Wheat breeders must effectively maintain and manage existing genetic diversity in order to continue the development of superior genotypes. It is therefore fundamental that the genetic relationships and diversity within the germplasm pools be thoroughly characterized and understood. Recently, DNA-based markers have provided powerful tools for genetic diversity analysis. This study investigates the usefulness of nuclear and chloroplast simple sequence repeat (SSR) markers in characterizing Pacific Northwest wheat (Triticum aestivum) breeding germplasm, and explores the patterns of genetic relatedness revealed by these markers. The 15 chloroplast SSRs were effective in differentiating between B-type, D-type, and barley (Hordeum vulgare) cytoplasms. Genetic distance estimates were determined for each pair of lines studied and analyzed using UPGMA clustering. The markers revealed five plastomic types within the B-type cytoplasm studied. Several lines of wheat in this germplasm, including important PNW cultivars like Madsen, were found to contain D-type cytoplasm rather than the B cytoplasm of wheat. Nuclear SSR assays using 24 markers revealed three major clusters of germplasms: PNW soft white winter wheat, Western
European-derived lines, and Great Plains accessions, as well as two clusters of more distantly related lines and genetic stocks. The primary defining characteristic of these clusters was regional adaptation. Subgroups of these major groups often clustered together on the basis of pedigree and market class. When nuclear and chloroplast SSR data was combined in analysis, the primary defining characteristic of the dendrogram became the type of cytoplasm rather than regional adaptation, with secondary divisions based on pedigree relationships. Cultivars released prior to 1950 were found to have a minimum of 20% of alleles in common for nuclear and chloroplast data combined, despite being unrelated via pedigree information. Heterogeneity was 2.3% for all marker/variety combinations. Overall, these sets of markers were found to be effective in characterizing the genetic relatedness of PNW wheat breeding germplasm.
Nuclear and Chloroplast Diversity of Pacific Northwest Wheat (*Triticum aestivum*) Breeding Germplasm.

by

Melanie Love Edwards

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Melanie Love Edwards, Author
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Nuclear and Chloroplast Diversity of Pacific Northwest Wheat (*Triticum aestivum*) Breeding Germplasm.

**Introduction**

The objectives of any wheat improvement program are to develop cultivars that are superior and stable in yield, resistant to biotic or abiotic stresses, and possess quality characteristic of value to the milling and baking industry. To accomplish this, wheat breeders capitalize upon the genetic diversity existing among elite germplasms, and unadapted germplasm from secondary gene pools. This genetic diversity must be properly managed to sustain long-term genetic gain. While there exist several methods for characterizing the genetic diversity based on phenotypic characteristics, comparison of the actual DNA sequence variation would provide a more direct measurement of genetic relatedness and variation. This may be accomplished through the use of DNA-based markers.

There are several DNA-based markers available and each has been used in evaluating genetic diversity of wheat germplasm. As these technologies are still under development, their applicability in wheat breeding germplasm remains to be fully explored. The Pacific Northwest wheat germplasm base is very appropriate to evaluating marker technologies. The germplasm of the Pacific Northwest includes cultivars from lines from around the world and spanning many different market
classes. Understanding of genetic relatedness of these lines could assist wheat breeders in management of diversity and developing long-term strategies to better exploit that diversity.

The objectives of this study were fourfold: i) to investigate the usefulness of simple sequence repeat markers for characterizing Pacific Northwest wheat breeding germplasm, ii) to analyze the cytoplasmic diversity available in this germplasm pool, iii) to explore nuclear diversity of this germplasm and to determine biological significance of genetic relatedness based on nuclear SSR markers, and iv) to determine the usefulness of a combined nuclear/chloroplast SSR data set and to investigate heterogeneity and underlying historical relatedness with this combined data set.
Literature Review

Maintenance of Genetic Variation

Crop improvement is accomplished by exploiting genetic diversity through breeding and selection. Plant breeders create diversity and maximize genetic gain through recombination of allelic variation. This is accomplished through various methods of crossing, backcrossing, selfing, cytoplasmic manipulation, and recurrent selection (Poehlman and Sleper 1995). Plant breeders use an array of strategies, from wide crosses with alien species to crosses among elite inbred lines, in attempts to maximize genetic gain to meet both long and short-term goals. Allelic variation is imperative for ongoing crop improvement efforts, and thus it is an important goal for breeders to effectively maintain and manage genetic diversity within their breeding germplasm.

Within a particular breeding program, the germplasm base can contain a wide variety of genetic material, from elite advanced lines to wild relatives or varieties from other regions. Germplasm pools also include breeding lines with specific alleles of interest, such as those for disease resistance, which may be deficient in many other traits. Prior to the initiation of genetic diversity studies, allelic variation existing within a breeding germplasm base was unclear. Assumptions regarding genetic diversity and similarity were based on pedigrees and phenotypic evaluation of important traits. Statistical
means of quantifying genetic variation were developed using pedigree analysis (Kempthorne 1969) or phenotypic data (Jain et al. 1975).

In the 1970’s, concern arose over lack of diversity, or uniformity, among commercial varieties developed through modern plant breeding. The United States experienced an epidemic of southern corn (Zea mays L.) leaf blight, caused by the fungus Bipolaris maydis, which destroyed 15% of the nation’s crop in 1970-71. At that time, 80% of the hybrid corn in the U.S. was planted with corn produced using male sterile Texas cytoplasm. Although this cytoplasm was useful for efficient production of hybrid seed, it rendered the crop vulnerable to southern corn leaf blight. The epidemic and crop losses led the 1972 US National Academy of Sciences to conduct an assessment of genetic vulnerability of major crops. The Council was concerned that modern breeding practices were systematically reducing genetic variability and biodiversity. Of particular concern to the Council was the use of narrow elite germplasm pools the focus of many breeding programs. Given a limited pool of elite, highly related germplasm, alleles have the potential to become rapidly fixed, through either natural or artificial selection, thus reducing the diversity of the germplasm pool and resulting cultivars.

The loss of alleles with neutral or adverse effect on agronomic traits may not reduce the potential for future crop improvement. However, given the complex nature of the genetic background, including epistasis, heterosis, and possible epigenetic effects, the
long-term consequences of the loss of alleles is unpredictable and could be highly negative. Therefore, researchers found the need to more effectively study, monitor, and manage genetic variation of germplasm pools and related species.

Rasmusson and Phillips (1997) suggested that new genetic variation can be generated without the addition of new genetic stocks. Using a study of elite germplasm from barley (*Hordeum vulgare* L.), they showed that selection gain continues even when using a narrow pool of elite lines. As these lines were presumed to be fixed for many of the same positive alleles, the authors argue that this gain may be due to *de novo* variation, epistasis, and/or epigenetic effects. The variation might arise from well-characterized genetic processes such as mutation, unequal crossing over, intragenic recombination, transposable element activity, DNA methylation, paramutation, or gene amplification. New alleles produced through these processes can have substantial effects on the plant phenotype due to epistasis, the interaction of a gene with a new genetic environment. Others reject their hypothesis (Smale et al. 2001), but there is little evidence to refute their premise. Evidence for the existence of *de novo* variation could dramatically alter strategies for long-term breeding and management of diversity. Whether genetic diversity is generated *de novo* or whether it is incorporated from existing allelic variation, quantification of available diversity remains an important goal in order to efficiently manage diversity and ensure continued genetic gain.
Quantification of Diversity

Prior to the availability of molecular markers, genetic diversity estimates were based on measures of coefficient of parentage (COP) and relatedness based on pedigree (Kempthorne 1969). While these measurements provide an estimate of relatedness among germplasm, the estimates are based on several false assumptions. Similarity estimates based on coefficients of parentage assume the following: i) parental lines of unknown pedigree are unrelated, ii) there is no selection pressure, and iii) both parents contribute equally in a cross. Later studies have shown that parental lines previously presumed to be completely unrelated actually may have up to 30% genetic similarity (Kim and Ward 1997, Melchinger et al. 1994, Russel et al. 1997), which undermines the first assumption of COP. The second assumption is often violated because breeding programs apply selection pressure for agronomically important attributes. Natural selection also exerts pressure on populations of crop plants. Finally, studies using molecular markers have confirmed that parents often do not contribute equally to the genetic material of their offspring (Lorenzen et al. 1995, Paull et al. 1998). Thus, pedigree comparisons are generally recognized as an ineffective means to quantify genetic diversity.

Elegant statistical approaches have been developed to quantify genetic variation in structured populations (Dudley 1982, Lynch and Walsh 1998). However, as breeding germplasm may not exist in the appropriate structured populations, this method is not applicable when analyzing diversity of a broad germplasm base. Morphological
markers were found to be useful in cases with high levels of diversity in important characters (Donini et al. 2000). Application is limited, however, by the available number of segregating morphological traits. Other studies have evaluated gene frequencies using electrophoretic patterns of isozymes or disease-resistance loci (Cox et al. 1986, Eagles et al. 2001, Sharp et al. 2001). However, the methods require knowledge and measurement of specific genes and do not address overall diversity. With the development of molecular marker technologies, DNA-based markers provide new, powerful, and efficient tools for measuring genetic diversity. Genetic diversity studies to date have used markers based on restriction fragment length polymorphism (RFLPs), amplified fragment length polymorphism (AFLPs), random amplified polymorphic DNA (RAPDs), simple sequence repeats (SSRs) or microsatellites, and inter simple sequence repeats (ISSRs). Each of these markers provides a measurement of genetic similarity or dissimilarity by comparing differences at the DNA sequence level. While a comparison of actual DNA sequences would provide a more complete measure of genetic diversity, limitations on resources make this impractical for full genome comparison.

DNA-based Markers

The most frequently used type of molecular marker to date has been RFLPs, due to their high level of distinguishable polymorphism and the ability to generate probes without prior sequence knowledge. RFLPs are detected by the use of restriction enzymes that cut genomic DNA at specific sequences, resulting in DNA fragments of
different sizes. RFLPs are visualized using Southern blot analysis with labeled probes that are either random genomic DNA or copies of transcribed genes (cDNA). RFLPs are normally codominant, as heterozygotes and homozygotes can be distinguished. Although there are few alleles per locus, RFLPs are useful as they are abundant throughout the genome (Lynch and Walsh 1998). They do, however, require a large amount of purified DNA for analysis (15 to 20 ug for wheat). The use of radioactivity also makes them a less desirable marker for high throughput diversity analysis.

PCR-based markers are becoming more frequently used, as these do not require radioactivity and the products are often relatively simple to visualize and score. They have been developed using three different strategies (Staub et al. 1996): i) markers that are amplified using single random primers, such as RAPDs, ii) markers using selective amplification of endonuclease-digested DNA fragments, i.e. AFLPs, and iii) markers using two primers that measure the variability of the target sequence between them (ISSRs and SSRs).

Short, randomly amplified pieces of DNA are the basis of markers in RAPDs. They are highly abundant within the genome. They offer no information about the location of the DNA being amplified, but provide opportunities for fingerprinting DNA about which little is known. They are dominant, in the sense that they do not allow for distinction between homozygous or heterozygous states. They are codominant in some cases, as occasionally RAPD bands of differing lengths can be assigned to the same
locus. They are visualized using ethidium bromide-stained agarose gels. They allow for the opportunity to amplify several different loci using a single primer, and require a minimal amount of DNA for analysis (10-25 ng). On the other hand, they are generally considered unreliable due to a lack of repeatability in the fingerprints that are generated, and due to the random nature of the primers used.

AFLPs are dominant, multilocus markers that exhibit high levels of polymorphism, and offer high resolution. They are produced using DNA markers of random origin on DNA fragments resulting from the action of restriction enzymes (Vos et al. 1995). These are visualized by using primers that are either fluorescently or radioactively labeled. AFLPs are useful because many markers can be generated with minimal primer testing, are highly polymorphic, and are relatively easy to score. Yet, these polymorphisms are less facile in interpretation. The multilocus nature of these markers reduces the ability to compare different alleles of the same locus to one another, since all alleles are measured on a presence/absence basis, regardless of locus.

SSRs are codominant loci that are highly polymorphic. SSRs have an added advantage in that the chromosomal locations for these are frequently known. Two primers are used in generating SSRs that are complementary to sequences on either side of a series of simple repeats. These repeats (di, tri, or tetranucleotide) differ in length, and these polymorphisms can be visualized using fluorescent labeling and electrophoresis on either agarose or polyacrylamide gels. The primers are developed from known
sequences. As more sequence data becomes available from large-scale genome projects, the number of species-specific SSRs is also increasing. Dinucleotide repeats are most commonly used. However, due to scoring difficulties, some researchers are choosing to employ more trinucleotide SSRs (M. Warburton, personal communication).

ISSRs are another PCR based marker technology that uses simple sequence repeats as the primer and measures the polymorphism of regions between these repeats. Nagaoka and Ogihara (1997) showed that ISSR polymorphism is similar to that of RFLPs in wheat, and higher than that obtained from RAPDs. As with SSRs, some of these markers are mapped, yet precise sequence information is unnecessary to produce them. Several studies have compared the efficacy of each of these molecular markers. Choice of marker technology depends largely on the objectives of each individual study, the time and financial resources available, equipment, qualification requirements, safety concerns, and availability of markers.

Wheat

Breeding efforts on wheat have been underway since the early 1800s. These efforts have impacted wheat’s architecture, yield, grain quality, and biotic and abiotic stress resistance, and presumably, genetic diversity within this species. Wheat (*Triticum aestivum* L.) often is considered “the most valuable single crop in the modern world” (Diamond 1997) and has been the subject of intense improvement efforts. It has been
cultivated in southwestern Asia, its geographic center of origin, for more than 10,000 years. It is predominantly a self-pollinated species. Individual cultivars, lines, and plants tend to be homozygous as alleles have become fixed through self-pollination.

Wheat is an allohexaploid with a comparatively large genome (13.3 gigabases), approximately three times larger than the genome of humans or corn. Modern bread wheat is the result of ancient hybridization events involving three different, related ancestral species. The three different genomes (A, B, and D) found in wheat are mostly homoeologous (orthologous) to one another and often contain duplications of genetic material. The large chromosome number ($2n=6x=42$) of wheat and polyploidy have been an obstacle to studying the genetics of wheat. However, its significance to human society and its long history of breeding make it an important choice for study of genetic diversity. Additionally, over 400,000 accessions are housed in collections all over the world, allowing for large-scale studies of \textit{a priori} genetic diversity and providing a broad genetic base for future breeding efforts (Poehlman and Sleper 1995).

In the past century, major advances in yield and productivity have been achieved in wheat. In the 1950’s, a concerted international breeding effort began that when combined with intense management, ultimately led to the “Green Revolution,” which changed the management practices for wheat production (Poehlman and Sleper 1995). New semidwarf varieties of wheat were developed and released by the International
Maize and Wheat Improvement Center (CIMMYT) that were able to grow under high fertilization without lodging, significantly increasing yield. These varieties were distributed worldwide through cooperative release and breeding efforts. In some cases, these new wheat varieties have replaced local landraces. The rapid adoption of semidwarfs and loss of local landraces increased concerns over genetic variability of crops and interests in quantifying allelic variation in germplasm.

Wheat Diversity

In response to recent concerns over narrowing genetic pools, and impact from the "Green Revolution", CIMMYT undertook a diversity study of all "CIMMYT-related" bread wheat from 1965 to 2000 (Smale et al. 2001). This study examined diversity at a molecular level using genetic markers. It also examined potential loss of variation due to the declining presence of landraces in the germplasm pools. The authors used several types of molecular markers as well as pedigree information to study the diversity remaining after intense breeding. They rejected the hypothesis of genetic narrowing in modern plant breeding efforts based on i) the reports regarding the selection of parental lines and ii) evidence of high allelic variation as determined using DNA-based markers. Although there are a limited number of major parental lines used in modern breeding programs, these programs incorporated a large number of landraces as donors of alleles for desirable traits (Smale et al. 2001). While these donors do not provide the genetic backbone of the released varieties, their utilization
refutes the assertion that breeding programs discard available diversity and utilize only elite cultivars for crossing.

Smale et al.’s study (2001) further addressed changes in diversity across time. While diversity estimates for each decade did vary, there was no linear correlation, and no significant difference among cultivars in the earliest decade studied versus among those in the most recent decade. The essence of these findings is similar to a study by Manifesto et al. (2001), where no evidence was found for the loss of genetic variation in Argentinean spring-wheat cultivars released from 1932 to 1995. While the amount of diversity did fluctuate over decades, no significant trend was found. As with the study by Smale et al. (2002), Manifesto et al. (2001) concluded that the genetic diversity had indeed changed qualitatively, but not quantitatively. A study of wheat from the United Kingdom since the 1930’s which used AFLPs, SSRs, storage proteins, and morphological characteristics likewise found no indication of decrease in diversity over time (Donini et al. 2000).

Selection of Markers for Wheat Diversity Studies

Roeder et al. 1998), ISSRs (Nagaoka and Ogihara 1997) and combinations of the above (Donini et al. 2000, Souza et al. 1994).

As previously noted, RFLPs are not a desirable marker for wheat due to the low level of polymorphism. While useful when other markers are unavailable, RAPDs are considered inferior because they are not repeatable and their chromosomal location is not normally known.

Barrett and Kidwell (1998) advocated the use of AFLPs rather than SSRs for wheat diversity studies, as the mean number of polymorphic bands per SSR primer is less than half that detected by AFLPs among the hexaploid wheats in their study. AFLP bands, however, may represent a number of loci and therefore may be difficult to score. Additionally, higher polymorphism is not necessarily indicative of a more optimal marker. In a study that used AFLPs to distinguish sister lines of Bobwhite, Warburton et al. (2002) found that the presence of wheat-alien translocations could bias genetic diversity estimates when using unmapped markers such as AFLPs.

Many researchers advocate the use of SSRs, as several hundred of these markers are mapped and publicly available (Fahima et al. 2002, Hammer et al. 2000, Pestsova et al. 2000, Plaschke et al. 1995, Roeder et al. 1998, Stephenson et al. 1998). The abundance of simple repetitive DNA in a genome has been attributed to slipped strand mispairing (Levinson and Gutman 1987). This process is believed to be a ubiquitous
force in the evolution of eukaryotic genomes. SSRs are thought to represent stepwise mutations, providing inference about phylogenetic relationships. However, it is important to point out that mutation rate in SSRs is high, and there are limited numbers of alleles per marker. Nauta and Weissing (1996) warn that many SSR loci, "much more than 15," are necessary to correctly infer a given phylogenetic relationship. A recent study has suggested that some of the variation at microsatellite loci may come from insertions or deletions (indels) in the flanking region rather than in the repeat motifs (Matsuoka et al. 2002). This reduces the ability to distinguish relationships as the stepwise mutation hypothesis becomes inaccurate. The relative contribution of indels and repeat length to the variation of SSR markers remains to be examined.

Regardless of phylogenetic limitations of microsatellites, SSRs remain useful to quantify the diversity within germplasm, as well as many other possible uses. Plaschke et al. (1995) suggested the use of SSRs for wheat cultivar identification. This is of increasing interest as intellectual property rights become more of an issue in crop improvement. Manifesto et al. (2001) found that a set of 10 SSRs were able to conclusivey differentiate between 105 lines of bread wheat.

ISSRs may provide another valuable tool for cultivar identification. A study using a series of 33 polymorphic ISSRs found that each was able to distinguish among 6 lines of cultivated wheat (Nagaoka and Ogihara 1997). Whether more ISSRS will be
needed or whether this set of ISSRs can distinguish closely related lines remains to be explored.

Chloroplast SSRs

Chloroplast DNA is a circular molecule that is maternally inherited in wheat and grass species. For these reasons, the chloroplast genome can be studied as a haplotype (Ishii et al. 2001). Previous studies in soybean have shown that closed populations of inbreeding crop species can remain genetically diverse for as many as 50 generations in a given area (Allard 1988). Lee et al. (1994) used chloroplast and mitochondrial DNA RFLPs to determine the number of distinct cytoplasmic genotypes in soybean. A group of females were chosen based on diverse phenotypes for development of new populations. These were found to have few cytoplasmic types, despite the higher levels of phenotypic variation. When these females were placed in a forced outcrossing situation, the cytoplasmic diversity declined substantially through subsequent crossings. This implied that some chloroplast interactions affected the fitness of the outcrossed offspring. The full implications of chloroplast/nuclear interactions remain unclear.

Variation in chloroplast DNA in ancestral species of wheat has been studied previously using RFLPs (Miyashita et al. 1994). Chloroplast haplotypes within cultivated wheat have not been thoroughly investigated. Using the DNA sequence of the wheat chloroplast genome (Ogihara et al. 2000), Ishii et al. (2001) developed 24
chloroplast SSR (cpSSRs). Twenty-one of these were found to be polymorphic, and were used to differentiate chloroplast (or plastome) haplotypes in wheat and its ancestral species. The values of diversity using these cpSSRs were found to match those determined by RFLP analysis. Although some have warned against using SSRs for phylogenetic evaluation due to size homoplasy (Doyle et al. 1998), Ishii et al. (2001) dismissed these concerns, noting that the polymorphic loci were from different regions of the genome and therefore would not be seriously affected by size homoplasy at individual loci. There was a high level of haplotype diversity between species, and some diversity was noted within species, even using a small number of lines.

Although cpSSRs have been used to differentiate closely related species, no studies have addressed plastome diversity within a cultivated species using cpSSRs. While Ishii et al.’s (2000) initial study indicates that common wheat has at least two chloroplast haplotypes, due to the high variability noted in cpSSRs, the possibility exists that there are several haplotypes that have not yet been identified. To date, the amount of chloroplast haplotype diversity within cultivated wheat has not been explored.
Materials and Methods

Plant Materials

In order to get an initial picture of diversity available in PNW wheat breeding germplasm, the genotypes included were selected to represent the major classifications that have been important in the PNW. This study included 174 genotypes chosen to represent significant parental lines of cultivars developed in the Pacific Northwest, commonly grown cultivars, experimental lines, and lines of interest that have similar adaptations of unique traits of value to Oregon State University’s wheat breeding program. Appendix 1 lists all accessions used, their Plant or Collection Identification numbers, and the source of seed used for this study. Appendix 4 lists the pedigrees for several of the major lines included in this study. All plants were grown under greenhouse conditions in Corvallis, OR for approximately 3 weeks before they were harvested for DNA extraction.

DNA Extraction

DNA extraction was performed using a protocol described by Liu and Whittier (1994) with modifications to increase throughput. DNA was extracted from a bulk of leaves from eight plants of each seed source. Tissue was kept on ice throughout the extraction procedure except during centrifugation. A 30-50 mg sample of total bulked tissue was cut into 1 cm pieces and placed in a 1.5 mL vial. Then 400 uL of cold DNA isolation buffer [10 mM Tris-HCl pH 9.5, 10 mM EDTA, 100 mM KCl, 0.5 M
sucrose, 4 mM spermidine, 1.0 mM spermine, 0.1 % (v/v) 2-mercaptoethanol, 2% (w/v) sarkosyl] was added to each tube. The samples were ground by placing a tungsten carbide bead in each tube and using a mixer mill (Retsch MM 300 USA) according to the manufacturer's directions for 1 min 30 sec at 30 sec⁻¹ on each side. Then, the tubes were centrifuged for 5 min at ~6000 g. After removing the tungsten beads with a magnet, 250 uL of phenol:chloroform (1:1 mixture) was added to each tube. The tubes were then mixed gently by hand and centrifuged for 25 min. at ~6000 g. The aqueous layer (300 uL) containing the DNA was transferred to new tubes. Approximately 30 uL of 3 M sodium acetate (pH 5.0) and approximately 750 uL of cold absolute ethanol were added to the supernatant to precipitate the DNA. These were mixed well and then centrifuged at ~6000 g for another 30 min. The alcohol was removed from the DNA pellet, and 0.5 mL of cold 70% ethanol was added to each tube to remove the salt. The tubes were again centrifuged for 30 min at ~6000 g. The alcohol was drawn off and pellets allowed to air-dry completely. DNA was dissolved in TE buffer (pH 8.0) containing 10 ug mL⁻¹ RNase to a concentration of 50 ng/uL and stored at −20 °C until used in PCR cycling.

SSR Markers

The nuclear SSR loci used in this study (Table 2) were developed by Roeder et al. (1998), and chloroplast SSR loci in this study (Table 1) were developed by Ishii et al. (2000). The nuclear markers are distributed throughout the genome with two chromosomes left uncovered (Figure 1). Primers were synthesized by MWG Biotech
Figure 1. Map of 21 wheat linkage groups with approximate location of the 24 gwm markers used in this study.
(Greensboro, NC). The reverse primer for each of these markers was fluorescently labeled with TET (4,7,2',7'-tetrachloro-6-carboxyflourescein), FAM (6-carboxyflourescein), or Hex (4,7,2',4',5',7'-hexachloro-6-carboxyflourescein) for fluorescence-based detection.

PCR amplifications were carried out in an MWG Primus 96 thermocycler in a 10 µL reaction mixture. Each reaction contained 10mM Tris-HCl (pH 9.0), 50mM KCl, 0.1% Triton X-100, 1.5 mM MgCl₂, 0.3 mM dNTPs, 0.03 U Taq polymerase (Promega), and 0.5 µM each of forward and reverse primers, with 100 ng of template DNA. The cycling parameters consisted of 3 minutes at 95 °C, followed by 45 cycles of 1 minute of 95 °C, 2 minutes at the pertinent annealing temperature and 1 minute at 74 °C. These cycles were then followed with a terminal extension of 10 minutes at 74 °C.

PCR products were diluted and sent to the Central Services Lab (CSL) at the Center for Gene Research and Biotechnology (Oregon State University) for fragment analysis using the ABI Prizm 3700® slab gel system and 3100® capillary system from Applied Biosystems (Foster City, CA). Allele sizes were determined using Genotyper® v 2.5.x Software (Applied Biosystems, Foster City, CA).
Data analysis

The nuclear markers are di-nucleotide repeats and therefore alleles were called based on two base pair differences in PCR product length. Chloroplast markers are single nucleotide repeats, and thus a single nucleotide difference in length should be considered a different allele. However, the CSL only guaranteed resolution to 0.5 base pairs. As this could result in some overlap in allele sizing, chloroplast alleles were called as with the nuclear markers on the basis of two base pair differences in PCR product length. While this reduces the precision of the diversity estimates, it increases the accuracy by reducing Type I error (calling alleles different that are actually the same). While some markers undoubtedly produce null alleles, all data points without allele sizes were treated as missing data, since null alleles and failed PCR cannot be distinguished. While this decreases the informativeness of markers that detect null alleles, it reduces the possibility of Type I error, increasing the accuracy of genetic diversity estimates using the entire marker set.

The number of alleles per locus, diversity estimates, number of taxon-specific alleles, and number of rare alleles (defined as occurring in less than 10% of the lines studied) were calculated with Microsat® v. 1.5d (Stanford, CA) and compared for the chloroplast SSR data alone, nuclear SSR data alone, and combined chloroplast and nuclear SSR data.
Three separate similarity matrices were produced for i) chloroplast SSR data, ii) nuclear SSR data, and iii) the entire data set using Microsat® v. 1.5d software, selecting the proportion of shared alleles statistic with 100 bootstraps. The matrix of the mean of bootstrap output was then analyzed by the SAHN cluster routine using the UPGMA (unweighted pair group method, arithmetic average) method of clustering using NTSYS software (Rohlfe 1992). The output was graphically represented as a dendrogram.
Results and Discussion

Chloroplast Diversity

Utility of Markers

Chloroplast markers for wheat have only recently been developed (Ishii et al. 2001), and have not yet been used to study wheat germplasm. The first objective of this study was to explore the effectiveness of these markers for diversity analysis of PNW wheat germplasm. Chloroplast SSR allele sizes for the genotypes studied here are presented in Appendix 2. Other chloroplast SSRs (cpSSRs) were tried (WCt16 and WCt24), but were found to be monomorphic at the two base pair level. These markers were eliminated from the overall analysis as they did not differentiate the germplasm and did not alter clustering patterns. Table 1 shows the number of rare alleles per locus and the number of taxon-specific alleles per locus. For the set of 15 chloroplast markers used, a total of 73 alleles were identified, with an average of 4.87 alleles per locus. This average was slightly higher than that of Ishii et al. (2000) who found an average of 4.13 alleles per locus for this set of cpSSRs. The exclusion of monomorphic markers from this study may account for the higher amount of polymorphism. For five of the markers, however, this study actually found slightly fewer alleles than previously reported. This may be related to scoring of alleles at a two base pair difference rather than a single nucleotide difference. Additionally, the plant material studied in Ishii et al. (2001) included more genetically divergent stocks,
Table 1. Allele frequencies for chloroplast simple sequence repeat markers.

<table>
<thead>
<tr>
<th>Marker</th>
<th>Total Alleles</th>
<th>Rare Alleles&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Lines containing Rare Alleles (%)&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Taxon-specific Alleles</th>
<th>Lines with most common allele (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wct1</td>
<td>3</td>
<td>1</td>
<td>1 (1)</td>
<td>1</td>
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</tr>
<tr>
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<td>35 (20)</td>
<td>3</td>
<td>111 (64)</td>
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<td>Wct11</td>
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<td>20 (11)</td>
<td>2</td>
<td>94 (54)</td>
</tr>
<tr>
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<td>2</td>
<td>16 (09)</td>
<td>1</td>
<td>157 (90)</td>
</tr>
<tr>
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<td>2</td>
<td>27 (16)</td>
<td>0</td>
<td>132 (76)</td>
</tr>
<tr>
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<td>2</td>
<td>0 (1)</td>
<td>0</td>
<td>87 (50)</td>
</tr>
<tr>
<td>Wct15</td>
<td>14</td>
<td>11</td>
<td>72 (41)</td>
<td>3</td>
<td>33 (19)</td>
</tr>
<tr>
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<td>0</td>
<td>117 (67)</td>
</tr>
<tr>
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<td>0</td>
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</tr>
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<td>3 (2)</td>
<td>0</td>
<td>92 (53)</td>
</tr>
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<td>1</td>
<td>164 (94)</td>
</tr>
<tr>
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<td>3</td>
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<td>1</td>
<td>154 (89)</td>
</tr>
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<td>15 (9)</td>
<td>0</td>
<td>93 (53)</td>
</tr>
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<td>4</td>
<td>14 (8)</td>
<td>2</td>
<td>105 (60)</td>
</tr>
<tr>
<td>Wct9</td>
<td>3</td>
<td>0</td>
<td>0 (0)</td>
<td>0</td>
<td>113 (65)</td>
</tr>
<tr>
<td>Total</td>
<td>73</td>
<td>44</td>
<td>233 (9)</td>
<td>14</td>
<td>1694 (65)</td>
</tr>
<tr>
<td>Mean/ Locus</td>
<td>4.87</td>
<td>2.93</td>
<td>15.53</td>
<td>0.93</td>
<td>112.93</td>
</tr>
</tbody>
</table>

<sup>a</sup> Rare alleles are those present in less than 10% of the lines.

<sup>b</sup> Percentage is based on a total of 174 lines.
including several species, and thus a lower level of diversity is to be expected from this study. The set of markers yielded an average of 2.93 rare alleles per locus and 0.93 taxon-specific alleles per locus. Seven of these markers, however, revealed no taxon-specific alleles, and if these are eliminated, the average number of taxon specific alleles increases to 1.75 per locus. WCt10 and WCt15 yielded the highest number of both rare and taxon specific alleles, constituting over 40 percent of both the rare and taxon specific alleles of this pool.

The percentage of lines containing rare alleles and the percentage of lines containing the most common allele were identified for each marker (Table 1). Some markers, such as WCt22, WCt4, and WCt12 are essentially monomorphic, with 89 to 94% of the lines containing the most common allele. Other markers (WCt11, WCt6, WCt8, WCt1, WCt14, WCt19), however, were able to separate the majority of lines into two or more groups, since 60% or less of the lines contained the single most common allele. Thus, the markers that revealed a high percentage of lines represented by the single most common allele are less useful for the study of the major clustering events. The measurement of percentage of lines containing rare alleles indicates a useful marker because it reflects both the number of rare alleles yielded by that marker and their frequency in the population studied.

For the entire pool of 174 lines, 9% of the lines contained rare alleles and 65% of the lines contained the single most common allele (Table 1). The most useful markers
were those that revealed a high percentage of lines containing rare alleles with a low percentage represented by the single most common allele. These also revealed several alleles that were present in more than 10% of the lines. The markers in this category were WCt1, WCt11, WCt14, WCt19, WCt6, and WCt15. While WCt10 revealed a high percentage of lines with rare alleles (20%), 63% of the remaining lines are represented by a single allele. Thus, for the purposes of differentiating major groups, this marker was less useful than the others listed above.

Cluster Analysis

The second objective of this study was to analyze the cytoplasmic diversity available in PNW wheat breeding germplasm. These markers were able to distinguish the three plasmon types in this study (Figure 2a, b, c, and d). Analysis using UPGMA yielded three major groups, represented by the B type cytoplasm, D type cytoplasm, and barley (*Hordeum vulgare*) cytoplasm. This is in concordance with previous observations that these cpSSRs are able to distinguish between plasmon types of *Triticum* and *Aegilops* (Ishii et al. 2001). The barley group was most distantly related to the other two groups and contained five lines that had been included to test the efficacy of wheat cpSSR markers in this species. As no nomenclature has been established for this cytoplasm, it has been labeled here in concordance with its nuclear genome as H type cytoplasm.
Figure 2a. Genetic relatedness tree from chloroplast SSR data, including B type cytoplasm, D type cytoplasm, and "H" type cytoplasm.
Figure 2b. Genetic relatedness tree from chloroplast SSR data, showing B type cytoplasm Group 1.
Figure 2c. Genetic relatedness tree from chloroplast SSR data, showing wheat B type cytoplasm Groups 2, 3, and 4.
Figure 2d. Genetic relatedness tree from chloroplast SSR data showing non-wheat chloroplast types including barley and two types of D-type cytoplasm, *Ae. tauschii* and VPM1-type.
Within PNW wheat germplasm, there appear to be at least four major clusters of B type cytoplasm (Group 1 in Figure 2b, and Groups 2, 3, and 4 in Figure 2c). These clusters do not have any obvious biological or parental basis for their differentiation. The four groups cluster together at coefficient 0.44, but are distinct from genotypes with D type and barley cytoplasm by almost as much difference as is exhibited within the wheat group (0.36). Wheat chloroplast Groups 1 and 2 are two major groups that separate at coefficient 0.35. These connect to Group 3 at coefficient 0.42, which then connects to Group 4 at coefficient 0.44.

Synthetic hexaploid wheats, produced by crossing durum wheat (\(T. turgidum, 2n = 4x = 28, AB\) genomes) with \(Ae. tauschii\) (\(2n = 2x = 14, D\) genome), have been shown to have potentially useful genetic variation for wheat improvement (del Blanco et al. 2001). M6 is a synthetic hexaploid wheat included in this study. It clustered with genotypes in Group 1 of wheat (Figure 2b). This was expected as durum wheat, which has B type cytoplasm, was used as the maternal parent in its development.

In addition to four major wheat cytoplasmic groups, three minor distinct groups were found. One group was represented by the cultivars Hatton, Jagger and Westbred 936, and Oberkulmer. Based on pedigree information, Hatton possesses the cytoplasm of an Iranian landrace (PI 142522). The nature of the cytoplasm of Jagger and Westbred 936 is unknown based on the available information. This study suggests that these cultivars share a common B type cytoplasm lineage that is quite distinct from the
majority of the cultivars studied. At coefficient 0.48, the line Oberkulmer connects with the other groups of the wheat B cytoplasm group (Figure 2d). This line is a Western European landrace of spelt wheat. Spelt wheat is considered a subspecies of *T. aestivum* (ssp. *spelta*), and thus was expected to have a distinct plastome from other wheat types.

The D type cytoplasm also constituted a group that was separate from either wheat or barley (Figure 2d). It is related to B type cytoplasm at the coefficient level of 0.79, intermediate between the relatedness level of wheat B plasmon type and barley H plasmon type, as would reflect genetic relatedness between the *Aegilops* and *Triticum* genera, which are more closely related to one another than either is to barley. This cluster is then subdivided into two groups at the coefficient level of 0.64, and contains the highest level of within-group variation. In fact, the two clusters may represent two distinct plastome types of *Aegilops*, one containing four lines of classic D type plastome from *Ae. tauschii* and one containing 10 lines that putatively have cytoplasm from *Ae. ventricosa*. Ishii et al. (2001) found that these cpSSR markers were sufficient to differentiate between various other species of *Triticum* and *Aegilops* (such as *Ae. speltoides*, *Ae. squarrosa*, *T. araraticum*, *T. dicoccoides*, *T. dicoccum*, *T. aestivum*, *T. spelta*, and *T. macha*). Thus it is not surprising that these markers differentiated the various cytoplasmic types in this study.
A cluster representing VPM1-related cytoplasm (Group 1 in Figure 2d) was identified which consists of ten wheat lines from both Europe and the PNW with resistance to the fungal disease strawbreaker foot rot (eyespot), caused by *Pseudocercospora herpotrichoides*. These lines have this resistance from the breeding line VPM1, which was developed from a cross of *Ae. ventricosa*/*T. aestivum*. Pedigree information for some of these lines can be found in Appendix 4. The maternal parent of VPM1, based on this analysis was *Ae. ventricosa*, thus VPM1 and any offspring for which it served as the maternal parent contain *Ae. ventricosa* type cytoplasm. This group is distinct from, but related to, the chloroplast type of *Ae. tauschii* (Group 2 in Figure 2d). Included in the group of VPM1 descendants is Madsen, which is a widely grown variety in the PNW. This finding demonstrates the successful alloplasmic lineage of wheat varieties.

Rendezvous is a Western European line that also has resistance to eyespot that was derived from VPM1 (Angus 2001). It appears to have *Ae. ventricosa* cytoplasm, which indicates that VPM1 was a maternal parent in its development. Other European lines that appear to have *Ae. ventricosa* cytoplasm are Roazon and FR-50.

Numerous lines derived from VPM1 do not cluster with the D type cytoplasm. Coda, Temple, and Weatherford all had VPM1 as a paternal parent, and thus have retained B cytoplasm. The pedigree of Hyak indicates VPM1 as the maternal parent, yet it appears in Group 1 (Figure 2b) of the B cytoplasm group. This suggests that the
actual pedigree for Hyak should indicate a different direction of crossing. Tyee should be the maternal parent, and VPM1/Moisson 421 the paternal parent, either in the original cross or the backcross. This would explain why Hyak clusters with the B cytoplasm rather than with all of the other lines descended from VPM1. WA 7690, which is listed as being a VPM1 descendent, and which contains eyespot resistance, however, clusters with the *Ae. tauschii* rather than with Group 2 of the D cytoplasmic lines. The reasons for this are unclear.

Barley lines were included in this study to test the efficacy of wheat chloroplast markers in this species. All markers in this group were able to amplify barley chloroplast DNA. These lines clustered separately from both D cytoplasm and B cytoplasm types and served to root the dendrogram at a clustering coefficient of 0.92 (Figure 2d). They were more closely related to one another than are the wheat lines in Groups 1 through 4, since the highest clustering coefficient within the barley group is 0.31.

**Conclusions**

The first objective of this study was to examine the usefulness of these markers in this germplasm. The 15 wheat chloroplast markers used in this study were able to differentiate three cytoplasmic types- B type, D type, and barley. They revealed at least five plastomic types within the wheat plasmon group studied. These markers
were also able to distinguish spelt wheat from common wheat, but were unable to
differentiate durum wheat from hexaploid wheat.

Two markers (WCt10 and WCt15) accounted for over 40% of the rare and taxon-
specific alleles. Several other markers were found to be particularly useful for
studying the chloroplast diversity of PNW wheat breeding germplasm because they
revealed several rare alleles and were also able to segregate these lines into two or
more distinct groups (WCt11, WCt6, WCt8, WCt1, WCt14, and WCt19).

The second objective of this study was to analyze the chloroplast diversity available.
Five plastomic types were found within the B cytoplasm group. In addition, several of
the lines in PNW wheat breeding germplasm appear to contain the cytoplasm of *Ae.
ventricosa* rather than that of wheat, including one of the most commonly grown
cultivars in the region, Madsen. This is an example of inadvertent widening of the
cytoplasmic diversity of breeding germplasm by introduction of eyespot resistance
from VPM1 material. Additionally, nuclear/cytoplasmic interactions may have effects
on desired traits and thus the presence of this alien cytoplasm in wheat lines is
significant. Thus, alloplasmic effects need to be further studied.
Nuclear Diversity

Utility of Markers

Complete allele sizing data from nuclear SSRs are shown in Appendix 3. The first objective of this study was to determine the usefulness of these markers in PNW wheat breeding germplasm. For this set of 24 nuclear markers, a total of 268 alleles were identified. The number of alleles per locus ranged from 4 for gwm608 to 30 for gwm282, with an average of 11.2 per locus (Table 2). Previous studies have shown a range of average alleles per locus for SSR markers from 4.2 (Stachel et al. 2000) to 18.1 (Huang et al. 2002). Genetic diversity of 500 European lines was assessed using 19 SSRs (Roeder et al. 2002), including 12 of those used in this study, and the average alleles per locus was 10.3. This is in contrast to the 18.1 alleles per locus reported by Huang et al. (2002), from a survey of accessions from the germplasm bank at the Institute for Plant Genetics and Crop Plant Research (IPK), Gatersleben (Germany). The average number of alleles per locus from this study was more similar to that of European germplasm than that of the germplasm bank. As both the current study and that of Roeder et al. (2002) involved a particular germplasm group consisting of predominantly winter wheat, this result was expected. The slightly higher measurement obtained from the current study is most likely due to the number of markers, the particular markers selected, and the addition of Ae. tauschii, M6, Oberkulmer and other unrelated wheats.
### Table 2. Allele frequencies for nuclear simple sequence repeat markers.

<table>
<thead>
<tr>
<th>Marker</th>
<th>Total Alleles</th>
<th>Rare Alleles</th>
<th>Lines containing Rare Alleles (%)</th>
<th>Taxon-specific Alleles</th>
<th>Lines with most common allele (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Xgwm3</td>
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<td>4</td>
<td>15 (9)</td>
<td>2</td>
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<td>26 (15)</td>
<td>2</td>
<td>73 (43)</td>
</tr>
<tr>
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<td>13</td>
<td>32 (18)</td>
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<td>49 (29)</td>
</tr>
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<td>61</td>
<td>1263</td>
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<tr>
<td>Mean</td>
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<td>8.1</td>
<td>36.2 (20)</td>
<td>2.5</td>
<td>52.6 (30)</td>
</tr>
</tbody>
</table>

*a* Rare alleles are those present in less than 10% of the lines. *b* Percentage is based on 171 lines.
Fourteen of the markers in this study were also in a recent study by Huang et al. (2002). Each of these markers, except gwm458, yielded a lower number of alleles per locus in this study than previously reported. The study by Huang et al. (2002) involved four times as many genotypes, including lines from 68 countries of five different continents. It is not unexpected that a study of a set of germplasm adapted to one particular region would exhibit less allelic variation than the broader international germplasm study.

The markers in this study showed an average of 8.08 rare alleles per locus and 2.54 taxon-specific alleles per locus. Five of the markers yielded no taxon-specific alleles. Gwm282 yielded both the highest number of taxon specific alleles and the highest number of alleles for a single marker (30). The distribution of alleles was compared with that reported by Huang et al. (2002). The distribution of alleles was not similar to those reported for the majority of markers. This study revealed fewer normally distributed markers and more randomly distributed markers than observed by Huang et al (2002). These results suggest that allelic distribution, and perhaps informativeness in general, is specific to the set of markers and populations studied rather than a function of the individual markers themselves.
Cluster Analysis

Major Clusters

The third objective of this study was to explore the nuclear diversity of this germplasm and to determine the biological significance of nuclear clustering patterns. Pedigree information was used to explain and characterize major clusters as based on nuclear SSR data (Appendix 4). The dendrogram from nuclear SSR data was inspected to locate clustering branches with several lines that had coefficients higher than 0.74. Five major clusters (Figure 3) were identified: Group 1 was represented by PNW soft white wheat clusters; Group 2 includes European-derived and related red wheat cultivars; cultivars in Group 3 a less distinct cluster or more distantly-related lines; Group 4 contains hard wheat cultivars from the Great Plains; and Group 5 includes lines used as genetic stocks, synthetics, and other distantly related cultivars. Group 1 and Group 2 cluster at a coefficient of 0.74. Group 4 then joins Groups 1 and 2 at coefficient 0.81. There were several subclusters within each of these major clusters. Lines in Group 3 clustered very loosely with the major groups (clustering coefficients higher than 0.84). The primary biological division for the major groups appears to be regional adaptation. This is consistent with a previous report of a wheat diversity study using SSR data (Roeder et al. 2002). As particular market classes are grown in different regions in the U.S., the clusters also appear to differentiate, although less distinctly, on market class.
Figure 3a. Genetic relatedness tree from nuclear SSR data with major clusters.
Figure 3b. Genetic relatedness tree from nuclear SSR data. Group 1: PNW Soft White Cultivars
Figure 3c. Genetic relatedness tree from nuclear SSR data. Group 2: European and Related Red Wheat Cultivars and Group 3: Distantly Related Cultivars.
Figure 3d. Genetic relatedness tree from nuclear SSR data. Group 4: Great Plains Hard Wheat Cultivars and Group 5: Genetic Stocks, Synthetics, and Distantly Related Cultivars.
AFLP analysis by Barrett and Kidwell (1998) suggested that divisions between market classes (hard vs. soft or red vs. white) within growth habit (winter, spring, or facultative) were not statistically supportable by clustering associations. In this study, while the primary factor in clustering appears to be regional, market class contributes to clustering within regional groups.

**Group 1: Pacific Northwest soft white wheat cultivars**

The first major group (converging at a clustering coefficient of 0.72) consists of soft white winter wheat cultivars from the PNW (Cluster 1 in Figure 3b). This group is further divided into four subsets on the basis of shared parental lines. Group 1a (coefficient 0.61) is composed of lines of club wheat and parental lines that provide much of the genetic foundation of the soft white class. Group 1b consists of lines closely related to Gaines with lineage based on parental lines Norm 10, Brevor, and Burt. This group includes the first major semi-dwarf varieties of wheat in the PNW released in the late 1960's. Group 1c (coefficient 0.71) cultivars were defined by commonalities with Stephens, and based on parental lines Nord Deprez and Pullman 101. Group 1d, which joins the clusters at coefficient 0.72, is linked through association with Luke, and represents the modern derivatives of Norin 10/ Brevor Group. Groups 1a and 1b cluster the most closely together (coefficient 0.67). Lines in Group 1a were used as parents in development of many lines in Group 1b.
Group 1a: Club wheat and soft white foundation cultivars

The first group (Group 1a in Figure 3b) is represented predominantly by club wheats, and includes such major cultivars as Elgin, Omar, Edwin, Hiller, and Tres. This Group also includes lines that are important progenitor stocks, such as Goldcoin, and modern variety clubs like Tres and Elgin, which have been used in the development of other cultivars. Additionally, several of them are parent/offspring duos (see pedigree information in Appendix 4). White club wheat was previously reported as the only category of winter wheat that consistently clustered together (69% of bootstrap trees) using AFLP data (Barret and Kidwell 1998).

Six club lines (Barbee, Coda, Albit, Hybrid 128, Little Club, and WA 7621) failed to be associated with Group 1a, and were dispersed throughout the other clusters. Little Club is a spring wheat, thus it is not unexpected that it segregated separately from the winter club group (in Group 3 in Figure 3c). It is also a major parent of Hybrid 128, which is in turn a major parental contributor of Albit (Group 4 in Figure 3d). WA 7621, Coda, and WA 7217 are all club wheats that have been bred for resistance to strawbreaker foot rot (eyespot) with parental contributions of common wheat and VPM1. They cluster with other of VPM1-related lines (Group 2b in Figure 3c). Barbee, also derived from a club by common wheat cross (but not VPM1 related), and its progeny WA 7217 were distinct and clustered more closely with common wheats than with the other club lines.
Group 1b: Gaines lineage based on Norin 10, Brevor, and Burt

The cluster most closely related to club wheats (Group 1b in Figure 3b) includes lines related to Gaines, or its parents Norin 10, Brevor, and Burt. This group includes the first PNW semi-dwarf varieties and the genetic background into which the semi-dwarf trait was introduced. These cluster closely with the club wheats because soft white common cultivars such as Gaines, Nugaines, Coulee, and Raeder have several common parental lines, including Goldcoin, which is an important ancestor of modern club wheats.

Group 1c: Stephens lineage based on Nord Deprez and Pullman 101

Groups 1a and 1b join a large cluster of soft white winter (SWW) wheat varieties at coefficient 0.70. This cluster (Group 1c in Figure 3b) is characterized by relationship to Stephens, a major SWW cultivar, and its progenitors Nord Deprez and Pullman 101. Stephens was released in 1978 by Dr. Warren Kronstad at Oregon State University. It has been a major cultivar in PNW production for over two decades. It clusters with its progeny lines such as ID 533, Lambert, Malcolm, Edwin, Brundage, and WA 7624. This cluster includes other lines based on Nord Deprez and Pullman 101, Hyslop, McDermid, and Hill 81 and their more recent offspring WA 7671, WA 7690, Madsen, and Weatherford. Also clustering in this group are 12 Oregon experimental lines that are largely based on parents from this cluster.
Group 1d: Luke lineage based on modern derivatives of Norin 10/Brevor

The final subset of the PNW cluster includes Luke and modern PNW cultivars related to Luke. These lines coalesce at coefficient 0.69. The majority of these cultivars (Luke, Daws, Lewjain, and Dusty) were released in the late 1970's and early 1980's from Washington. They represent the second generation of semi-dwarf improvement in Washington and are related through the progenitor lines Norin 10, which is the semi-dwarf gene donor, and Brevor. These lines, developed in Washington, are related to the Group 2b and share many adaptive characteristics.

Group 2: European and related red wheat cultivars

Group 2 was characterized by a grouping of developed European lines (Figure 3c). Cultivars from Western Europe have many similar adaptive characteristics to PNW soft whites and have been important parents in PNW varietal development efforts. Oregon State University has initiated new germplasm exchange and introgression efforts based on Western European material. The European lines included in this study coalesce at coefficient 0.74. This cluster was further divided into subgroups related to parental contribution; Group 2a includes all of the lines except those in Group 2d, and is defined by Western European cultivars with lineages based on Vilmorin 27, Group 2b (coefficient 0.47) consisting of a subset of lines related to VPM1, and Group 2c (coefficient 0.72) that contains a set of foundation cultivars used in development of the Great Plains hard red winter wheat.
**Group 2a: Western European lineage based on Vilmorin 27.**

Group 2a (Figure 3c) includes many Western European cultivars and two OSU experimental lines. These OSU lines have parental contribution from germplasm from the Netherlands. Within this cluster are several French cultivars derived from Vilmorin 27, including major cultivars Capelle Deprez, Nord Deprez, Isengrain, Talent, and Champlein. Jagger, a Great Plains hard red winter wheat is included in this cluster. It is derived from Stephens, which has parental contributions from Nord Deprez. Capitole and Moisson are both derived from Vilmorin 27 and another major French parental line, Etoile de Choisy, which is also included in this cluster. Renan and WA 7217 both have Norin 10 and Brevor in their backgrounds, as well as contributions from Vilmorin 27. This commonality, along with the Nord Deprez link, may explain why this group clusters more closely with PNW soft whites than does the Group from the U.S. Great Plains.

**Group 2b: Parents and derivatives of VPM1**

Within Group 2a, there is a tight cluster of lines that are closely related to VPM1 and its progeny, which is identified as Group 2b (Figure 3c). Marne was the common wheat parental line of VPM1 and clusters closely with it, at a coefficient of 0.24. Moisson is SWW wheat that is susceptible to strawbreaker foot rot (eyespot), an important fungal disease caused by *Pseudocercosporella herpotrichoides*, and was used in crosses with VPM1 to improve the yield and adaptive characteristics. VPM1 has been an important parent in PNW variety development, contributing eyespot
resistance into PNW wheat breeding germplasm. The two major lines derived from these crosses (VPM1/Moisson 421 and 951) both cluster more closely to Moisson (coefficient 0.25) than to VPM1 (coefficient 0.41) likely due to selection for the adaptive characteristics of Moisson.

**Group 2c: Foundation cultivars for Great Plains hard red winter**

Group 2c includes major cultivars and parents of Great Plains hard red winter wheat. Although the relationship with European materials is less obvious, these cultivars have origins in European landrace material, particularly from Eastern Europe, through Cheyenne, which is a selection from the landrace Crimean. Scout 66, Wanser, Hatton, and Century are all Cheyenne-derived.

**Group 3: Distantly related cultivars**

Lines in Group 3 (Figure 3c) appear to have no obvious basis, whether through pedigree or regional adaptation, for clustering together. They coalesce at a coefficient of 0.80. This high coefficient value within the cluster suggests that they are generally not closely related.

**Group 4: Great Plains hard wheat cultivars**

Group 4 (Figure 3d) is characterized by Great Plains hard wheat cultivars. Group 4 joins the previous sub-groups at coefficient 0.82. Within this diverse group, three closely related sub-groups stand out. Group 4a (coefficient 0.44) is a set of four lines
of hard white winter wheat that includes Arlin and progeny derived from single
crosses with Arlin. Group 4b (coefficient 0.55) is a small cluster of three hard spring
cultivars. This association is notable because of the few spring cultivars included in
this study. Group 4c contains Plainsman V and hard red wheats that have Plainsman
V or Kansas or Nebraska germplasm as common parents (N95L189, N96L1229,
Wesley, Karl 92).

**Group 5: Genetic stocks, synthetics, and distantly related cultivars**

A number of genetic stocks (M6, Norin 10, Chinese Spring, Ike, Oberkulmer, Cache,
and two *Ae. tauschii* accessions) showed little relationship (greater than coefficient
0.85) to the other groups (Group 5 in Figure 3d). M6 (the most different wheat in this
study with a coefficient of 0.95) is a synthetic wheat derived from a *T. turgidum/Ae.
Tauschii* cross. Norin 10 is the original donor of semi-dwarf genes into PNW cultivars.
Chinese Spring is an important stock for cytogenetic research. Ike is a HRW line
developed in Kansas with a different genetic base than other Great Plains wheats
included in this study. Oberkulmer is a spelt wheat, which is a different subspecies of
wheat than common hexaploid bread wheat. Finally, Cache is an older (1944) hard
red winter wheat developed in Utah, that was based on Kansas hard red parentage.

**Conclusions**

The markers in this study effectively clustered PNW wheat germplasm into groups
with commonalities based on parentage and origin. Approximately 20% of the lines
were grouped in ways not obvious by parental relationships or shared adaptation. Lines generally clustered with close relatives, and the predominant divisions appear to be based on regional adaptation (PNW vs. Europe vs. Great Plains). Additionally, although lines do not segregate conclusively on the sole basis of market class, the clustering pattern suggested that a commonality was market class. For instance, the European-derived group actually contains several U.S. hard red winter wheats in addition to the European hard red cultivars. Market class appears to be a shared characteristic within this group. This cluster of predominantly hard red wheats, however, is more closely related to PNW soft whites than to the other hard red wheats from the Great Plains, indicating that market class alone is not the primary segregating factor.

Overall, the amount of polymorphism, alleles per locus, and allelic distribution indicated by these markers indicate that the PNW wheat breeding germplasm contains a level of diversity on par with that of the European cultivars analyzed at the IPK (Roeder et al. 2002). The divergence of PNW soft white wheat from European-derived lines suggests opportunity to exploit European germplasm for further improvement of PNW cultivars.
Combined Nuclear/Chloroplast Analysis

Combined Clustering Patterns

The final objective of this study was to answer specific questions regarding the diversity of the PNW wheat breeding germplasm using genetic diversity estimates from the combined data sets. Clustering patterns for the entire set of markers, nuclear and chloroplast, were investigated for 165 lines included in both studies (Figure 4a). The structure of this combined dendrogram was compared to the individual dendrogram relationships yielded by chloroplast versus nuclear SSRs. The coefficients were intermediate (major branch points starting around 0.58) between those indicated by chloroplast (major branch points beginning at 0.32) and nuclear (major branch points starting around 0.74) data. The primary distinction in the combined tree is the separation of cultivars based on B versus D cytoplasmic types, which are labeled on Figure 4a. Within the B cytoplasmic type, the club wheats form a cluster, as well as the Stephens-related wheats (Group 1 and 2 respectively on Figure 4b). At coefficient 0.58, there is a large cluster that resembles the nuclear cluster formed by the European and PNW wheat together (Group 1 on Figure 4a), but the subclusters within that cluster do not separate into concise, pedigree based clusters such as those formed when nuclear data was analyzed alone. However, lines that are very closely related via pedigree (Appendix 4), such as sister lines or parent/offspring duos continue to cluster together.
Figure 4a. Genetic relatedness tree of PNW wheat breeding germplasm based on nuclear and chloroplast SSR data combined.
Figure 4b. Genetic relatedness tree from combined nuclear and chloroplast SSR data including club wheat and Stephens-related clusters.
Figure 4c. Genetic relatedness tree from combined nuclear and chloroplast SSR data including the D type cytoplasmic cluster.
The primary clustering commonality of nuclear clustering was geographical region, with secondary clustering based on market class. The chloroplast clustering of cultivars within the B type cytoplasm had no recognizable defining commonality. When the two types of markers are combined, the primary distinction becomes chloroplast type, which appears to distort the nuclear marker clustering. For geographical clustering, nuclear SSRs are more useful in this germplasm pool as based on known and expected cultivar relationships. Chloroplast and nuclear genetic relatedness measurements are not complimentary when the two data sets are combined. For instance, two lines might have the same chloroplast type yet be divergent at the nuclear level. An example of this from this study would be Roazon and Madsen, which cluster together based on chloroplast types, but are in entirely different major clusters based on nuclear data alone. It is therefore more useful to interpret the data separately rather than combining the data analysis.

**Historical Lines**

After 1949, a series of newer disease resistant lines began to be released in the PNW (Peterson et al. 2001). A second issue that the combined marker information was used to address is the historical genetic diversity of PNW wheat breeding germplasm. This study has examined 25 lines that were significant parents and/or progenitors of cultivars that were grown over a large proportion of the PNW that were released prior to 1950. The genetic diversity estimates from all markers were compared for these lines and a clustering analysis was performed (Figure 5). Proportion of shared alleles
Figure 5. Genetic relatedness tree of Pacific Northwest lines released prior to 1950.
ranged from 87.5% (Elgin and Elmar) to 20.8% (Nord Deprez and Cache). Although most of these lines were expected to be unrelated to one another, none of them share less than twenty percent of their alleles. This could serve as a base threshold of relatedness of genetic material for PNW wheat, regardless of pedigree.

Three of the lines in this study are represented by two different plant introduction (PI) numbers (Federation, Cheyenne, and Rex). The two PIs for Federation and Cheyenne (Appendix 1) were submitted to the National Small Grains Germplasm Repository. These clustered closely, as expected, although they were not quite as similar (0.27 for Federation and 0.236 for Cheyenne) as the parent/offspring duo of Elgin and Elmar. The two PIs for Rex (Appendix 1), however, segregated far from one another, with only 62.9% of alleles shared. When the pedigrees for these two lines were subsequently studied, it was discovered that they are actually two completely different releases. Rex 1 was released in 1962 from a French breeding program, while Rex 2 was released from an Oregonian program in 1933.

The historical lines divide into two specific clusters that were indicative of their roles in PNW wheat breeding programs. Group 1 (coefficient 0.56) consists of the lines that have formed the quality and adaptation backbone of PNW soft white cultivars. Group 2 (coefficient 0.59) consists of lines that have been used in PNW wheat breeding programs for particular trait introgression, such as disease resistance. There are several of these historical lines that cluster together in a stepwise manner (Group 3 in
Many of these are related by pedigree, and all are either club wheat or significant parental lines for club development.

The two lines that shared the fewest alleles were Nord Deprez and Cache. These lines are both hard red winter wheats but completely unrelated based on pedigree, released one year apart (1945 and 1944 respectively). Nord Deprez comes out of a French breeding program and Cache comes from Utah and was derived from the cultivar Turkey. It also corroborates the findings of Roeder et al. (2002) that the primary distinction seems to be based on geographical location.

**Heterogeneity**

The combined data in this study was also used to address the first objective, to ascertain the usefulness of these markers in this set of germplasm. This study yielded 2.3% heterogeneity for all marker/variety combinations, which is lower than previously reported 4.3% (Roeder et al. 2002). The markers selected for analysis in this study were chosen for ease of scoring, low copy number, which may account for this disparity. For the nuclear markers, 30.1% of the lines had at least one case of heterogeneity observed. This is higher than the 25% found by the European study using several of the same markers. Since this study contains several lines that are breeding lines or unreleased experimental lines, there is most likely higher heterogeneity than that of the pureline European cultivars used in the Roeder et al. (2002) study.
Conclusions

The markers used in this study were selected for high polymorphism and were able to differentiate even closely related or sister lines. All of the nuclear markers used yielded information of varieties and many clusters were related to commonalities in genetic background as based on pedigree comparisons. It is important to have good genome coverage when studying closely related lines as in this study. If the markers are tightly linked, there will be little recombination between them and genetic diversity estimates will be artificially lower than the actual genetic diversity throughout the rest of the genome. Three large wheat germplasm studies using SSRs have been recently published (Manifesto et al. 2000, Roeder et al. 2002, Huang et al. 2002) that used 15, 19, and 24 nuclear markers respectively. This study found the 24 nuclear markers used to be effective and informative, although the presence of some unexplained clustering relationships indicates that more markers might be advisable for future germplasm diversity studies of PNW wheat. The chloroplast markers were effective for differentiating major plasmon types between species and major chloroplast types within species also.

Nuclear markers identified more alleles per locus, with fewer lines on average being defined by the single most common allele. The higher number of alleles allowed more complex groupings than with chloroplast markers. The clusters were mostly found to
have biological basis, with the major distinction being region of adaptation and a secondary distinction based on market class.

Because these markers were able to distinguish between all cultivars included in this study, they could potentially be used in the future for breeding decisions. This information could be useful during gene introgression as a means of tracking the genetic background of the elite cultivar, thus accelerating the selection process toward more rapid regression to the elite cultivar's overall genome. While this method is not guaranteed because of scant genome coverage, it provides another tool that may decrease the amount of time required for breeders to achieve/identify the desired genetic background.

As new material is received into PNW wheat breeding germplasm, fingerprinting any unfamiliar material with this set of markers might help in categorizing genetic similarity or difference with existing germplasm. New material that falls into known clusters could then be integrated into the program as alternatives to others in that cluster. New material that clusters outside of known groups might be useful to introduce new allelic combinations for diversity management.

The chloroplast marker data shows alloplasmic lines within both PNW and European wheat breeding germplasm. The effect of alien cytoplasm on wheat phenotype remains largely unexplored. With the identification of existing cultivars with D type
cytoplasm, these effects could be more readily observable. This set of markers was sufficient to discriminate between B and D type markers, and would be useful in the future to identify which type of cytoplasm other cultivars contain. Additionally, decisions regarding cytoplasmic diversity would be facilitated by this data. Breeders could select the direction of crosses based on desired cytoplasmic type in the offspring. This information could help breeders to take steps that alleviate any concerns regarding cytoplasmic uniformity.

While this study provides valuable information about the nuclear genetic diversity of the cultivars studied, repeating the entire process for several of the nuclear markers would broaden the scope of the study. Over 500 European cultivars have been fingerprinted using several of the same markers (Roeder et al. 2002). Those allele sizes were confirmed and calibrated by repeating each one at least once. With this additional information for these lines, PNW wheat breeding germplasm could be compared and analyzed with this large European database. This would extend the usefulness of this database to wheat breeders in many regions.
References


Sharp, P.J., Johnston, S., Brown, G., McIntosh R.A., Pallotta, M., Carter, M., Bariana, H.S., Khatkar, S., Lagudah, E.S., Singh, R.P., Khiarallah, M., Potter, R., Jones,


APPENDICES
Appendix 1. List of plant material with abbreviations and seed source.

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A  Dr. R.E. Allan, USDA/ARS, Pullman WA
B  Dr. H. Bockelman, USDA National Small Grains Research Facility
C  Dr. P. Bruckner, Montana State University
D  Dr. X. Chen, USDA Pullman WA
E  Dr. A. Fritz, Kansas State University
F  R. Graybosch, USDA/ARS
G  Dr. D. Hole, Utah State University
H  Dr. E. Souza, University of Idaho
I  J. Bassinette, Oregon State University
J  Dr. P. Hayes, Oregon State University
K  Dr. R. Metzger, Oregon State University
L  Dr. C. J. Peterson, Oregon State University
M  Dr. C. Qualset, University of California, Davis
N  Dr. B. Gill, Kansas State University
Appendix 2. Chloroplast SSR allele sizes for the 174 genotypes studied.

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Appendix 4. Pedigrees of Major Cultivars with Nuclear Groupings.

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<td>Oro // Turkey / Florence /3/3* Elgin sel. 19 /4/ Elmar</td>
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<td>Suwon 92 /6* Omar /3/T. spelta / Coastal //3* Omar</td>
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<td>Hiller</td>
<td>la</td>
<td>1998</td>
<td>CI 13438 / Odin // CI 13645 / 101 /3/ M722712 /4/ Tres</td>
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<td>Temple</td>
<td>la</td>
<td>1997</td>
<td>Tres / VPM 1</td>
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<td>la</td>
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<td>Suwon 92 /4* Omar</td>
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<td>(Norin 10/Brevor, CI 13253, Sel. 14)/6/(Sel.3, CI 2692, Orfed/5/(Hybrid 50, Turkey Red/Florence//Fortyfold/ Federation/4/Oro/Turkey Red/Florence/3/Oro//Fortyfold/ Federation))/7/Burt</td>
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<td>1965</td>
<td>(Norin 10/Brevor, CI 13253, Sel. 14)/6/(Sel.3, CI 12692, Orfed/5/(Hybrid 50, Turkey Red/Florence//Fortyfold/ Federation/4/Oro/Turkey Red/Florence/3/Oro//Fortyfold/ Federation))/7/Burt</td>
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<td>Hill 81</td>
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<td>Yamhill / Hyslop</td>
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<td>Stephens//63-189/Bezostaja</td>
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<td>Lambert</td>
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<td>Nord Desprez/7 // (Pullman 101, CI13438, (Norin10/ Brevor CI 13253, Sel14/6 // (Turkey Red/Florence// Fortyfold/Federation/4 // Oro// Turkey Red//Florence/3 // Oro/Fortyfold//Federation, CI 12250, Sel27-15 /5 // Rio/Rex, CI 12597, sel53 .)</td>
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Appendix 4 (Continued).

   1a. Club Wheats and SW Foundation Cultivars.
   1b. Gaines Lineage Based on Norin 10, Brevor, and Burt.
   1c. Stephens Lineage Based on Nord Desprez and Pullman 101.

2. European and Related Red Wheat Cultivars.
   2a. European-derived Cultivars with Vilmorin 27-based Lineage.
   2b. Parents and Derivatives of VPM1.
   2c. Foundation Cultivars for Great Plains Hard Red Winter.

3. Distantly Related Cultivars.

   4a. Hard White Winter Lines Based on Arlin.
   4c. Modern Hard Red Winter Lineage with Contributions from PlainsmanV.

b Pedigrees were obtained from the National Plant Germplasm System.
Appendix 5. Primer locations and sequences.

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*a Ct is wheat chloroplast.*