Chapter 3
Oat

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Abstract Oat (*Avena sativa* L.) productivity is affected by crown rust (*Puccinia coronata* f. sp. *avenae*) and stem rust (*Puccinia graminis* f. sp. *avenae*) worldwide. Control of these diseases has been through the use of host resistance genes, but frequent changes in pathogen virulence provide a continuing threat to oat production. Wild oat species have been a major source of diversity for the improvement of cultivated oat. Many rust resistance genes, as well as genes providing resistance to other major oat diseases, have been found in wild oat species, landraces as well as in cultivated species and have been utilised in plant breeding. However, the transfer of resistance from wild diploid and tetraploid species to cultivated hexaploid oat is difficult because their chromosomes do not pair readily. Nevertheless, many improved oat cultivars possess alien-derived rust resistance genes and occupy considerable acreage in the major oat-producing regions of the world. This chapter reviews the major developments and their impacts on oat breeding, specifically through alien gene transfer from wild and related species.

Keywords Alien gene transfer • *Avena* • Disease resistance • Rust • Oat • Wild species

3.1 Introduction

Oat (*Avena sativa* L.) is an ancient cereal crop which has been cultivated at least since the time of Theophrastus (371–286 BC) and grown worldwide (Martens 1985). The genus *Avena* consists of diploid ($2n=2x=14$), tetraploid ($2n=4x=28$) and

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hexaploid ($2n=6x=42$) species, with a basic chromosome number of seven ($x=7$) (Thomas 1992). The hexaploid *Avena* genome is comprised of three subgenomes (A, C and D), which represents modifications of a common homologous chromosome series (Rajhathy and Thomas 1974). Diploid and tetraploid species are classified into A, B, C and D genome groups, with further subdivisions based on karyotypes and chromosome pairing in interspecific hybrids. The cultivated white hexaploid oat (*A. sativa* L.) spread from the Near East to Europe in the late Bronze Age, while the cultivated red oat (*A. byzantina* C. Koch) was the main form in North Africa and in Spain. Both species were introduced into North America in the sixteenth century (Coffman 1977).

One of the major constraints to oat production worldwide is plant disease (Harder and Haber 1992). Among several diseases that attack oat, crown rust and stem rust are the most damaging, affecting both yield and quality of oat grain and forage. Up to 35 % yield loss due to severe stem rust infection has been found in Canada (Martens 1978), while up to 50 % loss due to crown rust infection has been estimated in the United States (Simons 1985). Both rust diseases have primarily been controlled through the use of host resistance genes (McCallum et al. 2007). Many accessions of wild hexaploid and diploid oat have been found to be sources of desirable rust resistance genes for incorporation into cultivated oat. The identification of wild accessions with effective resistant genes is an important step in the process of developing locally adapted cultivars with improved crown rust and stem rust resistance. The genetic characterisation of rust resistance genes in *Avena* species has been carried out by researchers since the 1920s.

Parker (1920) was one of the earliest workers to investigate crown rust resistance in oat. He recognised the importance of determining the inheritance of rust resistance to plant breeding, and that linkage of crown rust resistance with undesirable traits could be a hindrance to crop improvement. Rust resistance types have been categorised broadly into specific (major, vertical, seedling, etc.) or general (minor, horizontal, partial or adult plant resistance (APR)). Specific resistance, usually governed by single genes, is expressed at all growth stages, and, while relatively easy to identify and incorporate into elite germplasm, has been frequently overcome by rust races with matching virulence. Partial resistance, usually conferred polygenically, does not prevent infection completely but reduces pustule size and numbers of spores produced and extends the latency period of pustule development (Portyanko et al. 2005). Partial resistance may be more durable than specific resistance because there is less selection pressure on the pathogen and therefore slows the evolution of virulence (Simons 1972). However, partial resistance is more difficult to use in plant breeding since several genes need to be incorporated, and is evaluated at the adult plant stage. Thus, specific resistance genes are desirable in plant breeding. While most of the hexaploid oat germplasm has been exploited in the search for new rust resistance genes, this chapter reviews the utilisation of alien genes to enhance rust resistance in oat.

3.2 Crown Rust

Crown rust, caused by the fungus *Puccinia coronata* f. sp. *avenae*, is a widespread and damaging disease of oat. Oat crown rust infection is favoured by periods of high leaf moisture (rainfall or dew) and moderate temperatures (21–25 °C) during the growing season (Carson 2011). Crown rust occurs commonly on wild *A. fatua* in the United States and Canada (Leonard 2003; Chong et al. 2011) and on *A. sterilis* and other wild oat species in the Mediterranean regions of southern Europe, Northern Africa and the Middle East (Zillinsky and Murphy 1967). Losses in both yield and grain quality commonly result from epidemics of crown rust (Simons 1985), with individual oat fields suffering total crop failure. Crown rust generally attacks the leaves and interferes with transport of photosynthesised sugars from leaves to the developing grain, which causes shrivelled grain with reduced quality. Badly rusted plants develop stunted root systems and have poor drought tolerance. Control of crown rust disease can be attained using fungicides, but disease resistance is the most effective, cost-efficient and environment friendly control method.

Breeding for resistance to crown rust began in 1919 (Simons 1985), and to date over 100 alleles have been described (Table 3.1). Crown rust resistance genes have

Table 3.1 Oat crown rust resistance genes

Gene	Original source	*Avena* species	Reference
Pc1	Red Rustproof	*A. byzantina*	Dietz and Murphy (1930)
Pc2	Victoria	*A. byzantina*	Murphy et al. (1937)
Pc2b	Anthony/Bond/Boone		Finkner (1954)
Pc3	Bond	*A. byzantina*	Hayes et al. (1939)
Pc3c	Ukraine	*A. sativa*	Weetman (1942)
Pc4	Bond	*A. byzantina*	Hayes et al. (1939)
Pc4c	Ukraine	*A. sativa*	Weetman (1942)
Pc5	Landhafer	*A. byzantina*	Litzenberger (1949)
Pc6	Santa Fe	*A. byzantina*	Litzenberger (1949)
Pc6c	Ukraine	*A. sativa*	Finkner (1954)
Pc6d	Trispernia	*A. sativa*	Finkner (1954)
Pc7	Santa Fe	*A. byzantina*	Osler and Hayes (1953)
Pc8	Santa Fe	*A. byzantina*	Osler and Hayes (1953)
Pc 9	Ukraine	*A. sativa*	Finkner (1954)
Pc9c	Santa Fe	*A. byzantina*	Simons and Murphy (1954)
Pc10	Klein 69B	*A. byzantina*	Finkner (1954)
Pc11	Victoria	*A. byzantina*	Welsh et al. (1954)
Pc12	Victoria	*A. byzantina*	Welsh et al. (1954)
Pc13	Clinton	*A. sativa*	Finkner et al.(1955)
Pc14	Ascencao	*A. byzantina*	Simons (1956)
Pc15	Saia	*A. strigosa*	Murphy et al. (1958)

(continued)

Table 3.1 (continued)

Gene	Original source	*Avena* species	Reference
Pc16	Saia	*A. strigosa*	Murphy et al. (1958)
Pc17	Saia	*A. strigosa*	Murphy et al. (1958)
Pc18	Glabrota	*A. glabrota*	Simons et al. (1959)
Pc19	CI 3815	*A. strigosa*	Simons et al. (1959)
Pc20	CI 7233	*A. abyssinica*	Simons et al. (1959)
Pc21	Santa Fe	*A. byzantina*	Chang (1959)
Pc22	Ceirch du Bach	*A. sativa*	McKenzie (1961)
Pc23	C.D 3820	*A. strigosa*	Dyck and Zillinsky (1962)
Pc24	Garry	*A. sativa*	Upadhyaya and Baker (1960)
Pc25	Garry	*A. sativa*	Upadhyaya and Baker (1960)
Pc26	Garry	*A. sativa*	Upadhyaya and Baker (1960)
Pc27	Garry	*A. sativa*	Upadhyaya and Baker (1960)
Pc28	Garry	*A. sativa*	Upadhyaya and Baker (1960)
Pc29	Glabrota	*A. glabrota*	Marshall and Myers (1961)
Pc30	CI 3815	*A. strigosa*	Marshall and Myers (1961)
Pc31	CI 4746	*A. strigosa*	Marshall and Myers (1961)
Pc32	CeirchLlwyd	*A. strigosa*	Marshall and Myers (1961)
Pc33	CeirchLlwyd	*A. strigosa*	Marshall and Myers (1961)
Pc34	D-60	*A. sterilis*	McKenzie and Fleischmann (1964)
Pc35	D-137	*A. sterilis*	McKenzie and Fleischmann (1964)
Pc36	CI 8081	*A. sterilis*	Simons (1965)
Pc37	CD 7994	*A. strigosa*	Dyck (1966)
Pc38	CW 491-4	*A. sterilis*	Fleischmann and McKenzie (1968)
Pc39	F-366	*A. sterilis*	Fleischmann and McKenzie (1968)
Pc40	F-83	*A. sterilis*	Fleischmann and McKenzie (1968)
Pc41	F-83	*A. sterilis*	Fleischmann and McKenzie (1968)
Pc42	F-83	*A. sterilis*	Fleischmann and McKenzie (1968)
Pc43	F-83	*A. sterilis*	Fleischmann and McKenzie (1968)
Pc44	Kyto	*A. sativa*	Martens et al. (1968)
Pc45	F-169	*A. sterilis*	Fleischmann et al. (1971a)
Pc46	F-290	*A. sterilis*	Fleischmann et al. (1971a)
Pc47	CI 8081A	*A. sterilis*	Fleischmann et al. (1971b)
Pc48	F-158	*A. sterilis*	Fleischmann et al. (1971b)
Pc49	F-158	*A. sterilis*	Fleischmann et al. (1971b)
Pc50	CW 486	*A. sterilis*	Fleischmann et al. (1971b)
Pc51	Wahl No.8	*A. sterilis*	Simons et al. (1978)
Pc52	Wahl No.2	*A. sterilis*	Simons et al. (1978)
Pc53	6-112-1-15	*A. sterilis*	Simons et al. (1978)
Pc54	CAV 1832	*A. sterilis*	Simons et al. (1978)
Pc55	CAV 4963	*A. sterilis*	Kiehn et al. (1976)
Pc56	CAV 1964	*A. sterilis*	Kiehn et al. (1976)
Pc57	CI 8295	*A. sterilis*	Simons et al. (1978)
Pc58	PI 295919	*A. sterilis*	Simons et al. (1978)
Pc59	PI 296244	*A. sterilis*	Simons et al. (1978)
Pc60	PI 287211	*A. sterilis*	Simons et al. (1978)

(continued)

Table 3.1 (continued)

Gene	Original source	*Avena* species	Reference
Pc61	PI 287211	*A. sterilis*	Simons et al. (1978)
Pc62	CAV 4274	*A. sterilis*	Harder et al. (1980)
Pc63	CAV 4540	*A. sterilis*	Harder et al. (1980)
Pc64	CAV 4248	*A. sterilis*	Wong et al. (1983)
Pc65	CAV 4248	*A. sterilis*	Wong et al. (1983)
Pc66	CAV 4248	*A. sterilis*	Wong et al. (1983)
Pc67	CAV 4656	*A. sterilis*	Wong et al. (1983)
Pc68	CAV 4904	*A. sterilis*	Wong et al. (1983)
Pc69	CAV 1387	*A. sterilis*	Harder et al. (1984)
Pc70	PI 318282	*A. sterilis*	CDL (2010)
Pc71	IA B437	*A. sterilis*	CDL (2010)
Pc72	PI 298129	*A. sterilis*	CDL (2010)
Pc73	PI 309560	*A. sterilis*	CDL (2010)
Pc74	PI 309560	*A. sterilis*	CDL (2010)
Pc75	IB 2402	*A. sterilis*	Fox et al. (1997)
Pc76	IB 2465	*A. sterilis*	Fox et al. (1997)
Pc77	IB 2433	*A. sterilis*	Fox (1989)
Pc78	IB 1454	*A. trichophylla*	Fox (1989)
Pc79	IB 1454	*A. trichophylla*	Fox et al. (1997)
Pc80	IB 3432	*A. sterilis*	Fox (1989)
Pc81	CI 3815	*A. strigosa*	Yu and Wise (2000)
Pc82	CI 3815	*A. strigosa*	Yu and Wise (2000)
Pc83	CI 3815	*A. strigosa*	Yu and Wise (2000)
Pc84	CI 3815	*A. strigosa*	Yu and Wise (2000)
Pc85	CI 3815	*A. strigosa*	Yu and Wise (2000)
Pc86	CI 3815	*A. strigosa*	Yu and Wise (2000)
Pc87	CI 3815	*A. strigosa*	Yu and Wise (2000)
Pc88	CI 3815	*A. strigosa*	Yu and Wise (2000)
Pc89	CI 3815	*A. strigosa*	Yu and Wise (2000)
Pc90	CI 3815	*A. strigosa*	Yu and Wise (2000)
Pc91	CW 57	*A. longiglumis*	Rooney et al. (1994)
Pc92	Obee/Midsouth	*A. strigosa*	Rooney et al. (1994)
Pc93	CI 8330		CDL (2010)
Pc94	RL 1697	*A. strigosa*	Aung et al. (1996)
Pc95	Wisc X 1588-2	*A. sativa*	Harder et al. (1995)
Pc96	RL 1730	*A. sativa*	Chong and Brown (1996)
Temp_*Pc97*	CAV 1180	*A. sterilis*	Chong et al. (2011)
Temp_*Pc98*	CAV 1979	*A. sterilis*	Chong et al. (2011)

been identified from four main sources: *A. byzantina*, *A. sativa*, *A. sterilis* and lower ploidy material (diploid oat, mainly *A. strigosa*). The best sources of genes for resistance to *P. coronata* can be found among wild relatives of oat in the regions of its origin (Manisterski and Wahl 1995). Of the wild relatives, *A. sterilis* is the most important source of resistance genes (Segal et al. 1980; Simons 1985) and can be

readily hybridised with cultivated oat. Although nearly 30 genes have been described in lower ploidy wild oat, relatively few have been used in oat breeding. Crown rust resistance genes (*Pc* genes) developed from the various sources are listed below.

3.2.1 A. byzantina

The first early successes in finding crown rust resistance genes were from *A. byzantina* introductions. *Pc1*, a dominant gene, was isolated from the cultivar Red Rustproof (Davies and Jones 1927), designated "S" by Dietz and Murphy (1930). Victoria, an introduction from Uruguay, was found to contain three genes: *Pc2* (Murphy et al. 1937), *Pc11* and *Pc12* (Welsh et al. 1954). Bond, from Red Algerian/Gold Rain out of Australia (Welsh et al. 1953), contained two dominant complementary genes for crown rust resistance: *Pc3* and *Pc4* (Hayes et al. 1939). *Pc5* was a gene found in Landhafer (Litzenberger 1949) and was an introduction from Germany, but it probably originated in South America (Coffman 1961). Another South American introduction was Santa Fe, which was the source of three resistance genes: *Pc6* (Litzenberger 1949), *Pc7* and *Pc8* (Osler and Hayes 1953). Klein was an *A. byzantina* introduction from Argentina which came to North America from Australia (Welsh et al. 1953), and Klein 69b was found to contain *Pc10* (Finkner 1954). Simons (1956) identified two genes in the variety Ascencao: one was determined to be *Pc2* while the second, *Pc14*, was shown to be epistatic to *Pc2*.

3.2.2 A. sativa

It would appear that *A. sativa* contains relatively few naturally occurring resistance genes useful against *P. coronata*. Ukraine (Hutica), an introduction from Russia, contained two dominant complementary genes, *Pc3c* and *Pc4c* (Weetman 1942). Finkner (1954) showed that two closely linked alleles, *Pc6c* and *Pc9*, conferred resistance in Ukraine. But a later work by Sanderson (1960) showed that Ukraine resistance was due to a single dominant gene, *Pc9*. Trispernia, an introduction from Romania (Welsh et al. 1953), contained three genes for resistance, one of which was *Pc6d* (Finkner 1954). *Pc13* was found to be present in the widely grown US oat cultivar Clinton (Finkner et al. 1955). *Pc22* was isolated from the Welsh variety Ceirch du Bach (McKenzie 1961). The cultivar Garry in Canada was found by Upadhyaya and Baker (1960) to possess three seedling genes (*Pc24*, *Pc25*, *Pc26*) and two APR genes (*Pc27*, *Pc28*). Kyto oat was found to contain the dominant gene *Pc44* (Martens et al. 1968). More recently, *Pc96* was identified in *A. sativa* (Chong and Brown 1996) and is currently effective against predominant races of *P. coronata* in North America (Chong et al. 2011), thus is useful for combining with other effective *Pc* genes.

3.2.3 *A. sterilis*

A. sterilis is a wild hexaploid oat species which is native in the Mediterranean regions (Wong et al. 1983). Accessions were collected in Israel and other Mediterranean countries during the 1960s and the early 1970s (Simons et al. 1978). The transfer of resistance from wild hexaploid *A. sterilis* to cultivated oat, *A. sativa*, was reported to be more successful than from other related wild species (Martens and Dyck 1989). *A. sterilis* has been the richest source of crown rust resistance genes of all species. To date there have been 43 genes described, many of which are linked or allelic (Table 3.1). Most *Pc* genes derived from *A. sterilis* have been defeated in North America, due to single gene deployment and rapid virulence changes in the *P. coronata* population. For example, *Pc68* was derived from *A. sterilis* and was one of the most effective major resistance genes deployed globally against crown rust, but virulence to this gene is now common in North America. Most of the *A. sterilis* genes for crown rust resistance are dominant or incompletely dominant, but there are exceptions as *Pc54* was shown to be an incompletely recessive gene (Martens et al. 1980).

At least 16 genes from *A. sterilis* have been deployed at various times in North America (Leonard 2003). *Pc38*, *Pc39* and *Pc68*, and to a lesser extent *Pc48*, have been used in developing resistant oat cultivars in the eastern prairie region of Canada. *Pc39* was the first gene derived from *A. sterilis* to be deployed in Canada, with the release of "Fidler" in 1980. This was followed by the release of a series of cultivars (such as "Dumont", "Robert" and "Riel") with both *Pc38* and *Pc39* from 1982 to 1993. *Pc38* and *Pc39* became ineffective in the eastern prairie region in the mid-1990s, due to a major shift in virulence to these two genes in the prairie rust population (Chong and Seaman 1997). Subsequently, a series of cultivars with the *Pc38 + 39 + 68* gene combination were released, starting with "AC Assiniboia" in 1995, followed by six other cultivars with the same gene combination. Since *Pc38* and *Pc39* were no longer effective in the 1990s, these cultivars basically were protected only by *Pc68*. In 1998, "Triple Crown" was released and its resistance was based on gene *Pc48*. In 2001, late-planted fields of this cultivar were severely damaged by crown rust (Chong and Zegeye 2004). By 2005 cultivars with the *Pc38*, *Pc39*, *Pc68* gene combination ("AC Assiniboia" and "Ronald") were severely damaged by crown rust (Chong et al. 2008), indicating that *Pc68* was no longer effective in Canada. Since then, two putative new genes from *A. sterilis* (*Temp_Pc97* and *Temp_Pc98*) have been described and are resistant to most current *P. coronata* races in Canada (Chong et al. 2011).

3.2.4 *Diploid and Tetraploid Oat*

Several wild diploid species of *Avena*, particularly *A. strigosa*, possess a high degree of resistance to crown rust. *A. strigosa* is primarily found in Western Europe and in

countries of the former USSR. This species was widely cultivated for grain-fodder (Holden 1979) and is currently grown to a limited extent in Germany, the United Kingdom (Wales) and Australia. It is also used as a fodder oat in Brazil (Leonard and Martinelli 2005). Transfer of genes for crown rust resistance from *A. strigosa* to hexaploid oat was initially accomplished by producing an autotetraploid of *A. strigosa* followed by crossing to *A. sativa* (Zillinsky and Derick 1960). However, the resistant hexaploid lines isolated in the later generations exhibited a high degree of sterility and cytological instability (Dyck and Zillinsky 1963). Wild diploid *A. strigosa* accessions have also been found to be a better source of adult plant resistance when compared to accessions of the tetraploid species, *A. barbata* (Cabral et al. 2011). There have been 22 genes described from *A. strigosa* (Table 3.1). Of these genes, only *Pc23* and *Pc94* have been incorporated into a stable *A. sativa* background (Dyck and Zillinsky 1963; Aung et al. 1996).

The lack of effective crown rust resistance genes in cultivated oat and the ability of the pathogen to produce new races have resulted in the continuous search for new sources of resistance. The useful lifetime of a resistance gene can be relatively short due to changes in virulence in the pathogen population following widespread deployment of an introduced resistance gene. Early oat breeding efforts incorporated resistance genes from cultivated hexaploid oat (Martens and Dyck 1989). When all available sources of resistance were defeated by the late 1950s, new sources of crown rust resistance were identified in *A. sterilis*. More than 40 resistance genes have been described, but few are useful for oat breeding. Moderate levels of virulence already existed in the *P. coronata* f. sp. *avenae* population to many of these genes, even though they had not previously been deployed in North America (Chong and Kolmer 1993). Some of the genes were tightly linked or allelic, and virulence to some of the genes was associated (Chong and Brown 1996; Leonard et al. 2005b). Few crown rust genes have been described from wild diploid and tetraploid species, even though they are a rich source of genetic diversity (Simons et al. 1959). *Pc91* is a highly effective gene derived from a cross between tetraploid *A. magna* Murphy and Terrell and diploid *A. longiglumis* Durr. (Rooney et al. 1994), with *A. magna* being the donor. *Pc91* is currently the most effective crown rust resistance gene available in North America (McCartney et al. 2011). *Pc94* was derived from *A. strigosa* (Aung et al. 1996) and was highly effective during 2002–2006 (Chong et al. 2008). Currently, oat breeders are interested in pyramiding *Pc91* and *Pc94* to slow the breakdown of these resistance genes. Pyramiding these genes in conjunction with APR genes may stabilise crown rust resistance.

3.3 Stem Rust

Stem rust is another major disease that threatens oat production worldwide. The disease is caused by the fungus *Puccinia graminis* Pers. f. sp. *avenae* Eriks. and E. Henn. The most severe epidemic recorded in Canada caused an estimated 35 % yield loss in the eastern prairie region in 1977 (Martens 1978). The most recent

Table 3.2 Oat Stem rust resistance genes

Gene	Original source	*Avena* species	Reference
Pg1	White Russian	*A. sativa*	Garber (1921)
Pg2	Green Russian	*A. sativa*	Dietz (1928)
Pg3	Joanette	*A. sativa*	Waterhouse (1930)
Pg4	HajiraRL1225	*A. sativa*	Welsh and Johnson (1954)
Pg5	RL 1225	*A. sativa*	Welsh and Johnson (1954)
Pg6	CD 3820	*A. strigosa*	Murphy et al. (1958)
Pg6a	CN 21997, CN 57130	*A. strigosa*	Zegeye 2008
Pg6b	CN 21996	*A. strigosa*	Zegeye 2008
Pg6c	CN 21998, CN 22000	*A. strigosa*	Zegeye 2008
Pg6d	CN 22001	*A. strigosa*	Zegeye 2008
Pg6e	CN 55115	*A. strigosa*	Zegeye 2008
Pg7	CD 3820	*A. strigosa*	Murphy et al. (1958)
Pg8	Hajira CI 8111	*A. sativa*	Browning and Frey (1959)
Pg9	Ukraine, Santa Fe	*A. sativa*	McKenzie and Green (1965)
Pg10	Illinois Hulless, CI 2824	*A. sativa*	Pavek and Myers (1965)
Pg11	Burt, CI 3034	*A. sativa*	McKenzie and Martens (1968)
Pg12	Kyto, CI 8250	*A. sativa*	Martens et al. (1968)
Pg13	PI 324798, CW 490-2	*A. sterilis*	McKenzie et al. (1970)
Pg14	Milford	*A. sativa*	Mac Key and Mattsson (1972)
Pg15	CAV 1830	*A. sterilis*	Martens et al. (1980)
Pg16	D203	*A. barbata*	Martens et al. (1979)
Pg17	IB 3056	*A. sterilis*	Harder et al. (1990)
Pg-a	*A. sterilis*/Kyto	*A. sterilis* + *sativa*	Martens et al. (1981)

epidemic of oat stem rust in Canada occurred in the eastern prairie region in 2002, with estimated yield losses of 6.6 % (worth $12.6 million) in Manitoba and 0.5 % (worth $1.0 million) in Saskatchewan (Fetch 2005). The disease can be effectively controlled with host resistance or with fungicides. However, fungicides can be an expensive option for producers besides having environmental impacts. Therefore, the most efficient, economical and environmentally sound method of controlling the disease is through the use of host resistance.

Currently, only 17 oat stem rust resistance genes (*Pg* genes) and the *Pg-a* complex have been described (Martens 1985; Fetch and Jin 2007) and are listed in Table 3.2. Most are from *A. sativa*, but a few are from wild oat (Martens 1985). Oat stem rust resistance genes are rare (Martens and Dyck 1989), and only a few genes (*Pg2*, *Pg13*, *Pg-a*) provide protection against the current races in the North American population of *P. g*. f. sp. *avenae* (Mitchell Fetch and Fetch 2011). Harder (1994) reported that only five genes (*Pg1*, *Pg2*, *Pg4*, *Pg9* and *Pg13*) had been intentionally deployed in Canadian oat cultivars, and most resistant cultivars likely possessed the *Pg2* + *Pg13* combination. This combination was effective against all stem rust races in North America, but new races (NA67, NA76) with virulence to these genes evolved and are common in North America (Fetch and Dunsmore 2004).

Virulence in the population of *P. g*. f. sp. *avenae* appears to be increasing (Mitchell Fetch and Fetch 2011); thus new genes are highly desirable. Only *Pg6*, *Pg10*, *Pg11*, *Pg12*, *Pg16* and the *Pg-a* complex confer resistance to NA67 and NA76 (Fetch and Dunsmore 2004). Genes *Pg10*, *Pg11*, *Pg12* and the *Pg-a* complex are from a hexaploid background. To date, only the *Pg-a* complex has been deployed in oat cultivars in Canada and the United States, but the frequency of virulent races to *Pg-a* is increasing in North America. The *Pg10* gene has been used in Canadian oat breeding programmes, but no cultivars have been developed to date. This gene confers characteristic large necrotic halos around rust pustules and on stems of adult plants (Harder 1999), and while no virulence has been detected in North America, there is virulence to *Pg10* in Ethiopia (Fetch, unpublished data). Gene *Pg11* is an APR gene and is effective to all races of oat stem rust, but is associated with chlorophyll deficiency (Harder et al. 1971) and is undesirable for breeding. Gene *Pg12* is effective only at the seedling stage (Martens 1985).

Since the virulence spectrum in *P. g*. f. sp. *avenae* is increasing and most known genes are either ineffective or undesirable, new genes are needed. A recent study evaluated nearly 10,000 lines from various species of *Avena* for resistance to race NA67. Results indicated that *A. strigosa* is the most promising source of resistance and that additional resistance genes in hexaploid oat are unlikely to be found (Gold Steinberg et al. 2005). Gene *Pg16* has been successfully transferred from the tetraploid *A. barbata* into hexaploid oat by irradiation (Brown 1985); however it is a 44-chromosome addition line and appears to reduce yield by about 10 % (J. Mitchell Fetch, unpublished). Efforts to reduce the chromosome number to 42 and maintain the resistance have not been successful. Gene *Pg6* derives from the diploid species *A. strigosa* and is resistant to most races of oat stem rust in North America except BLD (NA1) and CLD (NA70) (Fetch and Jin 2007). This gene reportedly was transferred into the American oat cultivar "Delredsa" (Rothman 1984), but multipathotype tests indicated *Pg6* was not present (Fetch, unpublished data). Recent efforts have been made by Zegeye (2008) to transfer resistance identified in the Gold Steinberg et al. (2005) study from *A. strigosa* into *A. sativa*. Efforts were partially successful, but resistant lines were chromosome addition lines, and no hexaploid derivatives containing *A. strigosa* resistance to oat stem rust has yet been developed.

3.4 Transfer of Rust Resistance from Wild Oat Accessions to Common Oat

There are many sources of rust resistance from diploid and tetraploid wild oat species. However, while transferring resistance from lower ploidy material to hexaploid wheat has been highly successful (Knott 1987), this has not been realised in oat. There are seven different genomes identified in diploid oat species and at least three in tetraploid species (Rajhathy and Thomas 1974). These genomes have differing affinities for pairing with the *A. sativa* genome, thus developing meiotically

stable progeny from interploidy crosses has been difficult. Interploidy transfer, particularly from diploid to hexaploid genomes, often requires special manipulations such as embryo rescue or development of a synthetic hexaploid, which can be crossed to a hexaploid cultivar (Innes and Kerber 1994). For example, *Pc91* is a highly effective gene in hexaploid oat that was transferred using a synthetic hexaploid derived from a cross between tetraploid *A. magna* Murphy and Terrell and diploid *A. longiglumis* Durr. (Rooney et al. 1994). In oat, diploid to hexaploid resistance gene transfers have also been facilitated by generation of autotetraploid, derived tetraploid and amphiploid lines (Sadanaga and Simons 1960). In contrast, the transfer of rust resistance genes from wild *A. sterilis* is easy as this species pairs readily with *A. sativa*.

The process of resistance gene transfer from wild to cultivated oat is often hindered by sterility barriers (Aung et al. 1977). Thus, generation of fertile progeny may involve the rescue of hybrids or F_1 embryos. The choice of the female and pistillate parent in interploidy crosses is also an important consideration, with the lower ploidy genotype being the preferred pistillate parent (Rajhathy and Thomas 1974). On the contrary, retaining the higher ploidy hexaploid as the pistillate parent yielded more vigorous F_1 seeds from interspecific crosses of hexaploid oat cv. "Wintaroo" and diploid *A. strigosa* genotypes (Cabral et al. 2013). Additionally, instances of suppressor genes/factors of the donor parent interfering with the expression of resistance in interspecific F_1 progeny have been reported. Rines et al. (2007) reported a suppressor factor in diploid line CI6954SP that contributed to susceptible F_1 progeny when crossed with *A. sativa*. The gene*Pc38* suppresses the expression of *Pc94* (Aung et al. 1996), which has been introgressed into *A. sativa* from *A. strigosa*.

Even if generation of fertile progeny from interspecific crosses is achieved, the introgression of resistance into the genome of hexaploid oat cultivars is very difficult to achieve by means of regular backcrossing procedures. This is mainly due to the low frequency of chromosome pairing between wild species with cultivated oat, consequently reducing the chance of recombination and gene transfer. Rajhathy and Thomas (1974) reported that a genotype of *A. longiglumis* (CW57) suppressed the activity of the gene(s) controlling regular bivalent pairing in *A. sativa* and induced pairing between nonhomologous chromosomes, resulting in translocation between two homologous chromosomes as well as between unrelated chromosomes. The CW57 gene(s) induced pairing between line RL1697 (*A. strigosa*) and line Sun II (*A. sativa*), which facilitated the transfer of *Pc94* crown rust into a hexaploid genetic background (Chong et al. 2011).

Though the transfer of resistance genes from wild species into hexaploid oat is difficult, several success stories and methods have been reported. Ladizinsky (1995) described the domestication of two wild tetraploid oat species not by selection of rare mutations but by transfer of genes into cultivated oat through hybridisation. He later developed a synthetic hexaploid oat (2000) by crossing the *A. strigosa* ($2n = 14$) cv. "Saia" with *A. magna* ($2n = 28$). Chromosome doubling of the resulting sterile triploid hybrid produced a synthetic hexaploid, which was intermediate between its parents in panicle shape and lemma colour. Progeny were similar to the tetraploid parent in spikelet structure and to the diploid parent in having a single, albeit

partially shrivelled seed per spikelet and low protein content. Fox (1989) crossed three tetraploid accessions with Rodney O (hexaploid *A. sativa*) and produced highly fertile progeny with resistance to crown rust races CR13 and CR 50, but two diploid accessions crossed with Rodney O did not produce any viable seeds.

Zillinsky and Derick (1960) first reported the transfer of genes from wild diploid *A. strigosa* into hexaploid oat. They created an autotetraploid line by doubling the chromosome number of diploid material using colchicine and crossed the progeny to hexaploid oat. However, these transfers were genetically unstable and autotetraploids were partially sterile (Dyck and Zillinsky 1962; Sadanaga and Simons 1960). Marshall and Myers (1961) directly crossed *A. strigosa* with *A. sativa* and had no difficulty in obtaining seeds, but were only water filled and became extremely shrivelled when dry. Much work was done with CD 3820, an *A. strigosa* line, where several genes for crown rust resistance were found. Dyck and Zillinsky (1963) showed the presence of two independent genes, *Pc15* and *Pc23*. *Pc15* proved to be located on a chromosome that failed to pair with any *A. sativa* chromosomes. In lines homozygous for *Pc15*, the chromosome number was 44 where *Pc15* was found on the extra chromosome pair. *Pc23* appeared to be completely incorporated into normal *A. sativa* (Dyck and Zillinsky 1963).

Rines et al. (2007) attempted two methods to transfer crown rust resistance from a diploid *A. strigosa* into a hexaploid *A. sativa*. The first method directly crossed the diploid line CI6954SP with a hexaploid to obtain tetraploid F_1 progeny, which were subsequently treated with colchicine to generate a synthetic octaploid for subsequent backcrossing to the hexaploid parent. The second method crossed CI6954SP with a tetraploid *A. murphyi* line to make a synthetic hexaploid for subsequent crossing into a hexaploid background. Although the direct method requires the laborious crossing and embryo rescue to develop a fertile octaploid line, it provided faster recovery of plants with high fertility, full transmission of resistance and desired plant and seed phenotypes. Similar work was done by Zegeye (2008) to directly transfer stem rust resistance from *A. strigosa* into hexaploid oat. The general crossing scheme and methodology followed is shown in Fig. 3.1. Crosses and reciprocal crosses between the diploid *A. strigosa* accessions and hexaploid *A. sativa* cultivar Sun II were made, and embryo rescue and colchicine treatment produced octoploid progeny. Synthetic octaploid seeds were larger than the parental seeds (Fig. 3.2) and the seedlings were more vigorous. Progeny were selfed to the F_2 and F_3 generation and backcrossed to Sun II. Cytological evaluation of resistant BC_1F_2 progenies found 43–47 chromosomes (Fig. 3.3) and progeny tests of BC_1F_2 and BC_1F_3 with NA67 identified resistant seedlings. Rajhathy and Thomas (1974) reported that the line Cw57 can be used to induce chromosome pairing between the "A_s" genome of *A. strigosa* and the "A" genome of *A. sativa*. Thus, F_1 octaploid seeds were produced from crossing diploid *A. longiglumis* (Cw57) with Sun II, which was subsequently crossed to highly resistant BC_1F_3 progeny lines containing 43–44 chromosomes from CN57130/Sun II//Sun II. F_1 hybrid seeds were obtained, which will be repeatedly backcrossed to Sun II until the resistance from *A. strigosa* is stabilised in a 42-chromosome background.

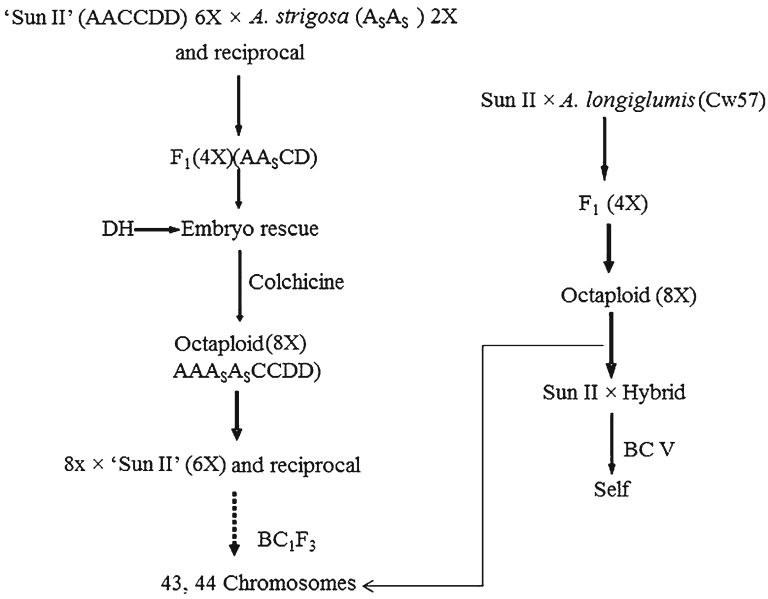

Fig. 3.1 Crossing scheme between diploid and hexaploid oat to transfer stem rust resistance from *A. strigosa* to *A. sativa*

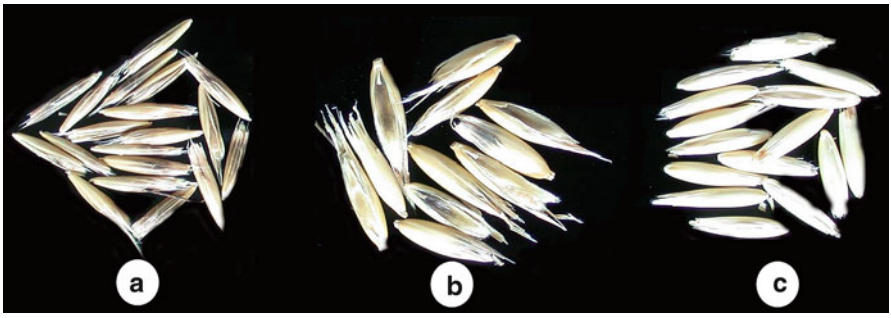

Fig. 3.2 Seeds from the diploid (**a**) *A. strigosa* (CN21997), (**b**) octaploid (CN21997/"Sun II") and (**c**) hexaploid *A. sativa* ("Sun II")

The use of irradiation to facilitate the transfer of resistance genes has also been reported. Mildew resistance was transferred from tetraploid *A. barbata* to cultivated oat *A. sativa* (Aung and Thomas 1976; Aung et al. 1977) using irradiation to induce translocations in a disomic addition line ($2n=6x=44$) of an *A. sativa* that contained a pair of *A. barbata* chromosomes carrying the mildew resistance gene. Sharma and Forsberg (1977) treated a monosomic substitution line with thermal neutrons and

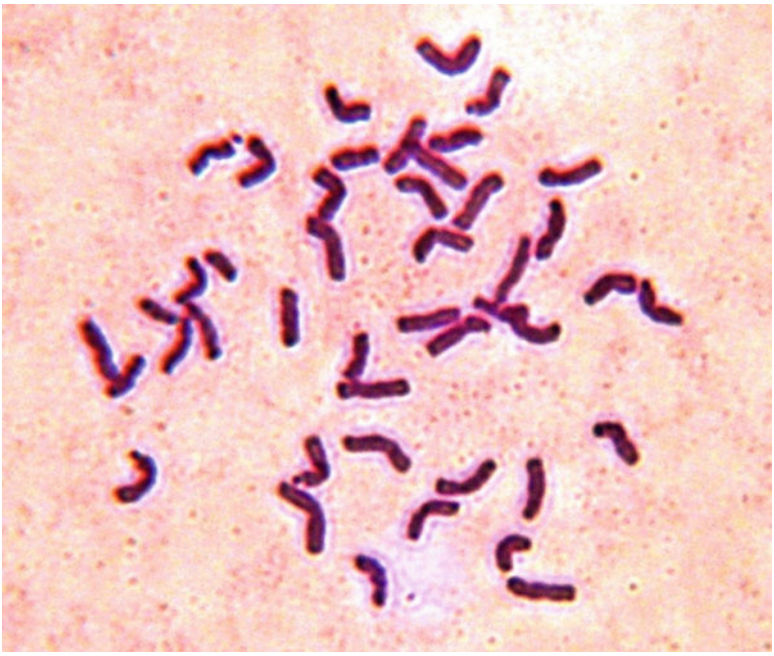

Fig. 3.3 Cytological evaluation depicting 44 chromosomes of a resistant BC_1F_2 seedling from CN21997/"Sun II"//"Sun II"

were successful in transferring the *Pc15* gene from *A. strigosa* into the cv. Clarian, which showed normal breeding behaviour and could be used in a breeding programme. The main limitation of the irradiation-induced gene transfers is that they are the products of reciprocal translocation and involve a deletion and duplication (Thomas 1992).

3.5 Relationship of Rust Resistance Genes and Molecular Markers

The exact position of rust resistance genes on oat chromosomes has not yet been described, because unlike the other cereal grains, there has not yet been any specific chromosome numbers allocated. Currently, there are 34 linkage groups mapped (Tanhuanpää et al. 2012), but work is underway to anchor molecular markers and develop a 21-chromosome map. Since no rust resistance genes have yet been located to a specific chromosome position, many genes could be alleles or the same gene since in most cases no full genetic studies exist. In crown rust, five linkage groups that have been identified and cultivars Santa Fe, Ukraine and Trispernia

have exhibited allelism or close linkage for at least one gene (Finkner 1954). A number of crown rust resistance genes are clustered in the oat genome, including *Pc46*, *Pc50* and *Pc68* (Wong et al. 1983); *Pc38*, *Pc62* and *Pc63* (Harder et al. 1980); *Pc39* and *Pc55* (Kiehn et al. 1976); *Pc35*, *Pc54* and *Pc96* (Martens et al. 1980; Chong and Brown 1996); and *Pc68*, *Pc44*, *Pc46*, *Pc50*, *Pc95* and *PcX* (Chong et al. 1994). Leonard et al. (2005a) suggested that genes *Pc39*, *Pc55* and *Pc71* may be identical or nearly identical alleles. It has also been postulated that gene *Pc94* might be close to or part of *PcA* (Rines et al. 2007). In stem rust, genes *Pg1*, *Pg2*and *Pg8* are clustered, *Pg3* and *Pg9* are linked, and *Pg4* and *Pg13* are associated (Martens 1985).

Crown rust and stem rust resistance genes have also been shown to be linked together. Martens et al. (1968) suggested that there were three alleles for crown rust resistance and two alleles for stem rust resistance at or near the *Pc44* locus, and *Pc44* was linked in repulsion to *Pg9*. *Pg9* was associated with crown rust resistance in Ukraine oat (McKenzie et al. 1965). The mapping of resistance gene analogues (RGA) on the Kanota × Ogle (KO) by Sanz et al. (2012) showed that both the nucleotide binding site (NBS) and protein kinase (PK)-based markers significantly co-localised with loci conferring resistance to *P. coronata*, i.e. *Pc39* (KO16_23), *Pc54*/*Pc59* and *Pc68* (KO4_12) and *Pc58* (KO17), as well as with a locus conferring resistance to *P. graminis*, i.e., *Pg13* (KO3 + 38).

Many race-specific resistance genes have been mapped, and markers that are closely linked to crown and stem rust genes have been identified (Table 3.3). An *avenin* protein marker is linked to *Pg3* and *Pg9* (Howes et al. 1992; Chong et al. 1994), and three *avenin* storage protein loci as well as two RGA markers are very tightly linked to *Pc68* (Satheeskumar et al. 2011). A random amplified polymorphic DNA (RAPD) marker has been linked in repulsion to *Pg3* (Penner et al. 1993a). The latter RAPD primers also produced a marker which, together with three restriction fragment length polymorphism (RFLP) markers and a third RAPD marker, were shown to be linked to *Pg9* (O'Donoughue et al. 1996). Gene *Pg13* has been mapped in two populations to linkage groups homologous to KO3 (O'Donoughue et al. 1996) and a second stem rust resistance gene *Pg4* (McKenzie et al. 1970). *Pg13* is also linked to a 56.6-kDa avenin storage protein marker (Howes et al. 1992; Chong et al. 1994). Personal Communication (2013) developed SCAR, CAPS and SSR markers based on amplified fragments linked to *Pg3*, *Pg9* and *Pg13* obtained using the RAPD primers ubc195, ubc269 and ubc254. Molecular markers can be used to facilitate pyramiding of genes, a breeding strategy designed to provide more durable control of rust by combining several resistance genes in one cultivar (Pedersen and Leath 1988).

Molecular markers can also be used in counter-selection. The gene *Pc38* would be an excellent choice, as it is known to suppress the action of genes *Pc62* (Wilson and McMullen 1997) and *Pc94* (Chong and Aung 1996). Molecular markers developed for any one particular rust resistance gene in a cluster will also be useful for the study of other disease resistance genes found within the same cluster. A KASP assay was developed from the previously reported nonredundant DArTs that co-segregated with *Pc91* (Gnanesh et al. 2013). The KASP assay was used for marker-assisted

Table 3.3 Molecular markers for oat crown and stem rust resistance genes

Gene	Marker	Linked marker/QTL name	Reference
Crown rust			
Pc38	RFLP	cdo673, wg420	Wight et al. (2004)
Pc39	RFLP	cdo666	Wight et al. (2004)
Pc48	RFLP	cdo337	Wight et al. (2004)
Pc54	RFLP	cdol435B	Bush and Wise (1996)
Pc58a,b,c	RFLP	PSR637, RZ516D	Hoffman et al. (2006)
Pc59	RFLP	cdo549B	Bush and Wise (1996)
Pc68	RAPD	ubc269	Penner et al. (1993b)
	SNP	*Pc68*-SNP1, *Pc68*-SNP2	Chen et al. (2006)
	AFLP	U8PM22, U8PM25	Kulcheski et al. (2010)
	SDS-PAGE	AveX, AveY, AveZ	Satheeskumar et al. (2011)
	RGA/RFLP	Orga1	Satheeskumar et al. (2011)
	SCAR	ubc269s SCAR	Personal Communication (2013)
Pc71	RFLP	cdo783, cdo1502	Bush and Wise (1998)
Pc81,82, 83,84,85	AFLP	isu2192, OP C18	Yu and Wise (2000)
	STS	Agx4, Agx9, Agx7	Yu and Wise (2000)
Pc91	RFLP	UMN145	Rooney et al. (1994)
	DArT	oPT-0350	McCartney et al. (2011)
	SCAR	oPT-0350-cdc	McCartney et al. (2011)
	KASP	oPT-0350-KOM4c2	Gnanesh et al. (2013)
Pc92	RFLP	OG 176	Rooney et al. (1994)
Pc94	AFLP	AF94a	Chong et al. (2004)
	SCAR	SCAR94-1, SCAR94-2	Chong et al. (2004)
	SNP	*Pc94*-SNP1a	Chen et al. (2007)
Pca	RGA/RFLP	isu2192	Kremer et al. (2001)
		L7M2.2	Irigoyen et al. (2004)
		b9-1	Sanz et al. (2012)
PcX	RFLP, RAPD	Xcdo1385F, XpOP6(A), Xacor458A	O'Donoughue et al. (1996)
Stem rust			
Pg3	RAPD	ACOpR-1, ACOpR-2	Penner et al. (1993a)
	SCAR/CAPS	*Pg3* SCAR/CAPS	Personal Communication (2013)
Pg4	SCAR/CAPS	ubc254s SCAR	Personal Communication (2013)
Pg9	Acid-PAGE	*avenin* band	Chong et al. (1994)
	RFLP, RAPD	Xcdo1385F, Xacor458A	O'Donoughue et al. (1996)
	SCAR/CAPS	*Pg9* SCAR/CAPS	Personal Communication (2013)
Pg13	SDS-PAGE	56.6-kDa polypeptide locus	Howes et al. (1992)
	RFLP, RAPD	Xmog12B, Xacor254C	O'Donoughue et al. (1996)
	SCAR	*Pg13* SCAR	Personal Communication (2013)
Sr_57130	AFLP	PacgMcga370	Zegeye (2008)

selection for crown rust resistance gene *Pc91* in an F_2 population developed from the cross of AC Morgan × Stainless (Fig. 3.4). Sanz et al. (2012) reported the PK-RFLP and PK profiling markers co-localise with *Pc71* (KO11_41 + 20) and *Pc91* (KO3 + 38), whereas clusters of mixed markers based on NBS and PK domains

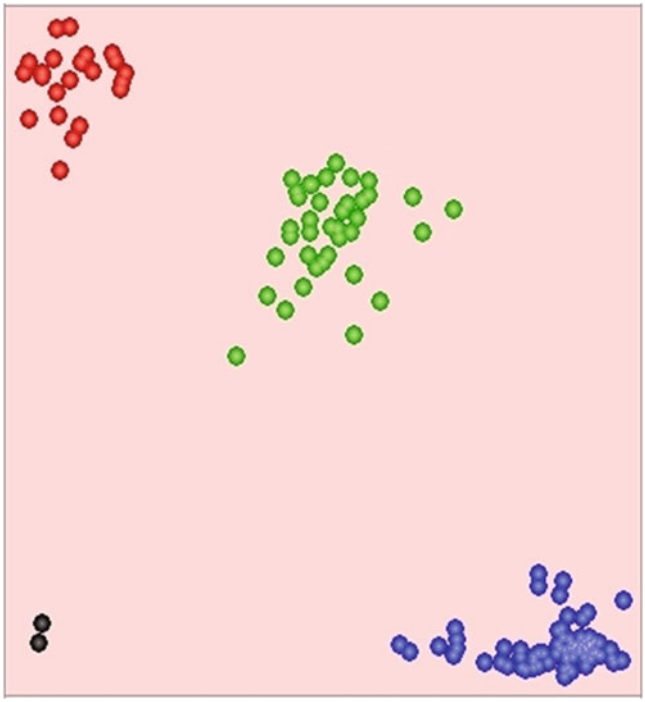

Fig. 3.4 Marker-assisted selection for crown rust resistance gene *Pc91* using oPt-0350-KOM4c2 KASP SNP assay in F_2 population (AC Morgan × Stainless). *Red* data points are carriers of *Pc91*, *blue* data points are non-carriers, *green* data points are segregating and *black* data points are no template controls

co-localise with genes *Pc38* (KO17), *Pc94* (KO17) and *PcX* (KO4_12). Comparative mapping of disease resistance loci with reference populations such as Kanota × Ogle (KO) (Wight et al. 2003), Ogle × TAM O-301 (Portyanko et al. 2001) and Ogle × MAM17-5 (OM) (Zhu and Kaeppler 2003) increases the number of potential molecular markers available for resistance genes and furthers our understanding of their organisation in the genome. The development of anchored markers on a 21-chromosome map is the first step in identifying the location of rust resistance genes and would help immensely in the identification of new resistance genes introgressed from wild species.

3.6 Future Outlook on Alien Introgression in Oat

Wild species are an important and abundant source of new rust resistance genes. Previous studies have identified numerous rust resistance genes in diploid and tetraploid wild species, but few have been successfully transferred. Although it

appears that initial transfer into chromosome addition lines is relatively simple, introgression and reduction to 42-chromosome cultivated oat have been difficult. New techniques are needed to find better methods of stabilising rust resistance from wild species, as virulence in *P. coronata* and *P. graminis* f. sp. *avenae* appears to be increasing worldwide.

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