University of Alberta

The potential of aspen clones and hybrids for enhanced forest management in Alberta.

by

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Dedication

I would like to dedicate this work to my family, especially to Cathy, my wife, our two sons Steven and Jack, and daughter Chloe. Your patience while writing my thesis will always be remembered.

Abstract

This thesis presents results from an industrial aspen tree improvement program for Alberta, evaluating a series of provenance, clonal and hybrid field trials. The goals were to (1) investigate geographic patterns of genetic variation in order to delineate breeding regions, (2) to assess the potential of clonal forestry systems to enhance forest productivity, and (3) to evaluate the potential of hybridization to enhance growth through hybrid vigor. Partitioning of genetic variance with geographic predictor variables suggests two breeding regions for Alberta should be appropriate: a Sub-Boreal Rocky Mountain Foothill region between 52°30'N and 56°N latitude, and a Boreal Mixedwood region between 56°N and 59°N latitude. Broad-sense heritabilities for height and diameter ranged from 0.36 to 0.64 on selected sites, allowing 5-15% genetic gains in height and 9-34% in diameter based on selections from current trials. The best genotypes within hybrid families could have some additional potential in improving yields.

Preface

This work is the result of a large collaborative effort of many forest industry partners, researchers, and the Alberta government. Following the significant increase in utilization of the deciduous forest resource in the province of Alberta in the mid 1980's, there was foresight to initiate a hardwood tree improvement program for the province. This thesis takes a first look at some of the data generated from tests that were established as part of the tree improvement initiative.

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1. Introduction

The western boreal hardwood forests cover approximately 60 million hectares, mainly in northern Alberta (Marshall 1999). These resources have historically been underutilized (Morley and Balatinecz 1993), and even today conifer management remains the dominant paradigm (Lieffers et al. 2002, Simard and Vyse 2006, Wagner et al. 2006, Vyse 2007). Until the mid 80s, conifer forest products were preferred for their superior fiber strength in both pulp and dimensional lumber products. However, this changed with advances in wood products technology, namely oriented strand boards (OSBs) that introduced oriented wafers of wood from poplars in combination with epoxy resins. OSBs are comparable in strength to conifer wood at a significantly lower price (Lowood 1997, APA 1999), and today they are widely used in construction as sheeting for exterior walls, roofs, and flooring (AZFRP 2008). As a consequence, a sharp increase in demand for deciduous forest resource occurred in the 1990s and numerous oriented strand board and pulp mills were built in Alberta at this time (Balatinecz et al. 2001)**.** Currently aspen represents approximately 42% of the combined conifer and deciduous annual harvest within the province of Alberta, making it an important local economic resource.

In 2007, about 10 million cubic meters of merchantable deciduous volume were harvested in Alberta, compared with 13 million cubic meters of conifer volume, which is close to the current annual allowable cut (SRD 2009). The deciduous forest component is dominated by approximately 80% aspen (*Populus*

tremuloides Michx.) with balsam polpar (*P. balsamifera* L.) and paper birch (*Betula papyrifera* Marsh.) making up the remaining 20%. Of these three species, birch has the best wood properties for solid wood products such as furniture and flooring, but it is susceptible to forest pests and diseases (Peterson et al. 1997). Balsam poplar and aspen have a lower specific gravity than birch which allows them to absorb resin and be compressed, which are desirable properties for OSB production (Balatinecz et al. 2001). In turn, aspen and balsam poplars have similar growth rates. However, aspen has an advantage of occurring naturally in single-species even-aged stands that regenerate clonally after fire disturbance (David et al. 2001). The abundance of sites suitable for aspen also exceeds that of balsam poplar (Farmer 1991). From an ecological and economic perspective, aspen therefore appears to be the most probable candidate for tree improvement because of a combination of natural abundance, reasonably good productivity, and favorable wood properties.

From a genetic perspective, viable tree improvement programs rely on high within-population genetic diversity in growth and adaptive traits for selection, high heritability of desired traits, capability for hybridization, and easy means of seed production or clonal propagation. Species of poplars generally have these characteristics (Dickmann 1983). However, vegetative propagation in aspen is not as simple as in other poplar species and needs to originate from roots (Farmer 1963, Zsuffa 1971). While no results from common garden experiments are available for Western Canada, low to moderate broad-sense heritabilities of wood

properties in aspen were estimated from naturally occurring clones (Yanchuk et al. 1984, Yankchuck et al. 1988). Moderate broad-sense heritabilities were also found in ecophysiological and growth traits in seedling experiments (Thomas et al. 1998a, b). Molecular genetic research with aspen has further shown high within and among population diversity in neutral markers (Cheliak and Pitel 1984, Hyun et al. 1987, Jelinski and Cheliak 1992, Rajora and Dancik 1992, Yeh et al. 1995).

Recognizing the potential for an aspen tree improvement program, an industrial cooperative, Western Boreal Aspen Corporation was formed in 1995 to develop a tree improvement strategy for Alberta, described by Li (1995). Because of aspen's ability to regenerate from root cuttings (Zsuffa 1975, Schier and Campbell 1978, Li and Wu 1996, Stettler et al. 1996), the initial plus tree selection from wild stands included collection of propagules that were replicated in clonal trial series. This allows an early assessment of broad-sense heritability and convenient access to plant material for controlled crosses. Because of the known potential of hybrid vigor in poplar (Mitton and Grant 1996), the breeding strategy also included exploratory crosses of native aspen with pollen from aspen species native to China, Korea, and Finland. Lastly, to develop a breeding program within the context of adaptation to local environments, the first stage of the tree improvement program also included a reciprocal transplant experiment with provenances covering much of the species range in western North America.

2. Thesis objectives

This thesis presents a synthesis of results from the initial tree improvement program efforts, evaluating a series of five provenance trials, thirteen clonal trials, and seven hybrid trials to investigate (1) to determine geographic patterns of genetic variation of aspen in western Canada in order to delineate seed zones and breeding regions, (2) to assess the potential of clonal forestry systems to enhance forest productivity, and (3) to evaluate the potential of hybridization to enhance growth through hybrid vigor. I use this data to make recommendations for the next stages of the tree improvement program, and I will review if current seed zones and breeding zones are appropriate, given new genetic data that is now available from provenance and clonal trials.

3. Literature review

3.1. Species distribution and biology

The native range of aspen in Canada stretches mountain areas in Mexico to Alaska, and across Canada from the Atlantic to the Pacific ocean, which makes aspen the most widely distributed tree species in North America (Little 1971, Burns 1990). Within its range, it can inhabit elevations from sea level to 3700 m and occupies a large variety of sites (Hall et al. 1982). Aspen is most abundant in the boreal forest region (Perala 1990). In contrast to other poplars, which prefer

moist growing sites, aspen is predominately found on upland sites (Peterson and Peterson 1992). However, it also does well on moist sites (Barnes 1966, Haeussler 1986). Aspen is a fast growing, relatively short-lived tree compared with conifer species of the boreal forest. It is considered a primary successional species, which can quickly colonize large areas after disturbance (Mitton and Grant 1996). Unlike paper birch and balsam poplar, aspen grows naturally in large single species stands (Peterson and Peterson 1992). Therefore aspen might also be a good candidate for intensive forest management from an ecological perspective.

Propagation of aspen can be either sexual or vegetative. After disturbance of natural stands, aspen most commonly regenerates through vegetative reproduction from roots (Farmer 1963, Zsuffa 1971, Haeussler 1986, Peterson and Peterson 1992) . Vegetative reproduction is hormonally controlled by dominance of auxin over cytokinin (e.g. loss of apical production of cytokinin) or increased cytokinin production in roots if soil temperature is high (indicating sunlight reaching the ground). The suckers take over the distal portion of the root system, which is the reason that clones expand in area (Farmer 1962). This growth pattern also allows aspen to colonize marginal sites with frequent disturbances, and results in aspen clones to represent arguably the oldest and largest known organisms (Zsuffa 1975, Dickmann 1983).

Less commonly, aspen reproduces through seed. Aspen is a dioecious angiosperm with male and female flowers on separate trees. It is one of the earliest species to

flower, typically in April. Seeds are small and have fine silky hairs, which aid in long distance wind dispersal. Seed can move more than 5-10 km (Zasada and Densmore 1979, Wyckoff 2002). Because of a lack of large seed endosperm, seed have a narrow window of viability. Unlike in most species, germination starts with the cotyledons, followed by the radicle. Therefore, adequate moisture and bare ground are required for successful germination (Wyckoff 2002). In much of aspen's natural range these conditions are rarely met, limiting reproduction by seed (Schreiner 1959, Haeussler 1986, Peterson and Peterson 1992, Mitton and Grant 1996).

3.2. Taxonomy and hybridization

Depending on the taxonomy used, *Populus* comprises approximately 30 to 40 species (Eckenwalder 1996). Many species naturally hybridize, which makes them sometimes difficult to taxonomically distinguish. The genus *Populus* is primarily found throughout Eurasia and North America, and species are grouped into five sections: The first section *Populus* contains aspen and white poplars (e.g. *Populus tremuloides*, *P. tremula*, *P. davidiana*, *P. alba* and *P. grandidentata*). The second section *Aigeiros* contains black poplars and cottonwoods (e.g. *P. nigra*, and *P. deltoides*). The third section *Tacamahaca* comprises eight species of balsam poplars (e.g. *P. balsamifera* and *P. trichocarpa*), and the remaining three sections are primarily comprised of subtropical and tropical species (Eckenwalder 1996). The sections are primarily distinguished by the morphology of

reproductive structures but the sections also differ in the way and how well they vegetatively reproduce, such as from stump sprouts (all taxonomic sections), cuttings (section *Aigeiros* and *Tacamahaca*), buried branches (*Aigeiros*), and root sprouts (all taxonomic sections) (Schreiner 1959).

Poplar species hybridize easily within taxonomic sections and often even between sections. There are few natural hybrids of aspen, which includes gray poplar in Europe (*Populus* × *canescens* (*P. alba* × *P. tremula*), known for drought resistance (Hall et al. 1982). Another notable natural hybrid is *P. alba* × *P. grandidentata,* known for good timber production on upland sites in the mid Western States (Dickmann 1983). *P.* × *euramericana* (Dode) Guin. (*P. deltoides* × *P. nigra*), also referred to as *P.* × *canadensis* Moench, is the most widely planted hybrid for wood production in Europe (Dickmann 1983). Another commercially important hybrid, *P.* × *interamericana* van Broekhuizen (*P. trichocarpa* x *P. deltoides*) has good disease resistance, excellent growth rates, and is widely used for plantations in the western United States (Zsuffa 1975, Wright 1976, Wu et al. 1992, Li and Wu 1996).

Superior growth and disease resistance have been attributed to the phenomenon of hybrid vigor or heterosis, defined as the performance of F_1 progeny being greater than either parent. It is thought to exist primarily in the first generation, and diminishing in subsequent generations (Li et al. 1998). The causes of hybrid vigor are not always well understood. Masking deleterious alleles (or dominance of

recessive alleles), and overdominance (the phenomena of heterozygotes resulting in a larger genetic effect than each of the homozygotes) have been suggested as the genetic basis of heterosis in aspen (Dickmann 1983).

Aspen species are good candidates to take advantage of hybrid vigor in a breeding program because there are three commercially important species in the northern hemisphere: *P. tremuloides* Michx. (Canada), *P. tremula* L. (Europe), and *P. davidiana* Schneid. (China/Korea). These three species likely have a direct common ancestor with a circumpolar distribution (Rajora and Dancik 1992). So far, aspen hybrids have been primarily used in Europe (Karacic et al. 2003). When breeding for hybrids, pollen is easier to ship and therefore females usually serve as the local parent. It should be noted, however, that chloroplast DNA is maternally inherited (Schreiner 1959, Mejnartowicz 1991), and there has been some speculation that this results in better adaptation to local environmental conditions, with females used as the local parent (Li et al. 1998). Reciprocal breeding experiments, however, did not indicate a difference (Kanaga et al. 2008).

3.3. Genetic variation and adaptation

Variation in aspen has been assessed three ways: (1) by morphological traits in naturally occurring aspen stands, taking advantage of the clonal population structure in aspen; (2) with molecular techniques, which can give precise values for within, among, and between population genetic variation for selectively

neutral genetic variation; (3) through provenance trials, which test seed sources collected throughout the range of a species in (sometimes multiple) common garden test environments; and (4) through progeny trials, where offspring from controlled crosses are grown in a common test environment to reveal genetic control and heritability of traits. Both provenance trials and progeny trials are planted in replicated experimental designs, where in the case of aspen, replicates can be also obtained through clonal propagation, allowing for the estimation of additional genetic parameters.

Provenance trial series over multiple environments are generally perceived as the best tool for studying genetic variation in adaptive traits, and for understanding adaptive strategies of trees in light of source environments, where samples for provenance trials have been collected. Progeny trials are most useful for estimating within-population genetic variation, heritability, and other genetic parameters that are required to develop selection and breeding strategies. Performance of genotypes in provenance and progeny trials should ideally be observed over a long period, so that growth and survival is evaluated in response to various environmental conditions, such as pests and climate extremes that genotypes may not be exposed to in every year. It is, however, expensive to establish and maintain such trials and this type of genetic information is usually only available for commercial forestry species of high economic importance (Zobel 1991).

3.3.1. Natural clones

Morphological features of trees in natural stands are normally impossible to infer genetic differences among individuals or populations because of the confounding effects of genetics and the environment. Aspen on the other hand can grow in clonal patches, and if site conditions are assumed to be uniform, broad-sense heritability (the ratio of among-clone variation to total observed variation) can be calculated. Barnes (1969) sampled five trees from each of 31 putative clones in Michigan. Broad-sense heritability for height and diameter at breast height were 0.45 and 0.36 respectively. Additionally he investigated the morphological characteristics leaf width, length, and petiole length and found very high broad-sense heritabilities of 0.80, 0.81, and 0.82 respectively. In a later study Barnes (1975) investigated nine morphological characteristics in 1257 clones at 206 locations in seven western states and the province of British Columbia. Univariate and multivariate analysis detected a significant south to north cline in morphology of aspen. Mitton and Grant (1980) counted growth rings taken from core samples of 106 putative clones of mature aspen trees within a 500 km square west of Bolder, Colorado. They inferred genetic variation and heritability in growth rates, finding a broad-sense heritability of 0.32. Another two studies investigated genetic variation in wood properties in naturally occurring clones in Alberta (Yanchuk et al. 1984, Yanchuk et al. 1988). They found significant differences among clones and moderate broad-sense heritabilities between 0.35 and 0.43 for wood density and fiber length respectively.

In all the above studies, clonal structure is usually inferred from fall phenology, with different shades of leaf coloration apparently delineating clones. As a note of caution, it has been shown that many different clones share the same timing of leaf color (Wyman et al. 2003), and that clones may not be reliably distinguished based on these or other morphological traits (Cheliak and Pitel 1984). This means that broad-sense heritabilities inferred from natural stands may be underestimates with some of the among-clonal variation falsely recorded as within-clone (i.e. environmental) variation. On the other hand, heritabilities in natural stands could also be overestimates. Ramets of a clone in natural stands are clustered rather than randomized. Clone effects may therefore be confounded with site variation, which will consequently be falsely attributed to variation among clones. The approach is therefore not a strong tool for reliably measuring genetic variation.

3.3.2. Molecular markers

Use of molecular markers is a useful tool in population genetics. Molecular markers characterize short sections of the DNA and typically represent selectively neutral differences in DNA sequences. A widely used marker that indirectly detects variation in DNA sequences are allozymes. Allozymes are different versions of a protein that can be separated by electrophoresis and imply different alleles encoding the proteins.

Even though genetic variation in molecular markers does not allow for inferences on adaptation, they are useful to assess overall genetic diversity within and among populations, and they may be used to infer the historical biogeography of a species including past population bottlenecks and geographic separation of subpopulations (Jaramillo-Correa et al. 2009). Within-population genetic diversity is believed to be important to a species for long term evolutionary potential (Newman and Pilson 1997, Westemeier et al. 1998, Booy et al. 2000). By implication, high within-population genetic diversity may also indicate potential for selection in tree improvement programs (Zobel 1991).

Genetic diversity is often measured as expected heterozygosity (H_e), which is not as sensitive to rare allies or sample size when comparing values across different studies. Alternative measures that are frequently reported are the proportion of polymorphic loci and mean number of alleles per locus (White 2007). Generally, genetic diversity in trees is high compared to other organisms. The range in expected heterozygosity in trees is typically between 0.05 at the low end and 0.20, which is considered high (White 2007). Generally, genetic variation in trees decrease with increased latitude (Stevens 1989). Also, species that occupy a large geographic area and are wind pollinated are expected to have high genetic diversity (Sork and Smouse 2006).

Aspen has been shown to have exceptionally high H_e values with high variation within and little among-population genetic variations. In a study of aspen genetic

diversity in Alberta with 222 trees in seven populations, Cheliak and Dancik (1982), found an overall H_e of 0.42 and an inbreeding coefficient of -0.23, indicating an excess of heterozygotes. They speculated that heterozygotes have selective advantages and are perpetuated by clonal propagation. The second study that covers a reasonable large portion of the aspen range is by Hyun et al. (1987) for Ontario with 200 trees in eight populations. Overall expected heterozygosity was high with H_e=0.24 and a fixation index of F=0.46 indicating a deficiency of heterozygotes. Hyun et al. (1987) reported 90% variability within populations and a small 6.8% proportion of gene diversity attributed among populations. The third notable study was conducted by Lund et al. (1992) in Minnesota with 347 trees from nine populations. They reported an average H_e of 0.22 and a fixation index close to zero.

Several other molecular marker studies with aspen have been conducted on smaller scales or with an emphasis on comparisons between allozyme and more advanced molecular marker methods (Mitton and Grant 1980, Cheliak and Pitel 1984, Rogstad et al. 1991, Jelinski and Cheliak 1992, Liu and Furnier 1993, Chong et al. 1994, Yeh et al. 1995, Wyman et al. 2003, Cole 2005, Namroud et al. 2005, DeWoody et al. 2008, Mock et al. 2008, De Woody et al. 2009). They generally support that within-population genetic variation in aspen is very high and other techniques detect comparable patterns of within and among population variation (De Woody et al. 2009).

3.3.3. Common garden trials

Unlike molecular markers, adaptive traits such as growth, survival, and insect and disease resistance are controlled by multiple genes as well as environmental factors. To distinguish environmental effects from genetic differences, trees are planted in a common garden trial, where environmental conditions are the same for all genotypes (residual environmental variation is randomized by means of an experimental design).

There are three common types of common garden tests: provenance, progeny, and clonal trials. Provenance tests are designed to evaluate adaptive variation among populations across a range of environments. Therefore, they typically include seed collections from much of the species' range, and they are typically planted in multiple sites to observe genotypic response to various environments. A progeny test design looks more closely at variation within a population and allows estimation of genetic parameters because some of the pedigree information is maintained. At least the mother is known if seeds were open pollinated, but full pedigree information is usually maintained if controlled crosses were made in a breeding experiment. Clonal tests take advantage of vegetative propagation to obtain exact replicates of the same individual genotype. Combinations of all tests are possible: for example, a provenance trial might have clonal or family structure, or a progeny test from a breeding experiment may be clonally replicated for better statistical power.

Partitioning of genetic variation in common garden tests can be used to calculate heritability, the proportion of the total variance in a phenotypic trait that is controlled by genes (rather than the environment). Heritability indicates to what degree a trait will be passed on to a subsequent generations. A heritability of one indicates all the observed phenotypic variation will be passed on to the next generation and zero indicates no transfer, i.e. all observed phenotypic variation is due to environmental factors. Heritability is further comprised of additive and non-additive genetic variation. Trees propagated through seed recombine their genes and only pass on the additive variation to their offspring. In clonal propagation, both additive and non-additive variation that arises from particular combination of genes can be captured. Therefore, broad-sense heritabilities that includes non-additive genetic effects is distinguished from narrow sense heritability, which applies to sexual reproduction. Heritability estimates are important in tree breeding, because they indicate the amount of improvement that can be accomplished by selection from one generation to the next.

Aspen has been shown to have relatively high heritabilities for growth traits. Thomas et al. (1998b) estimated genetic parameters using 29 clones from five populations in 2-year field trials and twelve-week growth chamber experiments. The populations were exposed to different environments at two sites at 50°N latitude and 1006m elevation and at 59°N latitude and 320m elevation in Alberta. Broad-sense heritability estimates for root collar diameter averaged across all

clones for two growing seasons at the southern site ranged from 0.29 to 0.56. Height was not evaluated because of deer browsing and no heritabilities for the northern site were calculated. In a growth chamber environment, which better controls for environmental variation than field tests, broad-sense heritabilities were generally high: root collar diameter, height, bud-burst, root-to-shoot ratio had heritabilities of 0.08, 0.74, 0.72, and 0.59, respectively. Although the estimates for root collar diameter were mixed, the result generally implies potential for response to selection in growth and adaptive traits at least at the juvenile stage.

In a second experiment by Thomas et al. (1998a) broad-sense heritabilities were estimated on various physiological traits measured as gas exchange rates on aspen grown in growth chambers using the same five populations and test sites as above. For the growth chambers the values for net assimilation, stomatal conductance, and photosynthetic water use efficiency were 0.28 to 0.80, 0.73 to 0.92, and 0.44 to 0.80, respectively. The same physiological measurements were also taken under field conditions, but no relationship between field trials and growth chamber results was found and the field trial results were much more variable than those of the growth chambers.

Two other studies based on clonal experiments in different study areas found moderately high heritabilities in adaptive and growth traits. Lindroth et al. (2007) conducted a common garden experiment comprised of twelve aspen clones in

Wisconsin to determine their susceptibility to ungulate browsing. For three tissue chemicals moderate to low broad-sense heritabilities for: salicortin, tremulacin, and condensed tannins where calculated as 0.35, 0.14, and 0.39 respectively, implying that selection for browse-resistant clones in a tree improvement program is possible. In another short-term common garden trial in Southern Utah, Kanaga et al. (2008) estimated broad-sense heritabilities for height growth of 0.45 across wet and dry sites.

Finally, there is one long-term common garden study with clones of aspen from Utah (St Clair et al. 2010). In this regional study in Northern Utah, 18 clones were propagated from roots and grown in a common garden for 27 years. Broad-sense heritabilities were estimated for growth traits after seven, 15, and 27 growing seasons. Broad-sense heritability for height was moderate with a declining trend over time 0.35, 0.33, and 0.26. Diameter at breast height showed similar values of 0.31, 0.34, and 0.25 respectively. Another long-term provenance trial exists for European aspen in Sweden. Stener and Karlsson (2004) used 16-year growth measurements for 280 hybrid *P. tremula* × *P. tremuloides* clones, grown on 10 agriculture sites to estimate heritabilities. They measured survival, damage, growth, and stem quality traits and found moderate broad-sense heritability of around 0.4 across all sites.

To summarize, aspen has been studied extensively in short term studies, which generally have revealed high broad-sense heritabilities and high within-population

genetic diversity for growth, adaptive and molecular marker traits. However, despite extensive research on aspen genetics there is no substantive body of research based on long-term field trials, needed to estimate gains from selection in commercial tree improvement programs. In Alberta, there had been no long-term provenance, progeny, or clonal trials with aspen until this research study started.

3.4. Seed zones and seed transfer guidelines

Geographic patterns of genetic variation have practical implications for reforestation programs. Forest managers have to ensure that seedlings are well adapted to the growing conditions of the planting site (Morgenstern 1996, Ying and Yanchuk 2006). Using planting stock for reforestation that originates within a restricted geographic area delineated as a seed zone aims at minimizing loss of productivity and forest health issues because of maladaptation. Alternatively, movement of seed can be allowed with seed transfer guidelines, also sometimes referred to as floating or flexible seed zones (Ying and Yanchuk 2006). Transfer guidelines avoid drawing fixed boundaries across continuous genetic clines by specifying a maximum distance and elevation movement from source location to a planting site to avoid maladaptation (Rehfeldt 1988, 1989).

Generally, there are two conceptual approaches to develop seed zones and seed transfer guidelines. The first aims at maximizing tree growth by comparing response functions of different genotypes over multiple test environments. The

approach usually employs univariate or multivariate curve fitting techniques to analyze growth and adaptive traits as a function of environmental or geographic predictor variables (Lindgren and Ying 2000). The second approach aims at minimizing risk based on the assumption that local sources are optimally adapted to the environments in which they occur.

It is generally difficult to translate genetic information from provenance trials into geographic zones or transfer guidelines, especially in complex landscapes. GIS-based techniques have been developed to delineate seed zone boundaries where response functions of differently adapted genotypes intersect or drop below a certain threshold (Hamann et al. 2000). For the risk-avoidance strategy, GIS-based seed zone optimization techniques are available that assign groups of similarly adapted genotypes to their corresponding environments (Parker 1992, O'Neill and Aitken 2004). However, seed zone systems in practical use have been developed by evaluating available genetic information, and subjectively deciding on reasonable transfer guidelines or seed-zone delineations that usually track ecological regions.

In Alberta, seed collected from natural stands is referred to as stream one material (ASRD 2009). For stream one material, the province uses seed zones to legislate movement of seed from collection location to planting site. These seed zones apply to all naturally collected seed based on a fine-scale ecosystem delineation of Natural Regions and Subregions of Alberta, which tracks elevational bands (NRC

2006). The seed zones regulate how far materials used in reforestation can be displaced from their place of origin. The limits on movement are based on the assumption that local tree populations are best adapted to the environments in which they occur (ASRD 2009).

Breeding regions are similar to seed zones to govern the deployment of genotypes from tree breeding programs. In Alberta, material from breeding programs is referred to as stream two material from controlled parentage programs. Breeding regions incorporate results from genetic progeny and provenance trials. Because more is known about the adaptation of genotypes in tree improvement programs, which are tested over a wide range of environments, the breeding regions are larger than seed zones. For aspen, three breeding regions were proposed for Alberta (Li 1995). In this paper Li (1995) anticipated a Northern Region I (approximately covering 55-57^{o} N, 114-120^{o} W), a southern Region II (approximately covering 53-55^{o}N, 114-120^{o} W), and an East Central Region III, which includes part of Saskatchewan, (approximately covering 54-56^{o} N, 107-144^{o} W).

3.5. Tree improvement with aspen

While seed zones and breeding regions account for genetic variation among populations, within-population genetic variation is of primary interest to tree improvement programs. Such programs normally aim at selecting genotypes for

improved growth, wood properties, and fiber characteristics. Aspen generally has high within-population genetic variation and moderate to high response to selection (reviewed above in section 3.3). Aspen tree improvement programs in Europe and the United States have taken advantage of this genetic resource.

3.5.1. Europe

Sweden has a record of tree improvement for European aspen (*Populus tremula* L.) that dates back to an industrial tree improvement program by the Swedish match stick industry in the 1930s and 1940s (Karacic 2005). These programs have seen a second wave of intense selection and breeding efforts in the 1970s sparked by the oil-crisis, which increased demand for bioenergy (Berg 2003). Sweden now satisfies 16% of its total energy demand from bioenergy (Rytter and Stener 2005). Early breeding programs in Sweden have focused on hybrid breeding, targeted as an alternative short-rotation crop on southern Sweden's agricultural lands. Superior hybrids are propagated as clones to take advantage of dominance and epistatic genetic variation. Finland also has a program of aspen and hybrid breeding aimed at high-quality paper production from uniformly short aspen fibers, but this program is only moderately well documented (Yu and Pulkkinen 2003).

There is a notable lack of studies that systemically compare the genetic gains of hybrid aspen compared with native aspen. However, data from short rotation

commercial plantations with hybrid aspen (*P. tremula* × *P. tremuloides*) in Sweden suggest that substantial gains can be expected over natural stand productivity. Mean annual increment of hybrids in Sweden were reported as 17 m^3/ha/year (Karacic et al. 2003) and 10 and 16 m^3/ha/year (Rytter and Stener 2005) over a wide variety of sites. This compares to estimates of European aspen productivity in natural stands between 5 m^3/ha/year (Linder et al. 1997) and 9 m^3/ha/year (Johansson 1999). Note that productivity improvements in this comparison could be due to genetic, silvicultural, or site factors.

3.5.2. United States

In the Lake States region of the United States (Michigan, Wisconsin, and Minnesota), aspen tree improvement programs started in the 1950s as a cooperative industrial effort, with up to 17 members, initiated by the Institute of Paper Chemistry. This program focused on selection of native trembling aspen, hybridization with European aspen, aiming at increased growth rates, disease resistance, and fiber quality (Li 1993). Aspen was primarily used for pulp production in the 1970s and 1980s, and subsequently for OSB in manufacturing. A decrease in the forest land base in the Lake States region from 13.2 million acres in 1970 to 11.9 million acres in 1987 also led to pressure to maximize productivity from the remaining land base (Einspahr 1990, Li 1993). Investment in tree improvement to grow more wood per acre was seen as a means to address both the increased demand and shrinking land base. The first genetic field trials

with native aspen were established in the 1970s (Anderson et al. 1990), and hybrid aspen trials were added in the mid 1980's (Einspahr 1990). In Minnesota, as of the late 1990s, there were approximately 15,000 acres planted with hybrid poplar (Streed 1999).

Early studies in Minnesota, comparing native aspen growth with that of European hybrids (*P. tremula* × *P. tremuloides*) suggested a 6-19% increase in height growth over a native control at age five (Benson 1967). Li (1993) in Minnesota conducted a hybrid breeding program using various combinations of *P. davidiana, P. alba, P. tremula, and P.* × *canescens.* He found various levels of improvement with all hybrids. Based on 15-year height measurements on hybrids derived from local *P. tremuloides* and European pollen from *P. tremula,* gains in height were 29 to 34%. There are no studies that report realized gains at rotation age from either hybrid or pure species tree breeding programs.

3.5.3. Alberta

Compared to tree improvement efforts with conifers, Alberta's aspen tree improvement program is relatively young for lack of commercial demand for relatively low-quality hardwood resources from aspen, poplar and birch in Alberta. Demand for forest products before the 1990s was almost exclusively met from conifer species and aspen was considered a forest weed. Demand for hardwoods increased rapidly in the 1990s because of technological advances that

allowed hardwood resources to be used for oriented strandboard products. As a consequence numerous oriented strand board and pulp mills were built in the province (Ondro 1991). At the same time several studies in the 1990s started to investigate the merits of a hardwood tree improvement program (Farmer 1991, Rajora 1991, Lester 1995, Ceulemans and Deraedt 1999). Li (1995) published the first breeding strategy based on breeding among native aspen within three proposed breeding regions (described above in section 3.4).

An industry-led tree improvement program in Alberta for aspen began in 1993, leading to the formal incorporation of the Western Boreal Aspen Corp (WBAC) in 2000. The tree improvement program was started with a series of provenance trials established in 1998 with sources collected throughout western Canada and Minnesota. This provenance trial series was established to examine geographic patterns of genetic variation across the region to allow for delineation of breeding region boundaries. The program then focused on plus-tree selections from wild stands, which were clonally propagated through root cuttings. From approximately 521 plus trees, 244 clones were successfully established in 15 clonal trials between 1999 and 2002. Superior clones were crossed to produce material for 10 progeny trials established between 2005 and 2008. The program also included hybrid breeding of native aspen (*P. tremuloides*) with pollen from United States, Chinese, and European aspen (*P. alba, P. davidiana* and *P. tremula*) established in 15 trials between 2001 and 2003.

No genetic gain estimates are available for improved aspen in Alberta. Generally, expectations for realized gains from broad range of species in long-running tree improvement programs are a 10% to 20% increase in productivity with each generation of selection and tree breeding. Additional gains in comparison to productivity in natural stands can be expected from intensive plantation forestry that includes weed control, spacing, and thinning (Li 1999, Pallett and Sale 2004, Binkley et al. 2010). Estimates for natural stand productivity of aspen in Alberta range from 2.5 m^3/ha/yr over a 90-year rotation (Thomas 1999) to 7.5 m^3/ha/yr for the first 30 years (Anderson and Luckert 2007). The industry-led tree improvement program in Alberta aims to approximately double the current yield, subject to the degree of genetic improvement and silvicultural prescriptions (Thomas 1999). This appears to be a reasonable target, given documented productivity values of hybrid poplar in shelterbelt plantations of around 15 m^3/ha/yr in Alberta (Ezra 1996) and realized gains from Scandinavian tree breeding programs reviewed above.

4. Materials and Methods

The basis for evaluating the potential of aspen tree improvement in Alberta in this thesis consists of 27 field trials that test clonal, hybrid, and provenance seedlot material (Table 1). The clonal trial series includes sources from Alberta and British Columbia (Figure 1) and the provenance trial covers seed sources from

British Columbia, Alberta, Saskatchewan and Minnesota (Figure 2). The hybrid trials include crosses of local Alberta sources with aspen from China, Europe, and the eastern United States.

4.1. Clonal trials

The amount of heritable genetic variation in growth traits were examined with clonal trials. The clonal trials were established in five general locations in Alberta, representing the land base of members of the forest industry cooperative (Figure 1). Plus trees were selected from natural stands based on good form, self-pruning in the lower half of the stem, and absence of insect and disease problems. A minimum distance of 1.5 km was required between selected trees to ensure they were genetically unrelated. Plus trees were clonally propagated from approximately 1.5 meters of hand excavated roots with a target diameter of 2.5cm. Root sections were collected between May and early June of each year.

Roots were processed by soaking in water and light rubbing to remove soil, followed by a 0.5% bleaching soak for 10-15 minutes for sterilization. Subsequently, 1.5m root segments were cut into smaller segments of approximately 30cm length, placed into 2-3 horticultural flats, covered with pearlite and drenched with fungicide. Horticultural flats were periodically irrigated to maintain moisture content until root sprouts appeared after approximately 10 days. Root sprouts that reached 1.5cm were harvested with a

scalpel over a period of approximately six weeks from the horticultural flats. The sprouts were stuck into pellets of peat growth media and placed in a growth chamber at 20°C and high humidity until they rooted within twelve days. Rooted sprouts subsequently were transferred into larger media and grown in a nursery setting under shade for two weeks before being moved to full light in July. In the fall of first growing season dormant stecklings were placed into cold storage for field planting in the subsequent spring.

In spring of 1999, a total of 509 overwinter dormant trees were planted in three test sites, representing 32 clones. The clonal representation at test sites was incomplete with 31, 17, and 21 clones planted at test sites 10, 41 and 60, respectively. In spring of 2001, 3,679 trees were planted in three test sites, representing 112 clones. The clonal representation at test sites was incomplete with 88, 31, and 53 clones planted at test sites 31, 81 and 60, respectively. In spring of 2002, a total of 6,012 trees were planted in three test sites, representing 118 clones. The clonal representation at test sites was incomplete with 104, 115 and 78 clones planted at test sites 10, 31 and 81, respectively. Some clones were planted in multiple years, with a total of 242 clones tested over all three years. All clonal trial test series used randomized block designs. The 1999 trial used two-tree row plots, replicated in four randomized complete blocks, while the reminder of the trials used four tree row plots, replicated in five randomized complete blocks. Because of the large size of the experiments, two separate randomized complete block experiments were established at Site 31 for the 2001

series to accommodate all clones. Similarly, two separate randomized complete block experiments were established at each site for the 2002 series. The target planting density was 2.5 meters by 3.0 meters, however slight variation in spacing occurred on some sites. Test sites were fenced to prevent animal browse and were managed for vegetation control comprised of a combination of chemical and mechanical means over the first three years with subsequent maintenance on a periodic basis. A double row of buffer trees was planted around all trials. Measurements of height and diameter at breast height were recorded after five, six, and eight growing seasons for the 1999, 2001, and 2002 trial series respectively. All measurements were taken in dormant season, usually in the fall and occasionally in the spring before leaf flush.

4.2. Hybrid trials

Hybrids were created by crossing local aspen (*P. tremuloides*) females with pollen from Chinese aspen (*P. davidiana*) from north-central China, European aspen (*P. tremula*) from Finland, and white poplar (*P. alba*) from Minnesota. Female material was a combination of potted orchard trees and cut branches in water. This dormant material was forced to flower in the greenhouse from February to April. All material was held in isolation cages or pollen bags with breeding completed before release of native pollen to minimize cross contamination.

The 2001 trial series was installed at four test locations (Table 1). The test design was a randomized complete block design with four-tree row plots and ten blocks. This series contained nine hybrid families. Families one to six were local female branches sent to Minnesota Aspen and Larch cooperative for breeding with *P. alba* pollen. Families seven, eight and nine were native female branches from Peace River, Drayton Valley, and Slave Lake sources respectively. The pollen for these crosses were *P. davidiana* from China, *P. tremula* from Finland, and *P. davidiana* from China, respectively.

The 2002 trial material was established in six experiments representing three regions. Tests were planted as randomized complete blocks with four-tree row plots and four blocks. This series contained 44 hybrid families, of which 42 used native Alberta female sources from Drayton Valley, Slave Lake, Grande Prairie, and Peace River regions of the province. Two non-native females of *P. davidiana* in the form of cut branches obtained from an arboretum in Ontario were also used. Pollen sources comprised six males native to Alberta and 40 pollen sources of *P. tremula* from Finland and *P. davidiana* from China and Korea.

All test sites had a target planting density of 2.5 meters by 3.0 meters, with slight variation in spacing at some sites. Test sites were intensively managed for control of vegetation for the first three years with subsequent maintenance on a periodic basis. Test sites were fenced to prevent animal browse. A double row of buffer trees surround all experiments. Measurements of height and diameter at breast

height at age six where taken in the dormant season predominantly in the fall and occasionally in the following spring before leaf flush.

4.3. Provenance trials

Regional genetic differences of aspen populations were examined with a provenance trial series established by a forest industry cooperative at five locations in western Canada in 1998 (Table 1, Figure 2). The planting locations and general collection locations were chosen to represent forest management areas of participating companies. A total of 43 half-sib families were tested in this experiment, with three to eleven families provided by each cooperative member from within their region, plus an additional five seed lots from Minnesota. In the subsequent text, I refer to half-sib families from this trial also as provenances.

Sowing of seed occurred in the spring of 1997 at a regional commercial nursery. Dormant seedlings were lifted at the end of the first growing season and held in cold storage over winter before being planted at all five test locations in the spring of 1998. All trials established with a border row of two trees. Seedlings that did not survive the first growing season in the field were replaced in the fall with surplus planting stock from the same treatment. All sites, except the northern British Columbia site (test site 70), were fenced to prevent animal browse. Sites were maintained with vegetation control for the first three years with a combination of mechanical and chemical means. Subsequent vegetation control

occurred on a periodic basis. Site number 70 was a forested and unmanaged site. However, it was still cleaned periodically with brush saws to remove vegetative competition. At each test site, provenances were planted in a randomized complete block design with six blocks in five tree row plots. Tree height at age nine was recorded in fall of 2006.

4.4. Data analysis

Prior to statistical analysis, all data were carefully examined for errors with boxplots and line plots to identify errors in measurements, data entry, or unusual growth patterns over multiple years (e.g. an unreasonable increment in one year that was reversed in the subsequent year). All individual tree data that was deemed unreasonable was set to missing values, which was possible without detrimental effects on the statistical power of the analysis, because all treatments were replicated in row plots. Subsequently, individual tree data from row plots were averaged to be used as experimental units in statistical analysis. Analysis of variance and variance component estimation was carried out with PROC MIXED of the SAS statistical software package (SAS Institute 2008), where site, block and genotype were specified as random factors. Average height and average diameter of genotypes (clones, provenances, and hybrids) were calculated with the least squares means method for each planting site.

Broad-sense heritabilities were determined separately for each clonal trial, and calculated as:

$$(1) \qquad H^2 = V_G/V_P,$$

where V_G is the total genetic variation represented by the variance component due to clones and V_P the phenotypic variation among clones represented by the variance component due to clones plus the residual error. Block effects were not included in the denominator.

To derive standard errors for heritability estimates, standard errors of variance components were generated with the COVTEST option of PROC MIXED (SAS Institute 2008). Using standard formulas of error propagation for addition, the standard error of V_P was determined as:

$$(2) \qquad SE_{Vp} = (SE_{Clone}^{2} + SE_{Error}^{2})^{½}$$

Subsequently, standard formulas of error propagation for division served to estimate the standard error of H^2:

$$(3) \qquad SE_{H^2} = H^2 \times ((SE_{Clone}/V_G)^{2} + (SE_{Vp}/V_P)^{2})^{½}$$

Seed zone delineations were carried out with a different variance partitioning approach that used geographic predictor variables to partition genetic variation observed in the provenance and clonal trial series. Least squares means of clones or provenances were grouped with multivariate regression tree analysis, implemented with the *MVpart* package v1.2-6 for the R programming environment (R Development Core Team 2008). Multivariate regression trees

analyze multiple traits (in this case height and DBH) from multiple sites simultaneously. For each trait to be equally weighted, all variables were standardized by subtracting the mean and division by the standard deviation of each trait at each test site, so that all traits are expressed in units of standard deviations from a site mean of zero.

Multivariate regression trees (MRT) are based on the same principles as Classification and Regression Trees (CART), but extended to more than one response variable (De'Ath 2002). MRT can be viewed as a constrained clustering methodology that is suitable for explanation as well as prediction. A set of clusters is grown by repeated binary splits of the genetic dataset. Splits are made using predictor variables as partitioning criteria (here, geographic variables), so that the homogeneity of the response variable (here, height and DBH) within the resulting groups is maximized. Homogeneity is evaluated as sums of squares of traits around the multivariate mean of observations in a cluster (De'Ath 2002).

5. Results

5.1. Geogaphic patterns of genetic variation

Significant genotype × environment interactions were present for all clonal and provenance trial series (Tables 2-9). The nature of interactions was visualized

with scatter plots and box plots (Figures 3-10), which I subsequently discuss in more detail for each trial series.

In the 1999 clonal series, rank changes of clones among pairs of sites are shown in Figure 3. This figure represents scatter plots among all pairs of sites for DBH (above the diagonal) and for height (below the diagonal). Note that in each scatter plot, only clones that were planted at both sites can be shown. Individual clones change ranks frequently (e.g. in the lower left scatter plot of Figure 3, the top performer for Height at Site 60 with 6m (red dot) is only an average performer at Site 10 with 4.5m). Groups of similar origin seem to rank more consistently across sites. The Slocan-North sources (yellow) are the worst performers at all sites followed by the Slocan-South sources (orange), while the remaining sources do not appear to be genetically distinct in height and diameter. The same performance ranking by groups is also visualized as boxplots (Figure 4), which generally shows the same trend but includes all clones (even those that are not shared among sites and that were excluded from Figure 3).

In the 2001 clonal series (Figures 5 and 6) had a smaller geographic sampling range and fewer clones replicated across all three test sites, but the results revealed somewhat similar patterns. The most northern sources from this series (DMI, green) showed the least performance at site 31 and 81. Local sources (AIN, purple) at site 81, and (MW, WEY, shades of blue) at site 31 were the best performers by a small margin. Interestingly, when looking at the scatter plots for

this trial, the best performing provenances are not local but southern sources that were transferred north. Local optimality appears to be only true for regional averages.

In the 2002 clonal series (Figure 7 and 8) is the most comprehensive series with complete replications. Again, there are similar results. BC sources (SLN, yellow and SLS, ochre) generally perform poorly. At the most southern site (31) all sources perform below average compared to the other sites (10, 81), with the sources that were transferred south (SLN, SLS, DMI, SLP) performing the worst. The local sources from the Foothill ecoregion (AIN, WEY) are the best performers on average as well as containing the best performing genotypes. The slight advantage of local sources is not apparent at the other sites (10 and 81). Rank changes among clones are less pronounced between Site 31 and Site 81 than among Site 10 and Site 31 or Site 10 and Site 81, indicating that different clones perform best at the northern site (Figure 7).

The 1998 provenance trial series (Figure 9 and 10) provides the most suitable data to analyze genotype × environment interactions, because it covers the greatest geographic range for both collections and test environments. Again, the sources from northern BC perform poorly (Figure 9 and 10, BCN, yellow). Sources from a wide geographic range including northern Alberta, central Alberta, the Alberta Foothills, and Saskachewan perform similarly across all sites. The surprise is the superior performance of Minnesota sources, transferred over a long-distance.

Only at the most northern sites (10 and 70) performance of the Minnesota seedlots was average.

5.2. Breeding region development

Figure 13 shows the result of variance partitioning for the 2002 clonal trial series using the multivariate regression tree approach. The 2002 clonal series was chosen because of the wide geographic coverage and complete replication over multiple test sites. The amount of genetic variation explained by each split of the dataset is represented by the length of the branches. Most variation within the 2002 clonal dataset (height and diameter at three sites) can be explained by a split at approximately 56°N latitude. Further splits separate the five most southern sources, which perform above average at all sites (Figure 13, group on the far right). The next split separates the two most northern sources in BC, which perform far below average at site 81 and 31 (group on far left). The last minor split separates sources from above and below 523m within the northen Alberta group.

Repeating the same analysis for the provenance trial, which covers a greater environmental range for test sites and source locations reveals similar patterns (Figure 14). Sources from the far north perform below average on all test sites (reaction norm represented by the far left group). The next split separates the Minnesota sources as well as the most southern sources from the Alberta Foothill

ecosystems, which has also been identified as superior in the 2001 clonal trial (Figure 14, group on far right). The last split explains only little additional genetic variation in the dataset and separates Alberta provenance at 56°N latitude, again an identical split as in the 2002 clonal trial.

5.3. Broad-sense heritability of growth traits

Assuming two breeding regions for Alberta, developed in the previous section, I separately analyzed northern clones at northern sites (Slocan and DMI sources planted at site 10) and southern sources at the southern planting site (all other sources at sites (31, 41, 81, and 60). Variance components and heritabilities for these putative breeding populations are shown in Tables 10 and 11.

Broad-sense heritabilities for height and diameter for the southern breeding region and southern collections by Weyerhaeuser, Millar Western Forest Products, Alberta-Pacific Forest Industries, Ainsworth Lumber, and Slave Lake Pulp Corporation were variable among individual trials (Table 10). Generally, Site 31 at Drayton Valley and Site 60 at Athabasca show high heritability values from 0.50 to 0.64. These were high-quality sites that were well maintained with uniform planting conditions. Given that Site 31 also contains the most clones within annual series, experiments at Site 31 (highlighted in bold in Table 10) appear to be the most promising to select for breeding and deployment. After removal of northern clones, the 1999 clonal trials only contained four to six

clones, which were not sufficient for accurate estimation of heritability in this series.

The northern collections by Slocan Forest Products and Daishowa-Marubeni International at the northern Site 10 yielded somewhat lower broad-sense heritabilities between 0.13 and 0.54, for height and diameter. Standard errors in this trial series were generally higher and the number of clones included in the trials were generally lower. Nevertheless, two experiments (highlighted in bold in Table 11) appear to be suitable to select clones for breeding and deployment with a total number of 42 clones.

5.3. Hybrid performance

All hybrid trials showed significant main effects for the site, type of cross, and hybrid family within cross type (Tables 12 to 15, Figures 11 and 12). The 2001 hybrid series, planted on four sites reveals a slight advantage of the *Populus tremuloides x P. alba* hybrid over two other types of crosses (*P. davidiana* and *P. tremula*) (Figure 11). However, only one pairwise comparison is significant for the 2001 series after Turkey adjustment: height at site 41 between the *P. alba* and *P. tremula* hybrids (p=0.0108). There were no significant interactions between genotypes and sites, either for the type of cross or for families within types of crosses.

In the 2002 hybrid series, *Populus tremuloides* × *P. davidiana* and *P. tremuloides* × *P. tremula* hybrid crosses were not significantly different from the native control seed lot in pairwise comparisons for individual sites. However, it is notable that the variation within the hybrids, and particularly within the *P. tremula* hybrid families is substantially larger than in the control lots. Also in this series, there were no significant interactions between genotypes and sites, either for the type of cross or for families within types of crosses.

6. Discussion

6.1. Delineation of seed and breeding zones

The analysis of geographic patterns of genetic variation confirms Li's (1995) preliminary delineation of breeding regions. In fact, his educated guess of three breeding regions for Alberta, which was not based on any genetic information, appears remarkably insightful. His proposed north-south split at 55°N latitude, corresponds almost exactly to our proposed 56°N latitude splits determined by regression tree analysis for both clonal and provenance trial data. However, there was no apparent east-west cline that would justify a third breeding region east of 114°W longitude, also proposed by Li (1995). The findings confirm observations by Barnes (1975), who investigated nine morphological characteristics in 1257 clones at 206 locations in seven western states and the province of British

Columbia. Univariate and multivariate analysis could only identify a significant south to north cline in morphology of aspen, not an east to west differentiation.

Regression tree analysis for the 2002 clonal trial series also identifies an elevational differentiation of genotypes within the first zone, north of 56° N latitude. Sources from above 500m within this zone consistently underperformed across all test sites in this trial series, which suggests that there should be an elevation limit to the northern breeding region. While I did not find an elevational cline in the southern breeding region, note that no high elevation clones or provenances were included, and the breeding region should therefore be restricted to the highest sampled provenances or clones.

6.2. Potential gains from aspen tree improvement

Across 13 clonal trials, broad-sense heritablilities in this study were on average 0.45 for height and 0.43 for diameter, similar to results observed in previous common garden trials. Thomas et al. (1998b) estimated heritability between 0.29 to 0.56 for root collar diameter in 2-year rooted cuttings. In a subsequent growth chamber experiment that better controls for environmental variation than field tests, broad-sense heritabilities ranged from 0.08 to 0.74 in diameter and height. In another short-term common garden trial in Southern Utah (Kanaga et al. 2008) estimated broad-sense heritabilities for height growth of 0.45. In a more

comprehensive long-term trial series, comparable in experimental design to this study, St Clair et al. (2010) found somewhat lower estimates of broad-sense heritability around 0.3.

The trials with the highest heritabilities and largest numbers of clones (highlighted in Tables 10 and 11), indicate a good potential for selecting superior clones for deployment prior to a first generation breeding cycle as a tree improvement strategy. To translate heritability values into gains in productivity, one has to determine selection differentials that can be achieved with the current trial series. High selection differentials require a large base population, which can be increased by combining clones planted at different sites. To rank clones across different genetic tests and planted in different years, height and diameter needs to be expressed as standard deviation from a test mean of zero. For the following calculations I therefore make the assumption that the average genetic worth of different clonal trial series is the same.

Clonal deployment of planting stock in Alberta requires at least 18 clones in a deployment population for reforestation (ASRD 2009). For the southern breeding region, 146 southern clones can be assessed at Site 31, allowing for a selection differential of 12% when selecting the top 18 clones. This results in a 15% gain in height and 34% in DBH, assuming an average broad-sense heritability at the selected sites (highlighted in Tables 10) of 0.55 and 0.57, for height and DBH respectively. The northern breeding region has smaller collection available at Site

10, with 42 northern clones. The Clone9-10-02 experiment is excluded because of low heritabilities (Table 11). This only allows a selection differential of 43% when selecting the top 18 clones. This results in a 5% gain in height and 9% gain in DBH, assuming an average broad-sense heritability at the selected sites (highlighted in Tables 10 and 11) of 0.44 and 0.5 for height and DBH, respectively.

As shown in Figure 4 and 8, many southern sources are growing well at the northern Site 10, which represents the northern breeding region. If southern clones from the 1999 to 2002 test series could be used in the northern breeding region, the top 18 clones would comprise six northern sources and twelve southern sources, yielding a 16% gain in height. The additional 11% gain would come at an increased risk associated with using non-local sources. Practitioners should probably avoid transfer distances from source to planting location that exceed 2-3° latitude even considering recent warming trends (Mbogga et al. 2009).

It should be kept in mind, however, that clonal selection is a "dead end" in tree improvement programs. No further gains are possible, once the deployment limit for individual clones is exhausted. In Alberta the proposed policy is for no more than one million ramets of a clone may be used on public lands. Controlled crosses of the best material and selection of offspring for desirable traits is the logical next step in an improvement program. To this end, a number of progeny

trials have recently been established by the industrial tree improvement cooperative between 2003 and 2006.

6.3. Local optimality of seed sources

The conceptual basis for the delineation of seed zones is that local sources are optimally adapted to local environments and should therefore not to be moved too far from the collection location to avoid mal-adaptation. The results interestingly suggest that this assumption is not correct for aspen in Western Canada. Instead, a northward movement of planting material almost always results in increased growth and a southward movement has a strong opposite effect.

For example, Figure 10 shows that the most northern provenances from British Columbia (color code: yellow) perform poorly when transferred south with the lowest height growth at the most southern test site (33). The provenances from northern Alberta (light green) perform somewhat more poorly than local sources at the southern test sites (33, 60, 90), but are the relatively best performers when transferred to the most northern test site (70). The provenances from central Alberta (light blue), Saskatchewan (pink), and the Foothills (dark blue) show similar growth across all test sites, and they also outperform the local sources when transferred to the most northern test site (70), but they are slightly inferior to the local sources when transferred to the Northern Boreal test site (10). The most surprising observation is the result of long-distance transfers of the

Minnesota seedlots. Except for the two most northern sites (70 and 10), they outperform all Canadian sources across test sites 60, 33, and 90 by a large margin. A similar effect was detected in the clonal series (Figure 4, 6 and 8). Also here, northern sources (SLN, SLS, and DMI) generally underperformed at southern sites (31, 41, and 81), whereas more southern sources (WEY, ALP, MW, AIN) generally performed better or on-par with local material at the northern site (10).

One possible explanation for this observation is adaptational lag. Adaptational lag refers to a mismatch of genotypes and environments, caused by a relatively fast environmental change and a comparably slow evolutionary response (Matyas 1990). Adaptational lag is not uncommon and is in fact part of any evolutionary change through directional natural selection. Even if adaptational lag does not pose a threat to a species' overall survival, it is a concern for forest management because it can result in suboptimal growth, poor forest health, and high rates of tree mortality. Even though these impacts could be viewed as a natural part of evolutionary change, most forest management systems would aim at maximizing forest health and productivity through intervention. Given the climate change trends towards drier and warmer conditions in western Canada (Mbogga et al. 2009), adaptational lag appears to be a plausible explanation for the observed non-optimality of local sources.

6.4. Potential of aspen hybrids

The assessment of hybrid performance across multiple test sites appears less promising overall than studies from other regions appear to suggest. In commercial plantations with hybrid poplar in Sweden, Karacic et al. (2003) and Rytter and Stener (2005) observed double the productivity than what was observed in natural stands by Linder et al. (1997) and Johansson (1999). Note that productivity improvements in this comparison includes genetic as well as silvicultural improvements. In direct comparisons in Minnesota with native aspen and various hybrids (*Populus tremuloides* × *P. davidiana,* × *P. alba,* × *P. tremula, and* × *P. canescens*), significant improvements between 29 to 34% increase in height growth over a native control at age 15 were observed (Li 1993). Improvements of comparable magnitude were only observed in the 2002 clonal series at the most southern test site (Figure 12, Site 31). All other differences were not statistically significant.

Although I cannot conduct a direct statistical comparison between the clonal and hybrid trial series, which were separate experiments, note that these trials were planted at the same time in adjacent blocks. I will therefore do an informal comparison in this discussion section, while acknowledging that site factors may be confounded with differences in clonal and hybrid performance. Clones of the 2001 series showed heights between 1.8 and 4m, with an average of 3m (Figure 6). Hybrids in the adjacent trial ranged from 2 to 3.5m, suggesting no advantage

(Figure 11). At site 81, the situation is similar, with native aspen on average 4.3m high and the top performing clones reaching 5m. None of the hybrids in the adjacent trials performed above the mean of the clonal trials.

The more extensive clonal and hybrid trial series in 2002 offer a more interesting comparison (Figure 8 versus 12). Here, the hybrid trials show greater variance in performance than the native aspen control lots, implying that superior hybrid genotypes could be identified, even if the average performance of hybrid crosses is on-par with native aspen. At site 10, the *P. tremula* hybrids showed the greatest variance with heights between 0.7 and 2.8. This compares to a range of height in clones between 1.5 and 3.9, with the best performing clones (WEY) transferred a substantial distance to the northern planting site. At site 31, *P. tremula* hybrids had heights between 2 and 3.5m (Figure 12), whereas clones ranged from 1.3 to 3m (Figure 8), giving the hybrids a slight advantage even if clones from other regions in Alberta were considered. Lastly, at site 81, *P. tremula* hybrids had heights between 2.3 and 5.2m (Figure 12), whereas clones ranged from 1.7 to 4.5m (Figure 12). Again, a slight advantage for the best hybrids compared to the best clones.

7. Conclusions and recommendations

Returning to the stated objectives of this thesis: (1) to determine geographic patterns of genetic variation of aspen in western Canada in order to delineate seed zones and breeding regions, (2) to assess the potential of clonal forestry systems to enhance forest productivity, and (3) to evaluate the potential of hybridization to enhance growth through hybrid vigor, I conclude with the following recommendations:

(1) Two breeding regions for aspen in Alberta, north and south of 56°N latitude appear appropriate. I should note that none of the clonal or provenance samples in Alberta were collected north of 59°N latitude and this should be a prudent limit for the northern breeding region. Similarly no material was tested south of 52°30'N, which would serve as a limit for the southern seed zone. The northern breeding region may include an elevation limit, since I detected a genetic difference along an elevational gradient in the 2002 clonal trial. This corresponds almost exactly to preliminary breeding zones that formed the basis of the current tree improvement program, that were delineated for Northwestern Alberta between 56° and 59°N and excludes the upper boreal highlands. Similarly, the current Alberta Foothill natural region matches the southern regression tree derived seed zone. The only suggestion for modification would be that transfer between eastern and western parts of Alberta at the same latitude and similar ecosystem types should be allowed, as I did not find any evidence of genetic differentiation even as far as central Saskachewan in the provenance trial.

(2) Broad-sense heritabilities estimated from multiple trials suggest that substantial genetic gains are possible through clonal selection as part of an aspen tree improvement program. Broad-sense heritabilities for height and diameter ranged from 0.36 to 0.64 on good sites. Clonal deployment of planting stock in Alberta requires at least 18 clones in a deployment population for reforestation. In a first round of selection from northern and southern breeding region with 42 and 146 clones respectively, 5-15% genetic gains in height and 9-34% in diameter could be achieved immediately through deployment of clones, prior to the first generation of breeding.

(3) It appears that intensive selection of the best hybrid families could have at least some potential in improving yields, and selecting particular clones within hybrids may increase yields even further (this remains unknown because the hybrid trials did not have a clonal structure). However, I did not find convincing evidence of hybrids consistently outperforming local sources. Given that deployment of hybrids entails its own risks, further investments in research is required to comprehensively assess the value of aspen hybrids for enhanced forest management in Alberta. Better information is needed about the origins of the non-local parents to assess the match with local climate conditions, and tests including more hybrid families that also have a clonal structure would make comparisons with native material more conclusive.

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Table 1. Site information, trial series, and measurement dates and types that were used for this study. The name of the trial consists of a trial identifier (e.g. Prov2-) a site identifier (e.g. -10-) and the year of establishment (e.g. -98 for spring 1998). The date of measurement is followed by the traits evaluated, with "H" standing for height, "R" for root collar diameter, and "D" for DBH. An asterisk indicates that the height was estimated based on first-order branches below the leader in the following year.

Site Information		Provenance Series 1998	Clonal Trial Series 1999	Clonal Trial Series 2001	Hybrid Trial Series 2001	Clonal Trial Series 2002	Hybrid Trial Series 2002
Number:	10	Prov2-10-98	Clone1-10-99		Hybrid1-10-01	Clone6-10-02	Hybrid12-10-02
Name:	Manning	Sep 02: H,D	July 99: H,R		Sep 01: H,R	Clone9-10-02	Sep 02: H,R
Region:	Northwestern AB	Sep 05: H,D	Sep 99: H,R,D		Sep 02: H,R	May 02: H. R	Sep 04: H,R,D
Latitude:	56°58'N		Sep 03: H,D		Sep 03: H,R,D	Sep 02: H,R	
Longitude:	117°44'W		Aug 05: H,D			Sep 04: H,R,D	
Elevation:	570 m		Nov 06: H,D			Sep 06: H. D	
Number:	11						Hybrid7-11-02
Name:	Manning						Sep 02: H,R
Region:	Northwestern AB						Sep 04: H,R,D
Latitude:	56°46'N						
Longitude:	117°28'W						
Elevation:	525 m						
Number:	31			Clone2-31-01	Hybrid3-31-01	Clone5-31-02	Hybrid8-31-02
Name:	Drayton Valley			Clone3-31-02	Sep 02: H	Clone8-31-02	Hybrid10-31-02
Region:	AB Foothills			Sep 02: H	Sep 03: H,D	Sep 02: H,R	Sep 02: H,R
Latitude:	53°12'N			Sep 03: H,D	Sep 05: H,D	Sep 04: H,R,D	Sep 04: H,R,D
Longitude:	115°13'W			Sep 05: H,D	Sep 06: H,D	Sep 05: H*	Sep 05: H*
Elevation:	887 m			Sep 06: H,D		Sep 06: H,D	Sep 06: H,D
Number:	33	Prov2-33-98					
Name:	Medicine Lake	Sep 04: H,D					
Region:	AB Foothills	Sep 05: H,D					
Latitude:	52°44'N						
Longitude:	114°47'W						
Elevation:	970 m						

continued …

Table 1. Continued

Site Information		Provenance Series 1998	Clonal Trial Series 1999	Clonal Trial Series 2001	Hybrid Trial Series 2001	Clonal Trial Series 2002	Hybrid Trial Series 2002
Number:	41		Clone1-41-99		Hybrid4-41-01		
Name:	Linaria		Sep 03: H,D		Oct 03: H,D		
Region:	Central AB		Oct 05: H*		Feb 07: H,D		
Latitude:	54°22'N		Oct 06: H,D				
Longitude:	114°10'W						
Elevation:	646 m						
Number:	60	Prov2-60-98	Clone1-60-99	Clone18-60-01			
Name:	Athabasca	Sep 99: H,D	Sep 01: H,R	Sep 01: H,R			
Region:	Central AB	Sep 00: H,D	Sep 02: H,R	Sep 02: H,R			
Latitude:	54°53'N	Sep 01: H,D	Sep 03: H,R,D	Sep 03: H,R,D			
Longitude:	113°18'W	Sep 02: H,D	Sep 05: H,D	Sep 05: H,D			
Elevation:	570 m	Sep 05: H,D	Sep 06: H,D	Feb 07: H-D			
Number:	70	Prov2-70-98					
Name:	Fort Nelson	Sep 02: H,D					
Region:	Northeastern BC	Sep 05: H,D					
Latitude:	58°32'N						
Longitude:	122°20'W						
Elevation:	335 m						
Number:	81			Clone 4-81-01	Hybrid5-81-01	Clone7-81-02	Hybrid9-81-02
Name:	Grovedale			Sep 01: H,R	Sep 01: H,R	Clone10-81-02	Hybrid11-81-02
Region:	West-Central AB			Sep 03: H,R	Sep 02: H,R	Sep 02: H,R	Sep 02: H,R
Latitude:	54°54'N			Sep 05: H*	Sep 03: H,R	Sep 04: H,R,D	Sep 04: H,R,D
Longitude:	118°57'W			Sep 06: H,D	Sep 05: H,R,D	Sep 06: H,D	Sep 05: H*
Elevation:	683 m				Jan 07: H,D		Sep 06: H,D
Number:	90	Prov2-90-98					
Name:	Prince Albert	Sep 05: H,D					
Region:	Central SK						
Latitude:	53°20'N						
Longitude:	105°36'W						
Elevation:	480 m						

Table 2. Analysis of variance for 8-year height measurements in trial series "Clone 1999"

Source of variation	df	MS	F-Value	P-Value
Clone	31	2.5	7.7	<0.0001
Block(Site)	9	3.5	10.8	<0.0001
Site	2	16.8	51.2	<0.0001
Clone×Site	35	0.9	2.6	<0.0001
Block×Clone(Site)	176	0.3		

Table 3. Analysis of variance for 8-year DBH measurements in trial series "Clone 1999"

Source of variation	df	MS	F-Value	P-Value
Clone	31	6.5	9.0	<0.0001
Block(Site)	9	7.1	9.8	<0.0001
Site	2	31.4	43.2	<0.0001
Clone×Site	35	1.2	1.6	0.0241
Block×Clone(Site)	176	0.7		

Table 4. Analysis of variance for 6-year height measurements in trial series "Clone 2001"

Source of variation	df	MS	F-Value	P-Value
Clone	111	2.4	10.3	<0.0001
Block(Site)	16	3.7	15.8	<0.0001
Site	2	124.0	524.5	<0.0001
Clone×Site	79	0.6	2.4	<0.0001
Block×Clone(Site)	820	0.2		

Table 5. Analysis of variance for 6-year DBH measurements in trial series "Clone 2001"

Source of variation	df	MS	F-Value	P-Value
Clone	111	5.1	11.0	<0.0001
Block(Site)	16	7.5	16.2	<0.0001
Site	2	208.7	452.5	<0.0001
Clone×Site	79	1.0	2.2	<0.0001
Block×Clone(Site)	817	0.5		

Table 6. Analysis of variance for 5-year height measurements in trial series "Clone 2002"

Source of variation	df	MS	F-Value	P-Value
Clone	117	1.4	9.1	<0.0001
Block(Site)	25	3.1	19.7	<0.0001
Site	2	172.5	1100.4	<0.0001
Clone×Site	174	0.4	2.8	<0.0001
Block×Clone(Site)	1072	0.2		

Table 7. Analysis of variance for 5-year DBH measurements in trial series "Clone 2002"

Source of variation	df	MS	F-Value	P-Value
Clone	117	2.2	9.6	<0.0001
Block(Site)	25	4.0	17.2	<0.0001
Site	2	223.4	959.5	<0.0001
Clone×Site	174	0.6	2.4	<0.0001
Block×Clone(Site)	1046	0.2		

Table 8. Analysis of variance for 9-year height measurements in trial series "Provenance 1998"

Source of variation	df	MS	F-Value	P-Value
Clone	42	4.7	12.9	<0.0001
Block(Site)	25	3.4	9.3	<0.0001
Site	4	327.8	899.7	<0.0001
Clone×Site	168	1.2	3.2	<0.0001
Block×Clone(Site)	1020	0.4		

Table 9. Analysis of variance for 9-year DBH measurements in trial series "Provenance 1998"

Source of variation	df	MS	F-Value	P-Value
Clone	42	3.2	6.0	<0.0001
Block(Site)	21	2.1	4.0	<0.0001
Site	4	822.8	1547.3	<0.0001
Clone×Site	159	1.4	2.6	<0.0001
Block×Clone(Site)	842	0.5		

Table 10. Number of clones included in trials, mean height and DBH of trials, variance components, and heritability estimates with standard errors (SE) for southern breeding region trials. Note that only clones and test sites south of 56°N latitude were included. The trials most promising for selecting superior clones (with the highest heritabilities and most clones within a series) are highlighted in bold.

	Trial code	Number	Trial	Variance components							
Variable	(ID-site-year)	of clones	mean	Clone	(SE)	Block	(SE)	Error	(SE)	H^2	(SE)
Height	Clone1-41-99	4	5.71	0.13	(0.20)	0.37	(0.40)	0.40	(0.20)	0.24	(0.39)
(m)	Clone1-60-99	6	4.91	0.56	(0.45)	0.14	(0.20)	0.52	(0.20)	0.52	(0.48)
	Clone2-31-01	**77**	**3.14**	**0.19**	**(0.04)**	**0.03**	**(0.02)**	**0.14**	**(0.01)**	**0.58**	**(0.13)**
	Clone3-31-01	46	2.82	0.21	(0.05)	0.03	(0.02)	0.17	(0.02)	0.55	(0.16)
	Clone4-81-01	20	4.76	0.30	(0.14)	0.11	(0.10)	0.58	(0.10)	0.35	(0.17)
	Clone18-60-01	53	3.51	0.38	(0.09)	0.01	(0.02)	0.31	(0.04)	0.55	(0.16)
	Clone5-31-02	**51**	**1.96**	**0.11**	**(0.03)**	**0.02**	**(0.02)**	**0.10**	**(0.01)**	**0.51**	**(0.14)**
	Clone7-81-02	28	3.28	0.23	(0.09)	0.19	(0.15)	0.33	(0.05)	0.41	(0.17)
	Clone8-31-02	**24**	**2.23**	**0.13**	**(0.04)**	**0.04**	**(0.03)**	**0.10**	**(0.02)**	**0.56**	**(0.22)**
	Clone10-81-02	22	3.73	0.11	(0.05)	0.11	(0.09)	0.28	(0.05)	0.27	(0.15)
DBH	Clone1-41-99	4	5.87	0.00		0.59	(0.64)	0.67	(0.29)	0.00	
(cm)	Clone1-60-99	6	6.20	0.91	(0.77)	0.00		0.92	(0.33)	0.50	(0.48)
	Clone2-31-01	**77**	**2.60**	**0.51**	**(0.10)**	**0.10**	**(0.07)**	**0.37**	**(0.03)**	**0.58**	**(0.13)**
	Clone3-31-01	46	2.18	0.40	(0.11)	0.10	(0.08)	0.41	(0.05)	0.49	(0.15)
	Clone4-81-01	20	4.45	0.64	(0.27)	0.17	(0.15)	0.89	(0.15)	0.42	(0.19)
	Clone18-60-01	53	3.61	0.62	(0.16)	0.03	(0.03)	0.60	(0.08)	0.51	(0.15)
	Clone5-31-02	**51**	**1.15**	**0.19**	**(0.05)**	**0.03**	**(0.03)**	**0.19**	**(0.02)**	**0.50**	**(0.14)**
	Clone7-81-02	28	2.71	0.36	(0.13)	0.28	(0.22)	0.55	(0.08)	0.39	(0.16)
	Clone8-31-02	**24**	**1.37**	**0.22**	**(0.07)**	**0.05**	**(0.04)**	**0.12**	**(0.02)**	**0.64**	**(0.25)**
	Clone10-81-02	22	3.15	0.18	(0.09)	0.20	(0.16)	0.52	(0.09)	0.25	(0.14)

Table 11. Number of clones included in trials, mean height and DBH of trials, variance components, and heritability estimates with standard errors (SE) for northern breeding region trials. Note that only clones and test sites north of 56°N latitude were included. The trials most promising for selecting superior clones (with the highest heritabilities and most clones within a series) are highlighted in bold.

	Trial code	Number	Trial	Variance components							
Variable	(ID-site-year)	of clones	Mean	Clone	(SE)	Block	(SE)	Error	(SE)	H^2	(SE)
Height	**Clone1-10-99**	**19**	**4.33**	**0.13**	**(0.07)**	**0.02**	**(0.03)**	**0.24**	**(0.05)**	**0.36**	**(0.21)**
(m)	**Clone6-10-02**	**23**	**2.63**	**0.12**	**(0.04)**	**0.11**	**(0.08)**	**0.11**	**(0.02)**	**0.52**	**(0.22)**
	Clone9-10-02	14	2.15	0.02	(0.02)	0.00	(0.01)	0.14	(0.03)	0.13	(0.13)
DBH	**Clone1-10-99**	**19**	**4.14**	**0.58**	**(0.25)**	**0.00**		**0.50**	**(0.10)**	**0.54**	**(0.27)**
(cm)	**Clone6-10-02**	**23**	**1.63**	**0.11**	**(0.04)**	**0.07**	**(0.06)**	**0.13**	**(0.02)**	**0.46**	**(0.19)**
	Clone9-10-02	14	1.35	0.06	(0.03)	0.03	(0.03)	0.15	(0.03)	0.27	(0.18)

Table 12. Analysis of variance for 6-year height measurements in trial series "Hybrid 2001". Type corresponds to the groups of hybrid families shown in Figure 11.

Source of variation	df	MS	F-Value	P-Value
Type	2	7.5	9.3	0.0001
Family(Type)	8	22.5	7.0	<0.0001
Site	3	51.3	42.3	<0.0001
Block(Site)	36	32.8	2.3	0.0001
Site×Type	4	0.8	0.5	0.7589
Site×Family(Type)	19	7.7	1.0	0.4524
Error	269	0.4		

Table 13. Analysis of variance for 6-year DBH measurements in trial series "Hybrid 2001". Type corresponds to the groups of hybrid families shown in Figure 11.

Source of variation	df	MS	F-Value	P-Value
Type	2	2.2	3.5	0.0320
Family(Type)	8	1.9	3.1	0.0021
Site	3	36.7	59.3	<0.0001
Block(Site)	36	1.0	1.6	0.0211
Site×Type	4	0.6	1.0	0.4370
Site×Family(Type)	19	0.8	1.3	0.1929
Error	269	0.6		

Table 14. Analysis of variance for 5-year height measurements in trial series "Hybrid 2002". Type corresponds to the groups of hybrid families shown in Figure 12.

Source of variation	df	MS	F-Value	P-Value
Type	2	6.8	16.0	<0.0001
Family(Type)	43	79.7	8.7	<0.0001
Site	2	92.0	215.3	<0.0001
Block(Site)	10	25.7	12.0	<0.0001
Site×Type	4	3.4	4.0	0.0040
Site×Family(Type)	45	18.0	1.9	0.0014
Error	256	0.2		

Table 15. Analysis of variance for 5-year DBH measurements in trial series "Hybrid 2002". Type corresponds to the groups of hybrid families shown in Figure 12.

Source of variation	df	MS	F-Value	P-Value
Type	2	4.1	7.5	0.0007
Family(Type)	41	54.3	4.8	<0.0001
Site	2	146.9	267.5	<0.0001
Block(Site)	10	34.8	12.7	<0.0001
Site×Type	4	3.4	3.1	0.0174
Site×Family(Type)	43	25.9	2.2	0.0001
Error	232	0.3		

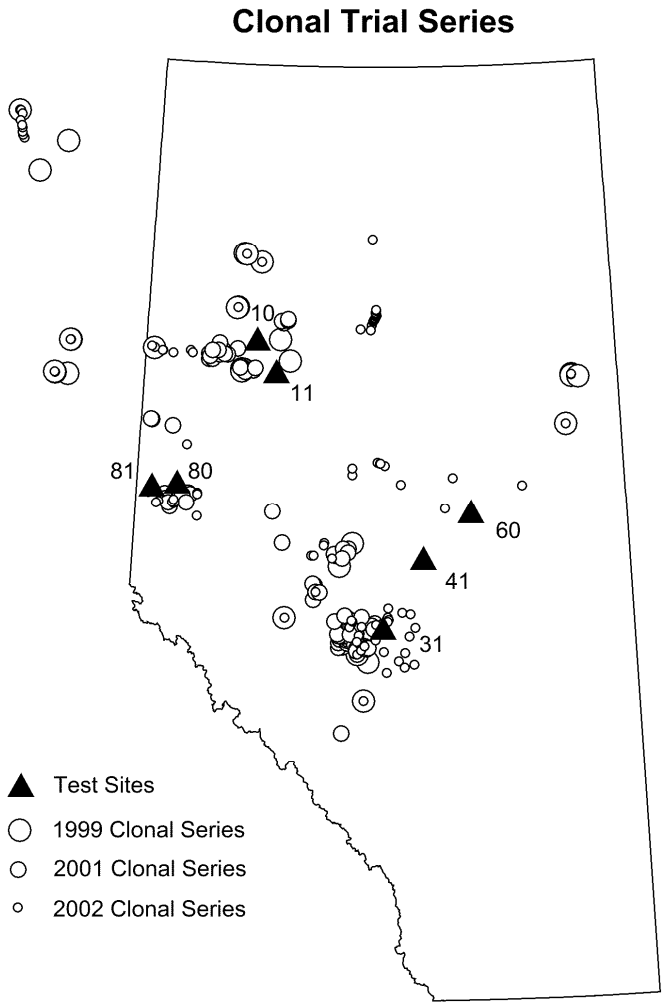


Figure 1. Sample sites for clone collections and test site locations of the clonal and hybrid trial series. The differently sized circles represent clones that were collected in different years and planted in different experiments described in Table 1.

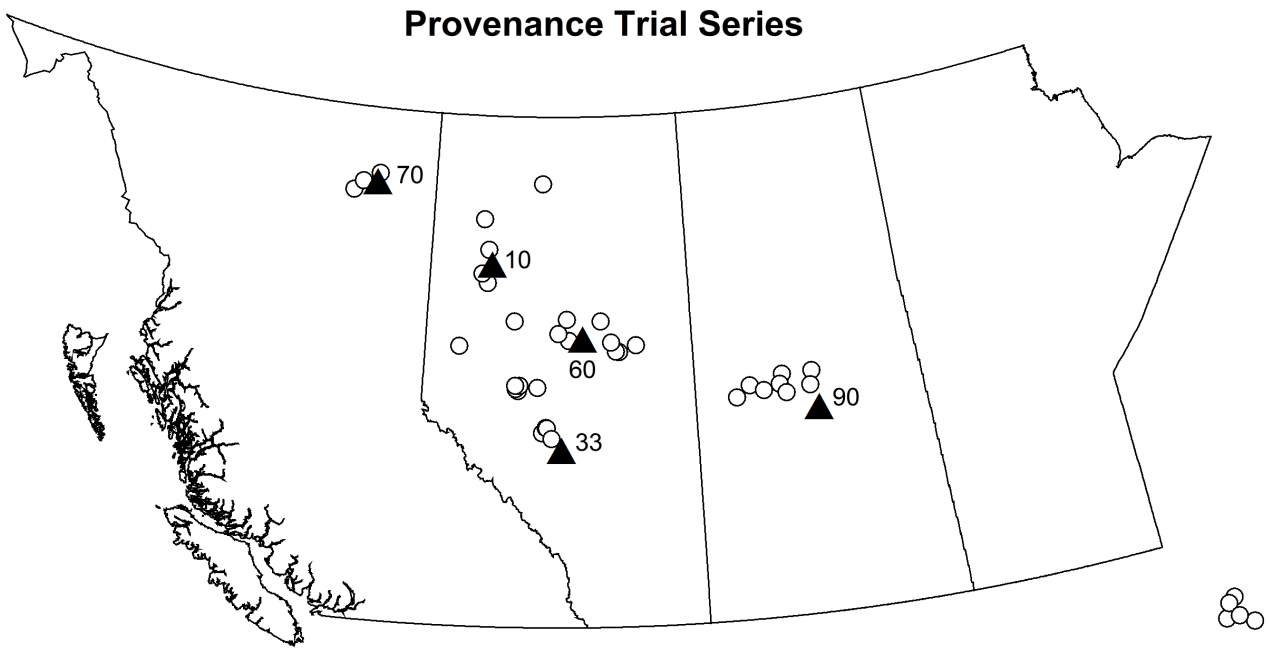


Figure 2. Sample and test site locations of the provenance trial series. Triangles represent test sites described in Table 1, circles represent source location of provenances planted at all test sites.

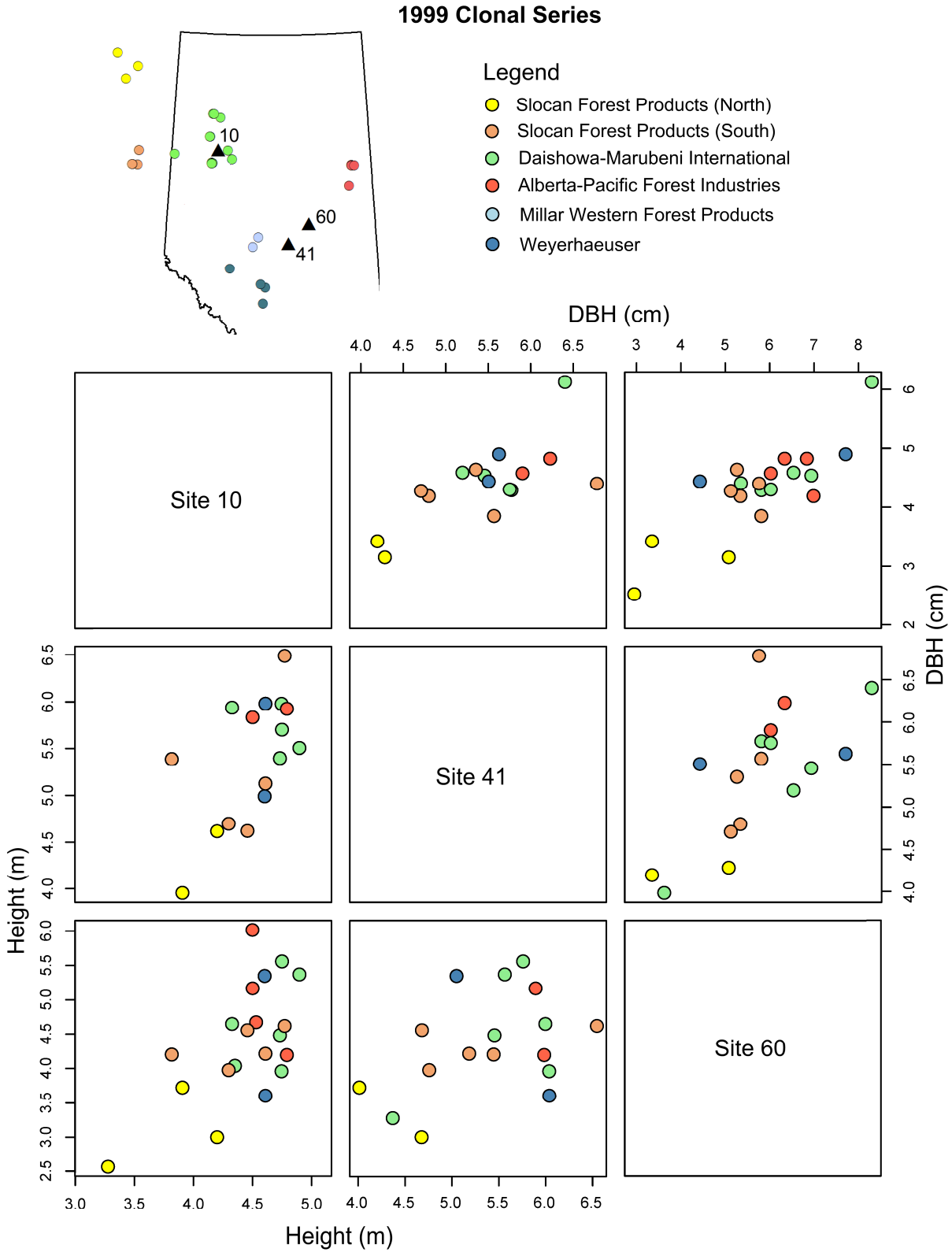


Figure 3. Rank changes of clones among pairs of sites for the 1999 clonal series. Scatter plots above the diagonal show 8-year DBH at two sites, and scatters below the diagonal show height. Note that in each scatter plot, only clones that were planted at both sites can be shown. The map above shows the location of test sites (triangles) and collection sites (circles).

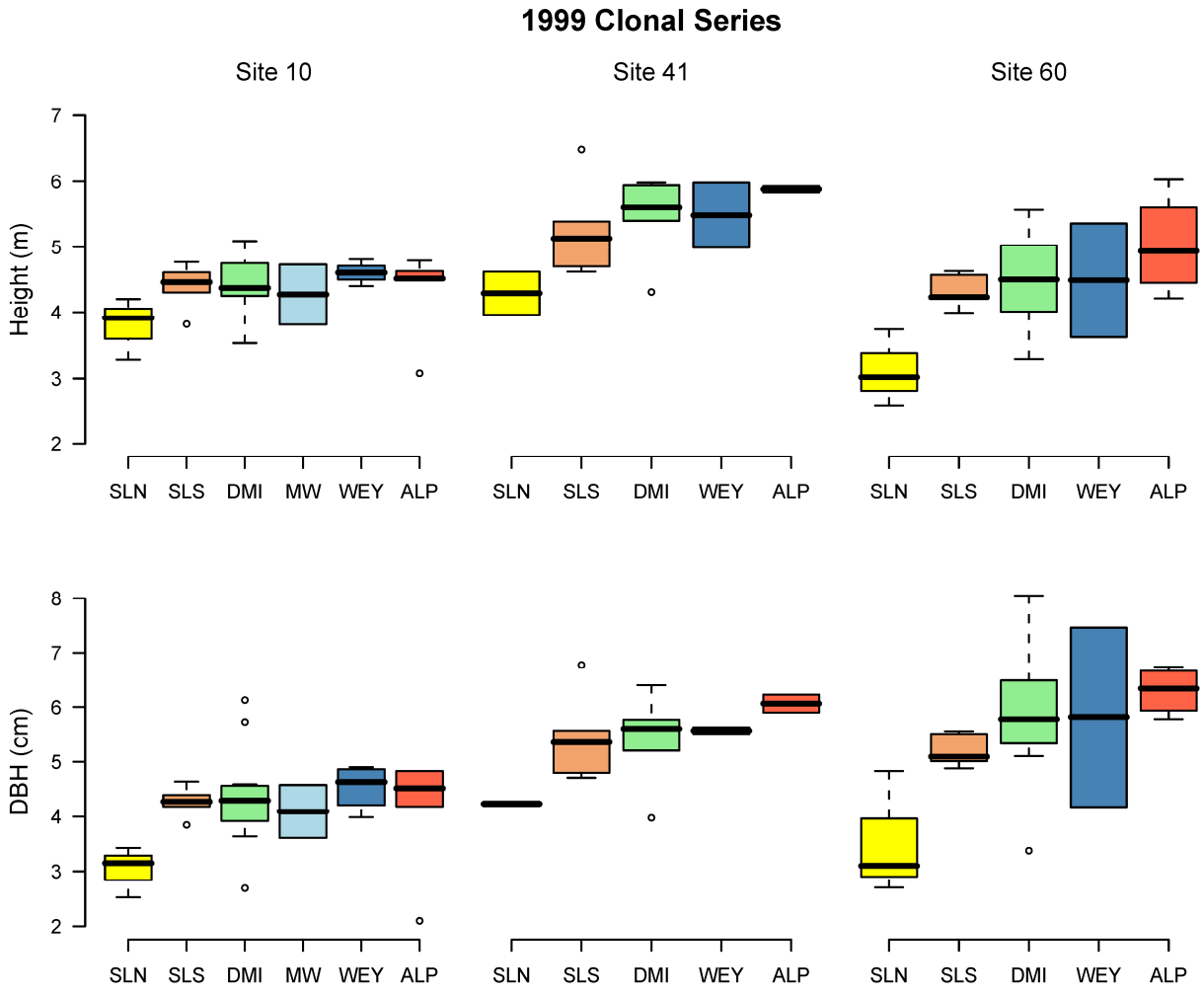


Figure 4. Range of aspen clone means for 8-year height and DBH at multiple test sites (the box plot indicates the range, the median, the 25th and 75th percentile of clonal means for each group. Outliers according to Tukey's inner fence criteria are indicated by circles). For abbreviation of forest management areas, refer to Figure 3.

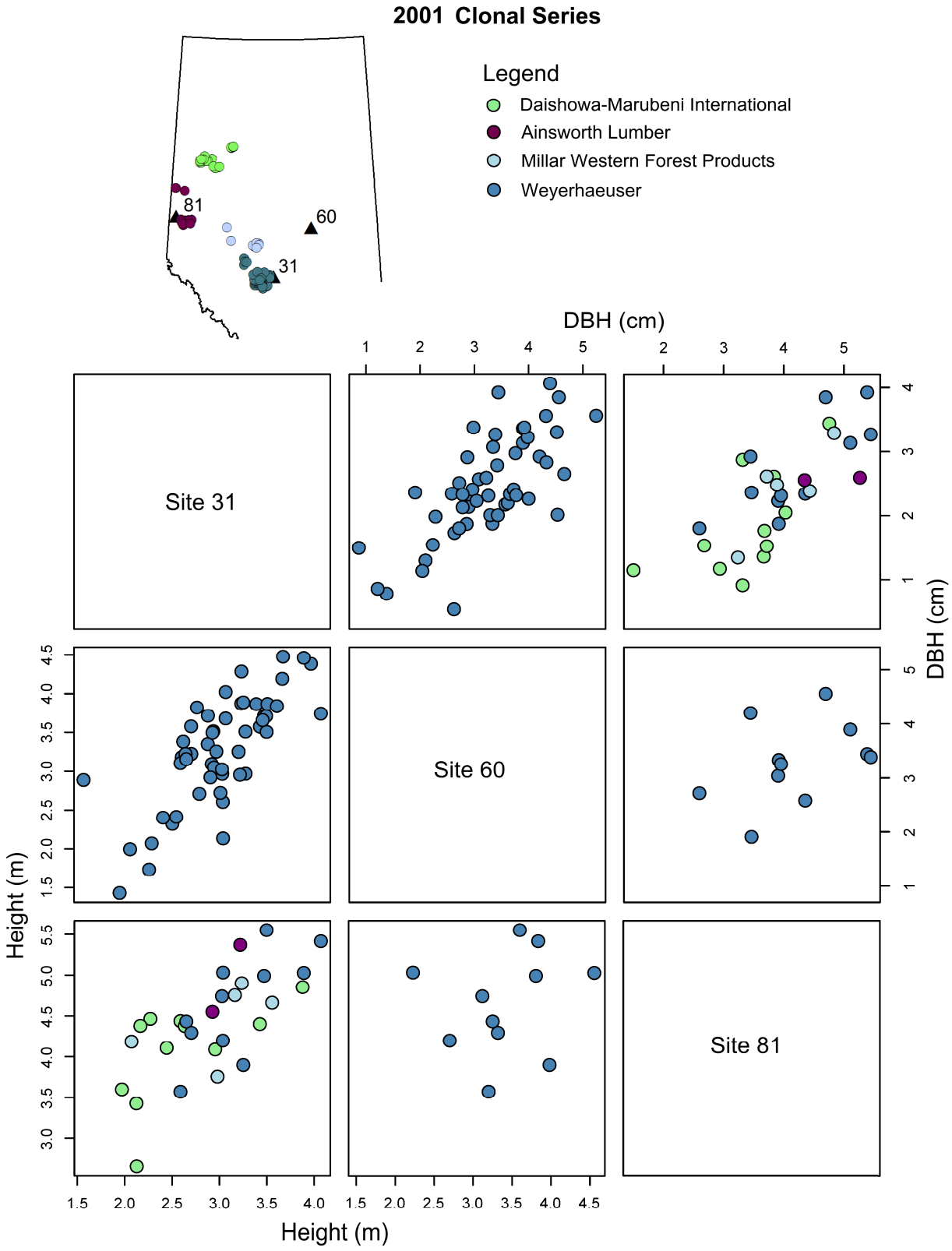


Figure 5. Rank changes of clones among pairs of sites for the 2001 clonal series. Scatter plots above the diagonal show 6-year DBH at two sites, and scatters below the diagonal show height. Note that in each scatter plot, only clones that were planted at both sites can be shown. The map above shows the location of test sites (triangles) and collection sites (circles).

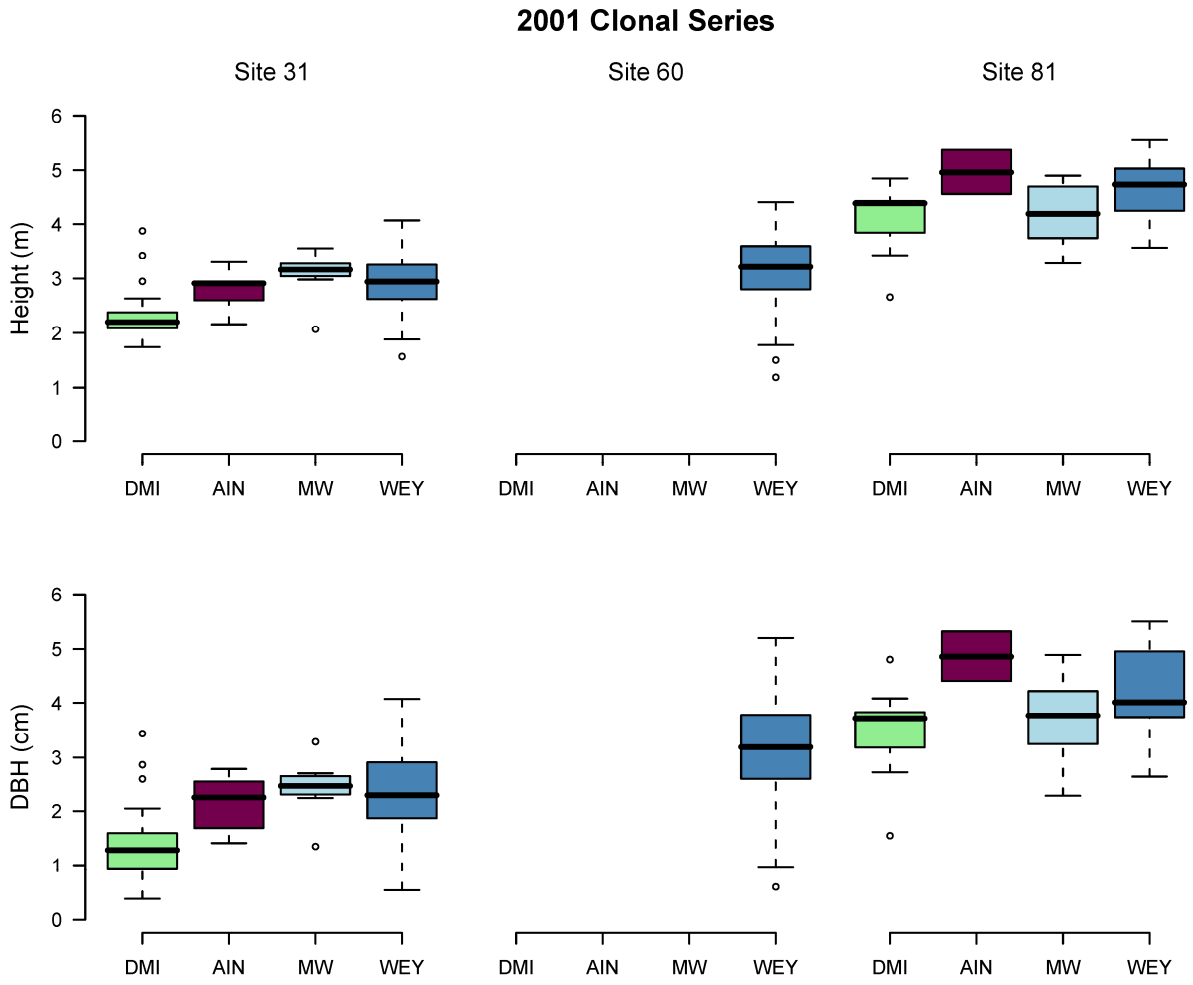


Figure 6. Range of aspen clone means for 6-year height and DBH at multiple test sites (the box plot indicates the range, the median, the 25th and 75th percentile of clonal means for each group. Outliers according to Tukey's inner fence criteria are indicated by circles). For abbreviation of forest management areas, refer to Figure 5.

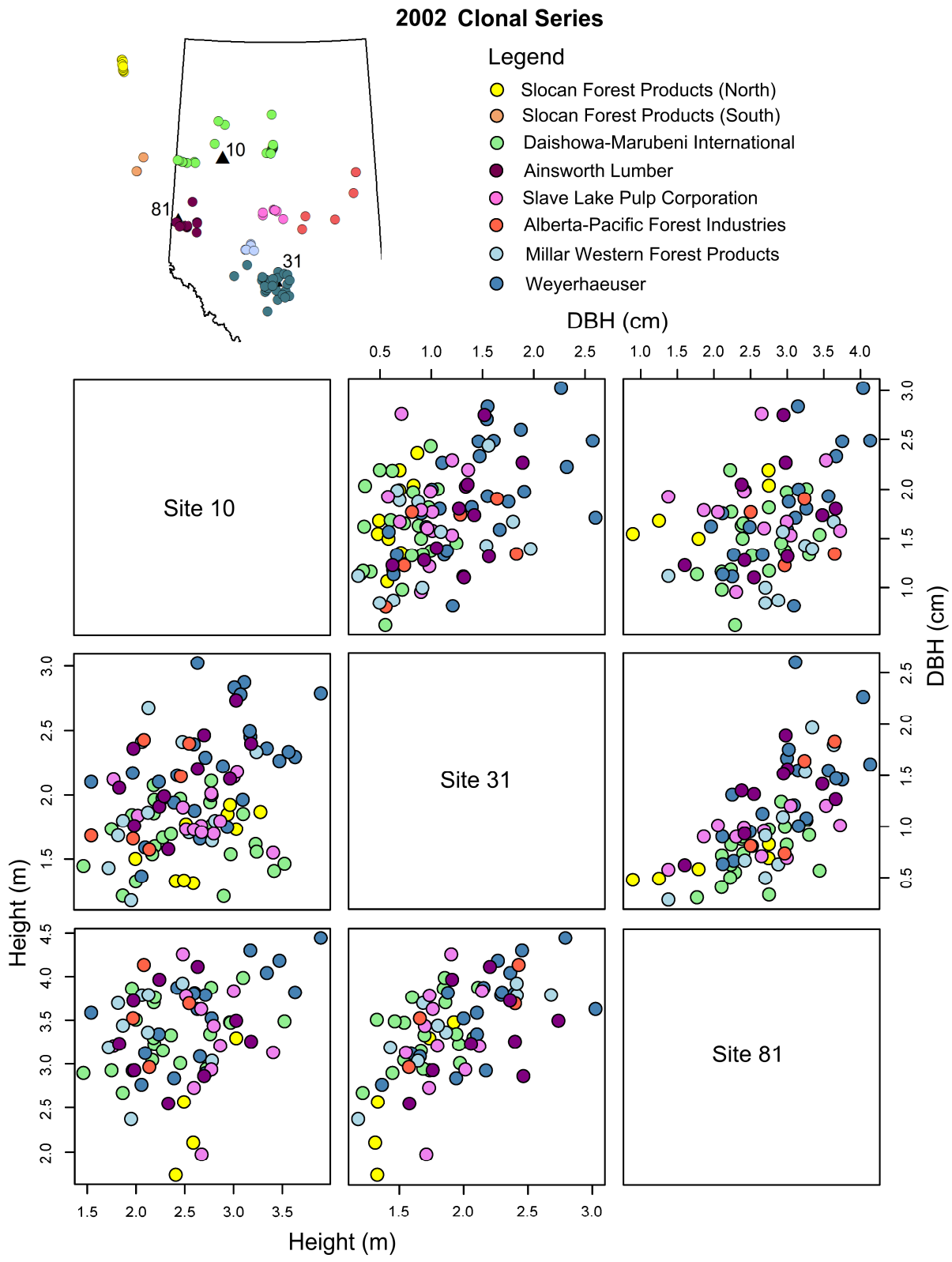


Figure 7. Rank changes of clones among pairs of sites for the 2002 clonal series. Scatter plots above the diagonal show 5-year DBH at two sites, and scatters below the diagonal show height. Note that in each scatter plot, only clones that were planted at both sites can be shown. The map above shows the location of test sites (triangles) and collection sites (circles).

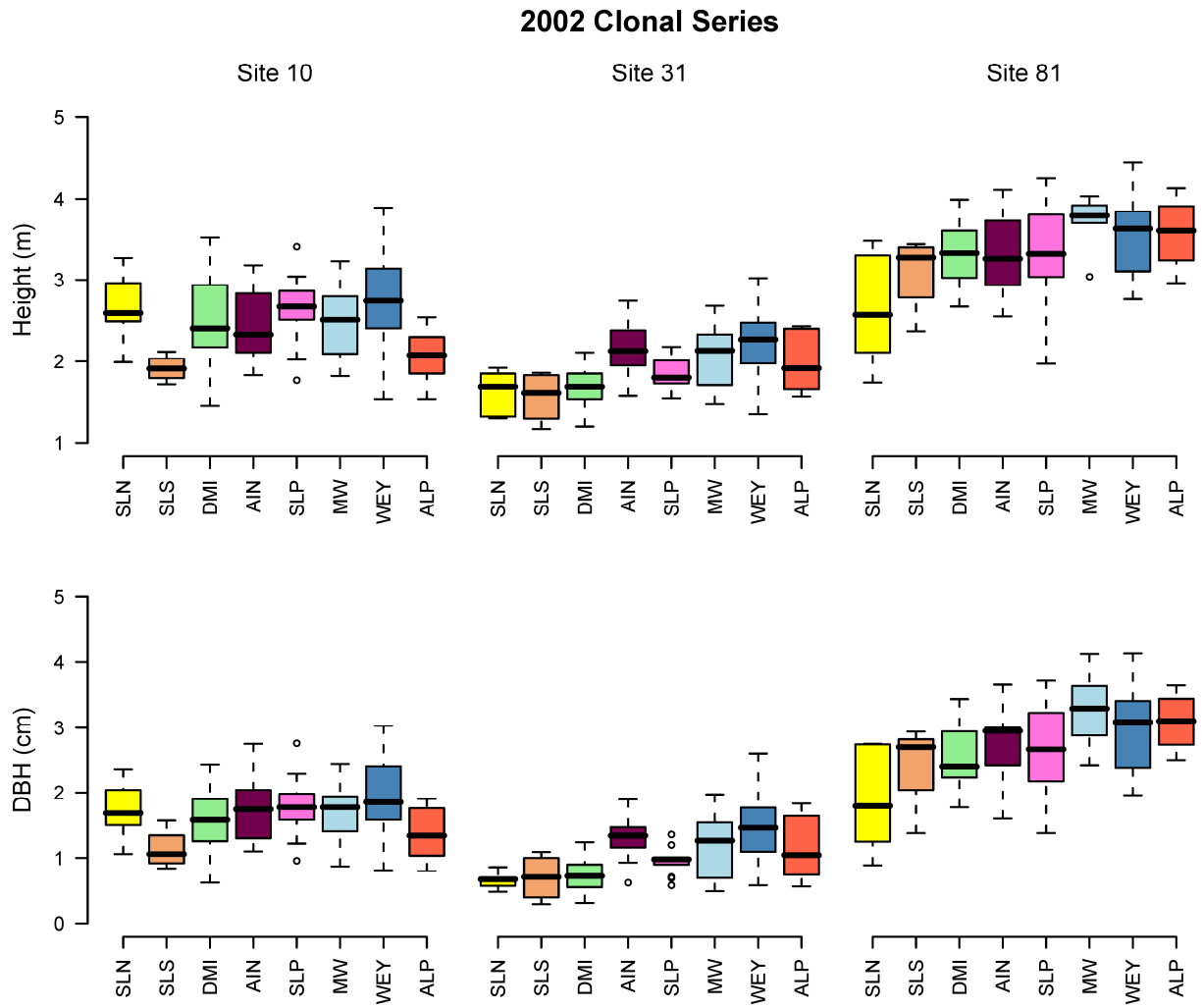


Figure 8. Range of aspen clone means for 5-year height and DBH at multiple test sites (the box plot indicates the range, the median, the 25th and 75th percentile of clonal means for each group. Outliers according to Tukey's inner fence criteria are indicated by circles). For abbreviation of forest management areas, refer to Figure 7.

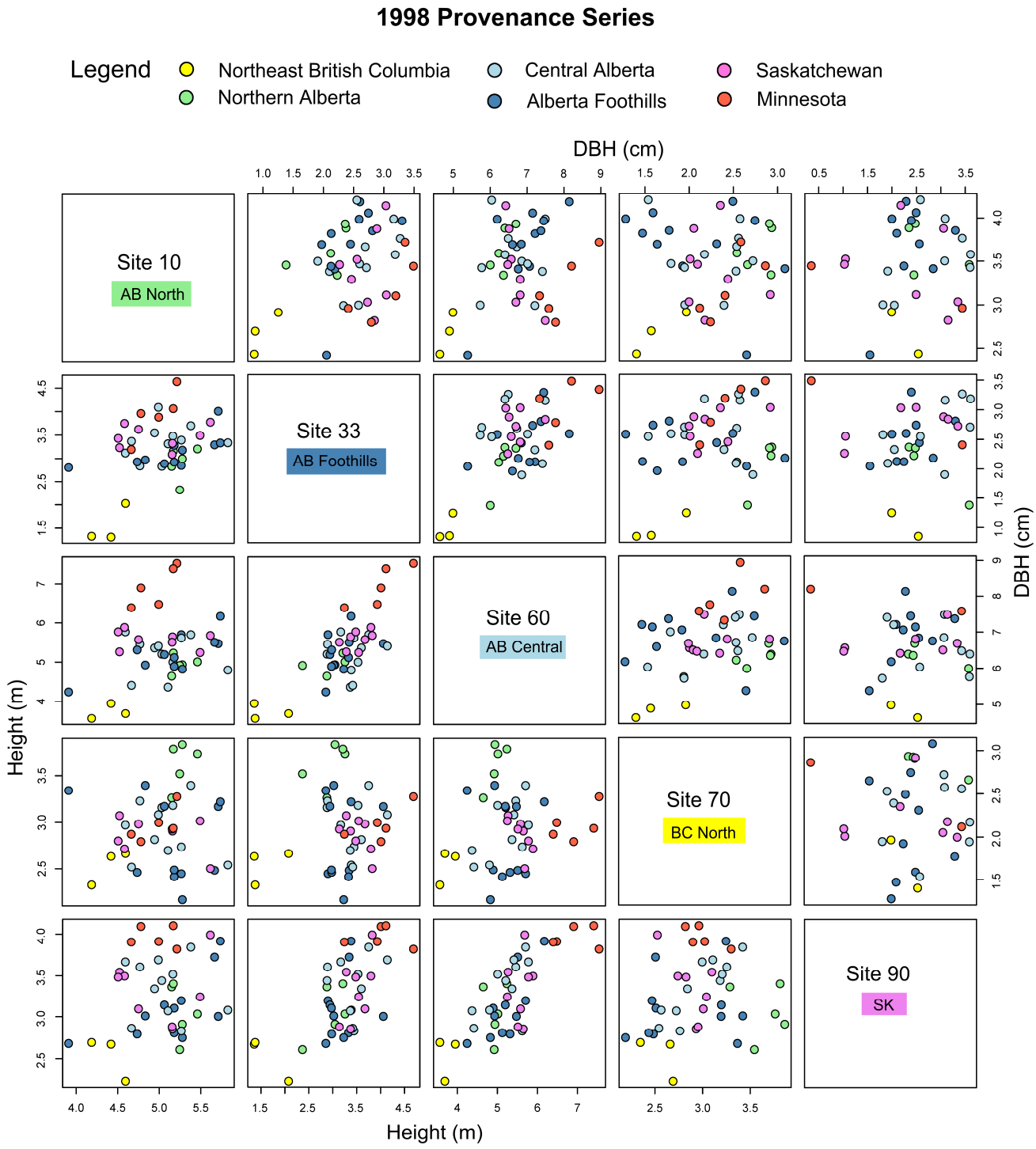


Figure 9. Rank changes of provenances among pairs of sites for the 1998 provenance series. Scatter plots above the diagonal show 9-year DBH at two sites, and scatters below the diagonal show height. Note that in each scatter plot, only clones that were planted at both sites can be shown.

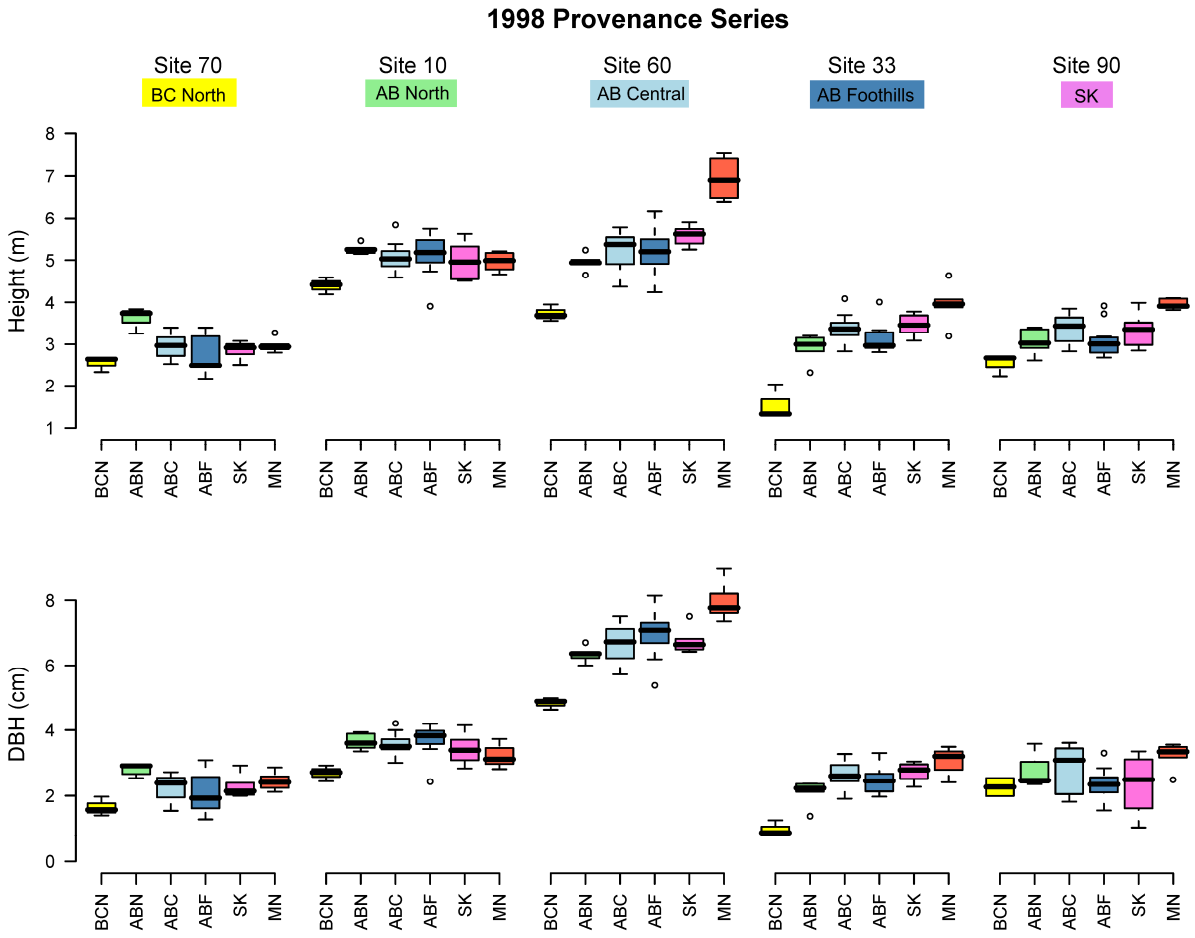


Figure 10. Range of aspen provenance means for 9-year height and DBH at multiple test sites (the box plot indicates the range, the median, the 25th and 75th percentile of provenance means for each group. Outliers according to Tukey's inner fence criteria are indicated by circles). For abbreviation of regional provenance collections, refer to Figure 9.

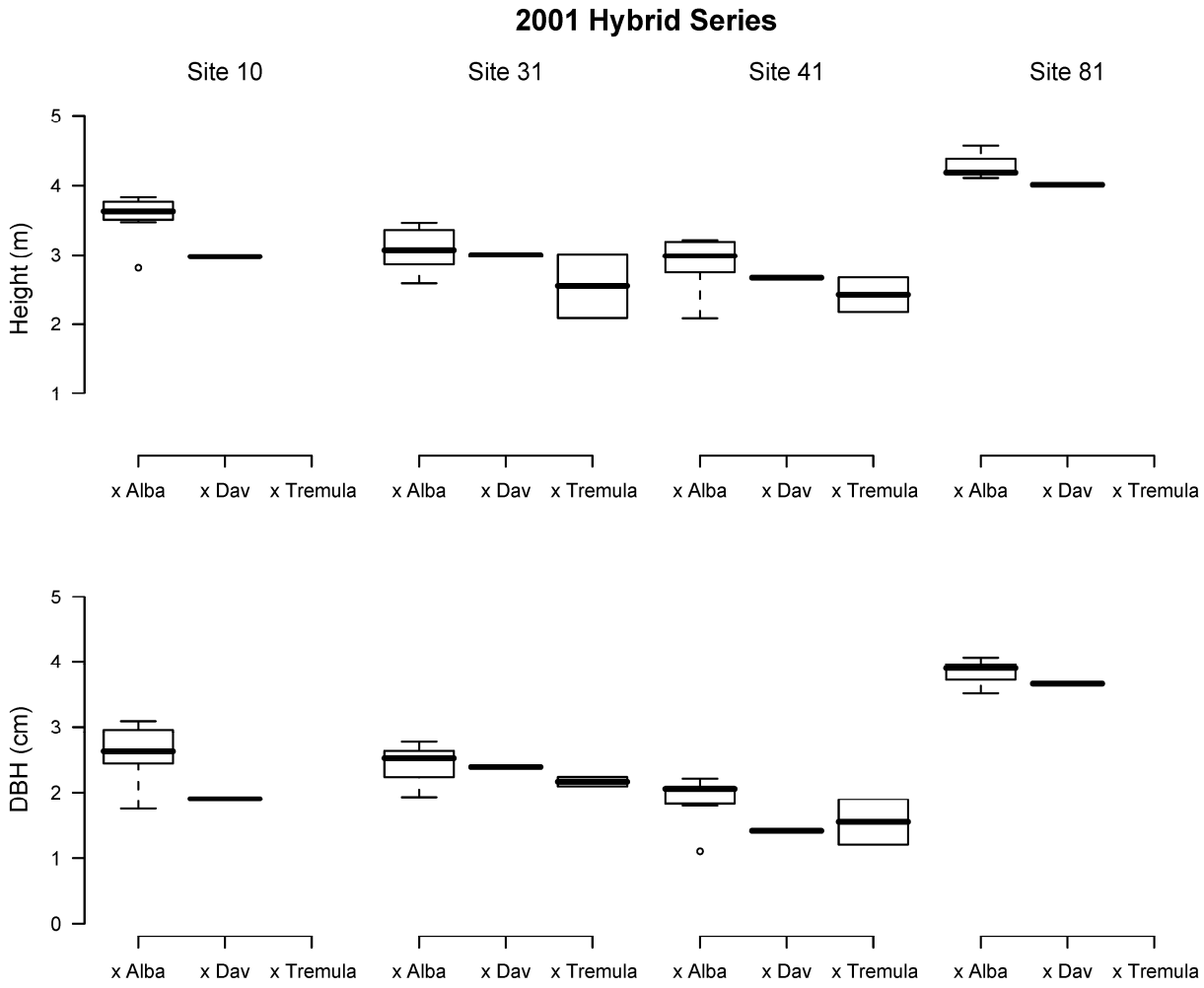


Figure 11. Range of 6-year height and DBH of aspen hybrids of the 2001 series planted at multiple test sites. Hybids are between native aspen that originate from Alberta (females), and pollen from white poplar from Minnesota (× Alba), pollen from Chinese aspen (× Dav) originating from central China, and pollen from European aspen (× Tremula) originating from Finland.

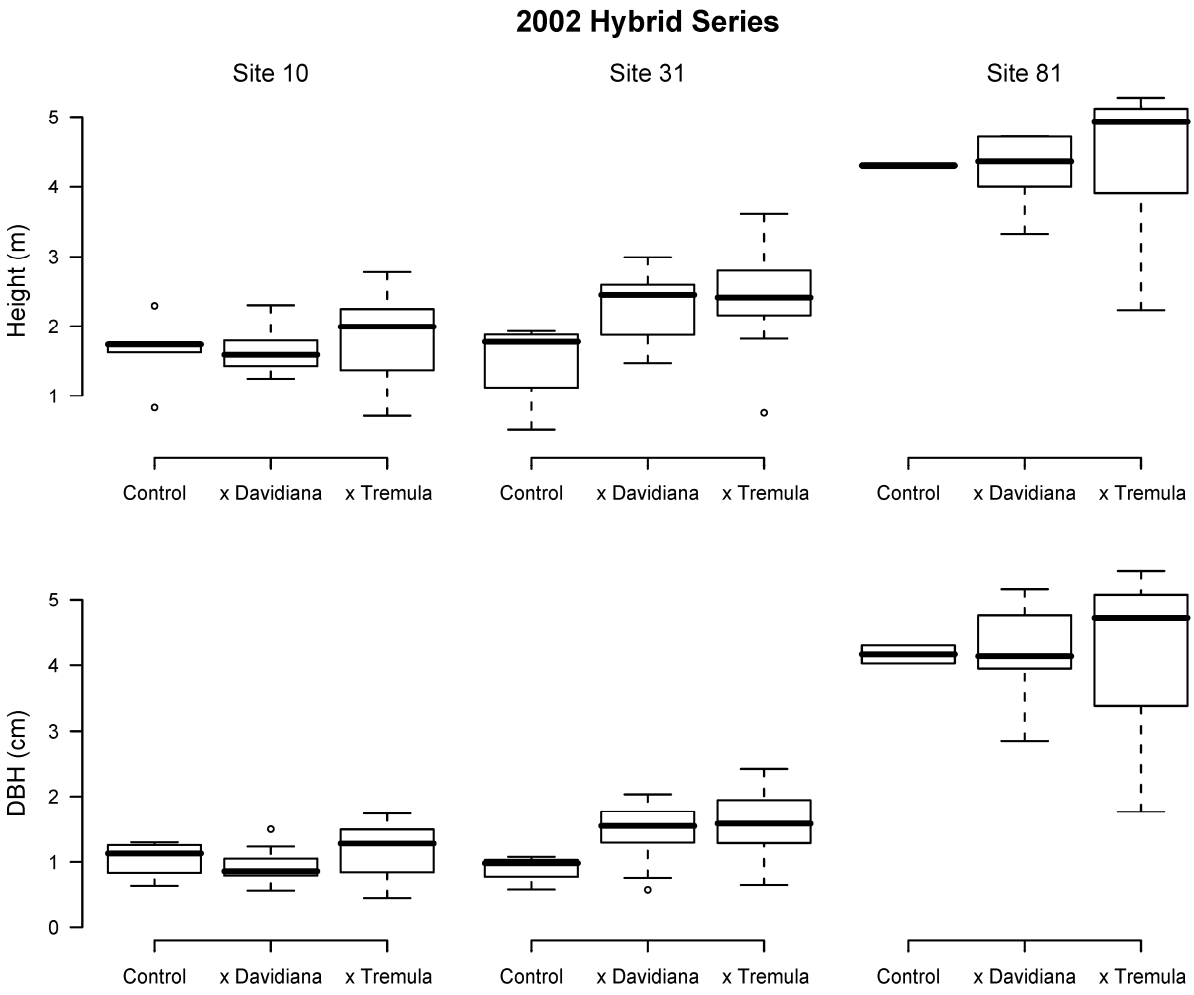


Figure 12. Range of 5-year height and DBH of aspen hybrids of the 2002 series planted at multiple test sites. Hybids are between native aspen that originate from Alberta (females), and pollen from Chinese aspen (× Davidiana) originating from central China, and pollen from European aspen (× Tremula) originating from Finland.

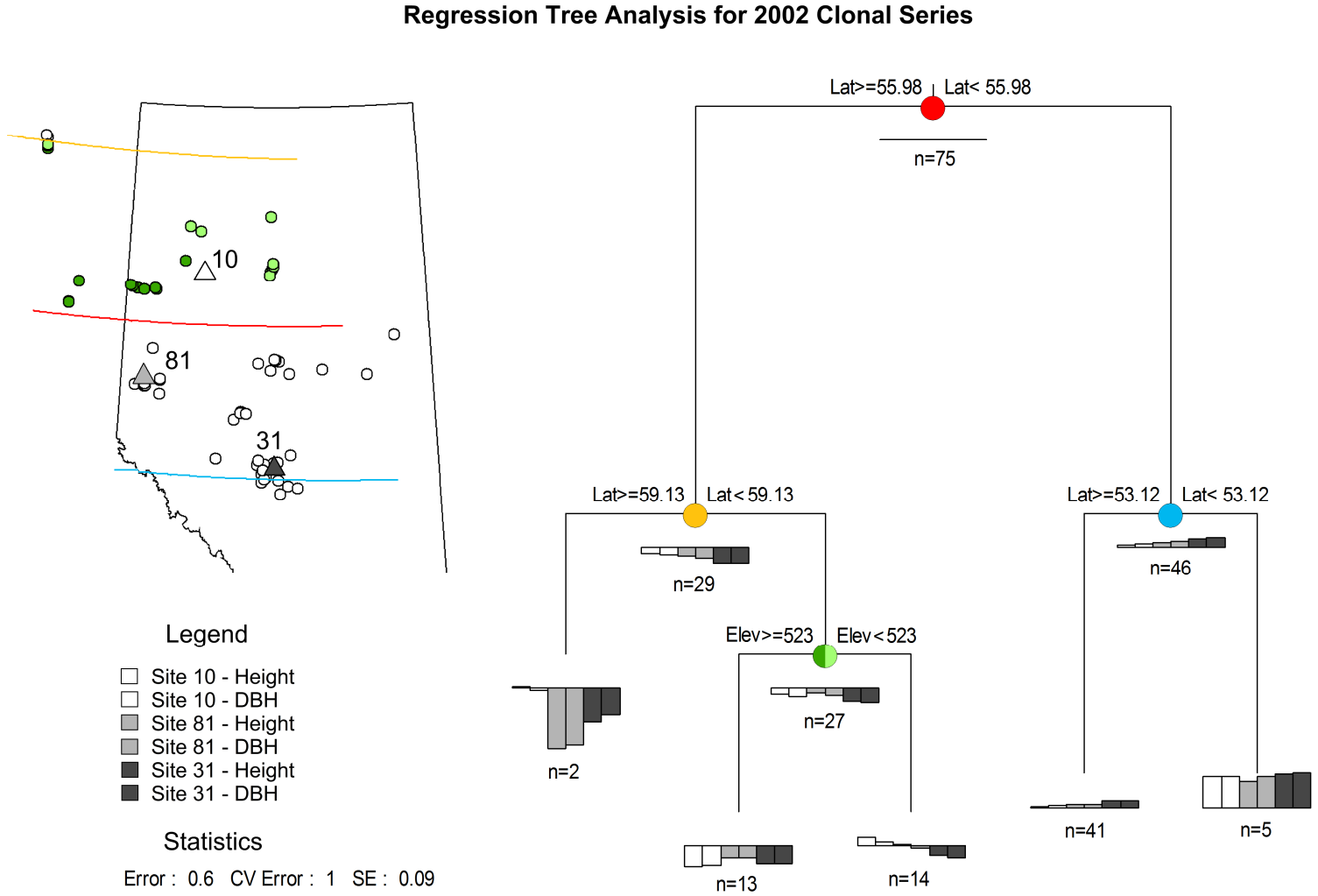


Figure 13. Regression tree analysis subdivides the data of the 2002 clonal series into 5 genetically distinct groups. Most variance in 6 variables (5-year DBH and height measured at 3 sites) is explained by three latitudinal splits at 53°, 56°, and 59°. The very northern provenances perform very poorly at all sites except site 10, where they show average growth. The 5 most southern sources perform above average at all sites. Sources from the boreal highlands (≥523m) perform somewhat below average at all sites while the northern lower elevation sources perform slightly above average at site 10 and slightly below average at site 31. A large group of the foothills and central Alberta n=41 shows a wide range of performance, but no geographic patterns of genetic variation.

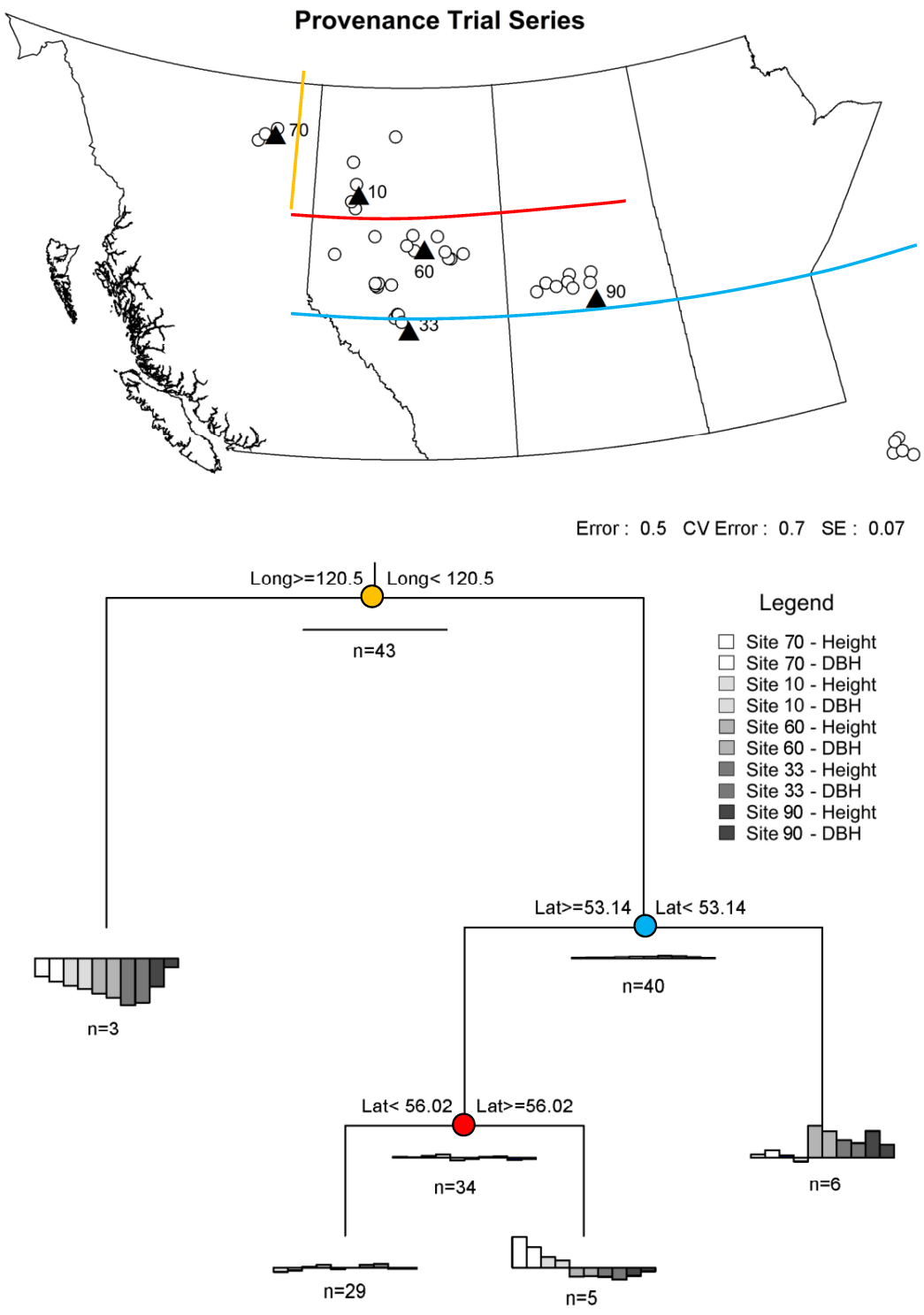
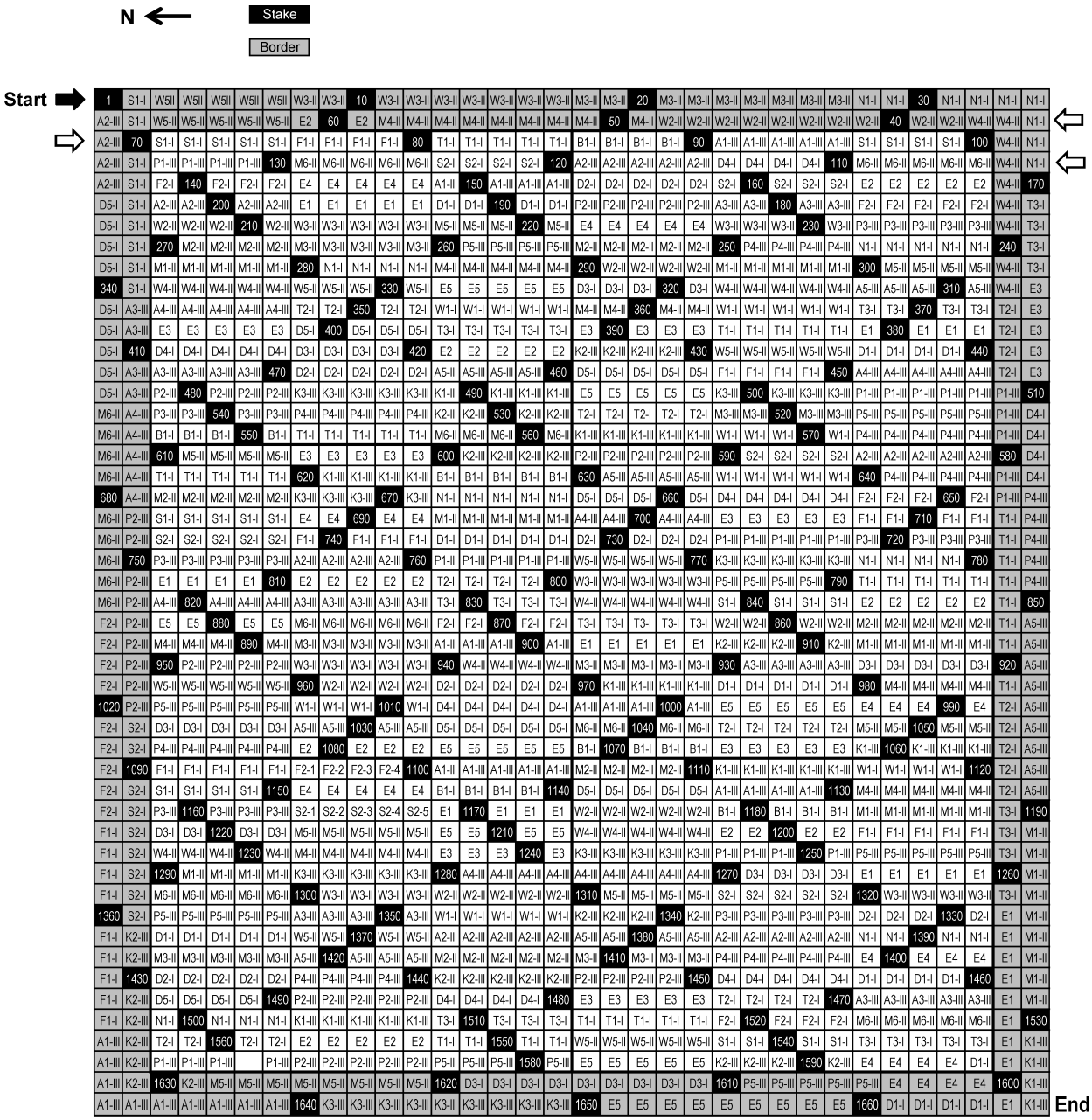


Figure 14. Regression tree analysis subdivides the data of the 1998 provenance series, consisting of 10 variables (9-year DBH and height measured at 5 sites) into 4 genetically distinct groups. For Alberta, the groups are split almost exactly as in Figure 15 although this is a different type of genetic trial. Notably, the most southern Alberta Foothill provenances are also in a separate group (here together with the Minnesota provenances) and perform above average on the three southern sites.

Appendix 1. Source information and treatment codes for the 1998 provenance trial series.

Family	Latitude	Longitude	Elevation	Family ID	Alpac ID	Member ID	Seedlot ID	Region
1	55.03	-118.73	649	N1-l	751	Ains	1	AB Foothills
2	56.41	-117.76	739	D1-l	752	DMI	94-5	AB North
3	57.12	-117.74	606	D2-l	753	DMI	95-2	AB North
4	56.61	-117.98	709	D3-l	754	DMI	95-5	AB North
5	57.78	-117.96	459	D4-l	755	DMI	95-8	AB North
6	58.56	-115.64	343	D5-l	756	DMI	96-1	AB North
7	55.19	-114.61	726	S1-I	757	SLP	1	AB Central
8	55.34	-115.01	646	S2-l	758	SLP	2	AB Central
9	58.20	-123.33	1177	F1-I	759	Slocan	40959	BC Northeast
10	58.60	-122.33	335	F2-l	760	Slocan	40960	BC Northeast
11	55.60	-116.67	632	T1-I	761	Tolko	1	AB Central
12	55.60	-116.67	632	T2-I	762	Tolko	2	AB Central
13	55.60	-116.67	632	T3-I	763	Tolko	3	AB Central
14	55.64	-114.69	709	W1-l	764	Wey SL	95001C	AB Central
15	54.18	-115.78	731	M1-ll	765	MWI	1	AB Foothills
16	54.10	-116.50	1018	M2-ll	766	MWI	3	AB Foothills
17	54.14	-116.58	868	M3-ll	767	MWI	4	AB Foothills
18	54.21	-116.44	803	M4-ll	768	MWI	5	AB Foothills
19	54.21	-116.44	803	M5-II	769	MWI	6	AB Foothills
20	54.21	-116.59	914	M6-ll	770	MWI	7	AB Foothills
21	53.20	-115.60	939	W2-ll	771	Wey	94003D	AB Foothills
22	53.31	-115.46	939	W3-ll	772	Wey	94006B	AB Foothills
23	53.30	-115.43	927	W4-II	773	Wey	34013B	AB Foothills
24	53.08	-115.26	912	W5-ll	774	Wey	94016A	AB Foothills
25	55.60	-113.41	762	A1-III	775	Alpac	C87-95 (AP1)	AB Central
26	54.93	-112.74	545	A2-lll	776	Alpac	K21-95 (AP2)	AB Central
27	54.94	-112.86	546	A3-lll	777	Alpac	Ward Pine Sands (AP3)	AB Central
28	55.14	-113.02	601	A4-lll	778	Alpac	KM33 West-96 (AP4)	AB Central
29	55.06	-112.11	624	A5-lll	779	Alpac	K59 Area-96 (AP5)	AB Central
30	54.20	-105.70	490	P1-lll	780	Wey PA	XTO 65-92	SK
31	54.20	-106.80	513	P2-lll	781	Wey PA	XTO 66-92	SK
32	54.00	-106.90	519	P3-lll	782	Wey PA	XTO 67-92	SK
33	53.90	-105.80	517	P4-lll	783	Wey PA	XTO 64-93	SK
34	53.80	-106.70	583	P5-lll	784	Wey PA	XTO 65-93	SK
35	54.03	-108.00	530	K1-lll	785	Mistik	XTO 66-93	SK
36	53.80	-108.50	710	K2-lll	786	Mistik	XTO 67-93	SK
37	53.90	-107.50	570	K3-lll	787	Mistik	XTO 68-93	SK
38	47.00	-93.00	384	E1	788	Mn	XTO 33-91	MN
39	47.20	-93.80	405	E2	789	Mn	XTP 53-92	MN
40	47.60	-93.40	424	E3	790	Mn	XTO 54-92	MN
41	47.50	-93.60	433	E4	791	Mn	XTO 48-94	MN
42	47.20	-93.40	395	E5	792	Mn	XTO 50-94	MN
43	58.40	-123.00	511	B1-l	793	BCMOF	1	BC Northeast

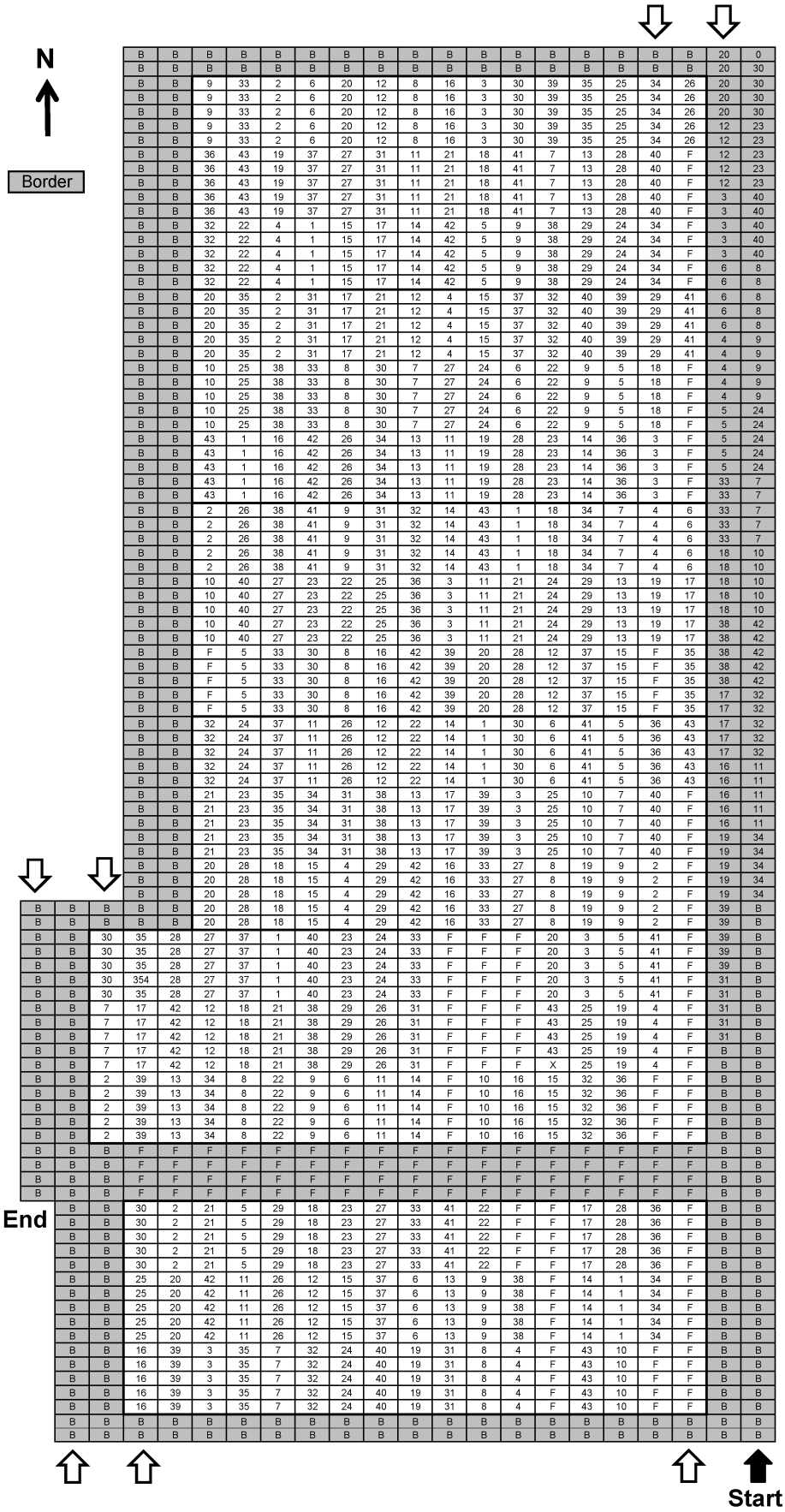
Appendix 2. Location, trial layout, and treatment codes for field trial "Provenance2-10-98" of the 1998 aspen provenance trial series.



Arrangement of replications

Rep 1	Rep 2
Rep 3	Rep 4
Rep 5	Rep 6

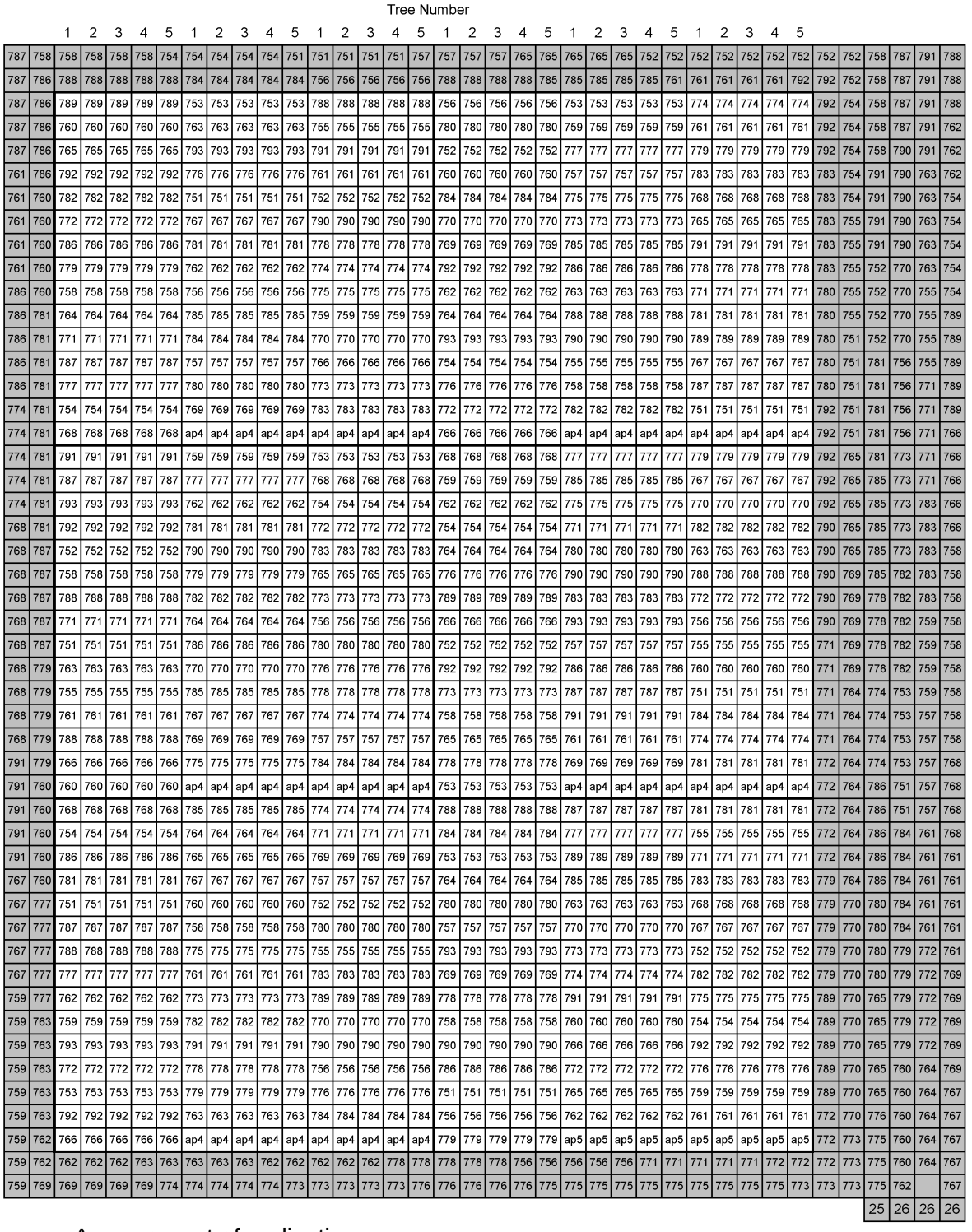
Appendix 3. Location and trial layout for field trial "Provenance2-33-98" of the 1998 aspen provenance trial series. (For treatment codes see Appendix 1).



Arrangement of replications

Rep 1
Rep 2
Rep 3
Rep 4
Rep 5
Rep 6

Appendix 4. Location and trial layout for field trial "Provenance2-60-98" of the 1998 aspen provenance trial series. (For treatment codes see Appendix 1).



Arrangement of replications

Rep 1	Rep 6
Rep 2	Rep 5
Rep 3	Rep 4

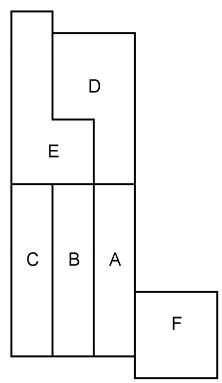
Appendix 5. Location and trial layout for field trial "Provenance2-70-98" of the 1998 aspen provenance trial series. (For treatment codes see Appendix 1).

N

Order

Treatment

Rep Layout



Tree Number

5	4	3	2	1
C	C	C	C	C
215	214	43	43	43
42	42	42	42	42
41	41	41	41	41
40	40	40	40	40
39	39	39	39	39
38	38	38	38	38
37	37	37	37	37
36	36	36	36	36
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31	31	31	31	31
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28	28	28	28	28
27	27	27	27	27
26	26	26	26	26
25	25	25	25	25
24	24	24	24	24
23	23	23	23	23
22	22	22	22	22
21	21	21	21	21
20	20	20	20	20
19	19	19	19	19
18	18	18	18	18
17	17	17	17	17
16	16	16	16	16
71	15	15	15	15
70	14	14	14	66
215	214	43	43	43
42	42	42	42	42
41	41	41	41	41
40	40	40	40	40
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38	38	38	38	38
37	37	37	37	37
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11	11	11	11	11
10	10	10	10	10
9	9	9	9	9
8	8	8	8	8
7	7	7	7	7
6	6	6	6	6
5	5	5	5	5
4	4	4	4	4
3	3	3	3	11
6	2	2	2	10
5	1	1	1	1

Tree Number

5	4	3	2	1	5	4	3	2	1
145	29	29	29	141	136	28	28	28	140
146	30	30	30	150	27	27	27	27	27
31	31	31	31	31	26	26	26	26	26
32	32	32	32	32	25	25	25	25	25
33	33	33	33	33	24	24	24	24	24
34	34	34	34	34	23	23	23	23	23
35	35	35	35	35	22	22	22	22	22
36	36	36	36	36	21	21	21	21	21
37	37	37	37	37	20	20	20	20	20
38	38	38	38	38	19	19	19	19	19
39	39	39	39	39	18	18	18	18	18
40	40	40	40	40	17	17	17	17	17
41	41	41	41	41	16	16	16	16	16
42	42	42	42	42	15	15	15	15	15
215	214	43	43	43	14	14	14	14	14
1	1	1	1	1	13	13	13	13	13
6	2	2	2	10	12	12	12	12	12
3	3	3	3	11	11	11	11	11	11
4	4	4	4	4	10	10	10	10	10
5	5	5	5	5	9	9	9	9	9
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7	7	7	7	7	7	7	7	7	7
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9	9	9	9	9	5	5	5	5	5
10	10	10	10	10	4	4	4	4	4
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12	12	12	12	12	6	2	2	2	10
65	13	13	13	61	5	1	1	1	1
215	214	43	43	43	215	214	43	43	43
42	42	42	42	42	42	42	42	42	42
41	41	41	41	41	41	41	41	41	41
40	40	40	40	40	40	40	40	40	40
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38	38	38	38	38	38	38	38	38	38
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35	35	35	35	35	35	35	35	35	35
34	34	34	34	34	34	34	34	34	34
33	33	33	33	33	33	33	33	33	33
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28	28	28	28	28	28	28	28	28	28
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26	26	26	26	26	26	26	26	26	26
25	25	25	25	25	25	25	25	25	25
24	24	24	24	24	24	24	24	24	24
23	23	23	23	23	23	23	23	23	23
22	22	22	22	22	22	22	22	22	22
21	21	21	21	21	21	21	21	21	21
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5	5	5	5	5	5	5	5	5	5
4	4	4	4	4	4	4	4	4	4
3	3	3	3	11	3	3	3	3	11
6	2	2	2	10	6	2	2	2	10
5	1	1	1	1	5	1	1	1	1

Tree Number

5	4	3	2	1	5	4	3	2	1
23	23	23	23	23	22	22	22	22	22
24	24	24	24	24	21	21	21	21	21
25	25	25	25	25	20	20	20	20	20
26	26	26	26	26	19	19	19	19	19
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33	33	33	33	33	12	12	12	12	12
34	34	34	34	34	11	11	11	11	11
35	35	35	35	35	10	10	10	10	10
36	36	36	36	36	9	9	9	9	9
37	37	37	37	37	8	8	8	8	8
38	38	38	38	38	7	7	7	7	7
39	39	39	39	39	6	6	6	6	6
40	40	40	40	40	5	5	5	5	5
41	41	41	41	41	4	4	4	4	4
42	42	42	42	42	3	3	3	3	11
215	214	43	43	43	6	2	2	2	10
					5	1	1	1	1

Appendix 6. List of clones, least squares means for 8-year height (m) and DBH (cm), and site ranks (based on the volume of a cone) for the 1999 clonal trial series. The three experiments Clone1-10-99, Clone1-41-99, and Clone1-60-99 are described in Table 1.

	Clone1-10-99			Clone1-41-99			Clone1-60-99		
Clone	Height	DBH	Rank	Height	DBH	Rank	Height	DBH	Rank
1003	4.80	5.4	2						
1004	4.75	4.3	16	5.88	5.6	6	3.97	5.6	12
1006				4.31	4.0	17	3.29	3.4	19
1007	4.75	6.1	1	5.60	6.3	4	5.57	8.1	1
1008	3.53	2.7	29						
1010	4.90	4.5	7	5.51	5.5	9	5.39	6.7	4
1011	4.73	4.6	8	5.40	5.2	12	4.50	6.3	6
1019	4.48	4.2	20						
1024	4.08	3.6	25						
1033	4.45	4.5	14				4.23	5.4	13
1034	4.33	4.3	18	5.94	5.8	5	4.66	5.8	9
1060	4.17	3.8	24						
3005	4.40	4.0	22						
3006	4.60	4.9	5	4.99	5.6	10	5.47	7.6	2
3008	4.81	4.8	3						
3012	4.61	4.4	15	5.98	5.5	7	3.73	4.3	18
4010	4.73	4.6	10						
4021	3.81	3.6	26						
6005	3.08	2.1	31						
6006	4.50	4.2	19				6.03	6.7	3
6007	4.50	4.6	11	5.99	6.2	2	5.18	5.8	7
6009	4.53	4.8	6				4.69	6.6	5
6028	4.63	4.5	13						
6090	4.79	4.8	4	5.93	6.2	3	4.21	6.1	8
7001	3.95	4.1	23	5.39	5.6	8	4.32	5.7	11
7002	4.30	4.2	21	4.70	4.8	13	4.00	5.2	15
7004	4.61	4.6	9	5.13	5.4	11	4.23	5.0	16
7005	4.77	4.4	12	6.49	6.8	1	4.74	5.6	10
7006	4.46	4.3	17	4.62	4.7	14	4.57	4.9	14
7013	4.20	3.4	27	4.62	4.2	15	3.02	3.1	20
7015	3.91	3.2	28	3.96	4.3	16	3.84	4.9	17
7019	3.24	2.5	30				2.58	2.7	21

Appendix 7. List of clones, treatment identifiers (TID) used in experiments, least squares means for 6-year height (m) and DBH (cm), and site ranks (based on the volume of a cone) for the 2001 clonal trial series. The four experiments Clone2-31-01, Clone3-31-01, and Clone18-60-01 are described in Table 1.

	Clone2-31-01				Clone3-31-01				Clone4-81-01				Clone18-60-01		
Clone	TID	Height	DBH	Rank	TID	Height	DBH	Rank	TID	Height	DBH	Rank	Height	DBH	Rank
1004					16	2.21	1.7	43	6	4.39	4.5	16			
1008					33	3.64	3.1	7	10	5.09	5.1	7			
1065	66	2.07	1.2	82											
1078					41	1.89	0.9	65							
1079					37	2.35	1.0	59	12	4.67	4.1	22			
1080					39	1.97	1.1	60							
1081					6	1.73	0.8	67	5	3.84	3.3	31			
1082					43	2.08	0.9	64							
1083					4	3.19	2.5	15	4	4.64	3.7	25			
1085					22	2.03	1.2	58	9	4.70	4.1	20			
1086					3	2.40	1.4	50	3	4.66	4.1	19			
1087					18	2.72	2.3	27	8	4.33	4.2	21			
1094	67	2.51	1.5	74											
1095	68	2.25	1.0	87											
1097	69	2.18	1.1	86	44	1.76	0.7	69							
1098	70	2.43	1.3	80											
1104	71	2.36	1.5	76					36	2.81	2.0	36			
1105					68	2.08	1.3	55							
1106	72	1.97	0.7	90											
1108	73	2.39	1.1	83	34	1.94	0.7	68	11	4.50	3.6	29			
1109	74	2.29	1.1	85											
1111	75	2.20	1.7	70	17	2.05	1.3	56	7	3.66	3.1	32			
1112	76	2.41	1.4	77											
3012	25	4.20	4.4	1									4.62	4.7	5
3014	2	4.11	4.2	3	11	3.67	3.5	3	27	5.27	5.1	6	4.69	4.9	3
3019	42	3.15	2.9	28									3.33	3.4	33
3020	15	2.81	2.4	53	29	2.59	1.9	37					3.81	3.9	20
3029	31	2.98	2.4	52	59	2.21	1.4	51					3.41	3.2	36
3030	34	3.11	2.5	46									3.58	4.0	22
3031	9	3.16	2.6	45	48	2.77	1.9	33					3.49	3.2	34
3032	55	3.18	2.7	40											
3033	52	3.00	2.3	54											
3034	16	3.64	3.5	11	20	3.30	2.8	11	30	5.23	5.5	5	3.94	4.2	13
3035	54	3.04	2.3	51											
3044	26	3.47	2.7	31									4.11	4.0	17
3045	61	3.46	3.4	12											
3046	3	3.00	2.3	55	21	2.40	1.5	47	31	4.53	4.3	18	3.46	3.7	28
3047	28	3.37	2.9	24	30	3.55	3.1	6					3.94	3.7	23
3067	33	2.74	1.9	64									2.63	2.7	46
3068	49	1.78	0.8	89									3.12	2.9	44
3073	63	3.14	2.7	38											
3074	47	2.78	2.3	56									2.72	2.8	45
3076	39	3.37	3.1	20	54	3.23	2.7	14					3.20	3.2	38
3080													3.93	4.6	10
3082	30	2.92	2.1	59	55	2.83	2.0	31					3.95	4.9	6
3083	1	3.43	3.3	13	1	3.07	2.6	16	23	4.14	3.8	27	4.12	4.5	9
3084	45	3.62	3.2	15									4.10	4.7	7
3085	37	3.91	3.9	4									4.71	5.6	1
3087	36	3.25	2.6	43	56	2.29	1.3	52					3.75	3.3	32

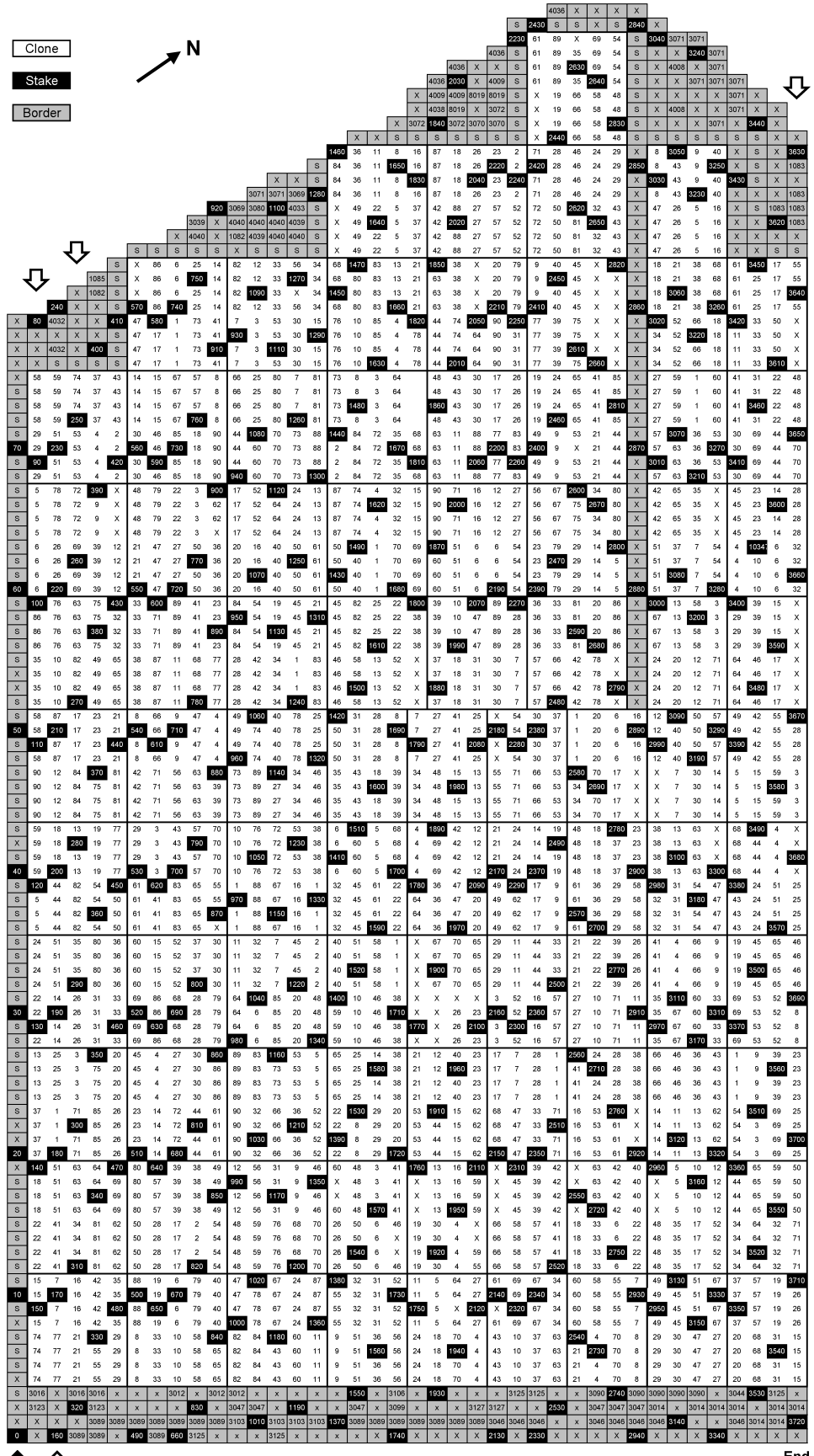
Appendix 7. Continued.

	Clone2-31-01				Clone3-31-01				Clone4-81-01				Clone18-60-01		
Clone	TID	Height	DBH	Rank	TID	Height	DBH	Rank	TID	Height	DBH	Rank	Height	DBH	Rank
3089	8	4.18	4.3	2	8	3.96	3.6	2	26	5.65	5.8	2	3.98	3.8	21
3090	64	2.66	1.6	71											
3095	10	3.13	2.4	49	5	2.94	2.3	22	24	5.27	4.7	10	2.36	2.9	47
3097	43	3.27	2.7	33									3.15	3.2	37
3098	11	3.32	2.8	27	23	2.75	1.9	36	32	4.43	3.8	24	2.84	2.2	49
3099	17	3.10	2.6	44	32	1.97	1.2	57					3.62	3.6	26
3100	46	2.88	2.1	61									3.46	3.0	41
3101	59	3.05	2.1	58											
3102	24	3.43	3.2	16	49	3.58	3.8	1					3.81	4.2	15
3103	6	3.63	3.6	10	71	3.39	3.0	9	34	5.79	5.8	1	3.74	3.7	25
3104	40	3.82	3.7	7	46	3.20	2.8	13					4.10	4.3	11
3105	51	2.34	1.4	78											
3106	27	3.88	3.6	8	40	3.45	3.0	8					4.42	4.9	4
3107	60	2.62	1.5	73											
3108	12	3.11	2.7	36	27	2.77	2.3	25					3.28	3.1	40
3109	22	3.77	3.9	5	64	3.12	2.8	12					3.89	4.3	14
3110	20	3.83	3.7	6	45	3.38	3.4	5					4.07	4.7	8
3111	13	2.82	2.0	63	12	2.36	1.6	44	28	3.81	3.0	33	3.34	3.1	39
3112	57	3.35	2.6	39											
3113	58	2.18	1.1	84									1.62	1.6	52
3114	50	3.25	2.7	34									2.95	4.0	27
3115	41	2.64	1.6	69									2.63	2.4	48
3116	29	2.29	1.2	81									2.23	1.6	51
3117	62	2.67	1.5	72											
3120	35	3.50	3.0	21	62	1.75	1.1	62					2.94	3.1	43
3122	38	3.17	2.8	30	60	2.24	1.6	46					4.05	4.3	12
3123	19	3.42	2.8	26	38	2.39	1.4	49					3.15	3.1	42
3124	4	3.24	3.1	22	14	2.06	1.3	54	29	4.67	4.3	17	3.44	3.5	31
3125	7	3.51	3.1	19									3.74	3.8	24
3126	14	3.33	2.4	47	24	2.80	1.6	42					4.25	3.8	19
3127	18	3.16	2.6	41									3.73	4.1	18
3128	21	3.34	2.9	23	65	3.12	2.4	19					4.52	5.0	2
3129	44	2.49	1.8	66									1.97	1.2	53
3131	5	3.12	2.3	50	7	2.93	2.3	23	25	5.03	4.4	14	3.26	3.6	30
3132	53	2.52	1.5	75									2.30	2.5	50
3133	56	2.62	1.7	67											
3135	32	3.25	3.4	14	61	2.88	2.6	17					3.91	4.1	16
3136	23	3.56	3.1	17	66	2.76	1.9	35					3.49	3.6	29
3137	48	3.45	3.7	9									3.19	3.3	35
3138	65	2.09	1.0	88											
4012									20	3.97	3.5	30			
4018									18	3.52	2.6	35			
4031					15	2.93	2.1	30	16	5.01	4.8	11			
4032					10	2.74	2.3	26	14	3.99	4.1	23			
4033					58	3.08	2.4	20							
4036					9	3.32	3.0	10	13	4.90	5.2	8			
4038					31	3.00	2.2	28	21	5.14	4.3	15			
4039					52	2.87	1.9	32							
4040					26	1.84	1.0	63	19	4.42	3.6	28			

Appendix 7. Continued.

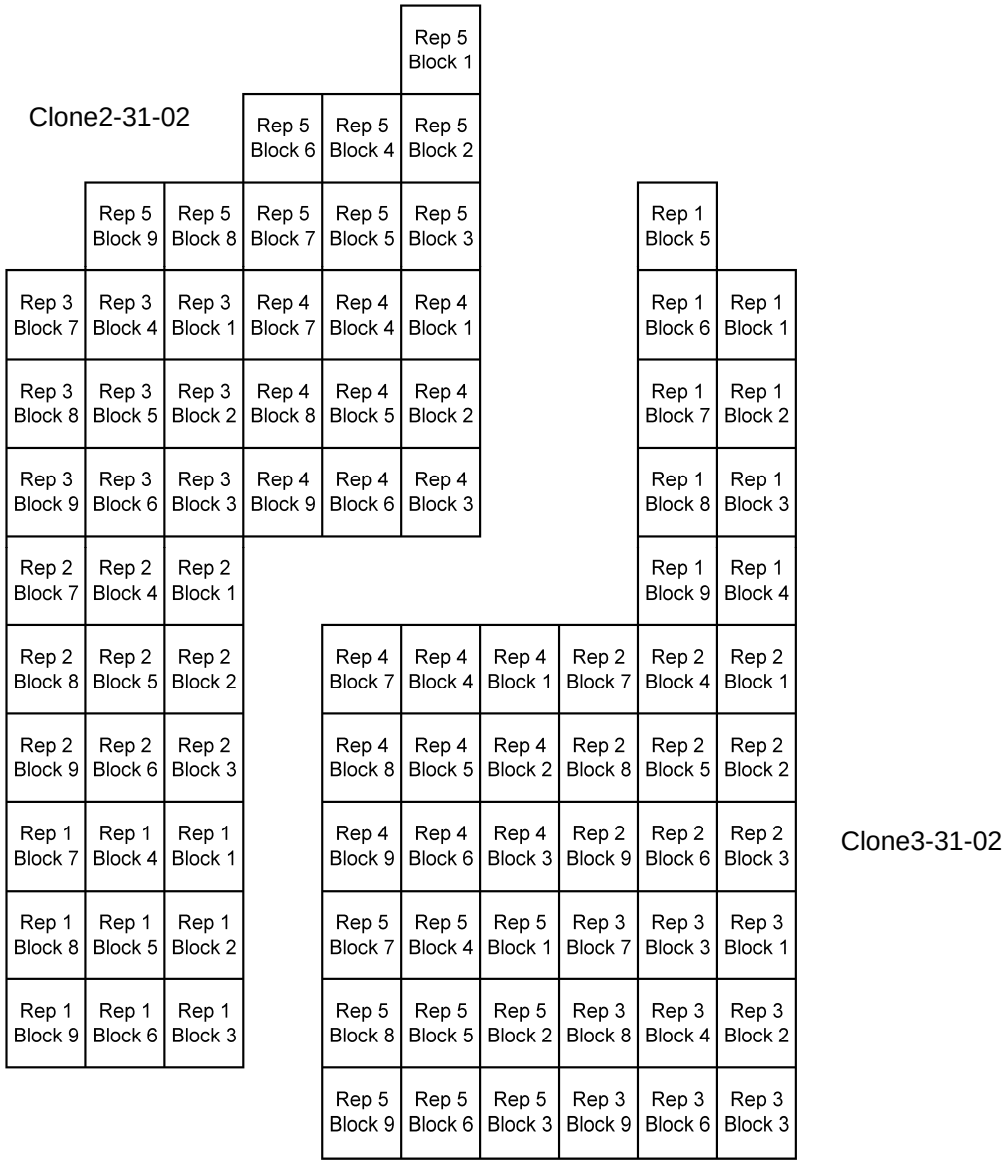
	Clone2-31-01				Clone3-31-01				Clone4-81-01				Clone18-60-01		
Clone	TID	Height	DBH	Rank	TID	Height	DBH	Rank	TID	Height	DBH	Rank	Height	DBH	Rank
8003	77	3.08	2.8	32	35	2.77	2.3	24	1	4.79	4.7	12			
8005	78	3.15	2.9	29											
8007	79	2.82	1.8	65											
8021	80	2.84	2.1	60	50	2.37	1.3	53							
8022					63	2.67	2.0	34							
8024	81	2.97	2.4	48											
8025	82	3.15	2.7	37											
8026	83	3.31	2.7	35	47	2.52	1.8	40							
8027	84	3.11	2.1	57											
8028					67	2.80	2.2	29							
8031	85	2.74	2.0	62											
8032	86	3.54	3.1	18											
8035	87	3.41	2.8	25	36	3.03	2.4	21	2	5.61	5.7	4			
8037	88	2.38	1.8	68	53	1.93	1.1	61							
Control Seedlots															
Ck1 WDV	89	3.07	2.7	42											
Ck2 Other	90	2.42	1.3	79											
Ctrl WDV					69	2.45	1.9	39							
Ctrl DMI					70	2.67	1.8	38							
DMI Excess									35	3.41	2.7	34			
MW 10									17	4.37	3.7	26			
MW 24									22	5.61	5.8	3			
MW 7									15	5.17	4.9	9			
WDV Excess									33	4.64	4.6	13			

Appendix 8. Location, trial layout, and treatment codes for field trials "Clone2-31-01" and "Clone3-31-01" of the 2001 aspen clonal trial series. (For treatment codes see Appendix 7).

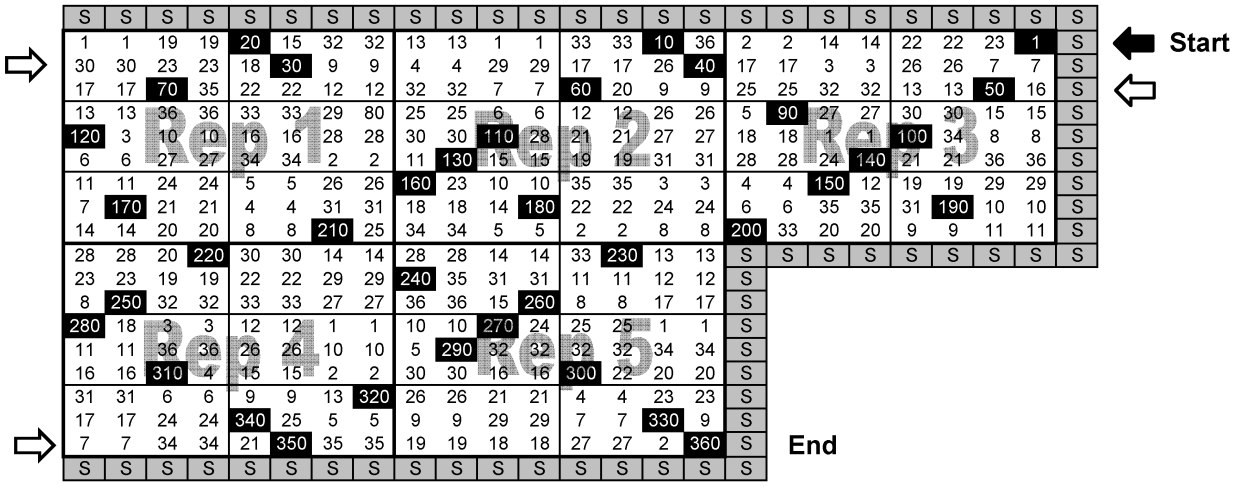


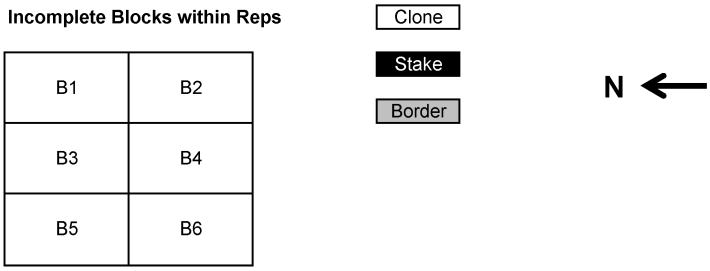
Appendix 8. Continued.

Layout of replications (Rep) and incomplete blocks within replications (Block).



Appendix 9. Location and trial layout for field trial "Clone4-81-01" of the 2001 aspen clonal trial series. (For treatment codes see Appendix 7).





Appendix 10. Location and trial layout for field trial "Clone18-60-01" of the 2001 aspen clonal trial series. (For treatment codes see Appendix 7).

N ←

B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	3100	3087	6009	3135	3074	3085	3120	3067	3110	3046	3089	3116	3085	3047	3127	3132	B	B
B	B	3100	3087	6009	3135	3074	3085	3120	3067	3110	3046	3089	3116	3085	3047	3127	3132	B	B
B	B	3098	3046	3114	3109	3084	3068	3031	3083	3044	3128	3123	3109	3029	3113	3034	3131	B	B
B	B	3098	3046	3114	3109	3084	3068	3031	3083	3044	3128	3123	3109	3029	3113	3034	3131	B	B
B	B	3113	3136	3108	3034	3014	3012	3089	3044	3135	3083	3109	3126	3098	3100	3124	3122	B	B
B	B	3113	3136	3108	3034	3014	3012	3089	3044	3135	3083	3109	3126	3098	3100	3124	3122	B	B
B	B	3034	3019	3128	3099	3124	3047	3106	3131	3031	3014	3136	3097	3068	3082	3020	3019	B	B
B	B	3034	3019	3128	3099	3124	3047	3106	3131	3031	3014	3136	3097	3068	3082	3020	3019	B	B
B	B	3108	3103	3095	3116	3020	3082	3127	3115	3103	3012	3044	3120	6009	3137	3115	3114	B	B
B	B	3108	3103	3095	3116	3020	3082	3127	3115	3103	3012	3044	3120	6009	3137	3115	3114	B	B
B	B	3097	3110	3084	3104	3126	3137	3125	3029	3104	3123	3074	3102	3083	3111	3103	3099	B	B
B	B	3097	3110	3084	3104	3126	3137	3125	3029	3104	3123	3074	3102	3083	3111	3103	3099	B	B
B	B	3076	3129	3111	3102	3123	3122	3132	3127	3095	3125	3129	3108	3076	3106	3046	3084	B	B
B	B	3076	3129	3111	3102	3123	3122	3132	3127	3095	3125	3129	3108	3076	3106	3046	3084	B	B
B	B	3095	3098	3137	3082	3097	3046	3102	3012	3111	3012	3076	3123	3074	3113	3137	3030	B	B
B	B	3095	3098	3137	3082	3097	3046	3102	3012	3111	3012	3076	3123	3074	3113	3137	3030	B	B
B	B	3135	3068	3085	3127	3108	3120	3099	3129	3095	3044	3103	3080	3099	3125	3019	3127	B	B
B	B	3135	3068	3085	3127	3108	3120	3099	3129	3095	3044	3103	3080	3099	3125	3019	3127	B	B
B	B	3126	3100	3083	3123	3111	3125	3089	3044	3109	3135	3083	3100	3132	3034	6009	3020	B	B
B	B	3126	3100	3083	3123	3111	3125	3089	3044	3109	3135	3083	3100	3132	3034	6009	3020	B	B
B	B	3122	3019	3136	3031	3132	3074	3087	3114	3116	3102	3122	3128	3098	3131	3067	3120	B	B
B	B	3122	3019	3136	3031	3132	3074	3087	3114	3116	3102	3122	3128	3098	3131	3067	3120	B	B
B	B	3110	3029	3082	3020	3131	3034	3103	3084	3047	3111	3128	3031	3097	3124	3126	3115	B	B
B	B	3110	3029	3082	3020	3131	3034	3103	3084	3047	3111	3128	3031	3097	3124	3126	3115	B	B
B	B	3106	3012	3113	3124	3115	3067	3105	3030	3087	3136	3110	3029	3082	3068	3108	3014	B	B
B	B	3106	3012	3113	3124	3115	3067	3105	3030	3087	3136	3110	3029	3082	3068	3108	3014	B	B
B	B	3047	3014	3104	3116	3128	3076	6009	3109	3085	3114	3046	3084	3106	3104	3095	3129	B	B
B	B	3047	3014	3104	3116	3128	3076	6009	3109	3085	3114	3046	3084	3106	3104	3095	3129	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B

Appendix 11. List of clones, treatment identifiers (TID) used in experiments, least squares means for 5-year height (m) and DBH (cm), and site ranks (based on the volume of a cone) for the first part of the 2002 clonal trial series. The three experiments Clone5-31-02, Clone6-10-02, and Clone7-81-02 are described in Table 1.

	Clone5-31-02				Clone6-10-02				Clone7-81-02			
Clone	TID	Height	DBH	Rank	TID	Height	DBH	Rank	TID	Height	DBH	Rank
1141	15	1.13	0.3	80	15	2.41	1.5	49	15	1.93	1.1	42
1142	62	1.59	0.6	59	62	2.33	1.2	61				
1143	51	1.69	0.7	49	51	3.10	2.2	12				
1144	30	1.15	0.3	78	30	2.23	1.4	58	30	1.56	0.6	43
1145	48	1.32	0.4	75	48	1.81	0.9	69				
1146	63	1.67	0.5	60	63	2.76	1.8	26				
1147	70	1.47	0.5	69								
1148	2	1.15	0.4	76	2	2.31	1.4	59	2	2.27	1.5	40
1149	31	1.56	0.5	63	31	2.85	2.0	21	31	2.90	2.3	25
1150	12	1.75	0.7	53	12	2.78	1.9	22	12	3.30	2.6	20
1151	67	1.59	0.5	61								
1152	32	1.43	0.5	67	32	2.54	1.5	48	32	2.65	2.1	33
1153	16	1.49	0.5	70	16	2.10	1.0	68	16	2.98	2.1	31
1154	47	1.03	0.3	82	47	2.72	1.5	46				
1155	49	1.79	0.8	44	49	2.27	1.4	60	49	2.83	2.2	28
1156	20	1.52	0.7	56	20	2.18	1.2	65	20	3.15	2.4	24
1157	23	1.48	0.5	68	23	3.05	2.0	18				
1158	1	1.93	0.9	34	1	2.59	1.9	30	1	3.70	3.1	9
1159	26	1.77	0.7	54	26	2.58	1.6	43	26	2.95	1.8	36
1160	24	1.59	0.5	72	24	2.60	1.5	44				
1161	27	1.36	0.8	51	27	2.79	1.7	35	27	3.29	2.6	21
1162	28	1.67	0.7	55	28	2.92	1.8	24	28	3.81	2.8	13
1163	53	1.23	0.2	83	53	3.08	1.7	28				
1164	55	1.38	0.8	48	55	3.06	2.3	11				
1165	3	1.29	0.4	77	3	3.34	2.0	14	3	3.31	2.1	29
3074	60	1.80	1.0	31	60	2.09	1.2	63				
3076	45	2.06	1.5	12	45	2.53	1.4	52	45	3.62	2.9	15
3082	34	1.53	0.8	45	34	2.56	1.7	37	34	2.91	2.0	34
3099	17	2.24	1.6	10	17	2.41	1.7	38	17	3.58	2.8	16
3118	54	1.57	0.4	73	54	2.70	1.4	55				
3119	46	2.70	2.4	1	46	2.93	2.3	9				
3137	6	2.05	1.0	30								
3139	21	2.09	1.3	20	21	3.29	2.3	7	21	4.00	3.6	3
3140	4	2.27	1.5	11	4	2.99	2.3	8	4	4.12	4.0	1
3141	42	2.66	2.2	2	42	2.83	2.1	19				
3142	37	2.12	1.4	16	37	3.45	2.7	2	37	3.64	3.0	12
3143	72	2.32	1.6	8								
3144	68	2.60	1.8	4	68	2.89	1.8	25				
3148	56	1.79	1.0	33	56	2.92	2.1	15				
3149	35	1.76	0.8	40	35	2.21	1.5	56	35	2.66	2.2	32
3150	58	2.04	1.3	24	58	2.71	1.7	36				
3152	5	2.18	1.3	18	5	3.16	2.2	13	5	3.86	3.5	5
3153	64	2.32	1.7	7	64	2.99	2.5	6				
3155	36	1.82	0.9	38	36	2.60	1.9	31	36	3.34	3.0	14

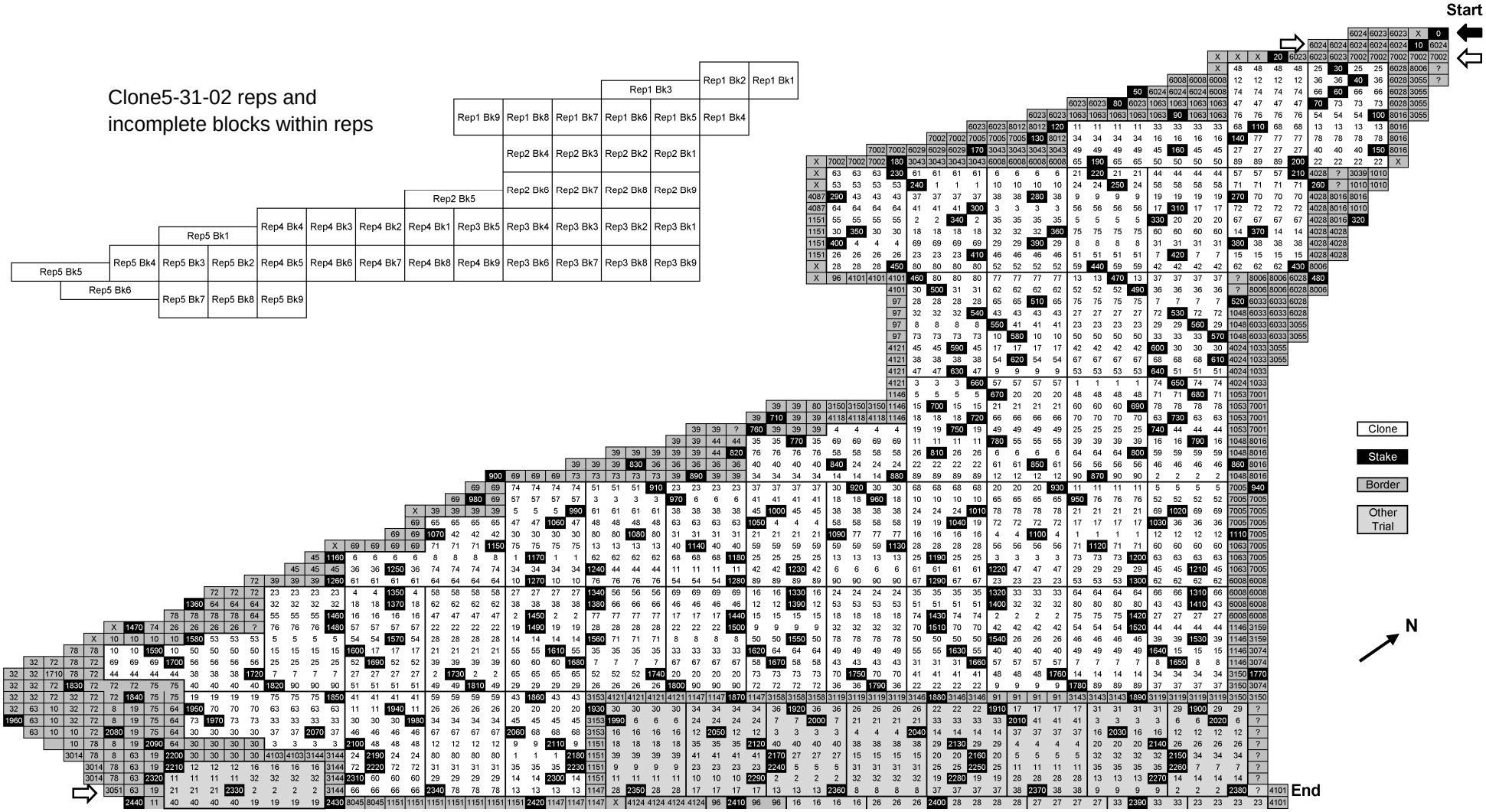
Appendix 11. Continued.

	Clone5-31-02				Clone6-10-02				Clone7-81-02			
Clone	TID	Height	DBH	Rank	TID	Height	DBH	Rank	TID	Height	DBH	Rank
3156	25	2.61	2.1	3	25	3.65	2.8	1	25	4.26	3.9	2
3157					6	2.55	1.5	50	6	2.72	1.8	37
3158	74	2.32	1.9	5								
3159	66	2.16	1.4	14	66	3.39	2.6	3				
4097	59	2.16	1.4	13	59	3.06	2.3	10				
4103	75	1.93	1.3	22								
4105	76	2.12	1.4	17								
4117	38	2.23	1.7	9	38	2.37	1.6	45	38	3.70	3.4	6
4118	61	1.53	0.5	65	61	2.36	1.7	39				
4119	77	2.15	1.2	23								
4121	69	1.98	1.1	27								
4122	43	1.47	0.5	66	43	2.60	1.8	32	43	2.86	2.3	27
4123	65	1.62	0.7	50	65	2.63	1.7	34				
4124	80	1.30	0.3	79								
4125	78	1.88	0.7	46								
5003	40	1.66	0.8	39	40	1.84	1.1	67				
5006	10	1.52	0.5	64	10	2.69	1.6	41	10	3.26	2.9	17
5007	39	1.37	0.6	62	39	3.23	2.6	4	39	2.99	2.5	23
5014	44	1.88	0.9	35	44	2.59	1.6	42	44	2.76	1.9	35
5017	33	1.58	0.8	42	33	2.46	1.4	54	33	3.45	2.5	22
5022	29	1.55	1.1	32	29	2.33	1.4	57	29	3.49	2.7	18
5023	13	1.62	0.8	43	13	2.69	1.8	29	13	3.03	2.3	26
5024	41	1.55	0.7	52	41	2.36	1.6	47	41	2.55	1.7	38
5025	14	1.96	1.1	29	14	2.82	2.1	16	14	3.44	3.1	11
5026	50	2.00	1.2	25	50	2.86	2.1	20				
5029									50	3.81	3.3	7
5032	11	1.53	0.4	74	11	2.43	1.7	40	11	2.00	1.3	41
8039	52	1.95	1.2	26	52	2.79	1.9	23				
8040	18	1.31	0.3	81	18	2.22	1.2	66	18	2.50	1.6	39
8041	9	2.56	1.7	6	9	2.85	2.1	17	9	3.52	3.1	10
8042	8	2.22	1.4	15	8	3.00	2.6	5	8	3.08	2.8	19
8043	7	1.97	1.1	28	7	2.34	1.5	51	7	3.94	3.5	4
8044	19	2.29	1.2	21	19	2.52	1.9	27	19	2.68	2.2	30
8045	22	1.82	0.9	36	22	2.11	1.3	62				
Control Seedlots												
Ctrl 1	90	1.64	0.7	47								
Ctrl 3	89	1.37	0.6	58								
T-91	71	1.63	0.6	57								
T-92	73	1.75	0.9	37								
T-94	57	1.90	1.4	19								
Ctrl 1/2/3									40	3.56	3.3	8

Appendix 12. List of clones, treatment identifiers (TID) used in experiments, least squares means for 5-year height (m) and DBH (cm), and site ranks (based on the volume of a cone) for the second part of the 2002 clonal trial series. The three experiments Clone10-81-02, Clone8-31-02, and Clone9-10-02 are described in Table 1.

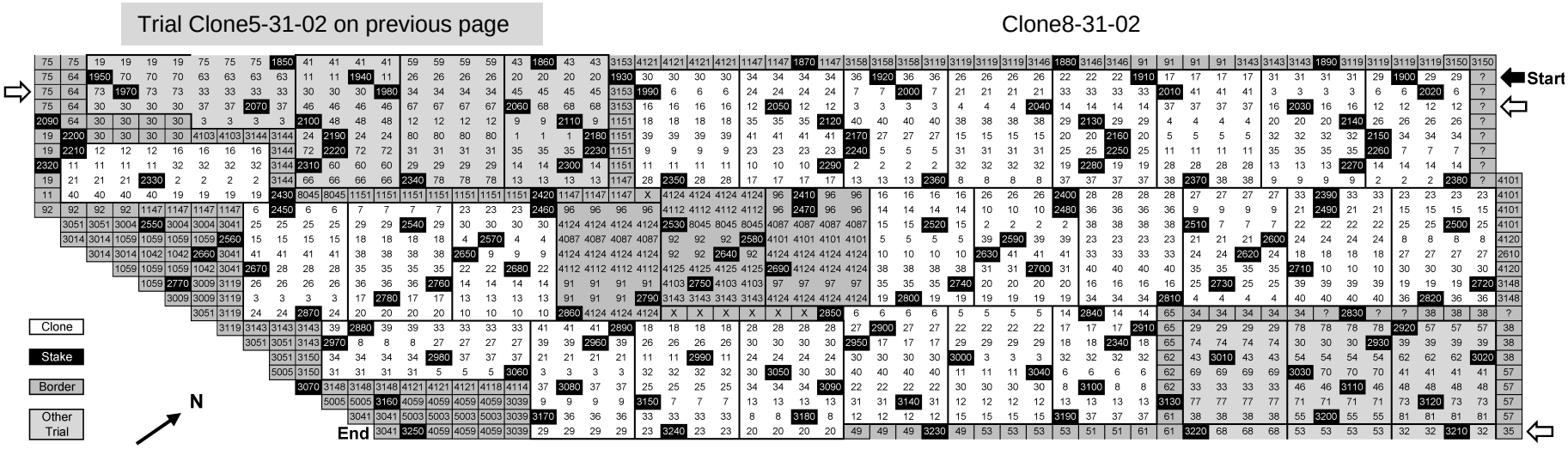
	Clone10-81-02				Clone8-31-02				Clone9-10-02			
Clone	TID	Height	DBH	Rank	TID	Height	DBH	Rank	TID	Height	DBH	Rank
1006	2	3.06	2.2	34	2	1.89	0.8	28	2	1.93	1.1	31
1010	3	3.88	3.1	14	3	2.04	1.1	20	3	2.36	1.5	15
1033	4	3.90	3.5	6	4	1.72	0.7	34	4	2.37	1.7	11
1039	5	3.33	2.4	31	5	1.72	0.6	36	5	2.34	1.3	23
1042	6	2.81	1.8	35	6	1.39	0.3	39	6	2.04	1.3	28
1048	7	3.79	3.0	18	7	1.50	0.5	37	7	2.18	1.3	24
1052	8	3.40	2.5	27	8	2.14	1.0	24	8	2.37	1.8	9
1053	9	3.03	2.4	33	9	1.62	0.7	33	9	1.64	0.8	38
1059	10	3.48	3.1	21	10	2.25	1.4	13	10	2.36	1.6	12
1063	11	4.04	3.4	8	11	2.02	1.1	22	11	2.14	1.5	19
3006					12	2.15	1.2	18				
3009	13	3.48	2.7	23	13	2.28	1.3	15	13	2.41	1.5	16
3014	14	3.91	3.4	10	14	3.20	2.7	1	14	2.81	1.9	4
3039	15	3.05	2.5	29	15	1.54	0.8	31	15	2.23	1.5	18
3041	16	3.69	3.1	15	16	2.28	1.4	14	16	1.72	1.0	36
3043	17	4.05	3.7	4	17	2.33	1.7	7	17	2.60	2.1	2
3051	18	3.10	2.4	32	59	2.35	1.5	9	18	2.14	1.3	27
3055	19	3.95	3.3	12	19	2.06	1.2	17	19	2.78	1.9	3
3060	20	3.41	2.4	30	20	1.77	0.8	30	20	2.27	1.3	25
4028	21	3.97	3.4	9	21	2.59	1.7	6	21	2.24	1.6	13
4029	22	3.97	3.5	7	22	2.86	2.1	2	22	2.31	1.5	14
4056	23	4.21	4.3	1	23							
4059	24	3.88	3.0	17	24	1.86	0.8	29	24	1.99	1.0	33
5001	25	3.38	2.4	28	25	2.30	1.0	21	25	1.95	1.1	32
5005	26	4.39	3.8	3	26	2.08	1.2	19	26	2.66	1.7	8
6005					27	1.86	0.7	32	27	1.72	0.9	37
6006					28	2.32	1.4	11	28	2.64	1.9	5
6008	29	3.14	2.6	26	29	1.75	0.9	26	29	2.31	1.9	7
6023	30	3.81	3.2	13	30	1.84	0.9	27	30	2.15	1.4	22
6024	31	4.42	3.9	2	31	2.61	2.0	3	31	2.26	1.5	17
6028	32	3.87	3.4	11	32	2.58	1.8	4	32	2.72	2.0	1
6033									33	1.91	1.0	35
7001	34	3.54	3.1	19	34	2.04	1.3	16	34	2.30	1.7	10
7002	35	3.37	2.8	22	35	1.61	0.6	35	35	1.90	1.0	34
7005	36	3.72	3.0	20	36	1.98	1.1	25	36	2.04	1.1	30
7006	37	2.55	1.5	36	37	1.36	0.4	38	37	2.13	1.3	26
8006	38	4.07	3.5	5	38	2.09	1.6	8	38	2.42	1.9	6
8012	39	3.83	3.1	16	39	2.54	1.7	5	39	2.15	1.5	20
8013	40	3.33	2.6	25	40	2.23	1.5	10	40	2.01	1.2	29
8016	41	3.21	2.7	24	41	1.94	1.1	23	41	2.16	1.4	21

Appendix 13. Location and trial layout for field trials "Clone5-31-02" and "Clone8-31-01" of the 2002 aspen clonal trial series. (For treatment codes see Appendix 11 & 12).

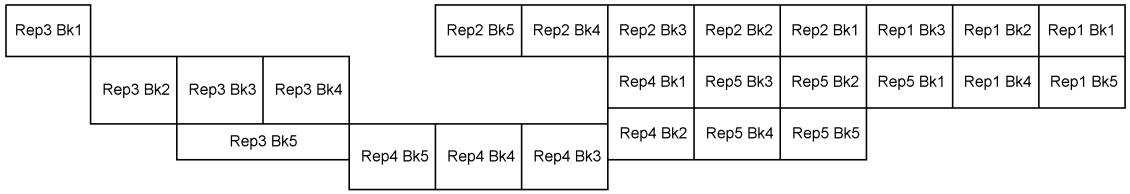


Trial Clone8-31-02 on next page

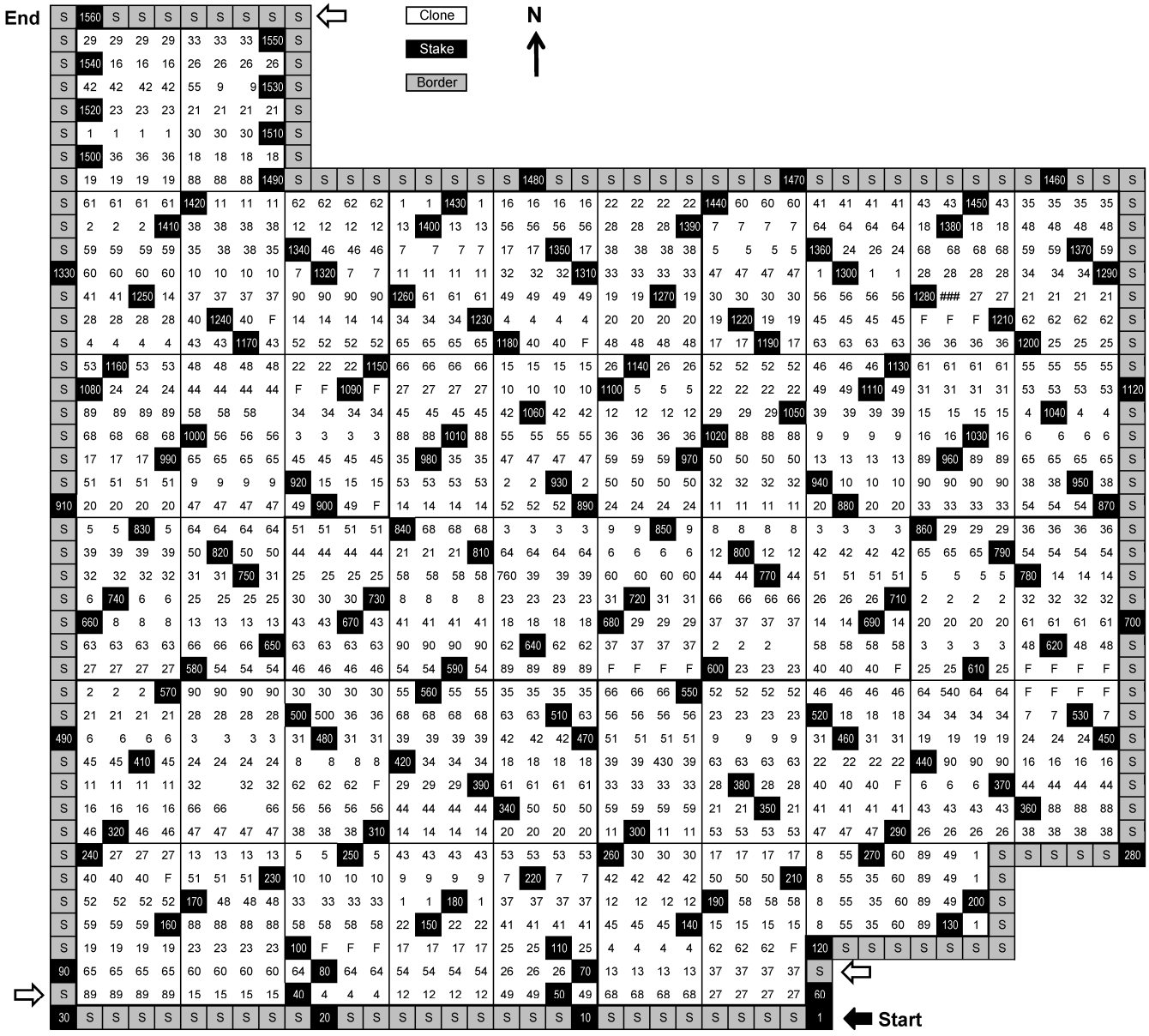
Appendix 13. Continued.



Clone8-31-02 reps and incomplete blocks within reps



Appendix 14. Location and trial layout for field trial "Clone6-10-02" of the 2002 aspen clonal trial series. (For treatment codes see Appendix 11).



Appendix 15. Trial layout for field trial "Clone7-81-02" of the 2002 aspen clonal trial series. (For treatment codes see Appendix 11).