populations) or to grazing mis-management (the winter-active cultivars). But, with low levels of seedling recruitment and generation turnover, only minimal changes of population mean through natural selection are likely to have occurred so far.

CSIRO plant-collecting expeditions by C. M. Donald and J. F. Miles in 1951 and by Neal-Smith in 1954 (Neal-Smith 1955) brought over 100 Mediterranean populations into Australia. None of these gave rise directly to a cultivar, but they have been essential for later hybridisation and selection programmes. Forty-two representative populations are kept in long-term storage conditions. Natural populations have effective seed dispersal systems which make seed harvesting inefficient and the resultant seed expensive. The price of seed of recent non-shedding cultivars eventually will be considerably lower than that of shedding cultivars and natural populations. It is unlikely that any wild accession will be sufficiently agronomically superior to seed-retaining cultivars to gain a share of the market. A temporary exception may be

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populations with a novel feature like salt tolerance (see later section), for which the inherently high seed price might be reduced by a community or government subsidy until a seed-retaining version is bred. Therefore the current search by the Victorian Department of Agriculture (M. W. Anderson pers. comm.) for a more productive, grazing-tolerant, but seed-shedding accession of the 'Australian' type, may not give rise to a cultivar directly, but will probably provide valuable material for a breeding programme. However, extensive sets of germplasm, such as those in the United States, New Zealand, and Australia, must be readily accessible as a source of genes, e.g., for pest and disease resistance, when these are needed.

SCIENTIFIC BASIS OF PHALARIS BREEDING

Quantitative inheritance

The selection theory used in phalaris breeding was elaborated primarily in Edinburgh, Scotland (Falconer 1981), and in Ames, Iowa (Kempthorne 1957). It was based on the earlier concepts of R. A. Fisher and Sewall Wright that the alleles at a large number of loci controlled the phenotype of continuously varying characters. Because the response in most traits depends on small changes in allele frequency at a large number of loci, and the "plus" allele is fixed at only a few loci in each generation, a similar-sized response to selection can be expected for many successive generations. Because relatively little selection has been applied to perennial grasses in southern Australia, apart from natural selection for survival traits in short-lived species, it can be expected that responses in many traits to artificial selection will continue for many generations.

Griffing, Latter, Morley, and Scowcroft guided the quantitative genetic aspects of phalaris breeding during 1956–70. Some theory was developed during a study of seed weight, seedling vigour, and heading date within 'Australian' (Latter 1965a,b). All three traits showed appreciable additive genetic variation, and therefore would respond to selection. It was predicted that seven generations of recurrent selection would be sufficient to increase the means for each trait beyond the range found in the 1951 and 1954 collections of Mediterranean accessions. Seedling weight was inherited almost independently of heading date, the genetic correlation coefficient being only 0.05. Because it was considered that more progress would be made in a genetically more diverse population, selection was not practised within 'Australian' but rather within a 26 line × 2 tester topcross which eventually gave rise to 'Sirosa' and 'Sirolan'. The genetic and plant breeding aspects of the early generations of this recurrent selection programme were documented by McWilliam & Latter (1970). Many limiting traits have now been investigated genetically. Except for one component of Al tolerance (Culvenor et al. 1986b), all traits showed continuous variation and quantitative inheritance. Heritabilities for most of these traits are shown in Table 1.

Physiology

McWilliam elucidated many aspects of flowering time responses to vernalisation and daylength, seedling growth rates in various temperature regimes, and germination responses to temperature, in a range of contrasting accessions (Cooper & McWilliam 1966; McWilliam 1968b). In particular, these studies revealed the high rate of leaf expansion at low temperature by accessions from the southern Mediterranean, and the high correlation between rate of leaf expansion and early seedling growth rate. This information guided the early development of the winter-active cultivars Sirosa and Sirolan. Similarly, studies on summer survival and bud dormancy in phalaris (Hoen 1966, 1968a,b; McWilliam & Kramer 1968; McWilliam 1968a; Oram 1983) explained the primary climatic limitation to the distribution of phalaris in southern Australia, and pointed to the need for cultivars specifically adapted to drier areas. The basis for improved seed production in phalaris before the discovery of the intact rachilla system of retention was provided by further studies on the agronomy (McWilliam & Schroeder 1974) and genetics (McWilliam 1963; Oram 1982) of seed yield.

Cytogenetics

Putievsky & Oram (1980) showed that *P. aquatica* is a segmental allotetraploid species. They also showed that many, but not all, hybrids between different Mediterranean ecotypes and geographic races showed meiotic chromosome abnormalities, partial pollen and ovule sterility, and break-down of self-incompatibility. All these phenomena indicated minor differences in gene sequences within the chromosomes. These would restrict recombination in some regions of the genomes in affected hybrids.

McWilliam (1962) examined the hybridisation of *P. aquatica* and hexaploid *P. arundinacea*, thus paving the way for the development of Siro 1146 hybrid phalaris. This heterotic hybrid was potentially useful for grazing and as mini-shelter belts in several parts of the country. However, it did not progress beyond the "experimental release" phase, because it could become a weed after spontaneous backcrossing to *P. aquatica* and selection of the least palatable, most fertile, and most vigorous plants (Oram & Schroeder 1989).

D. L. Hayman, J. R. McWilliam, K. Hoen, and R. N. Oram (unpubl. data) made 13 crosses among the 9 Old World species of *Phalaris*. Cytological studies on the 13 interspecific hybrids have elucidated the evolutionary relationships of the Old World species. *P. aquatica* was compatible with seven other species, but to date, none of the

Table 1 Narrow-sense heritability estimates in *P. aquatica*.

Trait and population	Heritability ± standard error	Method of estimation[1]	Reference
Seedling size			
Cv. Australian	0.17 ± 0.05	HS	Latter 1965b
Crossbreds	0.19 ± 0.07	FS-HS	McWilliam & Latter 1970
Weight per seed			
Cv. Australian	0.79 ± 0.06	D-O corr.	Latter 1965b
Date of ear emergence			
Cv. Australian	0.54 ± 0.13	HS corr.	Latter 1965b
Crossbreds	0.56 ± 0.05	FS-HS	McWilliam & Latter 1970
Herbage yield, winter			
Crossbreds			
Spaced plants	0.14 ± 0.06	FS-HS	McWilliam & Latter 1970
Swards	0.53 ± 0.10	HS Fam.	Oram & Schroeder 1987
Seed yield			
Crossbreds			
Spaced plants	0.52 ± 0.21	HS	Oram 1982
Swards	0.82 ± 0.06	HS Fam.	Oram & Schroeder 1987
Grazed sward density			
Crossbreds	0.39 ± 0.11	HS Fam.	Culvenor & Oram 1993
Rhizomatous spread			
Crossbreds	0.10 ± 0.10	HS	Culvenor & Oram 1993
Vernalisation requirement			
Cv. Australian	0.63 ± 0.06	Sel. response	McWilliam 1968
Bud dormancy			
Crossbreds			
Spaced plants	0.40 ± 0.16	HS	Oram 1984
Swards	0.36 ± 0.08	HS Fam.	Oram 1984
Aluminium tolerance			
Crossbreds			
Solution culture	0.59 ± 0.16	HS Fam.	Culvenor et al. 1986b
Field	0.13 ± 0.10	HS Fam.	Culvenor et al. 1986b
Alkaloid concentration			
Crossbreds	0.92	PO	Oram 1970
Herbage quality			
Crossbreds			
Protein	0.54	FS-HS	Oram et al. 1974
Fibre	0.43	FS-HS	Oram et al. 1974
Digestibility	0.60	FS-HS	Oram et al. 1974

[1]HS, within and between half-sibs families on individual plant basis; HS Fam., between half-sibs families in replicated swards; FS-HS, between full-sib families in half-sib groups in a North Carolina Design I experiment; HS corr., correlation among individuals in half-sib families; D-O corr., correlation between dams and half-sib offspring; PO, correlation between bi-parental means and progeny means; Sel. response, realized heritability in 4-generation selection experiment.

amphidiploids or backcrosses has contributed a commercial cultivar. However, the *P. aquatica* × *P. arundinacea* backcrossing programme should succeed in transferring Al tolerance genes into *P. aquatica*.

DELIBERATE SELECTION PROGRAMMES

Cultivars developed by limited selection within accessions

Only two or three generations of recurrent selection, primarily for higher seed retention in the ripe panicle, were practised within the introduced populations, 'El Gaucho', CPI 19331 and CPI 19305, to produce the cultivars Siro Seedmaster, Sirocco, and El Golea, respectively (see Table 2 and Oram 1990). 'El Gaucho', or 'Pergamino No. 1', was a cultivar of the 'Australian' type that had been selected for seed retention in Argentina. However, McWilliam (1963) found considerable, and highly heritable, variation within 'El Gaucho' for the morphological characters controlling seed retention of the 'Seedmaster' type. Three generations of selection for shorter, broader seeds and glumes, stiffer glumes, and shorter panicle branches gave 'Siro Seedmaster', which had much better seed retention than 'Australian'. On the other hand, when CPI 19331 and CPI 19305, wild populations from coastal and inland Morocco, respectively, were selected for the 'Seedmaster' mechanism of seed retention for two generations, there was limited response (Oram 1990).

Spontaneous mutation

During the search for possible ecotypic differentiation within 'Australian' (McWilliam et al. 1971), H. E. Schroeder found a single plant within a certified seed line from New South Wales which retained virtually all of its seed in the panicles at maturity. The ripe seeds were retained because they remained attached to the pedicel by the rachilla. The rachilla is normally pinched off by in-growing calluses on the two sterile lemmas at the base of the fertile floret. In the spontaneous mutant plant, the lower callus is displaced downwards and cannot function as the lower jaw of the pincer. The rachilla also is thickened. McWilliam & Gibbon (1981) suggested that homozygosity of the recessive alleles at four independent loci is necessary to produce the "intact rachilla" phenotype. Later evidence suggests that only three loci are involved, together with a small number of modifying loci (Oram unpubl. data). Outcrossing of the original mutant plant to the whole collection of 30 certified seed lines of 'Australian' and selection of four seed retainers in the F_2, gave rise to 'Uneta' (McWilliam & Gibbon 1981; Oram 1990).

The original spontaneous mutant represents the classical first domestication step in grasses used for grain or forage i.e. the suppression of a seed dispersal mechanism which is essential in the wild population but which limits seed yield under cultivation. It is desirable that the mutant genes in the original plant are eventually incorporated into all *P. aquatica* cultivars developed throughout the

Table 2 Cultivars of phalaris developed in Australia, the traits selected for in their development, and their present share of certified seed production.

Cultivar	Year of release or registration	Certified seed production 1992–93 (t)	Traits improved by recurrent selection before release
Semi-winter dormant group			
'Australian'	1904	38	No selection
'Seedmaster'	1965	4	Seed retention, seedling vigour
'Uneta'	1982	83	Seed retention, growth habit
Winter-active group			
'Sirocco'	1967	Nil	Seed retention
'El Golea'	1977	Nil	Seed retention
'Sirosa'	1974	392	Seedling vigour, fast winter growth, high seed yield
'Sirolan'	1978	65	As for 'Sirosa', and low tryptamine alkaloids, early flowering, and drought hardiness
'Holdfast'	1991	59	As for 'Sirosa', and seed retention, low tryptamines, and tolerance of roots to aluminium

world, at least those grown for seed in regions where seed shedding is normally induced by hot, dry, windy conditions during ripening.

Hybridisation and recurrent selection programmes

Cultivars Sirosa and Sirolan

These winter-active cultivars were developed by recurrent individual and family selection within a broadly based population created by topcrossing 26 diverse Mediterranean introductions onto 'Australian' and a Turkish accession, which was similar morphologically and physiologically to 'Australian' (D. L. Hayman, R. N. Oram & J. R. McWilliam unpubl. data). The F_1 families were evaluated in transplanted small swards at Canberra and Wagga Wagga. The families producing the most herbage in the second autumn and winter were recombined. The second generation plants were selected for seedling vigour and winter yield, giving 16 selected genotypes ("sires") that were clonally propagated and each crossed to four random genotypes out of a set of 64 other productive selections from the same population ("dams"). The 64 full-sib families in 16 half-sib groups in this North Carolina Design I progeny test were evaluated for 2 years at two sites. The most productive offspring were inter-pollinated, and the resultant half-sib families were sown in replicated, small, pure-grass swards, and also grown as replicated spaced-plant plots. Herbage yield was measured during autumn and winter in the swards, and flowering time, growth habit, and panicle characteristics were measured or observed on the spaced plants (McWilliam & Latter 1970).

The cycle was repeated in the 'Sirosa' progenitor population by selecting the best individual spaced plants in the families which yielded most in swards, and allowing the selected plants to inter-pollinate in isolation. In the 'Sirolan' progenitor populations, the selections from the first half-sib test were each crossed to a 'Sirocco' plant, the F_1 intercrossed, and selection within half-sib families was practised for 5 generations for a reduction in the dimethyltryptamine concentration in the herbage (Oram 1970). The dimethyltryptamine alkaloids were considered at that time to be the major determinants of herbage toxicity (Gallagher 1966). The progenitors of both 'Sirosa' and 'Sirolan' were selected for higher floret number per plant to increase seed yield potential (Oram 1982). Selection in both populations for the 'Seedmaster' type of seed retention had little effect.

Cultivar Holdfast

The original "intact rachilla" mutant was crossed with 'Sirolan' progenitors, 'Sirosa' progenitors, and with a set of 15 diverse Mediterranean accessions in three separate rounds of crossing, backcrossing to retaining plants from the previous round, and selection of retainers. Two generations of selection, each of 3 years duration, were practised on half-sib families in small swards at Temora, New South Wales, to improve persistence under dry conditions. The 200 genotypes selected from spaced plant rows at the end of each field test then were culled on root growth in the presence of 10 mg Al/l in nutrient solution at pH 4.1.

'Holdfast' is essentially a seed-retaining version of 'Sirosa'. 'Holdfast' has about 20% smaller seedlings and 20% lower yield of spaced plants in winter than 'Sirosa', but 'Holdfast' has 50–90% higher seed yield, and also is more tolerant of some acid soil conditions than 'Sirosa' (Oram & Schroeder 1992).

Future cultivars

Research conducted in the 1970s and 1980s has made possible the development of three new cultivars, the first pre-breeders seed of which is scheduled for production in each of the next 3 years (Table 3). The code names and characteristics of the populations are:

BP92

Research funded by the Meat Research Corporation in the early 1980s showed that the species *P. aquatica* is generally tolerant to high concentrations of soil manganese (Mn) (Culvenor 1985), but sensitive to Al (Culvenor et al. 1986a). However, two complementary dominant genes give a moderate degree of tolerance to Al, and within this class, there is extensive polygenic variation for higher tolerance (Culvenor et al. 1986b). Both forms of tolerance were exploited in 'Holdfast', but considerable polygenic variation should remain within 'Holdfast' and its close relatives. Therefore, 58 plants were selected from half-sib row trials on acid soils at Axe Creek and Swanpool, Victoria, and from sward trials near Canberra. These were inter-pollinated in isolation, and the half-sib progenies were sown in 1992 in duplicated 4-m rows on mildly acid, infertile groundwater recharge areas at Molyullah (near Benalla), Axe Creek (near

Bendigo), and at Ginninderra Experiment Station, Canberra. The performance of the progenies until April 1993 was used to select 18 parents as founders of the new cultivar, BP92. Under these field conditions, and assuming additive genetic effects, 'BP92' is predicted to be 20% more productive than 'Sirosa' and 'Holdfast'. It will be winter-active, and, like 'Sirosa', 'Sirolan', and 'Holdfast', will need rotational grazing in autumn and winter, and careful grazing control during early stem growth.

'Perla' retainer

This population is early-flowering, highly winter-active, seed-retaining, and has vigorous seedlings and summer-dormant buds. The latter trait enhances survival in regions with long, dry summers that are interrupted once or twice by brief wet spells (Oram 1984). The population was derived from crosses of the original intact rachilla mutant with 'Sirolan' precursors, followed by backcrossing twice to Moroccan accessions, predominantly cv. Perla koleagrass from California. It was selected for 4 generations under spaced plant conditions, and now 45 half-sib families are undergoing sward testing at Coolah, Merriwa, and Wagga Wagga, New South Wales, for three growing seasons. The parents of the new cultivar will be chosen on seed production potential from spaced plants of the most productive and persistent families.

'Uneta' × 'Australian'

Because 'Uneta' was derived from the original spontaneous mutant plant and 4 of its "grand children", its inbreeding coefficient is probably about 26%. This reduces its herbage and seed yield, so 12 'Uneta' genotypes were crossed with 12 unrelated 'Australian' plants. Forty-two second generation individuals were selected for good seed retention and large seeds. These were cloned and inter-pollinated in isolation. The resultant 42 half-sib families have been sown in replicated sward trials at Orange, Canberra, and Hamilton. These will be grazed heavily from autumn 1994 until August 1995. Yield and density estimates then will show whether enough of the families are equal to, or better than, the 8 control lines of certified or uncertified 'Australian' to warrant release of a new cultivar.

OPPORTUNITIES AND CONSIDERATIONS FOR FUTURE BREEDING IN PHALARIS

The current research projects which will form the basis of future breeding programmes are:

Aluminium tolerance

Accessions of both tetraploid and hexaploid *P. arundinacea* are more tolerant of Al than any phalaris population (Culvenor et al. 1986a), but grow too actively in summer to persist in most southern Australian locations. The F_1 hybrid, 'Siro 1146', between *P. aquatica* and hexaploid *P. arundinacea* is heterotic (McWilliam 1962) and Al-tolerant (Oram et al. 1990), but is unpalatable on fertile soil in summer; it also has the potential to generate a weedy, fertile form by backcrossing to *P. aquatica* (Oram & Schroeder 1989). Therefore, the possibility of transferring the Al tolerance genes of hexaploid and tetraploid *P. arundinacea* into *P. aquatica* by hybridisation and backcrossing has been investigated (Oram et al. 1990). The second cycle of field-testing and recombination is in progress: several more generations of field-testing on acid soils are warranted to produce a cultivar more Al-tolerant than BP92 (Oram et al. 1993a,b; Oram & Ridley 1994).

Table 3 Seed retaining cultivars planned for completion in the next 3 years.

Population code name	Year of first pre-basic seed production	Zone of adaptation	Improved traits
BP92	1994	Acid, skeletal soils on recharge ridges	Improved growth on acid, infertile soils
'Perla' retainer	1995	Drier margins	Like 'Sirocco', with summer-dormant buds
'Uneta' × 'Australian'	1996	Southerly and higher rainfall areas	More productive of seed and herbage than 'Uneta'

Persistence

The persistence of phalaris is presently receiving emphasis in view of a growing perception that the winter-active cultivars do not persist as well as 'Australian' under grazing. Grazing pressure, soil conditions, and drought all interact to affect survival of phalaris during the growing season and its regeneration from year to year. Phalaris usually survives drought better than the other temperate grasses introduced to southern Australia (Axelsen & Morley 1968). Stands of Australian phalaris set-stocked at 30 DSE/ha have survived several major droughts at Canberra (J. Donnelly pers. comm.), but may have lower survival at high than at low stocking rates on the Northern Tablelands of New South Wales (Hutchinson 1992).

Phalaris normally persists over a summer drought as dormant buds on the swollen bases of reproductive tillers. Survival of vegetative plants is possible but is lower than that of reproductive plants (Hoen 1968a). Bud dormancy in phalaris appears initially to be a continuation of apical dominance imposed by the elongating stems, to be replaced later by environmental suppression of bud growth (Hoen 1968b). Bud survival requires a moisture supply provided by deep roots (Hoen 1966; McWilliam & Kramer 1968). Soil conditions which constrain root penetration, such as acidity, tight, water-logged subsoil, and rock, can be expected to diminish survival.

Levels of bud dormancy differ between genotypes and are positively related to survival of plants in areas of southern Australia which have relatively severe summer drought occasionally interrupted by heavy rainfall (Oram 1983). Highly dormant cultivars survive better than the less dormant 'Australian' in the Riverina and south-western slopes of New South Wales (Oram & Hoen 1967; Oram & Freebairn 1984), and also in the hot, humid summers of Alabama, United States (Berry & Hoveland 1969). The less dormant 'Sirolan' also survives well in areas with severe summers because of the vigour of tillers which shoot after summer thunderstorms (Oram & Freebairn 1984). The optimal level of dormancy for a cultivar will depend on the particular environment in which it is to be grown (Oram 1984). A higher level of dormancy than is necessary for population survival can lead to a loss in summer growth and reduced animal performance in areas with moderate summers, e.g., the Southern Tablelands of New South Wales (R. Culvenor unpubl. data).

Severe or frequent utilisation of phalaris stands during the period of stem elongation can interfere with the strategy the species adopts to survive summer drought by reducing the number and size of dormant buds (Hill 1989; Culvenor 1993a), reducing the accumulation of carbohydrates and other nutrients in the stem bases (Richardson et al. 1932; McKell et al. 1966), and reducing the level of dormancy in spring to early summer (Hoen 1968b; Hill 1989; Culvenor 1993a). The susceptibility of phalaris to damage from spring utilisation is very dependent on seasonal conditions, with damage to persistence more likely if the onset of summer drought is early, and the summer conditions are severe but interrupted by some rainfall (Culvenor 1994). The winter-active cultivars seem to be more sensitive to spring management than the Australian type of phalaris (Hill & Watson 1989).

Future breeding of phalaris must emphasise persistence under suboptimal grazing and soil conditions. Oram & Ridley (1994) demonstrated that breeding for acid soil tolerance in phalaris need not be accompanied by a yield penalty on non-acid soils. The grazing tolerance of phalaris cultivars almost certainly interacts with soil conditions and the severity of grazing management. Although 'Australian' phalaris is not more Al-tolerant than 'Sirosa' or 'Sirolan' in nutrient solution (Culvenor et al. 1986a), reports suggest that it establishes and persists better on acid, infertile soils (e.g., Mahoney 1986). This may reflect at least partly its better grazing tolerance which allows it to survive other stresses.

'Australian' phalaris has a more prostrate, densely tillered habit than the winter-active cultivars, and therefore is better suited to heavy grazing (Culvenor & Oram 1992; Culvenor 1993b). Some change in the morphology of future cultivars towards the 'Australian' type appears warranted. The extent to which a more grazing-tolerant morphology can be combined with high winter growth rates is not known, but non-significant correlations between tiller density and winter growth rate in a broadly based population at Canberra suggest that progress in changing the morphology of the winter-active type is possible (Culvenor unpubl. data). Another population has been developed consisting of crosses and backcrosses between a highly winter-active breeding population and an 'Australian' type in which it is hoped that new combinations of morphology, winter growth rate, time of reproductive development, summer dormancy, and vernalisation requirement will be generated. Past experience in phalaris breeding indicates that ecotypic associations can be broken (McWilliam & Latter 1970).

'Australian' also has more capacity for rhizomatous spread than the winter-active cultivars (Culvenor & Oram 1992). This attribute is valuable for expanding into bare areas (Barker et al. 1993) and probably assists in recovery of stand density after damage from grazing or drought. Selection for spreading ability on a spaced plant basis is unlikely to succeed because of low heritability (Culvenor & Oram 1993). However, the same study revealed higher heritability for basal cover of grazed plots, presumably the result of a number of attributes which confer persistence under grazing. Superior families have been selected after 2 years of set-stocking at 20–30 DSE/ha and will be combined to form a new population after screening for Al tolerance. One or more generations of selection under continuous grazing on moderately infertile, mildly acid soils may give a winter-active, seed-retaining cultivar which has large seedlings, and is persistent under adverse conditions.

Herbage toxicity

Although only a few thousand sheep are killed annually in Australia by phalaris poisoning, heavy losses are common in some districts in most years, particularly Naracoorte, South Australia, and Esperance, Western Australia. These losses deter many graziers from sowing phalaris and thereby benefitting from its advantages over annual pasture grasses. Two toxins have been identified recently in addition to the N,N-dimethyltryptamines, hordenine, and β-carbolines previously reported (Oram 1970). The two toxins are N-methyltyramine (J. Edgar & N. Anderton pers. comm.) and cyanogenic glycosides (Bourke 1992). A study funded by the Meat Research Corporation has recently started. Its objectives are to search for low-toxin accessions or breeding lines, and, if found, to transfer the appropriate genes into agronomically acceptable cultivars.

Salt resistance

Two recent experiments showed some variation in growth in the presence of 160 m*M* NaCl (equal to $^1/_4$ seawater). Sirolan was the most productive with or without salt (R. N. Oram & J. E. Edlington unpubl. data). Measurements of Na^+ and Cl^- in the above-ground tissues showed that one Moroccan accession was able to exclude these ions equally as well as could a salt-tolerant accession of *Triticum tauschii*, and better than 'Tyrrell' tall wheatgrass. 'Australian' phalaris is recognised as moderately tolerant (Rogers & Bailey 1963). Further research may well show that a much more salt-tolerant phalaris than 'Australian' can be bred from the Moroccan accession. If so, specialised cultivars of phalaris will play a role in salinity mitigation in both groundwater recharge and discharge areas.

FUTURE RESEARCH AND DEVELOPMENT

The basic studies in quantitative genetics, physiology, and cytogenetics of phalaris have made the various breeding projects much more efficient and effective. Outcomes have become much more predictable. As more and more genetic improvement is made, progress will become more difficult, but new problems will arise, particularly from diseases and pests, and new methods will present new opportunities. To date, little tissue culture or genetic engineering research has been done on phalaris, because it is a minor plant in the context of Australian agriculture. Dr Vijay Kaul has produced embryogenic callus in 'Sirosa' at the Institute of Plant Sciences, Victorian Department of Agriculture (R. van Heeswijck pers. comm.). Molecular biology will probably make some contributions to phalaris improvement in the coming decades. Meanwhile, the evidence suggests that most progress will come from recurrent selection in sets of half-sib families selected under spaced plant and realistic sward conditions. To date, additive genetic variance in most traits subjected to selection has been larger than G × E effects, and hence recurrent selection for many generations has given more progress than would be possible from limited selection followed by extensive testing of a few synthetic populations. In future, rapid progress will depend on the identification of highly heritable components of limiting traits followed by multiple generations of selection under realistic, but controlled, conditions. Empirical direct selection will also be necessary for complex traits in which key components cannot be recognised, but long generation intervals, e.g., for persistence tests, will slow down the rate of genetic improvement.

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REFERENCES

Axelsen, A.; Morley, F. 1968: Evaluation of eight pastures by animal production. *Proceedings of the Australian Society for Animal Production 7*: 92–98.

Barker, D. J.; Lambert, M. G.; Dymock, N.; Gray, Y. S. 1993: Introduction, production, and persistence of five grass species in dry hill country. 5. Central Wairarapa, North Island, New Zealand. *New Zealand journal of agricultural research 36*: 29–39.

Berry, R. F.; Hoveland, C. S. 1969: Summer defoliation and autumn-winter production of *Phalaris* species and tall fescue varieties. *Agronomy journal 61*: 493–497.

Bourke, C. A. 1992: Toxins in pasture plants—phalaris toxicity. *Proceedings of the Australian Society of Animal Production 19*: 399–402.

Cooper, J. P.; McWilliam, J. R. 1966: Climatic variation in forage grasses. II. Germination, flowering and leaf development in Mediterranean populations of *Phalaris tuberosa*. *Journal of applied ecology 3*: 191–212.

Culvenor, R. A. 1985: Tolerance of *Phalaris aquatica* L. populations and some other agricultural species to excess manganese, and the effect of aluminium on manganese tolerance in *P. aquatica*. *Australian journal of agricultural research 36*: 695–708.

Culvenor, R. A. 1993a: Effect of cutting during reproductive development on the regrowth and regenerative capacity of the perennial grass, *Phalaris aquatica* L., in a controlled environment. *Annals of botany 72*: 559–568.

Culvenor, R. A. 1993b: Persistence of *Phalaris aquatica* L. in response to grazing. *Proceedings of the XVII International Grassland Congress*: 145–146.

Culvenor, R. A. 1994: The persistence of five cultivars of phalaris in response to cutting during reproductive development in spring. *Australian journal of agricultural research 45*: 945–962.

Culvenor, R. A.; Oram, R. N. 1992: The persistence of phalaris under grazing. *Proceedings of the 6th Australian Agronomy Conference*: 551. Melbourne, The Australian Society of Agronomy.

Culvenor, R. A.; Oram, R. N. 1993: Rhizomatous spread and persistence in phalaris. *Proceedings of the 10th Australian Plant Breeding Conference, Vol. II*: 27–28.

Culvenor, R. A.; Oram, R. N.; Fazekas de St. Groth, C. 1986a: Variation of tolerance in *Phalaris aquatica* L. and a related species to aluminium in nutrient solution and soil. *Australian journal of agricultural research 37*: 383–396.

Culvenor, R. A.; Oram, R. N.; Wood, J. T. 1986b: Inheritance of aluminium tolerance in *Phalaris aquatica* L. *Australian journal of agricultural research 37*: 397–408.

Falconer, D. S. 1981: Introduction to quantitative genetics, 2nd ed. London, Longman.

Gallagher, C. H.; Koch, J. H.; Hoffman, H. 1966: Diseases of sheep due to ingestion of *Phalaris tuberosa*. *Australian veterinary journal 42*: 279–284.

Hill, M. J. 1989: The effect of differences in intensity and frequency of defoliation on the growth of *Phalaris aquatica* L. and *Dactylis glomerata* L. *Australian journal of agricultural research 40*: 333–343.

Hill, M. J.; Watson, R. W. 1989: The effect of differences in intensity and frequency of defoliation on the growth of Sirolan phalaris in the field. *Australian journal of agricultural research 40*: 345–352.

Hoen, K. 1966: The effect of temperature and soil moisture on summer survival of two varieties of *Phalaris tuberosa*. *Australian journal of experimental agriculture and animal husbandry 6*: 280–282.

Hoen, K. 1968a: Summer dormancy in *Phalaris tuberosa* L. *Australian journal of agricultural research 19*: 227–239.

Hoen, K. 1968b: The effect of plant size and developmental stage on summer survival of some perennial grasses. *Australian journal of experimental agriculture and animal husbandry 8*: 190–196.

Hume, D. E.; Barker, D. J. 1991: Natural reseeding of five grass species in summer dry hill country. *Proceedings of the New Zealand Grassland Association 53*: 97–104.

Hutchinson, K. J. 1992: The grazing resource. *Proceedings of the 6th Australian Agronomy Conference*: 54–60. Melbourne, The Australian Society of Agronomy.

Kempthorne, O. 1957: An introduction to genetic statistics. New York, John Wiley & Sons.

Latter, B. D. H. 1965a: Quantitative genetic analysis in *Phalaris tuberosa*. I. The statistical theory of open-pollinated progenies. *Genetical research 6*: 360–370.

Latter, B. D. H. 1965b: II. Assortative mating and maternal effects in the inheritance of date of ear emergence, seed weight and seedling growth rate. *Genetical research 6*: 371–386.

Mahoney, G. P. 1986: The performance of the new phalaris cultivars in the field. Pp. 65–66 *in*: Proceedings of the DARA Pasture Specialists Conference, Glenormiston 1985. Melbourne, *Conference proceedings no. 4*. Department of Agriculture and Rural Affairs.

McCallum, D. A.; Thomson, N. A.; Judd, T. G. 1991: Experiences with deferred grazing at the Taranaki Agricultural Research Station. *Proceedings of the New Zealand Grassland Association 53*: 79–83.

McKell, C. M.; Whalley, R. D.; Brown, V. 1966: Yield, survival, and carbohydrate reserves of hardinggrass in relation to herbage removal. *Journal of range management 18*: 321–326.

McWilliam, J. R. 1962: Interspecific hybridization in phalaris: hybrids between *Phalaris tuberosa* and the hexaploid race of *Phalaris arundinacea*. *Australian journal of agricultural research 13*: 585–598.

McWilliam, J. R. 1963: Selection for seed retention in *Phalaris tuberosa* L. *Australian journal of agricultural research 14*: 755–764.

McWilliam, J. R. 1968a: The nature of the perennial response in Mediterranean grasses. II. Senescence, summer dormancy, and survival in *Phalaris*. *Australian journal of agricultural research 19*: 397–409.

McWilliam, J. R. 1968b: Nature and genetic control of the vernalization response in *Phalaris tuberosa* L. *Australian journal of biological sciences 21*: 395–408.

McWilliam, J. R.; Gibbon, C. N. 1981: Selection for seed retention in *Phalaris aquatica* L. *Proceedings of the XIV International Grassland Congress*: 269–272.

McWilliam, J. R.; Kramer, P. J. 1968: The nature of the perennial response in Mediterranean grasses. I. Water relations and summer survival in *Phalaris*. *Australian journal of agricultural research 19*: 381–395.

McWilliam, J. R.; Latter, B. D. H. 1970: Quantitative genetic analysis in *Phalaris* and its breeding implications. *Theoretical and applied genetics 40*: 63–72.

McWilliam, J. R.; Schroeder, H. E. 1974: The yield and quality of phalaris seed harvested prior to maturity. *Australian journal of agricultural research 25*: 259–264.

McWilliam, J. R.; Schroeder, H. E.; Marshall, D. R.; Oram, R. N. 1971: Genetic stability of Australian phalaris (*Phalaris tuberosa* L.) under domestication. *Australian journal of agricultural research* 22: 895–908.

Neal-Smith, C. A. 1955: Report on herbage plant exploration in the Mediterranean region. *FAO report no. 415*. Rome, Food and Agricultural Organization.

Nguyen, H. T.; Sleper, D. A. 1983: Theory and application of half-sib matings in forage grass breeding. *Theoretical and applied genetics 64*: 187–196.

Oram, R. N. 1970: Genetic and environmental control of the amount and composition of toxins in *Phalaris tuberosa* L. *Proceedings of the XI International Grassland Congress*: 785–788.

Oram, R. N. 1982: Genetics of total seed yield and its components in *Phalaris aquatica* L. *Australian journal of agricultural research 33*: 465–471.

Oram, R. N. 1983: Ecotypic differentiation for dormancy levels in oversummering buds of *Phalaris aquatica* L. *Botanical gazette 144*: 544–551.

Oram, R. N. 1984: Inheritance of conditional dormancy in over-summering buds of *Phalaris aquatica* L. *Euphytica 33*: 313–319.

Oram, R. N. 1990: Register of Australian herbage plant cultivars. 3rd ed. Melbourne, CSIRO, Australia.

Oram, R. N.; Clements, R. J.; McWilliam, J. R. 1974: Inheritance of nutritive quality of summer herbage in *Phalaris tuberosa* L. *Australian journal of agricultural research 25*: 265–274.

Oram, R. N.; Culvenor, R. A.; Ridley, A. M. 1993a: Breeding the perennial pasture grass *Phalaris aquatica* for acid soils. Pp. 17–22 *in*: Genetic Aspects of Plant Mineral Nutrition, Randall P. J.; Delhaize E.; Richards R. A.; Munns R. *ed.* Dordrecht, The Netherlands, Kluwer Academic Publishers.

Oram, R. N.; Freebairn, R. D. 1984: Genetic improvement of drought survival ability in *Phalaris aquatica* L. *Australian journal of experimental agriculture and animal husbandry 24*: 403–409.

Oram, R. N.; Hoen, K. 1967: Perennial grass cultivars for long leys in the wheat belt of southern New South Wales. *Australian journal of experimental agriculture and animal husbandry 7*: 249–254.

Oram, R. N.; Ridley, A. M. 1994 (in press): Quantitative genetic variation for acid soil tolerance in a *Phalaris aquatica* × *P. arundinacea* × *P. aquatica* backcross population. *Proceedings of the 3rd International Symposium on Plant-Soil Interactions at low pH.*

Oram, R. N.; Ridley, A. M.; Hill, M. J.; Hunter, J.; Hedges, D. A.; Standen, R. L.; Bennison, L. 1990: Improving the tolerance of *Phalaris aquatica* L. to soil acidity by introgression of genes from *P. arundinacea* L. *Australian journal of agricultural research 41*: 657–668.

Oram, R. N.; Ridley, A. M.; Hunter, J.; Schroeder, H. E.; Taylor, J. 1993b: Breeding phalaris for tolerance to a range of acid soils. *Proceedings of the XVII International Grassland Congress*: 1352–1354.

Oram, R. N.; Schroeder, H. E. 1987: Breeding *Phalaris aquatica* L. for improved productivity, adaptation and utility for ruminants. Pp. 309–311 *in*: Temperate pastures: their production, use and management, Wheeler, J. L.; Pearson, C. J.; Robards, G. E. *ed.* Melbourne, Australian Wool Corporation & CSIRO, Australia.

Oram, R. N.; Schroeder, H. E. 1989: Seasonal changes in palatability of hybrids between *Phalaris aquatica* and hexaploid *P. arundinacea*. *Proceedings of the XVI International Grassland Congress*: 241–242.

Oram, R. N.; Schroeder, H. E. 1992: Register of Australian herbage plant cultivars. 3(a). *Phalaris aquatica* L. cv. Holdfast. *Australian journal of experimental agriculture 32*: 261–262.

Putievsky, E.; Oram, R. N.; Malafant, K. 1980: Chromosomal differentiation among ecotypes of *Phalaris aquatica* L. *Australian journal of botany 28*: 645–657.

Richardson, A. E. V.; Trumble, H. C.; Shapter, R. E. 1932: The influence of growth stage and frequency of cutting on the yield and composition of a perennial grass—*Phalaris tuberosa*. *Council for Scientific and Industrial Research bulletin 66*.

Rogers, A. L.; Bailey, E. J. 1963: Salt tolerance trials with forage plants in south-western Australia. *Australian journal of experimental agriculture and animal husbandry 3*: 125–130.

Trumble, H. C. 1952: Grassland agronomy in Australia. *Advances in agronomy 4*: 1–65.