

INVITED REVIEW

Transgene escape: what potential for crop–wild hybridization?

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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 propagules 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

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& 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 Herbarium 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*, *Vitis*, 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, Bourdôt *et al.* 1999; Poaceae, Edgar & Connor 2000).

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 F_1 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.

Inviabile F_1 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 F_1 hybrids of some

Gossypium species resulting from negative interactions between parental alleles at a number of loci (Stephens 1950). Other reported F_1 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, F_1 hybrids may grow normally but be unable to reproduce.

Low F_1 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 F_1 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, F_1 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), *Mimulus* (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 F_1 generation, hybrid inviability or sterility is often not expressed until the production of F_2 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 & Bezar (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.¹

Information on the degree of reproductive compatibility between the crops and their wild relatives was obtained

¹ Species excluded from the crop list because they have no wild relatives. Naturalized crops: *Beta vulgaris* (beet), *Chamaecytisus palmensis* (tagasaste), *Cichorium intybus* (chicory), *Citrullus lanatus* (watermelon), *Colocasia esculenta* (taro), *Coronilla varia* (crown vetch), *Cydonia oblonga* (quince), *Dactylis glomerata* (cocksfoot), *Humulus lupulus* (hops), *Olea europaea* (olive), *Malus × domestica* (apple), *Pastinaca sativa* (parsnip), *Persea americana* (avocado), *Pisum sativum* (pea), *Pseudotsuga menziesii* (Douglas fir), *Pyrus communis* (pear), *Rheum rhabarbarum* (rhubarb), *Secale cereale* (rye), *Sequoia sempervirens* (coastal redwood), *Vitis vinifera* (grape). Casual crops: *Capsicum annuum* (capsicum), *Lens culinaris* (lentil), *Vaccinium corymbosum* (blueberry), *Zea mays* (corn). Cultivated only: *Feijoa sellowiana* (feijoa).

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*).

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 F_1 hybrids are known to be either (i) entirely sterile or (ii) F_1 viability and fertility are unknown. Here, transgene 'escape' may be limited to vegetative reproduction in sterile F_1 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.

Actinidiaceae

<i>Actinidia arguta</i> (kiwifruit)	cult.	1	Open pollination between <i>A. deliciosa</i> and <i>A. arguta</i>
<i>A. deliciosa</i> (kiwifruit)	nat.	1	(in either direction) produces viable and fertile F_1 hybrids (Fairchild 1927; Pringle 1986; M. McNeilage, personal communication).

Apiaceae

<i>Daucus carota</i> (carrot)	nat.	4	The compatibility of <i>D. carota</i> and the New Zealand native <i>D. glochidiatus</i> is unknown. However, the only reported interspecific cross involving carrot is <i>D. carota</i> × <i>D. capillifolius</i> (McCollum 1975), and a recent phylogenetic study places <i>D. glochidiatus</i> distant from <i>D. carota</i> relative to <i>D. capillifolius</i> (Vivek & Simon 1999).
<i>Daucus glochidiatus</i>	ind.		
<i>Apium graveolens</i> (celery)	nat.	1	<i>A. graveolens</i> × <i>A. nodiflorum</i> freely produce fertile hybrids (Pink & Innes 1984). <i>A. prostratum</i> and <i>A. graveolens</i> produce viable F_1 hybrids through hand pollination (reciprocally). F_1 hybrids have low pollen fertility (10%) but can be backcrossed easily to parental species (Daiwara <i>et al.</i> 1994; D'Antonio <i>et al.</i> 2001; C. Quiros, personal communication).
<i>Apium nodiflorum</i>	nat.		
<i>A. prostratum</i>	ind.		
<i>Petroselinum crispum</i> (parsley)	nat.	1	<i>A. graveolens</i> hybridizes with wild and cultivated parsley. The F_1 hybrids are fertile and produce viable F_2 hybrids (Honma & Lacy 1980).

Asteraceae

<i>Lactuca sativa</i> (lettuce)	nat.	1	<i>L. sativa</i> × <i>L. saligna</i> F_1 hybrids can be produced but have low fertility (Zohary 1991). <i>L. sativa</i> is fully interfertile with <i>L. serriola</i> (Lundqvist 1960; Kesseli <i>et al.</i> 1991; Zohary 1991). <i>L. virosa</i> is incompatible with <i>L. sativa</i> . Crosses generally lead to F_1 embryo abortion and/or F_1 sterility (Whittaker 1969; Eenink <i>et al.</i> 1982; Matsumoto 1991). However, a few BC_1 seeds were produced by large-scale pollination of F_1 plants (Maisonneuve <i>et al.</i> 1995).
<i>Lactuca saligna</i>	nat.		
<i>L. serriola</i>	nat.		
<i>L. virosa</i>	nat.		
<i>Helianthus annuus</i> (sunflower)	nat.	1	<i>H. annuus</i> hybridizes spontaneously with its annual diploid relatives in Section <i>Annui</i> (Rogers <i>et al.</i> 1982; Rieseberg & Wendel 1993; Heiser 1995). Hand-crossing trials also indicate reasonable interfertility between <i>H. annuus</i> and the perennial <i>H. salicifolius</i> (Atlagic <i>et al.</i> 1995), the cross producing F_1 hybrids with high pollen viability (64%). Although <i>H. annuus</i> × <i>H. tuberosus</i> (section <i>Divaricati</i>) F_1 hybrids have been produced with difficulty (e.g. Fambrini <i>et al.</i> 1996), they are typically sterile or have low fertility (Heiser 1995).
<i>Helianthus</i> × <i>laetiflorus</i> (= <i>H. rigidus</i> × <i>H. tuberosus</i>)	nat.		
<i>H. salicifolius</i>	nat.		
<i>H. tuberosus</i>	nat.		

Table 1 Continued

Brassicaceae (tribe Brassiceae)		
<i>Brassica juncea</i> (brown mustard)	nat.	1 Most <i>Brassica</i> species present in New Zealand, including wild relatives, are able to hybridize, although sometimes only with extreme difficulty (Bourdôt <i>et al.</i> 1999; Warwick <i>et al.</i> 2000; Salisbury 2002; Stewart 2002). High levels of interspecific reproductive compatibility are found between <i>B. rapa</i> and <i>B. napus</i> (U 1935; Wahiduzzaman 1987; Lu <i>et al.</i> 2001), <i>B. napus</i> and <i>B. juncea</i> (Wahiduzzaman 1987; Prakash & Chopra 1988; Frello <i>et al.</i> 1995). <i>B. rapa</i> also crosses easily with a variety of <i>Brassica</i> species (Ramanujam & Srinivasachar 1943; Choudhary & Joshi 2001). <i>B. oleracea</i> produces hybrids with difficulty with other <i>Brassica</i> species, including both crop and wild forms (e.g. Narain & Prakash 1972; Chiang <i>et al.</i> 1977; Akbar 1989).
<i>B. napus</i> (rape, canola, oilseed rape, fodder rape, swede)	nat.	
<i>B. oleracea</i> (cabbage, broccoli, kale, etc.)	nat.	
<i>B. rapa</i> (turnip, canola, oilseed rape)	nat.	
<i>Brassica fruticulosa</i>	nat.	Intergeneric hybridization is possible between crop brassicas and species in other genera within the tribe Brassiceae. In particular, hybridization is possible with <i>Diplotaxis muralis</i> , <i>D. tenuifolia</i> , <i>Eruca vesicaria</i> (syn. <i>E. sativa</i>), <i>Hirschfeldia incana</i> , <i>Raphanus raphanistrum</i> , <i>R. sativus</i> , <i>Sinapis alba</i> and <i>S. arvensis</i> , and some <i>Brassica</i> species, particularly <i>B. napus</i> and <i>B. rapa</i> (Bourdôt <i>et al.</i> 1999; Salisbury 2002). However, rates of hybridization in these crosses are typically very low. Native New Zealand members of Brassicaceae are more distantly related to crop brassicas (none are within the Brassiceae), and are therefore very unlikely to hybridize with crop species.
<i>B. nigra</i>	nat.	
<i>B. oxyrrhina</i>	nat.	
<i>B. tournefortii</i>	nat.	
<i>Diplotaxis muralis</i>	nat.	
<i>D. tenuifolia</i>	nat.	
<i>Hirschfeldia incana</i>	nat.	
<i>Raphanus sativus</i> (radish)	nat.	
<i>Raphanus raphanistrum</i>	nat.	
<i>Sinapis alba</i> (white mustard)	nat.	
<i>Sinapis arvensis</i>	nat.	
Convolvulaceae		
<i>Ipomoea batatas</i> (kumara)	nat.	4 <i>I. trifida</i> and <i>I. × leucantha</i> (neither present in New Zealand) are the only species known to be interfertile with the polyploid cultivated <i>I. batatas</i> (Diaz <i>et al.</i> 1996). Crossability between <i>I. batatas</i> and other <i>Ipomoea</i> species present in New Zealand has not been examined, but should be considered unlikely given the lack of crossability between <i>I. batatas</i> and most other closely related species.
<i>Ipomoea alba</i>	nat.	
<i>I. cairica</i>	ind.	
<i>I. indica</i>	nat.	
<i>I. pes-caprae</i>	ind.	
<i>I. purpurea</i>	nat.	
Cucurbitaceae		
<i>Cucumis melo</i> (rock, honeydew & musk melons)	cult.	3 Generally, attempts to hybridize the three <i>Cucumis</i> species present in New Zealand have failed; both Deakin <i>et al.</i> (1971) and Kho <i>et al.</i> (1980) attempted all six combinations between species present here. Only the crosses <i>C. sativus</i> × <i>C. melo</i> (Deakin <i>et al.</i> 1971) and <i>C. sativus</i> × <i>C. myriocarpus</i> produced fruits (Deakin <i>et al.</i> 1971; Kho <i>et al.</i> 1980). In other combinations, pollen failed to germinate (Kho <i>et al.</i> 1980), indicating strong prezygotic barriers. Hybrids between <i>C. sativus</i> (female) and <i>C. melo</i> (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 <i>C. sativus</i> were successful, but backcrosses to <i>C. melo</i> failed. Although <i>C. sativus</i> and <i>C. melo</i> can hybridize, neither species is naturalized in New Zealand.
<i>C. sativus</i> (cucumber)	cult.	
<i>Cucumis myriocarpus</i>	nat.	

Table 1 Continued

<i>Cucurbita maxima</i> (pumpkin)	nat.	4	Esquinas-Alcazar & Gulick (1983) reviewed crossability relationships between species of <i>Cucurbita</i> , including all present in New Zealand. All combinations produced seed except <i>C. ficifolia</i> × <i>C. moschata</i> . However, only the combination <i>C. moschata</i> × <i>C. pepo</i> produced fertile F ₁ plants. Fertile F ₁ plants have also been produced by Shiffriss & Cohen (1974) and Paris <i>et al.</i> (1985), and used to introgress traits into <i>C. moschata</i> . Barriers may depend on genotype, as several combinations reported to be compatible by Esquinas-Alcazar & Gulick (1983) could not be produced by Šiško <i>et al.</i> (2003), despite the use of embryo rescue. Furthermore, Whitaker & Bemis (1964) note 'there is no evidence for spontaneous hybridization among the cultivated <i>Cucurbita</i> [including <i>C. ficifolia</i>], although they have been grown side by side in fields and gardens for many generations'.
<i>C. moschata</i> (squash)	cult.	1	
<i>C. pepo</i> (squash, courgette)	nat.	1	
<i>Cucurbita ficifolia</i>	nat.		
Fabaceae			
<i>Lotus corniculatus</i> (birdsfoot trefoil)	nat.	3	Strong genic reproductive barriers prevail among <i>Lotus</i> species, and hybridization is generally impossible without assisted breeding (e.g. embryo rescue) (Caradus & Williams 1995). F ₁ hybrids are usually sterile (Somaroo & Grant 1972; Lautour <i>et al.</i> 1978; Yang <i>et al.</i> 1990).
<i>L. pedunculatus</i> (big trefoil)	nat.	3	
<i>L. tenuis</i> (narrow leaved trefoil)	nat.	3	
<i>Lotus angustissimus</i>	nat.		
<i>L. suaveolens</i>	nat.		
<i>Lupinus polyphyllus</i> (lupin)	nat.	3	Few <i>Lupinus</i> species are reproductively compatible. Embryo-rescue techniques have been used to produce F ₁ hybrids between some combinations (e.g. Przyborowski & Packa 1997), although these are typically sterile (Elliot <i>et al.</i> 1974). No taxa present in New Zealand are known to hybridize.
<i>Lupinus angustifolius</i>	nat.		
<i>L. arboreus</i>	nat.		
<i>L. luteus</i>	nat.		
<i>Medicago sativa</i> (lucerne)	nat.	2	<i>M. sativa</i> hybridizes spontaneously in Europe with <i>M. falcata</i> , and can be hand crossed with <i>M. glomerata</i> (de Vries <i>et al.</i> 1992; Langer 1995). F ₁ 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 <i>Medicago</i> hybrids (Nenz <i>et al.</i> 1996).
<i>Medicago arabica</i>	nat.		
<i>M. arborea</i>	nat.		
<i>M. glomerata</i>	nat.		
<i>M. lupulina</i>	nat.		
<i>M. minima</i>	nat.		
<i>M. nigra</i>	nat.		
<i>Phaseolus coccineus</i> (runner bean)	nat.	1	<i>P. coccineus</i> and <i>P. vulgaris</i> are completely interfertile (Debouck & Smartt 1995). However, <i>P. lunatus</i> is strongly reproductively isolated from both of these species (Alvarez <i>et al.</i> 1981).
<i>P. lunatus</i> (lima bean)	nat.	3	
<i>P. vulgaris</i> (French bean)	nat.	1	Interspecific hybridization in <i>Trifolium</i> is uncommon (Evans 1962) and breeding efforts rely largely on artificial methods (Quesenberry & Taylor 1976). However, some species combinations are compatible.
<i>Trifolium ambiguum</i> (Caucasian clover)	nat.	2	
<i>T. fragiferum</i> (strawberry clover)	nat.	4	
<i>T. hybridum</i> (aslike clover)	nat.	2	
<i>T. medium</i> (zigzag clover)	nat.	1	Caradus & Williams 1995). Hybridization between these species has been achieved through hand pollination, although F ₁ hybrid fertilities are unreported. In the UK, spontaneous hybridization between <i>T. pratense</i> and <i>T. medium</i> has been reported (Stace 1975).
<i>T. pratense</i> (red clover)	nat.	1	
<i>T. repens</i> (white clover)	nat.	2	
<i>T. resupinatum</i> (reversed clover)	nat.	4	
<i>T. subterraneum</i> (subterranean clover)	nat.	3	
<i>Trifolium angustifolium</i>	nat.		
<i>T. arvense</i>	nat.		

Table 1 Continued

<i>T. aureum</i>	nat.	
<i>T. campestre</i>	nat.	
<i>T. cernuum</i>	nat.	
<i>T. dubium</i>	nat.	
<i>T. glomeratum</i>	nat.	
<i>T. hirtum</i>	nat.	
<i>T. incarnatum</i>	nat.	
<i>T. micranthum</i>	nat.	
<i>T. ochroleucon</i>	nat.	
<i>T. ornithopodioides</i>	nat.	
<i>T. retusum</i>	nat.	
<i>T. scabrum</i>	nat.	
<i>T. striatum</i>	nat.	
<i>T. suffocatum</i>	nat.	
<i>T. tomentosum</i>	nat.	
<hr/>		
<i>Vicia cracca</i> (tufted vetch)	nat.	3 Strong crossing barriers in the genus <i>Vicia</i> result from
<i>V. disperma</i> (French tare)	nat.	3 chromosomal instability in F ₁ zygotes (Ladizinsky 1981). No
<i>V. faba</i> (faba bean)	nat.	3 known wild species of <i>Vicia</i> are crossable with the cultivated
<i>V. hirsuta</i> (hairy vetch)	nat.	3 faba bean. Embryo rescue and other methods are used to
<i>V. lathyroides</i> (spring vetch)	nat.	3 produce hybrid lines (Roupakias 1986; Muehlbauer <i>et al.</i> 1994).
<i>V. lutea</i> (yellow vetch)	nat.	3
<i>V. sativa</i> (common vetch)	nat.	3
<i>V. tetrasperma</i> (smooth tare)	nat.	3
<i>V. villosa</i> (fodder vetch)	nat.	3
<hr/>		
Grossulariaceae		
<i>Ribes nigrum</i> (black currant)	nat.	2 <i>R. nigrum</i> and <i>R. rubrum</i> (in separate subgenera) are
<i>R. rubrum</i> (red currant)	nat.	3 reproductively isolated (Keep 1995). Artificial F ₁ hybrids
		between <i>R. nigrum</i> and <i>R. uva-crispa</i> have been produced,
<i>Ribes odouratum</i>	nat.	although their fertility is unclear (reported in Nurminiemi
<i>R. sanguineum</i>	nat.	& Rognli 1993, p. 46). No cases of spontaneous hybridization
<i>R. uva-crispa</i>	nat.	between <i>Ribes</i> species have been recorded in the UK
		(Raybould & Gray 1993) or New Zealand.
<hr/>		
Liliaceae		
<i>Allium cepa</i> (onion)	nat.	1 <i>A. cepa</i> (2x = 16) and <i>A. fistulosum</i> L. (2x = 16) are closely
<i>A. fistulosum</i> (bunching onions, scallions)	cult.	1 related species (both within section <i>Cepa</i>) that can be readily
<i>A. porrum</i> (leek)	nat.	2 hybridized. Interspecific hybrids have been made for the
<i>A. sativum</i> (garlic)	nat.	3 purpose of transferring favourable characters from
		<i>A. fistulosum</i> into <i>A. cepa</i> (Peffley & Hou 2000). Backcrossing
		is difficult, but has been achieved (Cryder <i>et al.</i> 1991; Bark <i>et al.</i>
		1994). However, little genetic exchange appears to have taken
		place (Cryder <i>et al.</i> 1991). <i>A. cepa</i> is separated from most other
		<i>Allium</i> species by strong crossing barriers (Ulloa <i>et al.</i> 1995;
		van Raamsdonk <i>et al.</i> 2000, 2003) with hybrids typically sterile.
<i>Allium ampeloprasum</i>	nat.	<i>A. porrum</i> (leek) is cross-compatible with its close relatives
<i>A. neapolitanum</i>	nat.	<i>A. ampeloprasum</i> (present in New Zealand), <i>A. atroviolaceum</i> ,
		<i>A. bourgeui</i> and <i>A. commutatum</i> (Kik <i>et al.</i> 1997). No information
		was given about the fertility of the hybrids.
<i>A. roseum</i>	nat.	Hybrids have been obtained with <i>A. cepa</i> and <i>A. ampeloprasum</i>
		at very low frequencies using embryo rescue (Ohsumi
		<i>et al.</i> 1993; Yanagino <i>et al.</i> 2003).
<i>A. triquetrum</i>	nat.	Cultivated <i>A. sativum</i> is male sterile and propagated
		vegetatively (Havey 1995).
<i>A. vineale</i>	nat.	

Table 1 Continued

<i>Asparagus officinalis</i> (asparagus)	nat.	4 Extensive hand crosses conducted between <i>A. densiflorus</i> and the following species, <i>A. officinalis</i> , <i>A. acutifolius</i> , <i>A. albus</i> , <i>A. aphyllus</i> , <i>A. arborescens</i> , <i>A. falcatus</i> , <i>A. larinus</i> , <i>A. oligoclonos</i> , <i>A. setaceus</i> and <i>A. virgatus</i> , 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 <i>et al.</i> 1983). Hybridization between cultivated <i>A. officinalis</i> and the wild Asian species <i>A. schobioides</i> has been documented (Ochiai <i>et al.</i> 2002), although hybrid fertility was unreported. Compatibility between species present in New Zealand is unclear.
<i>Asparagus asparagoides</i>	nat.	
<i>A. scandens</i>	nat.	
<i>A. setaceus</i>	nat.	
Linaceae		
<i>Linum usitatissimum</i> (linseed, flax)	nat.	1 <i>L. usitatissimum</i> and <i>L. bienne</i> can freely produce fertile F ₁ hybrids (Green 1983). However, <i>L. usitatissimum</i> × <i>L. catharticum</i> are strongly isolated (Green 1983). Seetharam (1972) examined crossing relationships between wild <i>Linum</i> taxa (not present in New Zealand) and cultivated <i>L. usitatissimum</i> . 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 <i>L. monogynum</i> is unknown.
<i>Linum bienne</i>	nat.	
<i>L. catharticum</i>	nat.	
<i>L. monogynum</i>	ind.	
<i>L. trigynum</i>	nat.	
Myrtaceae		
<i>Eucalyptus delegatensis</i> (alpine ash)	nat.	4 Crossing barriers in the genus <i>Eucalyptus</i> are weak, particularly within subgenera (Griffin <i>et al.</i> 1988). Cases of 1 natural hybridization and introgression are common and 1 widespread (Pryor 1976; Griffin <i>et al.</i> 1988). Interfertile 1 crop-wild species combinations in New Zealand include: 1 <i>E. globulus</i> × <i>E. ovata</i> (McAulay 1938) <i>E. grandis</i> × <i>E. nitens</i> (Shelbourne <i>et al.</i> 1999) <i>E. gunnii</i> × <i>E. ovata</i> (Potts <i>et al.</i> 1987) 1 <i>E. nitens</i> × <i>E. globulus</i> (Tibbits 1988) <i>E. nitens</i> × <i>E. gunnii</i> (Tibbits 1988) <i>E. nitens</i> × <i>E. viminalis</i> (Tibbits 1988) <i>E. obliqua</i> × <i>E. pulchella</i> (Potts & Reid 1983) <i>E. regnans</i> × <i>E. obliqua</i> (Ashton 1984) <i>E. saligna</i> × <i>E. botryoides</i> (Passioura & Ash 1993) <i>E. tereticornis</i> × <i>E. robusta</i> (Griffin <i>et al.</i> 1988) Given the high level of interspecific reproductive compatibility in the genus, other interfertile combinations are likely to exist locally.
<i>E. fastigata</i> (brown barrel)	nat.	
<i>E. globulus</i> (Tasmanian blue gum)	nat.	
<i>E. grandis</i> (swamp gum)	nat.	
<i>E. nitens</i> (shining gum)	nat.	
<i>E. obliqua</i> (messmate)	nat.	
<i>E. regnans</i> (mountain ash)	nat.	
<i>E. saligna</i> (Sydney blue gum)	nat.	
<i>E. tereticornis</i> (forest red gum)	nat.	
<i>Eucalyptus botryoides</i>	nat.	
<i>E. cinerea</i>	nat.	
<i>E. gunnii</i>	nat.	
<i>E. ovata</i>	nat.	
<i>E. pulchella</i>	nat.	
<i>E. pilularis</i>	nat.	
<i>E. robusta</i>	nat.	
<i>E. tenuiramis</i>	nat.	
<i>E. viminalis</i>	nat.	
Oxalideaceae		
<i>Oxalis tuberosa</i> (yam)	nat.	4 No information was found on interspecific hybridization in <i>Oxalis</i> .
<i>Oxalis articulata</i>	nat.	
<i>O. corniculata</i>	nat.	
<i>O. debilis</i>	nat.	
<i>O. exilis</i>	ind.	
<i>O. hirta</i>	nat.	
<i>O. incarnata</i>	nat.	
<i>O. latifolia</i>	nat.	
<i>O. magellanica</i>	ind.	
<i>O. perennans</i>	nat.	
<i>O. pes-caprae</i>	nat.	
<i>O. purpurea</i>	nat.	
<i>O. rubens</i>	ind.	
<i>O. thompsoniae</i>	nat.	
<i>O. vallicola</i>	nat.	
<i>O. versicolor</i>	nat.	

Table 1 Continued

Passifloraceae		
<i>Passiflora edulis</i> (passionfruit)	nat.	2 The F ₁ combinations <i>P. edulis</i> × <i>P. caerulea</i> (Dixit & Torne 1978) and <i>P. edulis</i> × <i>P. incarnata</i> (Beal 1972) have been produced through hand pollination, although levels of hybrid viability and fertility are unclear. However, Soares-Scott <i>et al.</i> (2003) reports that aneuploidy typically results in F ₁ sterility in <i>Passiflora</i> . Most breeding efforts rely on embryo rescue and protoplast fusion (e.g. Barbosa & Vieira 1997), suggesting that natural hybridization is unlikely.
<i>Passiflora caerulea</i>	nat.	
<i>P. mixta</i>	nat.	
<i>P. mollissima</i>	nat.	
<i>P. pinnatistipula</i>	nat.	
<i>P. tetrandra</i>	ind.	Compatibility between cultivated species and the native <i>P. tetrandra</i> is not known but considered unlikely, as the native species belongs to a separate subgenus (Tetrapathaea).
Pinaceae		
<i>Picea abies</i> (Norway spruce)	nat.	2 Although spontaneous interspecific hybridization is frequent among <i>Picea</i> spp. (e.g. Gordon 1976; Rajora & Dancik 2000; Silim <i>et al.</i> 2001), it has not been reported between <i>P. abies</i> and <i>P. sitchensis</i> . Cross-pollination trials indicate that <i>P. abies</i> and <i>P. sitchensis</i> are reproductively compatible, although levels of hybrid fertility were not reported (Kleinschmidt 1979).
<i>Picea sitchensis</i> (Sitka spruce)	nat.	
<i>Pinus attenuata</i> (knobcone pine)	nat.	1 F ₁ hybrids can be produced through cross-pollination of <i>P. radiata</i> with <i>P. attenuata</i> (Dungey <i>et al.</i> 2003). F ₁ 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 <i>P. radiata</i> and <i>P. muricata</i> , <i>P. oocarpa</i> and <i>P. tecumumanii</i> is also possible but apparently difficult. Hybrid fertility for these combinations is unreported (Dungey <i>et al.</i> 2003).
<i>P. contorta</i> (shore pine)	nat.	
<i>P. muricata</i> (muricata pine)	nat.	
<i>P. nigra</i> (Corsican pine)	nat.	
<i>P. patula</i> (Mexican pine)	nat.	1 Spontaneous hybridization involving introgression occurs between <i>P. contorta</i> and <i>P. banksiana</i> where the two species are sympatric (Ye <i>et al.</i> 2002).
<i>P. pinaster</i> (maritime pine)	nat.	4 Extensive hand pollinations (Kormut'ak 1984) indicate a high level of compatibility between <i>P. sylvestris</i> and <i>P. mugo</i> . Natural hybridization and introgression also occur between these species (Christensen & Dar 1999). Crossing trials indicate that <i>P. sylvestris</i> can cross-breed freely with <i>P. patula</i> (Mirov 1967).
<i>P. ponderosa</i> (ponderosa pine)	nat.	
<i>P. radiata</i> (Monterey pine)	nat.	1
<i>P. strobus</i> (strobilus pine)	nat.	4 Combinations that are known to be incompatible include <i>P. contorta</i> × <i>P. sylvestris</i> ; <i>P. nigra</i> × <i>P. sylvestris</i> ; <i>P. nigra</i> × <i>P. banksiana</i> . Cross-pollination between these species apparently fails due to the inhibition of pollen germination and by degeneration of the internal contents of the ovule (Kormut'ak 1984). However, once formed, <i>Pinus</i> F ₁ hybrids are generally fertile (Williams <i>et al.</i> 2002).
<i>P. taeda</i> (loblolly pine)	nat.	
<i>Pinus banksiana</i>	nat.	
<i>P. halepensis</i>	nat.	
<i>P. mugo</i>	nat.	
<i>P. sylvestris</i>	nat.	
<i>P. taeda</i>	nat.	
Poaceae		
<i>Agrostis capillaris</i> (common bentgrass)	nat.	1 Most Northern Hemisphere <i>Agrostis</i> species are entirely interfertile and hybridize promiscuously (Smith 1995).
<i>A. castellana</i> (highland bentgrass)	nat.	1 Belanger <i>et al.</i> (2003) report high levels of interfertility (freely crossing through open pollination to produce highly fertile hybrids) between <i>A. stolonifera</i> and the following species: <i>A. capillaris</i> , <i>A. castellana</i> , <i>A. gigantea</i> and <i>A. canina</i> . Extensive natural introgression between <i>A. capillaris</i> and <i>A. stolonifera</i> has also been demonstrated using genetic markers (Lefebvre & Meerts 1989).
<i>Agrostis dyeri</i>	ind.	
<i>A. gigantea</i>	nat.	Reproductive compatibility between exotic and native <i>Agrostis</i> species is unknown.
<i>A. imbecilla</i>	ind.	
<i>A. magellanica</i>	ind.	

Table 1 Continued

<i>A. muelleriana</i>	ind.	
<i>A. muscosa</i>	ind.	
<i>A. oresbia</i>	ind.	
<i>A. pallescens</i>	ind.	
<i>A. personata</i>	ind.	
<i>A. petrici</i>	ind.	
<i>A. subulata</i>	ind.	
<i>A. stolonifera</i>	nat.	
<i>Avena sativa</i> (oats)	nat.	1 Cultivated hexaploid <i>A. sativa</i> is fully reproductively compatible with other hexaploid species including <i>A. fatua</i> and <i>A. sterilis</i> , but not with the tetraploid <i>A. barbata</i> or the diploid <i>A. strigosa</i> (Thomas 1995). Various studies have confirmed crop-wild introgression between <i>A. sativa</i> and its wild relatives (e.g. Derick 1933; Burdon <i>et al.</i> 1992).
<i>Avena barbata</i>	nat.	
<i>A. fatua</i>	nat.	
<i>A. sterilis</i>	nat.	
<i>A. strigosa</i>	nat.	
<i>Bromus inermis</i> (brome grass)	nat.	1 Compatibility relationships in the large genus <i>Bromus</i> are
<i>B. sitchensis</i> (upland brome)	nat.	4 relatively unknown. Cross-pollination of <i>B. inermis</i> with
<i>B. stamineus</i> (grazing brome)	nat.	4 <i>B. erectus</i> readily produces fertile F ₁ hybrids (Armstrong
<i>B. willdenowii</i> (prairie grass)	nat.	4 1990; Smith 1995). <i>B. inermis</i> can be also be hybridized with
<i>Bromus arenarius</i>	nat.	<i>B. arvensis</i> , <i>B. benekenii</i> , <i>B. pumpellianus</i> (Armstrong 1973, 1977,
<i>B. brevis</i>	nat.	1981), although none of these species are naturalized in
<i>B. commutatus</i>	nat.	New Zealand. Hybridization between <i>B. inermis</i> and <i>B. mollis</i>
<i>B. diandrus</i>	nat.	has been reported to be unsuccessful (Knowles 1944).
<i>B. erectus</i>	nat.	Hybridization is possible among many of the naturalized
<i>B. hordeaceus</i>	nat.	species; <i>B. commutatus</i> and <i>B. racemosus</i> are interfertile, and
<i>B. japonicus</i>	nat.	may hybridize in nature (Smith 1973). <i>B. mollis</i> can hybridize
<i>B. lithobius</i>	nat.	with at least <i>B. arenarius</i> , <i>B. commutatus</i> , <i>B. hordeaceus</i> ,
<i>B. madritensis</i>	nat.	<i>B. madritensis</i> , <i>B. racemosus</i> and <i>B. rubens</i> , as well as with
<i>B. mollis</i>	nat.	other species not present in New Zealand (Knowles 1944).
<i>B. racemosus</i>	nat.	Relationships with the other three crop species are
<i>B. sterilis</i>	nat.	completely unknown so further interfertile combinations
<i>B. tectorum</i>	nat.	may exist in New Zealand.
<i>B. valdivianus</i>	nat.	
<i>Festuca arundinacea</i> (tall fescue)	nat.	1 Several cultivated species of <i>Festuca</i> (including the three
<i>F. ovina</i> (sheep fescue)	nat.	1 present in New Zealand) are interfertile (Smith 1995), and
<i>F. rubra</i> (fine fescue)	nat.	1 can also hybridize with some <i>Lolium</i> and <i>Vulpia</i> spp., including
<i>Festuca actae</i>	ind.	<i>V. bromoides</i> (Stace & Cotton 1974; Barker & Stace 1982).
<i>F. contracta</i>	ind.	Reproductive compatibility between exotic and native
<i>F. coxii</i>	ind.	<i>Festuca</i> species in New Zealand is unstudied.
<i>F. deflexa</i>	ind.	
<i>F. filiformis</i>	nat.	
<i>F. luciarum</i>	ind.	
<i>F. madida</i>	ind.	
<i>F. matthewsii</i>	ind.	
<i>F. multinodis</i>	ind.	
<i>F. novae-zelandiae</i>	ind.	
<i>F. ultramafica</i>	ind.	
<i>Vulpia myuros</i>	nat.	
<i>V. bromoides</i>	nat.	
<i>Holcus lanatus</i> (Yorkshire fog)	nat.	1 <i>H. lanatus</i> is reproductively compatible with <i>H. mollis</i> and
<i>H. mollis</i>	nat.	the two species are known to hybridize spontaneously
		(Stace 1975).
<i>Hordeum vulgare</i> (barley)	nat.	1 Cultivated barley hybridizes spontaneously in nature with its
<i>Critesion marinum</i> (syn. <i>Hordeum marinum</i>)	nat.	wild subspecies (including <i>H. vulgare</i> ssp. <i>distichon</i>) and with
		<i>H. spontaneum</i> (Harlan 1995). <i>H. vulgare</i> is not known to
		be reproductively compatible with any other species in the
		genus (Harlan 1995). <i>Critesion marinum</i> hybridizes freely with
		cultivated wheat <i>T. aestivum</i> (Guadagnuolo <i>et al.</i> 2001b).

Table 1 Continued

<i>Lolium multiflorum</i> (rye grass)	nat.	1	<i>L. multiflorum</i> and <i>L. perenne</i> are completely interfertile and hybridize naturally (Hubbard 1968). Fertile <i>Lolium</i> × <i>Festuca</i> hybrids also form readily and can backcross into the parental species (Smith 1995).
<i>L. perenne</i> (perennial rye grass)	nat.	1	
<i>Lolium remotum</i>	nat.		
<i>L. rigidum</i>	nat.		
<i>L. temulentum</i>	nat.		
<i>Paspalum dilatatum</i> (dallisgrass)	nat.	3	Like most species in the genus, <i>P. dilatatum</i> 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).
<i>Paspalum conjugatum</i>	nat.		
<i>P. distichum</i>	nat.		
<i>P. orbiculare</i>	nat.		
<i>P. paniculatum</i>	nat.		
<i>P. pubiflorum</i>	nat.		
<i>P. urvillei</i>	nat.		
<i>P. vaginatum</i>	nat.		
<i>Phalaris aquatica</i> (phalaris)	nat.	1	<i>P. aquatica</i> and <i>P. arundinacea</i> can be crossed readily and F ₁ hybrids are viable and fertile (Smith 1995). Lowe & Bowdler (1981) report using a <i>P. aquatica</i> × <i>P. canariensis</i> hybrid in an experiment, but no information is given about the production of this hybrid. No reports were found of hybridization between crop <i>Phalaris</i> species and the other three naturalized species.
<i>P. arundinacea</i> (canary grass)	nat.	1	
<i>Phalaris angusta</i>	nat.		
<i>P. canariensis</i>	nat.		
<i>P. minor</i>	nat.		
<i>P. paradoxa</i>	nat.		
<i>Sorghum bicolor</i> (sorghum)	nat.	1	The diploid <i>S. bicolor</i> is interfertile with its wild subspecies, and also with a number of other species in the genus, including the tetraploid <i>S. halapense</i> (Doggett & Prasada Rao 1995). Arriola & Ellstrand (1996) reported extensive spontaneous hybridization between cultivated <i>S. bicolor</i> and experimentally planted <i>S. halapense</i> . F ₁ hybrids are fertile (Warwick & Black 1983).
<i>Sorghum halepense</i>	nat.		
<i>Triticum aestivum</i> (wheat)	nat.	1	Cultivated hexaploid <i>T. aestivum</i> is interfertile with other hexaploid varieties including <i>T. aestivum</i> var. <i>compactum</i> (Feldman <i>et al.</i> 1995). <i>T. aestivum</i> is also widely compatible with species in the genus <i>Aegilops</i> (goat grasses), although F ₁ hybrids are typically sterile. No <i>Aegilops</i> species are present in New Zealand. Genetic evidence exists of introgressive hybridization between cultivated <i>T. aestivum</i> and sympatric wild <i>C. marinum</i> (Guadagnuolo <i>et al.</i> 2001a).
<i>Critesion marinum</i> (syn. <i>Hordeum marinum</i>)	nat.		
Rosaceae			
<i>Fragaria</i> × <i>ananassa</i> (strawberry)	nat.	2	Cultivated strawberries and wild <i>F. vesca</i> can be crossed but seed set is typically low. F ₁ hybrids show low viability and are usually apomictic (Li <i>et al.</i> 2000). Marta <i>et al.</i> (2004) reported partial asymmetric compatibility between <i>F. × ananassa</i> and <i>D. indica</i> when the latter species is used as the seed parent. F ₁ hybrids showed strong viability but their fertility was not examined.
<i>Fragaria vesca</i>	nat.		
<i>Duchesnea indica</i>	nat.		
<i>Prunus armeniaca</i> (apricot)	nat.	4	Interfertility among species within <i>Prunus</i> subgenera is high: a feature extensively used for breeding purposes (Watkins 1995). For many intersubgeneric combinations, although F ₁ female fertility is low, greater F ₁ male fertility can facilitate backcrossing to parental taxa (Watkins 1995). Crossing barriers within subgenus <i>Prunophora</i> (plums, apricots) are notably weak, particularly within sect. <i>Euprunus</i> . Members of this section in New Zealand include <i>P. domestica</i> , <i>P. cerasifera</i> , <i>P. salicina</i> and <i>P. spinosa</i> . Cultivated <i>P. domestica</i> and wild <i>P. spinosa</i> are known to hybridize spontaneously in the UK (Stace 1975). In subgenus <i>Cerasus</i> , introgressive hybridization with cultivated <i>P. cerasus</i> also threatens native populations of <i>P. fruticosa</i> in Eastern Europe (Wójcicki & Marhold 1993).
<i>P. avium</i> (sweet cherry)	nat.	4	
<i>P. cerasus</i> (sour cherry)	nat.	4	
<i>P. domestica</i> (European plum)	cas.	1	
<i>P. persica</i> (peach/nectarine)	nat.	1	
<i>P. salicina</i> (Japanese plum)	nat.	1	

Table 1 Continued

<i>Prunus campanulata</i>	nat.	<i>P. armeniaca</i> × <i>P. salicina</i> is the most commonly cultivated hybrid (plumcot). This F ₁ hybrid is generally fertile but in some instances may be pollen sterile. Backcrosses to either plum or apricot result in more fertile hybrids (M. Malone, personal communication).
<i>P. cerasifera</i>	nat.	
<i>P. laurocerasus</i>	nat.	
<i>P. lusitanica</i>	nat.	
<i>P. mahaleb</i>	nat.	
<i>P. serrulata</i>	nat.	
<i>P. spinosa</i>	nat.	
<i>Rubus fruticosus</i> (blackberry)	nat.	1 <i>Rubus</i> 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 <i>et al.</i> 1995) but hybridization is sometimes possible between subgenera (Gustafsson 1942; Jennings 1995; Alice <i>et al.</i> 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) <i>R. flagellaris</i> (locally naturalized) can hybridize easily with tetraploid races of both raspberry and blackberry (Finn <i>et al.</i> 2002). In both cases F ₁ fertility is variable but generally high (Finn <i>et al.</i> 2002). <i>R. argutus</i> can also hybridize with cultivated blackberry to produce viable and fertile F ₁ hybrids (Finn <i>et al.</i> 2002; H. Swartz personal communication). Finn <i>et al.</i> (2002) report interfertility between <i>R. idaeus</i> and both <i>R. phoenicolasius</i> and <i>R. rosifolius</i> . While the <i>R. rosifolius</i> hybrids are apparently weak and not able to survive to sexual maturity, <i>R. phoenicolasius</i> hybrids are viable and fertile. Many of the exotic blackberry species in New Zealand are tetraploids from the European <i>R. fruticosus</i> group: <i>R. procerus</i> , <i>R. erythrops</i> , <i>R. cissburiensis</i> , <i>R. echinatus</i> , <i>R. lacinatus</i> (cultivated in the USA), and one diploid species, <i>R. ulmifolius</i> . These species are all usually apomictic, thus preventing hybridization. However, some will occasionally reproduce sexually when grown under elevated temperatures (H. Hall, personal communication). Natural interspecific hybridization has been reported between <i>Rubus</i> taxa from remote regions of origin (e.g. in Hawaii between <i>R. rosifolius</i> (North American) and <i>R. hawaiiensis</i> (Hawaii), Randell <i>et al.</i> 2004), suggesting a potential for hybridization between other native and exotic <i>Rubus</i> species in New Zealand. However, extensive reciprocal hand crosses between two native taxa (<i>R. australis</i> and <i>R. squarrosus</i>) and both cultivated raspberry (<i>R. idaeus</i>) and blackberry (<i>R. fruticosus</i>) all failed to produce seed (H. Hall, unpublished).
<i>R. idaeus</i> (raspberry)	nat.	
<i>Rubus australis</i>	ind.	
<i>R. argutus</i>	nat.	
<i>R. cardiophyllus</i>	nat.	
<i>R. cissburiensis</i>	nat.	
<i>R. cissoides</i>	ind.	
<i>R. echinatus</i>	nat.	
<i>R. erythrops</i>	nat.	
<i>R. flagellaris</i>	nat.	
<i>R. laciniatus</i>	nat.	
<i>R. leptothyrsos</i>	nat.	
<i>R. mollior</i>	nat.	
<i>R. mucronulatus</i>	nat.	
<i>R. nemoralis</i>	nat.	
<i>R. ostryifolius</i>	nat.	
<i>R. parvus</i>	ind.	
<i>R. phoenicolasius</i>	nat.	
<i>R. polyanthemus</i>	nat.	
<i>R. procerus</i>	nat.	
<i>R. rosifolius</i>	nat.	
<i>R. rugosus</i>	nat.	
<i>R. schmidelioides</i>	ind.	
<i>R. squarrosus</i>	ind.	
<i>R. tuberculatus</i>	nat.	
<i>R. ulmifolius</i>	nat.	
<i>R. vestitus</i>	nat.	
Rutaceae		
<i>Citrus</i> × <i>paradisi</i> (= <i>C. maxima</i> × <i>C. sinensis</i>) (grapefruit)	cult.	1 In general <i>Citrus</i> species hybridize readily. Intergeneric hybridization between <i>Citrus</i> , <i>Poncirus</i> , <i>Fortunella</i> , <i>Eremocitrus</i> and <i>Microcitrus</i> species is also not uncommon — a feature that has been used extensively in crop breeding.
<i>C. aurantium</i> (sour orange)	cult.	

Table 1 Continued

<i>C. clementina</i> (Clementine mandarin)	cult.	1	However, many cultivars (within <i>Citrus</i>) 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 <i>et al.</i> 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 <i>Citrus</i> 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 <i>et al.</i> 1995).
<i>C. limon</i> (lemon)	cas.	1	
<i>C. sinensis</i> (orange, sweet, navel)	nat.	1	
<i>C. unshiu</i> (satsuma mandarin)	cult.	3	
<i>Poncirus trifoliata</i> (bitter orange)	cult.	1	
Salicaceae			
<i>Populus</i> × <i>canadensis</i> (poplar)	nat.	1	Poplar cultivars grown in New Zealand are the products of hybridization variously between <i>P. nigra</i> , <i>P. deltoides</i> , <i>P. trichocarpa</i> , <i>P. alba</i> and <i>P. tremula</i> . These cultivars and the parental taxa hybridize freely with each other and other <i>Populus</i> species (Raybould & Gray 1993). Natural hybridization and introgression between cultivated and wild species is also commonly reported (e.g. Cagelli & Lefevre 1995; Fossati <i>et al.</i> 2003).
<i>P.</i> × <i>canescens</i> (= <i>P. alba</i> × <i>P. tremula</i>)	nat.	1	
<i>P.</i> × <i>gileadensis</i>	nat.	1	
<i>P. alba</i> (white poplar)	nat.	1	
<i>P. deltoides</i> (eastern cottonwood)	nat.	1	
<i>P. nigra</i> (black, Lombardy poplar)	nat.	1	
<i>P. tremula</i> (European aspen)	nat.	1	
<i>Populus trichocarpa</i>	nat.		
<i>P. yunnanensis</i>	nat.		
Salix spp. (willows)			
<i>Salix</i> × <i>calodendron</i>	nat.	1	Crossing barriers in the genus <i>Salix</i> are typically weak. Hybridization is frequent in nature and has been exploited to develop new cultivars (Faulkner 1995). Molecular and morphological characters have been used to study numerous cases of introgression between wild populations, including <i>S. alba</i> and <i>S. fragilis</i> (Beismann <i>et al.</i> 1997; Triest <i>et al.</i> 1999), <i>S. cinerea</i> and <i>S. phylicifolia</i> (Meikle 1992), and <i>S. sericea</i> and <i>S. eriocephala</i> (Hardig <i>et al.</i> 2000).
<i>S.</i> × <i>chrysocoma</i>	nat.		
<i>S.</i> × <i>reichardtii</i>	nat.		
<i>S.</i> × <i>rubens</i>	nat.		
<i>S.</i> × <i>sepulcralis</i>	nat.		
<i>S. alba</i>	nat.		
<i>S. babylonica</i>	nat.		
<i>S. cinerea</i>	nat.		
<i>S. daphnoides</i>	nat.		
<i>S. elaeagnos</i>	nat.		
<i>S. fragilis</i>	nat.		
<i>S. glaucophylloides</i>	nat.		
<i>S. gracilistyla</i>	nat.		
<i>S. matsudana</i>	nat.		
<i>S. purpurea</i>	nat.		
<i>S. viminalis</i>	nat.		
Solanaceae			
<i>Nicotiana tabacum</i> (tobacco)	nat.	3	Significant genomic incompatibility exists among <i>Nicotiana</i> species, preventing natural hybridization among most combinations (Gerstel & Sisson 1995). F ₁ hybrids produced artificially between <i>N. tabacum</i> and <i>N. rustica</i> , <i>N. alata</i> and <i>N. glauca</i> are generally inviable or completely sterile (Nikova <i>et al.</i> 1999; Kuboyama & Takeda 2000; Trojak-Goluch & Berbec 2003).
<i>Nicotiana alata</i>	nat.		
<i>N. glauca</i>	nat.		
<i>N. rustica</i>	nat.		
<i>N. sylvestris</i>	nat.		
Solanum			
<i>Solanum betaceum</i> (tamarillo)	nat.	3	<i>S. lycopersicon</i> (tomato) can cross freely with its close relatives (species formerly in the genus <i>Lycopersicon</i> ; Hogenboom 1979; Rick <i>et al.</i> 1987; Wolters <i>et al.</i> 1994). However, none of these taxa are naturalized in New Zealand. Studies attempting to introgress traits from other <i>Solanum</i> species present in New Zealand typically have used somatic hybridization, indicating the presence of strong barriers to hybridization. Hybridization in <i>S. tuberosum</i> (potato) is constrained to its close, tuber-forming, relatives (Conner 1994; Simmonds 1995). Crosses between potato and the wild species <i>S. dulcamara</i> and <i>S. nigra</i> failed to produce viable offspring, despite hundreds or thousands of pollinations
<i>S. lycopersicum</i> (tomato)	nat.	3	
<i>S. muricatum</i> (pepino)	nat.	3	
<i>S. tuberosum</i> (potato)	nat.	2	
<i>S. melongena</i> (eggplant)	cult.		
<i>Solanum americanum</i>	ind.		
<i>S. aviculare</i>	ind.		
<i>S. carolinense</i>	nat.		
<i>S. chenopodioides</i>	nat.		
<i>S. crispum</i>	nat.		
<i>S. diflorum</i>	nat.		

Table 1 Continued

<i>S. dulcamara</i>	nat.	(Conner 1994; Eijlander & Stiekema 1994; McPartlan & Dale 1994), although Eijlander & Stiekema (1994) did manage to produce viable (though weak and sterile) hybrids between <i>S. nigrum</i> and <i>S. tuberosum</i> (with <i>S. nigrum</i> as female) through embryo rescue. Extensive crossing trials have been conducted between cultivated potato (as the pollen donor) and the following species: <i>S. aviculare</i> , <i>S. brevidens</i> , <i>S. laciniatum</i> , <i>S. muricatum</i> , <i>S. nigrum</i> , <i>S. furcatum</i> , <i>S. chenopodioides</i> , <i>S. dulcamara</i> , <i>S. jasminoides</i> , <i>S. physalifolium</i> , <i>S. pseudocapsicum</i> and <i>S. melongena</i> . All failed to produce any seed (Conner & Zhang, unpublished). <i>S. melongena</i> (eggplant) can cross with several closely related species (e.g. Omidiji 1979). Interfertility has been demonstrated with <i>S. torvum</i> (McCammon & Honma 1983). <i>S. torvum</i> is present in New Zealand but exists only casually (is not known to have self-maintaining populations in the wild). F ₁ hybrid fertility between these species is unclear. No information exists for hybridization in <i>S. betaceum</i> (tamarillo) or <i>S. muricatum</i> (pepino) with species naturalized in New Zealand. Hybrids have been made between <i>S. muricatum</i> and its close relatives <i>S. caripense</i> , <i>S. basendopogon</i> , and <i>S. chochoae</i> (Stiefkens <i>et al.</i> 1999; Prohens <i>et al.</i> 2002). Bohs (1991) and Pringle & Murray (1991) crossed <i>S. betaceum</i> 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, <i>S. betaceum</i> is distantly related from all other <i>Solanum</i> species present in New Zealand (Olmstead & Palmer 1997).
<i>S. jasminoides</i>	nat.	
<i>S. laciniatum</i>	ind.	
<i>S. linnaeanum</i>	nat.	
<i>S. marginatum</i>	nat.	
<i>S. mauritianum</i>	nat.	
<i>S. nigrum</i>	nat.	
<i>S. physalifolium</i>	nat.	
<i>S. pseudocapsicum</i>	nat.	
<i>S. rantonnei</i>	nat.	
<i>S. rostratum</i>	nat.	
<i>S. villosum</i>	nat.	

*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; Ellstrand 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. *Acaena* (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; Nurminiemi & Rognli 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 world's 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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