INVITED REVIEW

Transgene escape: what potential for crop–wild hybridization?

T. T. ARMSTRONG,* R. G. FITZJOHN,† L. E. NEWSTROM,† A. D. WILTON† and W. G. LEE†
*Manaaki Whenua Landcare Research, Private Bag 92 170, Auckland, New Zealand, †Manaaki Whenua Landcare Research, PO Box 69, Lincoln, Canterbury, New Zealand

Abstract

To date, regional surveys assessing the risk of transgene escape from GM crops have focused on records of spontaneous hybridization to infer the likelihood of crop transgene escape. However, reliable observations of spontaneous hybridization are lacking for most floras, particularly outside Europe. Here, we argue that evidence of interspecific reproductive compatibility derived from experimental crosses is an important component of risk assessment, and a useful first step especially where data from field observations are unavailable. We used this approach to assess the potential for transgene escape via hybridization for 123 widely grown temperate crops and their indigenous and naturalized relatives present in the New Zealand flora. We found that 66 crops (54%) are reproductively compatible with at least one other indigenous or naturalized species in the flora. Limited reproductive compatibility with wild relatives was evident for a further 12 crops (10%). Twenty-five crops (20%) were found to be reproductively isolated from all their wild relatives in New Zealand. For the remaining 20 crops (16%), insufficient information was available to determine levels of reproductive compatibility with wild relatives. Our approach may be useful in other regions where spontaneous crop–wild hybridization has yet to be well documented.

Keywords: biosafety, crops, GM crop risk assessment, hybridization, introgression, New Zealand, reproductive compatibility, wild relatives

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Introduction

A primary concern relating to the full release of GM crops is that transgenes will escape from the confines of agriculture, possibly leading to unforeseen or negative environmental consequences (Snow & Morán Palma 1997; Hails 2000; Newstrom et al. 2003; Ellstrand 2003). Much of this concern centres on the expectation that if wild species or crops acquire transgenes promoting resistance to pests, diseases, or other abiotic stresses, they could invade or persist in agricultural areas or natural ecosystems (e.g. Snow et al. 2003). Concerns such as these have motivated the development of transgene containment strategies that aim to allow the cultivation of transgenic crops while minimizing the risk of transgene escape.

There are three main avenues by which a transgene may escape. First, plants containing the transgene may persist after harvesting (either vegetatively or as seed) and form populations capable of spreading to surrounding cultivated land and adjoining native habitats. Second, the transgene may be transferred via pollination to a conspecific crop or naturalized population of the same species and spread beyond the confines of agriculture. Last, the transgene may be transferred via pollination and interspecific hybridization to another crop species (either in cultivation or naturalized) or to a closely related wild species, leading to its escape from containment.

In this review we focus specifically on the potential for transgenes to escape via hybridization. Although transgene escape through seed, vegetative propagation, or intra-specific cross-pollination are important in the context of GM crop risk assessment; they are not addressed here. Our focus reflects particular concern about introgression of crop transgenes into other species via hybridization, rather than through gene flow between crops and cultivated or naturalized populations of the same crop species.

The crops assessed in this review for New Zealand are also widely cultivated in temperate latitudes (Lazarides...
& Hince 1993; Smartt & Simmonds 1995). Although New Zealand is not a centre of crop domestication it possesses a great diversity of naturalized exotic crop relatives (Allan 2000), many of which are well established throughout temperate and subtropical regions of the world (Holm et al. 1979; Randall 2002).

Like many recently settled archipelagos, New Zealand is particularly vulnerable to the establishment and spread of introduced plants (Lonsdale 1999). Within 150 years of European settlement, more than 20 000 plant species have been introduced to New Zealand. Of these 2109 species have become naturalized (i.e. self-sustaining in the wild), and at least 240 now have a considerable negative impact on both agricultural activity and indigenous biodiversity (Webb et al. 1988; Wilton & Breitwieser 2000; P. Williams, personal communication). In this context, a primary concern relating to the potential impact of crop transgene escape via hybridization in New Zealand is the possibility of increasing the invasiveness of existing weeds or creating new, aggressive weeds resistant to herbicides, abiotic stresses or insect herbivores. Particular concern centres on the transfer of any traits that could limit control options in conservation areas (Eichelbaum et al. 2001).

Also considered in this review is the potential for hybridization between crops and species indigenous to New Zealand. In other regions similarly distant from the centres of crop domestication, several examples have been found of locally indigenous species that have hybridized freely with introduced crops (e.g. in Chenopodium, Vitus, and Rubus in North America: Smartt & Simmonds 1995; Ellstrand 2003). Because a high value is placed on protecting the genetic integrity of indigenous species in New Zealand (Eichelbaum et al. 2001), the escape of transgenes into indigenous species is considered to be undesirable regardless of the potential for any direct hazard from the trait. This issue is of particular concern given the significance of New Zealand’s unique, insular flora.

Surveys of the potential for crop transgene escape have been conducted in western European countries, notably the Netherlands (de Vries et al. 1992), the UK (Raybould & Gray 1993), Norway (Nurminiemi & Rognli 1993) and Switzerland (Ammann et al. 1996). A feature common to these assessments is their emphasis on evidence of spontaneous hybridization (i.e. natural, unassisted sexual reproduction between taxa in the field) to infer the potential for crop–wild gene flow. This is reflected by Nurminiemi & Rognli (1993: p. 3), who argue that ‘if a [spontaneous] hybrid has not been found in a wild population … it is assumed that the possibility for this to happen is very small.’ Similarly, de Vries et al. (1992: p. 1) argue that ‘the absence of certain hybrids in the State Herbarium can be interpreted as a decisive indication that such a hybrid does not occur in the wild’ and thus, that ‘if a hybrid has not been observed previously in the wild, experiments for the possible hybridization between a cultivated plant and a wild species of the same genus need not be carried out.’ Whilst this approach may be valid for the most intensively studied floras where spontaneous hybridization is well known, for much of the world such data is entirely lacking (Ellstrand 2003).

Importantly, studies demonstrate that spontaneous hybridization can be highly context dependent, ephemeral and variable in time and space (Harlan 1992; Ladizinsky 1998; Lutman 1999; Spillane & Gepts 2001). Whilst local evidence of spontaneous crop–wild hybridization is compelling, observations from one region may not be universally applicable. For example, radish (Raphanus sativus) and jointed charlock (Raphanus raphanistrum) hybridize extensively in California, only sporadically and locally in the UK, and not at all in the Netherlands (Ellstrand 2003). Given the spatial and temporal variability of spontaneous hybridization and the influence of context-dependent factors in the prepollination stage, we argue that experimental evidence of reproductive compatibility is an important component of risk assessment.

Experimental hybridization studies are not without their own limitations. Clearly, the ease with which a crop and its wild relatives can be hybridized through manual cross-pollination reveals little about the potential influence of prepollination or other ecological barriers in the field. However, data on the degree of intrinsic reproductive compatibility between species is useful precisely because it is independent of the ecological context in which the species occur. If two species are known to be reproductively incompatible, then spontaneous hybridization between them is unlikely to happen anywhere. Conversely, if species can be freely hybridized in the glasshouse, research can be directed at determining the effectiveness of prepollination barriers in the field.

Since few reports of spontaneous crop–wild hybridization exists in New Zealand, we focus here on experimental analyses of interspecific reproductive compatibility reported in the literature. In the following section, we first define key terms, and then provide an overview of postpollination barriers in plants (i.e. the genetic and chromosomal basis of reproductive compatibility).

Hybridization

Hybridization is extremely widespread in nature, and is increasingly seen as an important evolutionary phenomenon (Arnold 1997). A recent survey of five floras found that at least 11% of angiosperm species freely hybridize with close relatives (most commonly congeneric species) (Ellstrand et al. 1996). Cases of intergeneric hybridization are less commonly encountered, and tend to be more concentrated in some plant families (e.g. Brassicaceae, Bourdöt et al. 1999; Poaceae, Edgar & Connor 2000).

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Species are genetically isolated from one another by various barriers to reproduction, the strength of which can vary along a continuum. At one extreme, hybridization may be impossible, or confined only to the production of sterile F₁ hybrids. At the other extreme, reproductive barriers may be absent, facilitating extensive introgression (i.e. repeated hybridization involving backcrossing into parental taxa) between hybridizing taxa (Rieseberg et al. 1995). It is noteworthy that some of the best examples of introgressive hybridization involve domesticated plants and their wild relatives (Gregorius & Steiner 1993; Rieseberg & Wendel 1993; Rieseberg 1997).

The breeding relationships of numerous important crops and their close relatives have been well studied (e.g. reviews in Smartt & Simmonds 1995). Indeed, many crops are known to successfully hybridize variously with other cultivars, subspecies, wild congeners, and occasionally species in other genera (Ellstrand 2003). In some cases this has led to widespread genetic exchange via introgression between cultivated crops and sympatric populations of wild relatives (e.g. Burdon et al. 1992; Arriola & Ellstrand 1996).

However, prepollination barriers can act to prevent spontaneous hybridization between reproductively compatible species. Grant (1994) and Levin (2000) provide excellent reviews of prepollination barriers, including isolation arising from the breeding system, floral (mechanical) isolation, ethological (pollinator) isolation, temporal isolation and ecological or geographical isolation. In contrast, postpollination barriers prevent hybridization once pollen has been transferred to the stigma.

Reproductive compatibility: genetic and chromosomal factors

Diverse genetic and chromosomal factors influence the likelihood of successful interspecific hybridization. These factors can act at different stages in the sequence of events beginning with cross-pollination and (potentially) resulting in the exchange of genes between different taxa.

Following cross-pollination, genetic incompatibility between heterospecific pollen and the recipient stigma can prevent fertilization in some groups (Grant 1994). For example, in Nicotiana and Lycopersicon it has been demonstrated that mutations in S alleles and changes in their level of expression by modifier genes can alter interspecific cross compatibility by preventing pollen from reaching the ovary and penetrating the micropyle (Li et al. 1997). Where interspecific fertilization is not prevented, the potential for further genetic exchange is determined by the viability and fertility of the hybrid progeny.

Inviable F₁ hybrid embryos may either be aborted prior to seed maturation or give rise to plants that are unable to grow normally or to reproduce (Levin 2000). One example is the deleterious ‘corky’ syndrome in F₁ hybrids of some Gossypium species resulting from negative interactions between parental alleles at a number of loci (Stephens 1950). Other reported F₁ developmental abnormalities caused by negative interactions (often between homologous dominant genes) include the suppression of apical dominance, profuse branching, and dwarfism (Chu & Oka 1972; Abbo & Ladizinsky 1994). Alternatively, F₁ hybrids may grow normally but be unable to reproduce.

Low F₁ hybrid fertility or complete sterility results either from the action of specific genes affecting the stringency of meiotic disjunction in hybrids (Jenkins & Jimenez 1995) or from interspecific differences in chromosome number, ploidy level, or chromosomal arrangement (Chandler et al. 1987), leading to the formation of aneuploid gametes (Smartt & Simmonds 1995; Arnold 1997; Rieseberg & Carney 1998). Even in the absence of ploidy differences, fertility in hybrids can decline as parental heterozygosity for chromosomal rearrangements increases (Croullebois et al. 1989; Rieseberg & Wendel 1993), with larger rearrangements having a greater impact on fertility than smaller ones (Chandler et al. 1987). For example, heterozygotes for inversions, fusions, or reciprocal translocations can all yield aneuploid gametes that are either sterile or produce inviable zygotes.

Analysis of hybrids between Lens culinaris and Lens ervoides, for example, reveals that heterozygosity for a single chromosomal translocation can greatly lower fertility in F₁ hybrids (Tadmor et al. 1987). Studies in Helianthus also demonstrate that taxa differing by translocations and paracentric inversions can have reduced fertility due to the failure of meiotic disjunction in their first or later generation hybrids (Chandler et al. 1987; Abbo & Ladizinsky 1994; Quillet et al. 1995; Rieseberg et al. 1995). Similarly, F₁ hybrid sterility in Vicia results from meiotic failure associated with chromosomal incompatibility (Ladizinsky 1998). Notwithstanding these examples, chromosomal heterozygosity does not always result in reproductive isolation (Sites & Moritz 1987; Coyne et al. 1993).

In many groups the action of specific genes may be more important determinants of compatibility. Negative interactions between homologous genes in the parental taxa can prevent hybridization (Dobzhansky 1937; Wu & Palopoli 1994). For example, Li et al. (1997) demonstrated that genic incompatibility among rice (Oryza) taxa is the result of a single cytoplasmic gene causing both male and female hybrid sterility. Reproductive isolation resulting from genic rather than chromosomal factors is apparent in a number of other genera including Lotus (Caradus & Williams 1995), Melilotus (Sano & Kita 1978), Minulius (Macnair & Christie 1983; Christie & Macnair 1984), Oryza (Oka 1974; Wan et al. 1996), Stellaria (Croullebois et al. 1989), and Triticum (Hermson 1963). Because recombination between parental genomes does not occur until the formation of gametes in the F₁ generation, hybrid inviability or sterility is often not expressed until the production of F₂ and backcross hybrids.
Assessing the potential for crop–wild hybridization in New Zealand

Our analysis of the potential for transgene escape via hybridization mirrors the natural hierarchy of barriers to interspecific gene exchange. First, we identify which species are closely related and therefore may be interfertile. Second, we obtain evidence on the extent to which these species can cross under experimental conditions (i.e. their level of reproductive compatibility).

Survey methods

We compiled a list of all crops grown in New Zealand using data from Petrie & Bezari (1997); MAF (2003–04); Statistics New Zealand (2004) and HortResearch (2004). The list included all transgenic crops developed or field tested in New Zealand (Christey & Woodfield 2001). Excluded were a number of minor crops (e.g. Achillea spp., Hypericum spp.) and ornamental species grown for the trade in cut flowers (e.g. Cymbidium, Dianthus).

A list of all wild relatives was then assembled for each crop by identifying congeneric indigenous and naturalized exotic species (including other crops) using the New Zealand Plant Names Database (Allan Herbarium 2000). Because this review focuses explicitly on the potential for interspecific hybridization, taxonomic units below the rank of species (e.g. subspecies, varieties, races) are not considered. In families where intergeneric hybridization is known to be prominent (Apiaceae, Brassicaceae, Poaceae) members of other genera were also considered. Only those crop relatives with self-maintaining wild populations were included (i.e. indigenous and naturalized exotic species). Exotic species known not to persist outside cultivation (i.e. casual species) were excluded. These ‘biostatus’ categories (e.g. naturalized or casual) are used in the New Zealand Plant Names Database based on definitions modified by Webb et al. (1988) and Heenan et al. (1998, 1999). 25 crops found to have no close relatives present in New Zealand, and therefore no opportunity for interspecific hybridization, were excluded from the crop list.

Information on the degree of reproductive compatibility between the crops and their wild relatives was obtained from a range of sources. Initially, the citation databases CAB Abstracts (1973–2004) and ISI Web of Knowledge (1988–2004) (http://isi02.isiknowledge.com, the Thomson Corporation 2005) were extensively searched for relevant publications. We also included earlier studies derived from citation lists in recent journal articles and key texts such as Smartt & Simmonds (1995). Significant additional information about crossing relationships was also obtained by directly contacting crop breeders (see Acknowledgements).

We derived four ‘Hybridization Potential’ categories to reflect the level of reproductive compatibility, and therefore potential for hybridization, between crops and their wild relatives.

Hybridization Potential (HP) category 1: Strong evidence exists of substantial reproductive compatibility (i.e. where manual or open-pollination results in the production of viable, fertile F1 hybrids, and later generation hybrids are also known to be fertile) between the crop and at least one other wild relative in New Zealand.

HP category 2: Cross-pollination between the crop and at least one other wild relative can produce F1 hybrids, but either these hybrids are completely sterile or their viability and fertility is unknown. In such cases, transgene ‘escape’ may be limited to vegetative reproduction in sterile hybrids.

HP category 3: The crop and all other related species present in New Zealand are known to be reproductively isolated (i.e. F1 hybrids cannot be produced through manual pollination, although hybridization may in some cases be possible using embryo rescue or protoplast fusion methods, etc.).

HP category 4: Insufficient information on compatibility relationships between the crop and its wild relatives was available to evaluate the potential for hybridization.

Results

We identified 123 important food, fodder and forestry crop species from 48 genera in New Zealand. The associated crop-relative list contained 199 exotic naturalized species from 41 genera, and 37 indigenous species from 14 genera. Evidence indicating the level of reproductive compatibility between the crops and their wild relatives is provided in Table 1. From this survey, crops were assigned to the four HP categories.

HP category 1: Sixty-six (66) of the 123 crops surveyed (54%) were reproductively compatible with at least one closely related indigenous or naturalized exotic species in the New Zealand flora (e.g. Agrostis capillaris, Lactuca sativa, Lolium spp.).

HP category 2: Crop–wild compatibility relationships were less clear for 12 crops (10%) either because (i) hybrid viability or, more frequently, fertility was not reported (e.g. Medicago sativa × M. glomerata), or (ii) F1 hybrids are known to be completely sterile (e.g. Passiflora edulis × P. caerulea).

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Table 1 The potential for hybridization between crops (common names given in brackets) and their indigenous and naturalized close relatives (indented) in New Zealand. The biostatus of each taxon is indicated in the second column using the following abbreviations: indigenous to New Zealand (ind.); naturalized exotic (nat.); casual (cas.); cultivated only (cult.). Naturalized crops are also considered as wild relatives in relation to other congeneric crops.

The potential for hybridization (HP) is indicated in the third column by the following four categories:
1 Evidence exists of substantial reproductive compatibility between the crop and at least one other indigenous or naturalized species (including naturalized crops).
2 All crop-wild F1 hybrids are known to be either (i) entirely sterile or (ii) F1 viability and fertility are unknown. Here, transgene ‘escape’ may be limited to vegetative reproduction in sterile F1 hybrids.
3 The crop and all other related species present in New Zealand are known to be completely reproductively isolated.
4 Insufficient information was available on compatibility relationships between the crop and its wild relatives to determine the potential for hybridization.

<table>
<thead>
<tr>
<th>Family</th>
<th>Taxon</th>
<th>Biostatus</th>
<th>HP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Actinidiaceae</td>
<td>Actinia arguta (kiwifruit)</td>
<td>cult.</td>
<td>1 Open pollination between A. delicosa and A. arguta</td>
</tr>
<tr>
<td></td>
<td>A. arguta (kiwifruit)</td>
<td>nat.</td>
<td>1 (in either direction) produces viable and fertile F1 hybrids (Fairchild 1927; Pringle 1986; M. McNeilage, personal communication).</td>
</tr>
<tr>
<td>Apiaceae</td>
<td>Daucus carota (carrot)</td>
<td>nat.</td>
<td>4 The compatibility of D. carota and the New Zealand native D. glochidiatus is unknown. However, the only reported interspecific cross involving carrot is D. carota × D. capitifolius (McCollum 1975), and a recent phylogenetic study places D. glochidiatus distant from D. carota relative to D. capitifolius (Vivek &amp; Simon 1999).</td>
</tr>
<tr>
<td></td>
<td>Daucus glochidiatus</td>
<td>ind.</td>
<td>1 A. graveolens × A. nodiflorum freely produce fertile hybrids (Pink &amp; Innes 1984).</td>
</tr>
<tr>
<td></td>
<td>Apium graveolens (celery)</td>
<td>nat.</td>
<td>1 A. graveolens hybridizes with wild and cultivated parsley. The F1 hybrids are fertile and produce viable F2 hybrids (Honma &amp; Lacy 1980).</td>
</tr>
<tr>
<td></td>
<td>Apium nodiflorum</td>
<td>nat.</td>
<td>1 A. graveolens hybridizes with wild and cultivated parsley. The F1 hybrids are fertile and produce viable F2 hybrids (Honma &amp; Lacy 1980).</td>
</tr>
<tr>
<td></td>
<td>A. prostratum</td>
<td>ind.</td>
<td>1 A. graveolens hybridizes with wild and cultivated parsley. The F1 hybrids are fertile and produce viable F2 hybrids (Honma &amp; Lacy 1980).</td>
</tr>
<tr>
<td>Asteraceae</td>
<td>Lactuca sativa (lettuce)</td>
<td>nat.</td>
<td>1 L. sativa × L. saligna F1 hybrids can be produced but have low fertility (Zohary 1991).</td>
</tr>
<tr>
<td></td>
<td>Lactuca saligna</td>
<td>nat.</td>
<td>1 L. sativa is fully interfertile with L. serriola (Lundqvist 1960; Kesseli et al. 1991; Zohary 1991).</td>
</tr>
<tr>
<td></td>
<td>L. serriola</td>
<td>nat.</td>
<td>1 L. virosa is incompatible with L. sativa. Crosses generally lead to F1 embryo abortion and/or F1 sterility (Whittaker 1969; Eenink et al. 1982; Matsumoto 1991). However, a few BC1 seeds were produced by large-scale pollination of F1 plants (Maisonuneuve et al. 1995).</td>
</tr>
<tr>
<td></td>
<td>L. virosa</td>
<td>nat.</td>
<td>1 L. virosa is incompatible with L. sativa. Crosses generally lead to F1 embryo abortion and/or F1 sterility (Whittaker 1969; Eenink et al. 1982; Matsumoto 1991). However, a few BC1 seeds were produced by large-scale pollination of F1 plants (Maisonuneuve et al. 1995).</td>
</tr>
<tr>
<td></td>
<td>Helianthus annuus (sunflower)</td>
<td>nat.</td>
<td>1 H. annuus hybridizes spontaneously with its annual diploid relatives in Section Annui (Rogers et al. 1982; Rieseberg &amp; Wendel 1993; Heiser 1995). Hand-crossing trials also indicate reasonable interfertility between H. annuus and the perennial H. salicifolius (Atlagic et al. 1995), the cross producing F1 hybrids with high pollen viability (64%).</td>
</tr>
<tr>
<td></td>
<td>Helianthus × laetiflorus (≡ H. rigidus × H. tuberosus)</td>
<td>nat.</td>
<td>1 Although H. annuus × H. tuberosus (section Diouricata) F1 hybrids have been produced with difficulty (e.g. Fambrini et al. 1996), they are typically sterile or have low fertility (Heiser 1995).</td>
</tr>
</tbody>
</table>
Brassicaceae (tribe Brassiceae)

Brassica juncea (brown mustard) nat. 1 Most Brassica species present in New Zealand, including wild relatives, are able to hybridize, although sometimes only with extreme difficulty (Bourdôt et al. 1999; Warwick et al. 2000; Salisbury 2002; Stewart 2002). High levels of interspecific reproductive compatibility are found between B. rapa and B. napus (U 1935; Wahiduzzaman 1987; Lu et al. 2001), B. napus and B. juncea (Wahiduzzaman 1987; Prakash & Chopra 1988; Frello et al. 1995). B. rapa also crosses easily with a variety of Brassica species (Ramanujam & Srinivasachar 1943; Choudhary & Joshi 2001).

B. oleracea (cabbage, broccoli, kale, etc.) nat. 1 B. rapa also crosses easily with a variety of Brassica species (Ramanujam & Srinivasachar 1943; Choudhary & Joshi 2001).

B. rapa (turnip, canola, oilseed rape) nat. 1 Intergeneric hybridization is possible between crop brassicas and species in other genera within the tribe Brassiceae. In particular, hybridization is possible with Diplotaxis muralis, D. tenuifolia, Eruca vesicaria (syn. E. sativa), Hirschfeldia incana, Raphanus raphanistrum, R. sativus, Sinapis alba and S. arvensis, and some Brassica species, particularly B. napus and B. rapa (Bourdôt et al. 1999; Salisbury 2002). However, rates of hybridization in these crosses are typically very low.

B. napus (rape, canola, oilseed rape, fodder rape, swede) nat. 1 Interspecific crosses between R. sativus and R. raphanistrum have been reported (Lee & Snow 1998). In addition, intergeneric crosses with R. sativus have been reported with several species, including B. juncea (Gupta 1997), B. napus (Paulmann & Röbbelen 1988; Gupta 1997), B. oleracea (Ellerström 1978; Gupta 1997), B. rapa (Ellerström 1978), and S. arvensis (Mizushima 1950).

Raphanus sativus (radish) nat. Interspecific hybrids have been reported between S. alba and both B. napus (Heyn 1977) and B. nigra (Choudhary & Joshi 2000).

Sinapis alba (white mustard) nat. 1 Interspecific crosses between R. sativus and R. raphanistrum have been reported (Lee & Snow 1998). In addition, intergeneric crosses with R. sativus have been reported with several species, including B. juncea (Gupta 1997), B. napus (Paulmann & Röbbelen 1988; Gupta 1997), B. oleracea (Ellerström 1978; Gupta 1997), B. rapa (Ellerström 1978), and S. arvensis (Mizushima 1950).

Sinapis arvensis nat. 1 Interspecific hybrids have been reported between S. alba and both B. napus (Heyn 1977) and B. nigra (Choudhary & Joshi 2000).

Convolvulaceae

Ipomoea batatas (kumara) nat. 4 I. trifida and I. × leucantha (neither present in New Zealand) are the only species known to be interfertile with the polyploid cultivated I. batatas (Diaz et al. 1996). Crossability between I. batatas and other Ipomoea species present in New Zealand has not been examined, but should be considered unlikely given the lack of crossability between I. batatas and most other closely related species.

Cucurbitaceae

Cucumis melo (rock, honeydew & musk melons) cult. 3 Generally, attempts to hybridize the three Cucumis species present in New Zealand have failed; both Deakin et al. (1971) and Kho et al. (1980) attempted all six combinations between species present here. Only the crosses C. sativus × C. melo (Deakin et al. 1971) and C. sativus × C. myriocarpus produced fruits (Deakin et al. 1971; Kho et al. 1980). In other combinations, pollen failed to germinate (Kho et al. 1980), indicating strong prezygotic barriers. Hybrids between C. sativus (female) and C. melo (male) have been produced (van der Knaap & de Ruiter 1978), although only a few hybrids were produced from thousands of pollinations. Backcrosses from the hybrid to C. sativus were successful, but backcrosses to C. melo failed. Although C. sativus and C. melo can hybridize, neither species is naturalized in New Zealand.
Cucurbita maxima (pumpkin) nat. 4 Esquinas-Alcazar & Gulick (1983) reviewed crossability relationships between species of Cucurbita, including all present in New Zealand. All combinations produced seed except C. ficifolia × C. moschata. However, only the combination C. moschata × C. pepo produced fertile F₁ plants. Fertile F₁ plants have also been produced by Shifriss & Cohen (1974) and Paris et al. (1985), and used to introgress traits into C. moschata. Barriers may depend on genotype, as several combinations reported to be compatible by Esquinas-Alcazar & Gulick (1983) could not be produced by Izik et al. (2003), despite the use of embryo rescue. Furthermore, Whitaker & Bemis (1964) note ‘there is no evidence for spontaneous hybridization among the cultivated Cucurbita [including C. ficifolia], although they have been grown side by side in fields and gardens for many generations’.

<table>
<thead>
<tr>
<th>Fabaceae</th>
<th></th>
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<tbody>
<tr>
<td><strong>Lotus corniculatus</strong> (birdsfoot trefoil)</td>
<td>nat. 3 Strong genic reproductive barriers prevail among Lotus species, and hybridization is generally impossible without assisted breeding (e.g. embryo rescue) (Caradus &amp; Williams 1995). F₁ hybrids are usually sterile (Somaroo &amp; Grant 1972; Lautour et al. 1978; Yang et al. 1990).</td>
</tr>
<tr>
<td><strong>L. pedunculatus</strong> (big trefoil)</td>
<td>nat. 3</td>
</tr>
<tr>
<td><strong>L. tenuis</strong> (narrow leaved trefoil)</td>
<td>nat. 3</td>
</tr>
<tr>
<td><strong>Lotus angustissimus</strong></td>
<td>nat.</td>
</tr>
<tr>
<td><strong>L. suaveolens</strong></td>
<td>nat.</td>
</tr>
<tr>
<td><strong>Lupinus polyphyllus</strong> (lupin)</td>
<td>nat. 3 Few Lupinus species are reproductively compatible. Embryo-rescue techniques have been used to produce F₁ hybrids between some combinations (e.g. Przyborowski &amp; Packa 1997), although these are typically sterile (Elliott et al. 1974).</td>
</tr>
<tr>
<td><strong>L. arboresus</strong></td>
<td>nat.</td>
</tr>
<tr>
<td><strong>L. luteus</strong></td>
<td>nat.</td>
</tr>
<tr>
<td><strong>Medicago sativa</strong> (lucerne)</td>
<td>nat. 2 M. sativa hybridizes spontaneously in Europe with M. falcata, and can be hand crossed with M. glomerata (de Vries et al. 1992; Langer 1995). F₁ hybrid fertility levels for the latter combination are not reported. No other locally present combinations are interfertile. Breeders rely on embryo rescue and protoplast fusion to produce Medicago hybrids (Nenz et al. 1996).</td>
</tr>
<tr>
<td><strong>Medicago arabica</strong></td>
<td>nat.</td>
</tr>
<tr>
<td><strong>M. arborea</strong></td>
<td>nat.</td>
</tr>
<tr>
<td><strong>M. glomerata</strong></td>
<td>nat.</td>
</tr>
<tr>
<td><strong>M. lupulina</strong></td>
<td>nat.</td>
</tr>
<tr>
<td><strong>M. minima</strong></td>
<td>nat.</td>
</tr>
<tr>
<td><strong>M. nigra</strong></td>
<td>nat.</td>
</tr>
<tr>
<td><strong>Phaseolus coccineus</strong> (runner bean)</td>
<td>nat. 1 P. coccineus and P. vulgaris are completely interfertile (Debouck &amp; Smartt 1995). However, P. lunatus is strongly reproductively isolated from both of these species (Alvarez et al. 1981).</td>
</tr>
<tr>
<td><strong>P. lunatus</strong> (lima bean)</td>
<td>nat. 3</td>
</tr>
<tr>
<td><strong>P. vulgaris</strong> (French bean)</td>
<td>nat. 1</td>
</tr>
<tr>
<td><strong>Trifolium ambiguum</strong> (Caucasian clover)</td>
<td>nat. 2 Interspecific hybridization in Trifolium is uncommon (Evans 1962) and breeding efforts rely largely on artificial methods (Quesenberry &amp; Taylor 1976). However, some species combinations are compatible.</td>
</tr>
<tr>
<td><strong>T. fragiferum</strong> (strawberry clover)</td>
<td>nat. 4</td>
</tr>
<tr>
<td><strong>T. hybridum</strong> (aslike clover)</td>
<td>nat. 2 T. repens can hybridize with T. ambiguum, T. hybridum (both locally naturalized) and T. iltisnocarpum (Evans 1962; Stace 1975). Spontaneous hybridization between T. pratense and T. medium has been reported (Stace 1975).</td>
</tr>
<tr>
<td><strong>T. medium</strong> (zigzag clover)</td>
<td>nat. 1 Caradus &amp; Williams (1995). Hybridization between these species has been achieved through hand pollination, although F₁ hybrid fertilities are unreported. In the UK, spontaneous hybridization between T. pratense and T. medium has been reported (Stace 1975).</td>
</tr>
<tr>
<td><strong>T. pratense</strong> (red clover)</td>
<td>nat. 1</td>
</tr>
<tr>
<td><strong>T. repens</strong> (white clover)</td>
<td>nat. 2</td>
</tr>
<tr>
<td><strong>T. resupinatum</strong> (reversed clover)</td>
<td>nat. 4</td>
</tr>
<tr>
<td><strong>T. subterraneum</strong> (subterranean clover)</td>
<td>nat. 3</td>
</tr>
<tr>
<td><strong>Trifolium angustifolium</strong></td>
<td>nat.</td>
</tr>
<tr>
<td><strong>T. arvense</strong></td>
<td>nat.</td>
</tr>
</tbody>
</table>
T. aureum nat.
T. campestre nat.
T. cernuum nat.
T. dubium nat.
T. glomeratum nat.
T. hirtum nat.
T. incarnatum nat.
T. micranthum nat.
T. ochroleucon nat.
T. ornithopodioides nat.
T. retusum nat.
T. scabrum nat.
T. striatum nat.
T. suffocatum nat.
T. tomentosum nat.

Vicia cracca (tufted vetch) nat. 3 Strong crossing barriers in the genus Vicia result from chromosomal instability in F1 zygotes (Ladizinsky 1981). No known wild species of Vicia are crossable with the cultivated faba bean. Embryo rescue and other methods are used to produce hybrid lines (Roupakias 1986; Muehlbauer et al. 1994).

V. disperma (French tare) nat. 3
V. faba (faba bean) nat. 3 known wild species of Vicia are crossable with the cultivated faba bean. Embryo rescue and other methods are used to produce hybrid lines (Roupakias 1986; Muehlbauer et al. 1994).
V. lathyroides (spring vetch) nat. 3
V. lutea (yellow vetch) nat. 3
V. sativus (common vetch) nat. 3
V. tetrasperma (smooth tare) nat. 3
V. villosa (fodder vetch) nat. 3

Grossulariaceae
Ribes nigrum (black currant) nat. 2 R. nigrum and R. rubrum (in separate subgenera) are reproductively isolated (Keep 1995). Artificial F1 hybrids between R. nigrum and R. uva-crispa have been produced, although their fertility is unclear (reported in Nurminiemi & Rognli 1993, p. 46). No cases of spontaneous hybridization between Ribes species have been recorded in the UK (Raybould & Gray 1993) or New Zealand.
Ribes aduratum nat.
R. sanguineum nat.
R. uva-crispa nat.

Liliaceae
Allium cepa (onion) nat. 1 A. cepa (2x = 16) and A. fistulosum L. (2x = 16) are closely related species (both within section Cepa) that can be readily hybridized. Interspecific hybrids have been made for the purpose of transferring favourable characters from A. fistulosum into A. cepa (Pefley & Hou 2000). Backcrossing is difficult, but has been achieved (Cryder et al. 1991; Bark et al. 1994). However, little genetic exchange appears to have taken place (Cryder et al. 1991). A. cepa is separated from most other Allium species by strong crossing barriers (Ulloa et al. 1995; van Raamsdonk et al. 2000, 2003) with hybrids typically sterile.
Allium ampeloprasum nat. A. porrum (leek) is cross-compatible with its close relatives A. ampeloprasum (present in New Zealand), A. atrovioletaceum, A. bourgeui and A. commutatum (Kik et al. 1997). No information was given about the fertility of the hybrids.
A. roseum nat. Hybrids have been obtained with A. cepa and A. ampeloprasum at very low frequencies using embryo rescue (Ohsumi et al. 1993; Yanagino et al. 2003).
A. triquetrum nat. Cultivated A. sativum is male sterile and propagated vegetatively (Havey 1995).
Asparagus officinalis (asparagus) nat. 4 Extensive hand crosses conducted between *A. densiflorus* and the following species, *A. officinalis*, *A. acutifolius*, *A. albus*, *A. aphyllus*, *A. arborescens*, *A. falcatus*, *A. laricinus*, *A. oligoclonos*, *A. setaceus* and *A. virgatus*, produced no hybrid seed (McCollum 1988). Interspecific crossing in the genus is generally considered extremely difficult and breeding attempts rely on protoplast fusion, typically producing sterile *F*₁ hybrids (Falavigna *et al.* 1983). Hybridization between cultivated *A. officinalis* and the wild Asian species *A. schobioides* has been documented (Ochiai *et al.* 2002), although hybrid fertility was unreported. Compatibility between species present in New Zealand is unclear.

### Linaceae

*Linum usitatissimum* (linseed, flax) nat. 1 *L. usitatissimum* and *L. bienne* can freely produce fertile *F*₁ hybrids (Green 1983). However, *L. usitatissimum* × *L. catharticum* are strongly isolated (Green 1983). Seetharam (1972) examined crossing relationships between wild *Linum* taxa (not present in New Zealand) and cultivated *L. usitatissimum*. Levels of hybrid seed set were typically high and normal meiotic pairing was observed in most *F*₁ hybrid combinations. Interfertility of cultivated flax with the native *L. monogynum* is unknown.

### Myrtaceae

*Eucalyptus delegatensis* (alpine ash) nat. 4 Crossing barriers in the genus *Eucalyptus* are weak, particularly within subgenera (Griffin *et al.* 1988. Cases of natural hybridization and introgression are common and widespread (Pryor 1976; Griffin *et al.* 1988). Interfertile crop–wild species combinations in New Zealand include: *E. globulus* × *E. ovata* (McAulay 1938) *E. grandis* × *E. nitens* (Shelbourne *et al.* 1999) *E. gunnii* × *E. ovata* (Potts *et al.* 1987) *E. nitens* × *E. globulus* (Tibbits 1988) *E. nitens* × *E. gunnii* (Tibbits 1988) *E. nitens* × *E. viminalis* (Tibbits 1988) *E. obliqua* × *E. pulchella* (Potts & Reid 1983) *E. regnans* × *E. obliqua* (Ashton 1984) *E. saligna* × *E. botryoides* (Passioura & Ash 1993) *E. tereticornis* × *E. robusta* (Griffin *et al.* 1988) Given the high level of interspecific reproductive compatibility in the genus, other interfertile combinations are likely to exist locally.

### Oxalideaceae

*Oxalis tuberosa* (yam) nat. 4 No information was found on interspecific hybridization in *Oxalis*.
Passifloraceae

Passiflora edulis (passionfruit) nat. 2 The F1 combinations P. edulis × P. caerulea (Dixit & Torne 1978) and P. edulis × P. incarinata (Beal 1972) have been produced through hand pollination, although levels of hybrid viability and fertility are unclear. However, Soares-Scott et al. (2003) reports that aneuploidy typically results in F1 sterility in Passiflora. Most breeding efforts rely on embryo rescue and protoplast fusion (e.g. Barbosa & Vieira 1997), suggesting that natural hybridization is unlikely.


Pinaceae

Picea abies (Norway spruce) nat. 2 Although spontaneous interspecific hybridization is frequent among Picea spp. (e.g. Gordon 1976; Rajora & Dancik 2000; Silim et al. 2001), it has not been reported between P. abies and P. sitchensis. Cross-pollination trials indicate that P. abies and P. sitchensis are reproductively compatible, although levels of hybrid fertility were not reported (Kleinschmidt 1979).

Picea sitchensis (Sitka spruce) nat.

Pinus attenuata (knobcone pine) nat. 1 F1 hybrids can be produced through cross-pollination of P. radiata with P. attenuata (Dungey et al. 2003). F1 hybrids are known to be viable and fertile, although hybrid pollen fertility is apparently lower than in parental species (H. Dungey, pers. comm.). Hybridization between P. radiata and P. muricata, P. oocarpa and P. tecumumanii is also possible but apparently difficult. Hybrid fertility for these combinations is unreported (Dungey et al. 2003).

Pinus contorta (shore pine) nat. 1 P. radiata with P. attenuata (Dungey et al. 2003). F1 hybrids are known to be viable and fertile, although hybrid pollen fertility is apparently lower than in parental species (H. Dungey, pers. comm.). Hybridization between P. radiata and P. muricata, P. oocarpa and P. tecumumanii is also possible but apparently difficult. Hybrid fertility for these combinations is unreported (Dungey et al. 2003).

Pinus muricata (muricata pine) nat. 2 F1 hybrids can be produced through cross-pollination of P. radiata with P. attenuata (Dungey et al. 2003). F1 hybrids are known to be viable and fertile, although hybrid pollen fertility is apparently lower than in parental species (H. Dungey, pers. comm.). Hybridization between P. radiata and P. muricata, P. oocarpa and P. tecumumanii is also possible but apparently difficult. Hybrid fertility for these combinations is unreported (Dungey et al. 2003).

Pinus nigra (Corsican pine) nat. 4 F1 hybrids can be produced through cross-pollination of P. radiata with P. attenuata (Dungey et al. 2003). F1 hybrids are known to be viable and fertile, although hybrid pollen fertility is apparently lower than in parental species (H. Dungey, pers. comm.). Hybridization between P. radiata and P. muricata, P. oocarpa and P. tecumumanii is also possible but apparently difficult. Hybrid fertility for these combinations is unreported (Dungey et al. 2003).

Pinus patula (Mexican pine) nat. 1 Spontaneous hybridization involving introgression occurs between P. contorta and P. banksiana where the two species are sympatric (Ye et al. 2002).

Pinus ponderosa (ponderosa pine) nat. 4 Extensive hand pollinations (Kormut’ak 1984) indicate a high level of compatibility between P. sylvestris and P. mugo. Natural hybridization and introgression also occur between these species (Christensen & Dar 1999). Crossing trials indicate that P. sylvestris can cross-breed freely with P. patula (Mirov 1967).

Pinus strobus (strobos pine) nat. 4 F1 hybrids can be produced through cross-pollination of P. radiata with P. attenuata (Dungey et al. 2003). F1 hybrids are known to be viable and fertile, although hybrid pollen fertility is apparently lower than in parental species (H. Dungey, pers. comm.). Hybridization between P. radiata and P. muricata, P. oocarpa and P. tecumumanii is also possible but apparently difficult. Hybrid fertility for these combinations is unreported (Dungey et al. 2003).

Poaceae

Agrostis capillaris (common bentgrass) nat. 1 Most Northern Hemisphere Agrostis species are entirely interfertile and hybridize promiscuously (Smith 1995).

A. castellana (highland bentgrass) nat. 1 Belanger et al. (2003) report high levels of interfertility (freely crossing through open pollination to produce highly fertile hybrids) between A. stolonifera and the following species: A. capillaris, A. castellana, A. gigantea and A. canina. Extensive natural introgression between A. capillaris and A. stolonifera has also been demonstrated using genetic markers (Lefebvre & Meerts 1989).

A. gigantea nat. Reproductive compatibility between exotic and native Agrostis species is unknown.

A. imbecilla ind.

A. magellanica ind.
<table>
<thead>
<tr>
<th>Species</th>
<th>Origin</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. muelleriana</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>A. muscosa</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>A. oresbia</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>A. pallescens</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>A. personata</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>A. petriei</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>A. subulata</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>A. stolonifera</td>
<td>nat.</td>
<td></td>
</tr>
<tr>
<td>A. sativa</td>
<td>nat.</td>
<td>1 Cultivated hexaploid A. sativa is fully reproductively compatible</td>
</tr>
<tr>
<td>Avena sativa (oats)</td>
<td></td>
<td>with other hexaploid species including A. fatua and A. sterilis, but</td>
</tr>
<tr>
<td>A. barbata</td>
<td>nat.</td>
<td>not with the tetraploid A. barbata or the diploid A. strigosa (Thomas</td>
</tr>
<tr>
<td>A. fatua</td>
<td>nat.</td>
<td>1995). Various studies have confirmed crop-wild introgression between</td>
</tr>
<tr>
<td>A. sterilis</td>
<td>nat.</td>
<td>A. sativa and its wild relatives (e.g. Derick 1933; Burdon et al. 1992).</td>
</tr>
<tr>
<td>A. strigosa</td>
<td>nat.</td>
<td></td>
</tr>
<tr>
<td>Bromus inermis (brome grass)</td>
<td>nat.</td>
<td>1 Compatibility relationships in the large genus Bromus are</td>
</tr>
<tr>
<td>B. sitchensis (upland brome)</td>
<td>nat.</td>
<td>relatively unknown. Cross-pollination of B. inermis with</td>
</tr>
<tr>
<td>B. stamineus (grazing brome)</td>
<td>nat.</td>
<td>4 B. erectus readily produces fertile F₁ hybrids (Armstrong 1990;</td>
</tr>
<tr>
<td>B. wildenowii (prairie grass)</td>
<td>nat.</td>
<td>Smith 1995). B. inermis can be also be hybridized with B. arcensis,</td>
</tr>
<tr>
<td>B. brevis</td>
<td>nat.</td>
<td>none of these species are naturalized in New Zealand. Hybridization</td>
</tr>
<tr>
<td>B. commutatus</td>
<td>nat.</td>
<td>between B. inermis and B. mollis has been reported to be unsuccessful</td>
</tr>
<tr>
<td>B. diandrus</td>
<td>nat.</td>
<td>(Knowles 1944). Hybridization is possible among many of the naturalized</td>
</tr>
<tr>
<td>B. erectus</td>
<td>nat.</td>
<td>species; B. commutatus and B. racemosa are interfertile, and</td>
</tr>
<tr>
<td>B. hordeaceus</td>
<td>nat.</td>
<td>may hybridize in nature (Smith 1973). B. mollis can hybridize</td>
</tr>
<tr>
<td>B. japonicus</td>
<td>nat.</td>
<td>with at least B. arenarius, B. commutatus, B. hordeaceus, B. madritenis,</td>
</tr>
<tr>
<td>B. liebicus</td>
<td>nat.</td>
<td>B. madritensis, B. racemosa and B. rubens, as well as with other</td>
</tr>
<tr>
<td>B. mollis</td>
<td>nat.</td>
<td>other species not present in New Zealand (Knowles 1944). Relationships</td>
</tr>
<tr>
<td>B. racemosa</td>
<td>nat.</td>
<td>with the other three crop species are completely unknown so further</td>
</tr>
<tr>
<td>B. sterilis</td>
<td>nat.</td>
<td>interfertile combinations may exist in New Zealand.</td>
</tr>
<tr>
<td>B. tectorum</td>
<td>nat.</td>
<td></td>
</tr>
<tr>
<td>B. vulvianus</td>
<td>nat.</td>
<td></td>
</tr>
<tr>
<td>Festuca arundinacea (tall fescue)</td>
<td>nat.</td>
<td>1 Several cultivated species of Festuca (including the three present</td>
</tr>
<tr>
<td>F. ovina (sheep fescue)</td>
<td>nat.</td>
<td>in New Zealand) are interfertile (Smith 1995), and</td>
</tr>
<tr>
<td>F. rubra (fine fescue)</td>
<td>nat.</td>
<td>1 can also hybridize with some Lolium and Vulpia spp., including V.</td>
</tr>
<tr>
<td>Festuca actae</td>
<td>ind.</td>
<td>bromoides (Stace &amp; Cotton 1974; Barker &amp; Stace 1982). Reproductive</td>
</tr>
<tr>
<td>F. contracta</td>
<td>ind.</td>
<td>compatibility between exotic and native Festuca species in New Zealand</td>
</tr>
<tr>
<td>F. coxii</td>
<td>ind.</td>
<td>is unstudied.</td>
</tr>
<tr>
<td>F. deflexa</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>F. filiformis</td>
<td>nat.</td>
<td></td>
</tr>
<tr>
<td>F. luciarum</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>F. madida</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>F. matthevsi</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>F. multinodis</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>F. novae-zelandiae</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>F. ulvulsum</td>
<td>ind.</td>
<td></td>
</tr>
<tr>
<td>Vulpia myuros</td>
<td>nat.</td>
<td></td>
</tr>
<tr>
<td>V. bromoides</td>
<td>nat.</td>
<td></td>
</tr>
<tr>
<td>Holcus lanatus (Yorkshire fog)</td>
<td>nat.</td>
<td>1 H. lanatus is reproductively compatible with H. mollis and the two</td>
</tr>
<tr>
<td>H. mollis</td>
<td>nat.</td>
<td>species are known to hybridize spontaneously (Stace 1975).</td>
</tr>
<tr>
<td>Hordeum vulgare (barley)</td>
<td>nat.</td>
<td>1 Cultivated barley hybridizes spontaneously in nature with its wild</td>
</tr>
<tr>
<td>Critesion marinum (syn. Hordeum marinum)</td>
<td>nat.</td>
<td>subspecies (including H. vulgare ssp. distichon) and with H. spontaneum (Harlan 1995). H. vulgare is not known to be reproducitively compatible with any other species in the genus (Harlan 1995). Critesion marinum hybridizes freely with cultivated wheat T. aestivum (Guadagnuolo et al. 2001b).</td>
</tr>
</tbody>
</table>
Lolium multiflorum (rye grass) nat. 1
L. perenne (perennial rye grass) nat. 1
Lolium rematum
L. rigidum
L. temulentum
Paspalum dilatatum (dallisgrass) nat. 3
Paspalum conjugatum
P. distichum
P. orbiculare
P. paniculatum
P. pubiflorum
P. urvillei
P. vaginatum
Paspalum dilatatum
P. conjugatum
P. distichum
P. orbiculare
P. paniculatum
P. pubiflorum
P. urvillei
P. vaginatum
Phalaris aquatica (phalaris) nat. 1
P. arundinacea (canary grass) nat. 1
Phalaris angusta
P. canariensis
P. minor
P. paradoxa
Phalaris aquatica
P. arundinacea
Phalaris angusta
P. canariensis
P. minor
P. paradoxa
Phalaris aquatica and P. arundinacea can be crossed readily and F₁
hybrids are viable and fertile (Smith 1995). Lowe & Bowdler (1981) report using a P. aquatica × P. canariensis hybrid in an
experiment, but no information is given about the production
of this hybrid. No reports were found of hybridization between
crop Phalaris species and the other three naturalized species.
Sorghum bicolor (sorghum) nat. 1
Sorghum halepense
Triticum aestivum (wheat) nat. 1
Critesion marinum (syn. Hordeum marinum)
Rosaceae
Fragaria × ananassa (strawberry) nat. 2
Fragaria vesca
Duchesnea indica
Prunus armeniaca (apricot) nat. 4
P. avium (sweet cherry) nat. 4
P. cerasus (sour cherry) nat. 4
P. domestica (European plum) cas.
P. persica (peach/nectarine) nat. 1
P. salicina (Japanese plum) nat. 1
Subtable 1 Continued

<table>
<thead>
<tr>
<th>Species</th>
<th>Nativity</th>
<th>Remarks</th>
</tr>
</thead>
</table>
| Lolium multiflorum and L. perenne are completely interfertile and
hybridize naturally (Hubbard 1968). Fertile Lolium × Festuca
hybrids also form readily and can backcross into the
parental species (Smith 1995). |
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hybridize naturally (Hubbard 1968). Fertile Lolium × Festuca
hybrids also form readily and can backcross into the
parental species (Smith 1995). |
| Like most species in the genus, P. dilatatum is an obligate
apomict, limiting the potential for interspecific gene flow.
Breeding efforts using sexual lines generally result in
the production of sterile hybrids (Burson & Bennet 1976;
Burson 1995). |
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apomict, limiting the potential for interspecific gene flow.
Breeding efforts using sexual lines generally result in
the production of sterile hybrids (Burson & Bennet 1976;
Burson 1995). |
| The diploid S. bicolor is interfertile with its wild subspecies,
and also with a number of other species in the genus, including
the tetraploid S. halapense (Doggett & Prasada Rao 1995). Arriola
& Ellstrand (1996) reported extensive spontaneous hybridization
between cultivated S. bicolor and experimentally planted
S. halapense. F₁ hybrids are fertile (Warwick & Black 1983). |
| Cultivated hexaploid T. aestivum is interfertile with other
hexaploid varieties including T. aestivum var. compactum
(Feldman et al. 1995). T. aestivum is also widely compatible
with species in the genus Aegilops (goat grasses), although
F₁ hybrids are typically sterile. No Aegilops species are present
in New Zealand. Genetic evidence exists of introgressive
hybridization between cultivated T. aestivum and sympatric
wild C. maritimum (Guadagnuolo et al. 2001a). |
| Cultivated strawberries and wild F. vesca can be crossed but
seed set is typically low. F₁ hybrids show low viability and
are usually apomictic (Li et al. 2000). Marta et al. (2004) reported partial asymmetric compatibility
between F. × ananassa and D. indica when the latter species is
used as the seed parent. F₁ hybrids showed strong viability
but their fertility was not examined. |
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in New Zealand. Genetic evidence exists of introgressive
hybridization between cultivated T. aestivum and sympatric
wild C. maritimum (Guadagnuolo et al. 2001a). |
| Interfertility among species within Prunus subgenera is high:
a feature extensively used for breeding purposes (Watkins 1995).
For many intersubgeneric combinations, although F₁ female
fertility is low, greater F₁ male fertility can facilitate backcrossing
to parental taxa (Watkins 1995). Crossing barriers within
subgenus Cerasus, introgressive hybridization with cultivated P. cerasus
also threatens native populations of P. fruticosa in Eastern
Europe (Wójcicki & Marhold 1993). |
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a feature extensively used for breeding purposes (Watkins 1995).
For many intersubgeneric combinations, although F₁ female
fertility is low, greater F₁ male fertility can facilitate backcrossing
to parental taxa (Watkins 1995). Crossing barriers within
subgenus Cerasus, introgressive hybridization with cultivated P. cerasus
also threatens native populations of P. fruticosa in Eastern
Europe (Wójcicki & Marhold 1993). |
Rubus fruticosus (blackberry)  nat.  1  Rubus is a large cosmopolitan genus (> 750 spp.) with complex taxonomy and variable reproductive mechanisms (Jennings 1995). Full fertility in crosses occurs mostly between closely related taxa (Steele & Hodgdon 1963; Kraft et al. 1995) but hybridization is sometimes possible between subgenera (Gustafsson 1942; Jennings 1995; Alice et al. 1997) especially when high polyploids are used (particularly as the maternal parent) (H. Hall, personal communication) Diploid raspberries can be crossed with tetraploid blackberries, but typically produce sterile, or very weakly fertile triploid hybrids (C. Finn, personal communication).

R. idaeus (raspberry)  nat.  1  interfertility between R. idaeus and both R. phoenicolasius and R. rosifolius. While the R. rosifolius hybrids are apparently weak and not able to survive to sexual maturity, R. phoenicolasius hybrids are viable and fertile. Many of the exotic blackberry species in New Zealand are tetraploids from the European R. fruticosus group: R. procerus, R. erythrops, R. cissburiensis, R. echinatus, R. lacinatus (cultivated in the USA), and one diploid species, R. ulmifolius. These species are all usually apomictic, thus preventing hybridization. However, some will occasionally reproduce sexually when grown under elevated temperatures (H. Hall, personal communication).

R. leptothyrsos  nat.  Natural interspecific hybridization has been reported between R. taxa from remote regions of origin (e.g. in Hawaii between R. phoenicosianus and R. rosinolius) R. rosinolius (North American) and R. hawaiianus (Hawai'i), Randell et al. 2004), suggesting a potential for hybridization between other native and exotic Rubus species in New Zealand. However, extensive reciprocal hand crosses between two native taxa (R. australis and R. squarrosus) and both cultivated blackberry species in New Zealand are tetraploids from the European R. fruticosus group: R. procerus, R. erythrops, R. cissburiensis, R. echinatus, R. lacinatus (cultivated in the USA), and one diploid species, R. ulmifolius. These species are all usually apomictic, thus preventing hybridization. However, some will occasionally reproduce sexually when grown under elevated temperatures (H. Hall, personal communication).

R. ostryifolius  nat.  Natural interspecific hybridization has been reported between R. taxa from remote regions of origin (e.g. in Hawaii between R. phoenicosianus and R. rosinolius) R. rosinolius (North American) and R. hawaiianus (Hawai'i), Randell et al. 2004), suggesting a potential for hybridization between other native and exotic Rubus species in New Zealand. However, extensive reciprocal hand crosses between two native taxa (R. australis and R. squarrosus) and both cultivated blackberry species in New Zealand are tetraploids from the European R. fruticosus group: R. procerus, R. erythrops, R. cissburiensis, R. echinatus, R. lacinatus (cultivated in the USA), and one diploid species, R. ulmifolius. These species are all usually apomictic, thus preventing hybridization. However, some will occasionally reproduce sexually when grown under elevated temperatures (H. Hall, personal communication).

R. parvus  ind.  Rubus taxa from remote regions of origin (e.g. in Hawaii between R. phoenicosianus and R. rosinolius) R. rosinolius (North American) and R. hawaiianus (Hawai'i), Randell et al. 2004), suggesting a potential for hybridization between other native and exotic Rubus species in New Zealand. However, extensive reciprocal hand crosses between two native taxa (R. australis and R. squarrosus) and both cultivated blackberry species in New Zealand are tetraploids from the European R. fruticosus group: R. procerus, R. erythrops, R. cissburiensis, R. echinatus, R. lacinatus (cultivated in the USA), and one diploid species, R. ulmifolius. These species are all usually apomictic, thus preventing hybridization. However, some will occasionally reproduce sexually when grown under elevated temperatures (H. Hall, personal communication).

R. polyanthemus  nat.  Natural interspecific hybridization has been reported between R. taxa from remote regions of origin (e.g. in Hawaii between R. phoenicosianus and R. rosinolius) R. rosinolius (North American) and R. hawaiianus (Hawai'i), Randell et al. 2004), suggesting a potential for hybridization between other native and exotic Rubus species in New Zealand. However, extensive reciprocal hand crosses between two native taxa (R. australis and R. squarrosus) and both cultivated blackberry species in New Zealand are tetraploids from the European R. fruticosus group: R. procerus, R. erythrops, R. cissburiensis, R. echinatus, R. lacinatus (cultivated in the USA), and one diploid species, R. ulmifolius. These species are all usually apomictic, thus preventing hybridization. However, some will occasionally reproduce sexually when grown under elevated temperatures (H. Hall, personal communication).

R. procerus  nat.  Natural interspecific hybridization has been reported between R. taxa from remote regions of origin (e.g. in Hawaii between R. phoenicosianus and R. rosinolius) R. rosinolius (North American) and R. hawaiianus (Hawai'i), Randell et al. 2004), suggesting a potential for hybridization between other native and exotic Rubus species in New Zealand. However, extensive reciprocal hand crosses between two native taxa (R. australis and R. squarrosus) and both cultivated blackberry species in New Zealand are tetraploids from the European R. fruticosus group: R. procerus, R. erythrops, R. cissburiensis, R. echinatus, R. lacinatus (cultivated in the USA), and one diploid species, R. ulmifolius. These species are all usually apomictic, thus preventing hybridization. However, some will occasionally reproduce sexually when grown under elevated temperatures (H. Hall, personal communication).

R. rugosus  nat.  Natural interspecific hybridization has been reported between R. taxa from remote regions of origin (e.g. in Hawaii between R. phoenicosianus and R. rosinolius) R. rosinolius (North American) and R. hawaiianus (Hawai'i), Randell et al. 2004), suggesting a potential for hybridization between other native and exotic Rubus species in New Zealand. However, extensive reciprocal hand crosses between two native taxa (R. australis and R. squarrosus) and both cultivated blackberry species in New Zealand are tetraploids from the European R. fruticosus group: R. procerus, R. erythrops, R. cissburiensis, R. echinatus, R. lacinatus (cultivated in the USA), and one diploid species, R. ulmifolius. These species are all usually apomictic, thus preventing hybridization. However, some will occasionally reproduce sexually when grown under elevated temperatures (H. Hall, personal communication).

R. schmidelioides  ind.  Natural interspecific hybridization has been reported between R. taxa from remote regions of origin (e.g. in Hawaii between R. phoenicosianus and R. rosinolius) R. rosinolius (North American) and R. hawaiianus (Hawai'i), Randell et al. 2004), suggesting a potential for hybridization between other native and exotic Rubus species in New Zealand. However, extensive reciprocal hand crosses between two native taxa (R. australis and R. squarrosus) and both cultivated blackberry species in New Zealand are tetraploids from the European R. fruticosus group: R. procerus, R. erythrops, R. cissburiensis, R. echinatus, R. lacinatus (cultivated in the USA), and one diploid species, R. ulmifolius. These species are all usually apomictic, thus preventing hybridization. However, some will occasionally reproduce sexually when grown under elevated temperatures (H. Hall, personal communication).

R. squarrosus  ind.  Natural interspecific hybridization has been reported between R. taxa from remote regions of origin (e.g. in Hawaii between R. phoenicosianus and R. rosinolius) R. rosinolius (North American) and R. hawaiianus (Hawai'i), Randell et al. 2004), suggesting a potential for hybridization between other native and exotic Rubus species in New Zealand. However, extensive reciprocal hand crosses between two native taxa (R. australis and R. squarrosus) and both cultivated blackberry species in New Zealand are tetraploids from the European R. fruticosus group: R. procerus, R. erythrops, R. cissburiensis, R. echinatus, R. lacinatus (cultivated in the USA), and one diploid species, R. ulmifolius. These species are all usually apomictic, thus preventing hybridization. However, some will occasionally reproduce sexually when grown under elevated temperatures (H. Hall, personal communication).

R. ulmifolius  nat.  Natural interspecific hybridization has been reported between R. taxa from remote regions of origin (e.g. in Hawaii between R. phoenicosianus and R. rosinolius) R. rosinolius (North American) and R. hawaiianus (Hawai'i), Randell et al. 2004), suggesting a potential for hybridization between other native and exotic Rubus species in New Zealand. However, extensive reciprocal hand crosses between two native taxa (R. australis and R. squarrosus) and both cultivated blackberry species in New Zealand are tetraploids from the European R. fruticosus group: R. procerus, R. erythrops, R. cissburiensis, R. echinatus, R. lacinatus (cultivated in the USA), and one diploid species, R. ulmifolius. These species are all usually apomictic, thus preventing hybridization. However, some will occasionally reproduce sexually when grown under elevated temperatures (H. Hall, personal communication).

R. vestitus  nat.  Natural interspecific hybridization has been reported between R. taxa from remote regions of origin (e.g. in Hawaii between R. phoenicosianus and R. rosinolius) R. rosinolius (North American) and R. hawaiianus (Hawai'i), Randell et al. 2004), suggesting a potential for hybridization between other native and exotic Rubus species in New Zealand. However, extensive reciprocal hand crosses between two native taxa (R. australis and R. squarrosus) and both cultivated blackberry species in New Zealand are tetraploids from the European R. fruticosus group: R. procerus, R. erythrops, R. cissburiensis, R. echinatus, R. lacinatus (cultivated in the USA), and one diploid species, R. ulmifolius. These species are all usually apomictic, thus preventing hybridization. However, some will occasionally reproduce sexually when grown under elevated temperatures (H. Hall, personal communication).

Rutaceae

Citrus × paradisi (= C. maxima × C. sinensis) (grapefruit)  cult.  1  In general Citrus species hybridize readily. Intergeneric hybridization between Citrus, Poncirus, Fortunella, Eremocitrus and Microcitrus species is also not uncommon — a feature that has been used extensively in crop breeding.

C. aurantium (sour orange)  cult.  1  In general Citrus species hybridize readily. Intergeneric hybridization between Citrus, Poncirus, Fortunella, Eremocitrus and Microcitrus species is also not uncommon — a feature that has been used extensively in crop breeding.
C. clementina (Clementine mandarin)  cult.  1  However, many cultivars (within Citrus) are male-sterile and some also produce seed apomictically (nucellar seed). As these factors will influence the potential for hybridization, gene-flow potential should be assessed on a cultivar-specific basis (Roose et al. 1995; A. Currie, pers. comm.). For example, satsuma mandarins and navel oranges (the two major New Zealand citrus crops) typically produce sterile pollen. However, hybrid fertility in Citrus is generally high (Agarwal 1987) and cultivars of other local citrus crops (including sweet orange, grapefruit, lemon, bitter orange and clementine mandarin) can (variously) cross with little difficulty (Agarwal 1987; Roose et al. 1995).

Salicaceae

Populus × canadensis (poplar)  nat.  1  Poplar cultivars grown in New Zealand are the products of hybridization variously between P. nigra, P. deltoides, P. trichocarpa, P. alba and P. tremula. These cultivars and the parental taxa hybridize freely with each other and other Populus species (Raybould & Gray 1993). Natural hybridization and introgression between cultivated and wild species is also commonly reported (e.g. Cagelli & Lefevre 1995; Fossati et al. 2003).

Solanaceae

Nicotiana tabacum (tobacco)  nat.  3  Significant genomic incompatibility exists among Nicotiana species, preventing natural hybridization among most combinations (Gerstel & Sisson 1995). F1 hybrids produced artificially between N. tabacum and N. rustica, N. alata and N. glauca are generally inviable or completely sterile (Nikova et al. 1999; Kuboyama & Takeda 2000; Trojak-Goluch & Berbec 2003). S. lycopersicon (tomato) can cross freely with its close relatives (species formerly in the genus Lycopersicon; Hogenboom 1979; Rick et al. 1987; Wolters et al. 1994). However, none of these taxa are naturalized in New Zealand. Studies attempting to introgress traits from other Solanum species present in New Zealand typically have used somatic hybridization, indicating the presence of strong barriers to hybridization. Hybridization in S. tuberosum (potato) is constrained to its close, tuber-forming, relatives (Conner 1994; Simmonds 1995). Crosses between potato and the wild species S. dulcamara and S. nigra failed to produce viable offspring, despite hundreds or thousands of pollinations.
†F1 hybrids cannot be produced through hand crossing (although hybridization may be possible with the use of embryo rescue, protoplast fusion or other artificial methods).

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Table 1 Continued

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<tr>
<th>Species</th>
<th>HP Category</th>
<th>Notes</th>
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<tr>
<td>S. dulcamara</td>
<td>nat.</td>
<td>(Conner 1994; Eijlander &amp; Stiekema 1994; McPartlan &amp; Dale 1994), although Eijlander &amp; Stiekema (1994) did manage to produce viable (though weak and sterile) hybrids between S. nigrum and S. tuberosum (with S. nigrum as female) through embryo rescue. Extensive crossing trials have been conducted between cultivated potato (as the pollen donor) and the following species: S. aviculare, S. brevidens, S. laciniatum, S. muricatum, S. nigrum, S. furcatum, S. chenopodioides, S. dulcamara, S. jasminoides, S. physalifolium, S. pseudocapsicum and S. melongena. All failed to produce any seed (Conner &amp; Zhang, unpublished). S. melongena (eggplant) can cross with several closely related species (e.g. Omidiji 1979). Interfertility has been demonstrated with S. torvum (McCammon &amp; Honma 1983). S. torvum is present in New Zealand but exists only casually (is not known to have self-maintaining populations in the wild). F1 hybrid fertility between these species is unclear. No information exists for hybridization in S. betaceum (tamarillo) or S. muricatum (pepino) with species naturalized in New Zealand. Hybrids have been made between S. muricatum and its close relatives S. caripense, S. basendopogon, and S. cochoae (Stiefkens et al. 1999; Prohens et al. 2002). Bohs (1991) and Pringle &amp; Murray (1991) crossed S. betaceum with nine species. Hybrids were produced in low numbers in a few of these crosses, but none of these species are present in New Zealand. However, S. betaceum is distantly related from all other Solanum species present in New Zealand (Olmstead &amp; Palmer 1997).</td>
</tr>
<tr>
<td>S. jasminoides</td>
<td>nat.</td>
<td></td>
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<tr>
<td>S. laciniatum</td>
<td>ind.</td>
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<tr>
<td>S. linearum</td>
<td>nat.</td>
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<tr>
<td>S. marginatum</td>
<td>nat.</td>
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<td>S. mauritianum</td>
<td>nat.</td>
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<td>S. nigrum</td>
<td>nat.</td>
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</tr>
<tr>
<td>S. physalifolium</td>
<td>nat.</td>
<td></td>
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<tr>
<td>S. pseudocapsicum</td>
<td>nat.</td>
<td></td>
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<tr>
<td>S. rantonneti</td>
<td>nat.</td>
<td></td>
</tr>
<tr>
<td>S. rostratum</td>
<td>nat.</td>
<td></td>
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<tr>
<td>S. villosum</td>
<td>nat.</td>
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*Hand- or open-pollination results in the production of viable, fertile F1 hybrids and/or, introgressive hybridization between the species occurs in nature.

†F1 hybrids cannot be produced through hand crossing (although hybridization may be possible with the use of embryo rescue, protoplast fusion or other artificial methods).

In most cases additional information was needed to determine the likelihood of introgression beyond F1 hybrid formation. Where F1 hybrids are known to be sterile, transgene ‘escape’ would be confined to vegetative propagation of F1 hybrids.

**HP category 3:** Twenty-five (25) crops (20%) were found to be entirely reproductively isolated from all their wild relatives in New Zealand (e.g. Phaseolus lunatus, Solanum tuberosum, Vicia cracca).

**HP category 4:** For 20 crops (16%), information on compatibility relationships with wild relatives was not available (e.g. Asparagus officinalis and Oxalis tuberosa).

Little information on experimental hybridization was found for 5 of the 37 indigenous species related to crops. Indigenous celery (Apium prostratum) is highly interfertile with cultivated celery (Apium graveolens) (Daiwara et al. 1994; C. Quiros, personal communication). Potato (Solanum tuberosum) and the indigenous Solanum aviculare and Solanum laciniatum are reproductively incompatible (Conner & Zhang, unpublished). Both cultivated blackberries (Rubus fruticosus) and raspberries (Rubus idaeus) are incompatible with the indigenous taxa Rubus australis and Rubus squarrosus (H. Hall, unpublished). For the remaining 32 indigenous species that are congeneric with crops, no information was available.

**Discussion**

This review has established that 54% of New Zealand’s major food, fodder and forestry crops are reproductively compatible with related indigenous or naturalized exotic species. However, reproductive compatibility as demonstrated under experimental conditions merely indicates a potential for spontaneous hybridization, the actual likelihood of which is contingent upon the influence of various prepollination barriers. For example, species capable of hybridizing have to be in close enough proximity to permit the transfer of pollen. Field surveys are therefore required to determine the range overlap between crops and their compatible wild relatives (e.g. Heenan et al. 2004 for Brassica in New Zealand).

Even where species do coexist, other prepollination barriers may act to reduce opportunities for natural hybridization (Rieseberg & Carney 1998). These include nonsynchronous flowering, reliance on different pollinators, and the influence of breeding systems (Grant 1994; Levin...
2000). Such barriers are also likely to vary with respect to local conditions and in ways that may be difficult to predict (Harlan 1982; Ladizinsky 1998; Ellisstrå 2003). Furthermore, because pollen competition alone can restrict hybridization between potentially interfertile taxa (Arnold et al. 1993), the results of manual-pollination trials may exaggerate the potential for spontaneous hybridization.

Consequently, the actual likelihood of spontaneous hybridization occurring between compatible crop–wild combinations may be very small in many cases. However, the fact that hybridization between these species can be achieved (often with remarkable ease) in glasshouse settings argues that such crops should be treated differently to those for which hybridization with a wild relative is known to be impossible.

Our survey for New Zealand showed that in all but one case, compatible crop–wild combinations involved naturalized exotic rather than indigenous species. This result is unsurprising given the predominance of naturalized exotic species in the vascular flora (53%) and the fact that New Zealand is not a centre of crop domestication. Spontaneous hybridization between indigenous and exotic species is a phenomenon yet to be widely studied but some evidence for non-crop genera in New Zealand has been reported, e.g. Acacia (Rosaceae) (Webb et al. 1988), Carpobrotus (Aizoaceae) (Chinnock 1972), and Epilobium (Onagraceae) (Raven & Raven 1976). Whilst these examples do not involve crops, they indicate the potential for crop–wild hybridization involving indigenous species in other species-rich cosmopolitan genera containing cultivated crops, e.g. Festuca and Agrostis (Poaceae), Rubus (Rosaceae), Linum (Linaceae) and Oxalis (Oxalidaceae). Although hybridization in some of these groups may be difficult to detect morphologically, molecular markers can now be readily developed, and have been applied to examine introgression between indigenous and exotic taxa (including crops) elsewhere (e.g. Triest et al. 1999; Guadagnuolo et al. 2001b; Randell et al. 2004). The lack of information on compatibility between exotic crops and indigenous species in New Zealand highlights an important gap likely to exist for many other countries.

By contrast, this review uncovered a considerable body of information on compatibility relationships between crops and exotic naturalized species in New Zealand. Most of these crops are extensively cultivated outside New Zealand (Smartt & Simmonds 1995) and many of their wild relatives are widely distributed throughout temperate and subtropical countries (Holm et al. 1979; Randall 2002). For example, of the 199 naturalized crop relatives assessed in this study (84%) are also native to or have become naturalized in Australia (Sindel 1997; Shepherd et al. 2001), 82% in the USA (USDA, NRCS 2004), 76% in the UK (Stace 1997), 54% in California (Jepson Online Interchange 2005) and 49% in Ecuador and Peru (Missouri Botanical Gardens 2002-). Not only do these examples emphasize the homogenizing influence of human activity on global plant distributions, they also suggest that our findings may be relevant to other regions.

Due to differences in scope and emphasis, our results are only partially comparable with those of other surveys (i.e. de Vries et al. 1992; Nurminiem & Rogali 1993; Raybould & Gray 1993; Ammann et al. 1996). Previous surveys (viz. the Netherlands, Norway, and Switzerland) have focused largely on local records of spontaneous hybridization and have included very detailed information on crop and wild relative distributions and abundances to evaluate the potential ecological impacts of transgene escape at a regional level. Furthermore, we explicitly limit our analysis to the potential for interspecific hybridization rather than intraspecific gene flow. In contrast, previous reviews have often (although not consistently) included subspecies, varieties or recognized feral races in their analysis of the potential for crop–wild transgene escape. Lastly, most surveys have examined relatively few crop species: 46 crops in the Netherlands, 33 crops in the UK, and 22 crops in Switzerland compared to 186 crops in Norway and 123 crops in New Zealand.

Another important contrast is that previous surveys have not generally reported positive evidence of known incompatibility. By working explicitly with the full range of locally present wild relatives, and by including confirmed reports of reproductive incompatibility (HP category 3), we have identified crops that cannot hybridize with any relatives present in the local flora. Our approach also attempts to highlight where no information is available (HP category 4) and this in itself is useful for risk assessment.

A limitation common to all risk assessment surveys of this kind is that they present data in a highly summarized and interpreted form and are difficult to extend or update directly. We are currently developing the New Zealand Plant BioSafety Database to capture hybridization information in a more comprehensive, extensible, and transparent format.

This work has reviewed evidence useful for assessing the potential for hybridization between some of the worlds’ major temperate crops and their widely naturalized close relatives. The majority of these crops have been genetically modified, highlighting the urgent need for information to assist regulatory agencies to make decisions and develop containment strategies. Regional surveys of reproductive compatibility between crops and the indigenous and naturalized flora represent an important component of GM crop risk assessment, particularly in countries lacking detailed information about local spontaneous hybridization.

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