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**Genetic and environmental effects on rooting ability
of dormant unrooted hybrid poplar cuttings**

by

Ronald S. Zalesny Jr.

A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Forestry (Forest Biology-Wood Science)

Program of Study Committee:
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Iowa State University

Ames, Iowa

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Major Professor

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For the Major Program

DEDICATION

The majority of my personal and professional development has come from people I know and interact with on some level. Yet people I have not met also influenced me during certain points in time. I dedicate this dissertation and its research to the memory of Karen Krull-Haissig and her husband, Bruce Haissig. Karen was a unique world-class educator who touched the lives of many people. Karen was a great friend who taught me at a very young age that life has no boundaries and that a person should never settle for anything. She has been a guardian angel looking over me since her accidental death in 1995. Her influence never dwindles, and her legacy will never fade. Although I never knew Bruce on a personal level, I somehow feel as if I did. Bruce guided Don Riemenschneider and Ed Bauer who, along with Rick Hall, melded me into the scientist I am today. The research described in this dissertation would not have been possible without their assistance. Bruce also published numerous manuscripts, which were invaluable to me during my studies of rooting. Unfortunately Karen and Bruce are not with us anymore, but maybe in some very little way this dissertation can act as a symbol that their memory will remain forever.

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ABSTRACT

Genotypes with enhanced rooting ability are crucial for deployment of intensively cultured *Populus* plantations. Rooting of dormant, unrooted cuttings is the first biological prerequisite to stand establishment. The primary objective was evaluating three developmental systems affected by site conditions: lateral and adventitious root ontogenies, root/shoot growth rates, and temperature dependent physiologies. The study tested rooting ability of 21 clones from five taxonomic backgrounds ((*Populus deltoides* x *Populus trichocarpa*) x *P. deltoides* 'BC₁'; *P. deltoides* 'D'; *P. deltoides* x *Populus maximowiczii* 'DM'; *P. deltoides* x *Populus nigra* 'DN'; *P. nigra* x *P. maximowiczii* 'NM') at Ames, Iowa; Waseca, Minnesota; and Westport, Minnesota, across three planting dates during 2001 and 2002. The experimental design was randomized complete blocks with 12 blocks per planting date and a single 20 cm cutting per clone per block. Spacing was 1.2 x 2.4 m, with two border rows of unrooted cuttings. Trees were harvested 14 days after planting. Lateral roots, callus roots, callus, shoots, and leaves were dissected from each cutting and oven dried for dry weight determination. The dissected plant components were photographed and an image analysis system was used to determine dimensions and numbers. Height following establishment was also determined. Aboveground and belowground temperatures were recorded to estimate growing degree days (GDD). Precipitation data were compiled. Data on aboveground and belowground growth were analyzed using analyses of variance, variance component analyses, and principal component analyses according to the Statistical Analysis System. The percentage of cuttings rooted among clones ranged from 21.8 – 86.1%. Significant clone-mean correlations among traits suggested that a few dependent variables could explain the variation in rooting among genotypes. Broad-sense heritabilities for root dry weight and top dry weight ranged from 0.09 – 0.11 and 0.31 – 0.38, respectively. BC₁ clones exhibited the highest root dry weight, while NM and DM clones produced the highest top dry weight. Clonal and taxonomic group shoot:root ratios ranged from 5 – 77 and 11 – 71, respectively. Genotype x environment (G x E) interactions existed for most traits, with belowground GDD accounting for most environmental variation. Clonal performance was stable over all year x site combinations, except for Westport 2002 where root growth was relatively poor. Rooting increased with increasing belowground GDD for all taxonomic groups. Least-squares regression models indicated very similar taxonomic group responses

for each rooting trait. A minimum of four days with at least four GDD per day, along with precipitation dispersed throughout the growing period, were needed for above-average rooting. Controlled environment studies are needed to identify specific temperature thresholds that promote rooting. Clonal survival rates decreased about 10% from June to October. Clone NM6 performed well relative to others, while clone DN34 performed poorly.

CHAPTER 1. INTRODUCTION

Dissertation Structure

This dissertation follows a traditional format including five chapters relating to the introduction, literature review, materials and methods, results and discussion, and conclusions.

Chapter 1 provides a section of terminology, followed with an introduction to short rotation woody crops, regional hybrid poplar implications, and the genus *Populus*. General characteristics, taxonomy, and genetics and breeding of *Populus* are discussed.

Chapter 2 provides a literature review addressing inheritance and correlation of growth parameters, anatomy and genetics of rooting, and factors affecting rooting. Factors addressed relate to physiology, propagation, soil, and temperature. A brief review of rooting study methods is also given. Destructive and non-destructive sampling techniques are described, along with information regarding rooting parameters.

Chapter 3 provides detail on materials and methods. General information about site and clone selection precedes a section describing data acquisition. Data include those obtained from image analysis, dry weight determinations, tree growth measurements, and environmental weather stations. The chapter concludes with a detailed description of experimental design and data analysis. The field plot layout, models, and expected mean squares are highlighted.

Chapter 4 provides results and discussion relating to separate analyses of initial root development and tree growth. The general structure of each analysis consists of an evaluation of genotypic effects, site effects, genotype x environment interactions, and performance relative to commercial standards. An evaluation of environmental effects is also included in the initial root development analysis.

Chapter 5 provides a summary and recommendations for future research directions.

Lists of figures and tables, acknowledgements, and an abstract precede Chapter 1.

Appendices, works cited, and a biographical sketch follow Chapter 5.

Definitions of Terms

The following definitions are from The Dictionary of Forestry (Helms 1998) (H) and Anatomy of Seed Plants (Esau 1977) (E).

Acropetal Development:	Produced or becoming differentiated in a succession toward the apex of an organ. The opposite of basipetal but means the same as basifugal. (E)
Adventitious:	Pertaining to a plant part that develops outside the usual order of time, position, or tissue. An adventitious root arises from parts of the plant other than a preexisting root, e.g. from a stem or leaf. (H)
Anticlinal:	Commonly refers to orientation of cell wall or plane of cell division; perpendicular to the nearest surface. Opposite of periclinal. (E)
Basipetal Development:	Produced or becoming differentiated in a succession toward the base of an organ. The opposite of acropetal and basifugal. (E)
Catkin:	A unisexual pendulous inflorescence consisting of a central stem, scaly bracts, and sessile flowers without petals. (H)
C-effect:	A non-heritable effect common among individuals that is not due to genetic covariation. C-effects may include maternal effects, a non-random environment, or a common physiological condition of donor tissue used for cloning. (H)
Clone:	A vegetatively propagated organism, or a group of such organisms consisting of an ortet and its ramets. (H)
Coppice:	The production of new stems from stump or roots, or any shoot arising from an adventitious or dormant bud near the base of a woody plant that has been cut back. (H)
Dioecious:	Pertaining to a species having male and female flowers (or strobili) produced on separate plants. (H)
Heritability:	The proportion of variability of a character due to heredity, the remainder being due to environment. (H)
Heterosis:	A characteristic exhibited when the mean hybrid phenotype exceeds the range of the parents. (H)
Ontogeny:	The developmental history of an individual organism over its life cycle from zygote to maturity. (H)

Definitions of Terms (continued)

Ortet:	The original plant (ancestor) from which a vegetatively propagated clone has been derived. (H)
Pedigree:	A record of parentage, often including data on performance of the parents and of other relatives. (H)
Periclinal:	Commonly refers to orientation of cell wall or plane of cell division; parallel with the circumference or the nearest surface of an organ. Opposite of anticlinal. (E)
Propagule:	A plant part such as a bud, tuber, root, shoot, or spore used to propagate an individual vegetatively, or the individual resulting from vegetative propagation. (H)
Provenance:	The original geographic source of seed, pollen, or propagules. (H)
Ramet:	An individual member of a clone vegetatively propagated from an ortet. (H)
Root Primordium:	An organized group of root cells at the early stage of differentiation within the pericycle that develops into a lateral root. (H)
Scion:	An aerial plant part, often a branch tip, that is grafted onto the root-bearing part (rootstock) of another plant. (H)
Stool:	A living stump (capable of) producing sprouts. (H)
Translocation:	The long-distance transport of water, minerals, and organic compounds, including plant-growth regulators within plants. (H)

Short Rotation Woody Crops

The United States has drastically depleted much of its stock in native forests. Recent attention focuses on increasing production from intensively managed plantations (Sedjo 1997). Such plantations usually consist of clones and hybrids of one or a few species (monoclonal plots), compared with extensive mixtures in native stands (DeBell and Harrington 1993). Mixed plantations (polyclonal plots with multiple genotypes) have been designed to increase productivity (DeBell and Radwan 1979) and species diversity, while decreasing intragenotypic competition. However, increased productivity with polyclonal stands is not a guarantee. DeBell and Harrington (1997) failed to show consistent yield advantages of polyclonal plantings over monoclonal plantings. Nevertheless, intensive culture has been pursued because production from such plantations reduces pressure on native forests (Gladstone and Ledig 1990). Teynor and Edberg (1996) reported that the Minnesota Department of Agriculture predicts an aspen shortage within 10 – 20 years due to a lack of suitable aspen stumpage within harvestable diameter classes. There currently exists large stumpage of mature aspen (over 50 years) and young aspen (less than 15 years) but limited stumpage in the middle age class (20 – 40 years). This is alarming since industrial timber products annually harvested in the Lake States consist primarily of pulpwood. Piva (1998) reported that 49% of Lake States pulpwood roundwood harvested and 72% of Minnesota pulpwood roundwood harvested in 1996 consisted of aspen. Perry et al. (2001) cited data from the Minnesota Department of Natural Resources (1997) that 30,000 – 40,000 hectares of former cropland and former conservation reserve program land will be converted to tree plantations before 2005.

Short rotation intensive culture forestry systems mirror agronomic practices (Hansen et al. 1983). Site selection and site preparation precede plantation establishment. Disease and pest control, weed control, and fertilizer application follow planting. Uniformly sized trees are harvested. Hybrid poplars (referring to *Populus* spp. and *Populus* hybrids) are excellent intensive culture species and have been vegetatively propagated for hundreds of years. Hybrid poplars have been studied more than any other tree species (Dickmann 2001), and have been extensively planted outside their native range (Heilman 1999).

Short rotation woody crop systems, synonymous with hybrid poplar plantations in this dissertation, are supply systems where selected, genetically improved tree species are planted on a prepared site for multiple societal benefits (Tuskan 1998). Poplar plantations provide fiber supplies, energy (liquid fuels and biomass for electricity), phytoremediation, raw material for engineered lumber products, cordwood (firewood), riparian stabilization, agroforestry opportunities, wildlife habitat, and aesthetic values (Heilman 1999, Joslin and Schoenholtz 1997, NCFES 1996, Ranney and Mann 1994, Tolbert and Wright 1998, Treeby 1978). Robison and Raffa (1998, page 1) listed environmental and economic costs of such plantations as soil erosion, pest impacts, pesticides, nutrient depletion, fertilizers, processing byproducts, reduced genetic diversity, and energy inputs. Despite such costs, research is being conducted in breeding and selecting disease resistant, pest tolerant, fast growing hybrid poplars adapted to regional environments (Knowe et al. 1998, Lortz et al. 1994, Ostry and Anderson 1995, Riemenschneider et al. 2001, Robison and Raffa 1997, Tuskan 1997, Walsh et al. 1996, Wu and Stettler 1994). Tuskan (1998) stated that 80% of short rotation intensive forestry research is devoted to hybrid poplars.

Regional Hybrid Poplar Implications

The focus on the production of alternative fuels as a source of energy is increasing in the North Central United States (Husain et al. 1998). Intensively cultured poplar plantations are beneficial to the industrial fiber supplies of other areas of the United States and have gained attention in the North Central region. Interest is focused on hybrid poplars because they are fast growing, relatively easy to vegetatively propagate, and require shorter harvest cycles than native aspen (Heilman 1999). Hybrid poplar has the potential to grow approximately 6 – 8 times faster than native aspen in the Lake States. Potential stand productivity of hybrid poplar is predicted to be between 3 – 5 dry tons per acre per year, compared with native aspen potential stand productivity of 0.4 – 0.7 dry tons per acre per year (Netzer et al. 2002, Netzer and Tolsted 1999, Riemenschneider et al. 2001).

Failure to conduct proper site management can cause severe economic losses (Buhler et al. 1998). Lack of weed control may result in complete loss of the planting. It is essential to assess the effects of various site management strategies, including the use of chemical and mechanical techniques, if high yields are to be realized (Hansen 1994, Hansen et al. 1994, Heilman and Norby 1998, Lindquist 1986). Buhler et al. (1998) noted that effective weed

control can potentially double productivity. Marino and Gross (1998) found highly significant growth reductions with increased levels of weed competition. Water and nutrient deficiency also likely contribute to stunted growth.

Clonal development is a major part of the aforementioned hybrid poplar research efforts (Riemenschneider et al. 2001). Primary traits of interest include those associated with pathogen and insect resistance and those associated with tree growth and development. Primary pathogen and insect parameters include but are not limited to leaf diseases, stem diseases, and insect pests. Tree growth and development parameters include but are not limited to height, diameter, biomass, specific gravity, and stem form. A detailed discussion of these traits is beyond the scope of this dissertation. Ostry et al. (1988a) provided comprehensive detail about insect, pathogen, and animal pests of poplar. Table 1 lists additional literature sources for interested readers.

Table 1. Literature sources for leaf rusts, stem cankers, and pests of hybrid poplar.

Disease/Insect	Species	Source
Leaf rust	<i>Melampsora larici-populina</i> /	Beare et al. 1999
	<i>M. allii-populina</i>	
	<i>M. larici-populina</i>	Cervera et al. 1996
	<i>M. larici-populina</i>	Lèfevre et al. 1998
	<i>M. larici-populina</i>	Lèfevre et al. 1994
	<i>M. medusae</i>	Newcombe 1998
	<i>M. medusae</i>	Newcombe et al. 1996
	<i>M. medusae</i>	Newcombe et al. 1994
	<i>M. medusae</i>	Prakash and Heather 1989
	<i>M. medusae</i>	Rajora et al. 1994
	<i>M. medusae</i>	Tabor et al. 2000
Stem canker	<i>M. medusae</i>	Widin and Schipper 1980
	<i>Hypoxylon mammatum</i>	Bucciarelli et al. 1998
	<i>H. mammatum</i>	Enebak et al. 1999
	<i>H. mammatum</i>	Ostry and Anderson 1995
	<i>Septoria musiva</i>	Lo et al. 1995
	<i>S. musiva</i>	Ostry et al. 1989
	<i>S. musiva</i>	Ostry et al. 1988b
Insect pest	<i>S. musiva</i>	Waterman 1946
	<i>Chrysomela scripta</i>	Bingaman and Hart 1993
	<i>C. scripta</i>	Bingaman and Hart 1992
	<i>C. scripta</i>	Kang et al. 1997
	<i>C. confluens</i>	Floate et al. 1993
	<i>Phratora californica</i>	James and Newcombe 2000
	<i>Malacosoma disstria</i>	Robison and Raffa 1997

Furthermore, breeding for enhanced rooting ability is a key component of hybrid poplar clonal development (Stout and Schreiner 1933), since as much as 42% of tree biomass has been apportioned to the roots (Scarascia-Mugnozza et al. 1997). Francis (1985) reported that roots comprised 27% of pulpwood-sized *Populus deltoides* biomass. Likewise, Baker and Blackmon (1977) attributed 30% of biomass to roots. Studying the quantitative inheritance of rooting ability may provide information for the development of improved cultural technologies. Such practices may enhance the potential for success of commercial plantation deployment because rooting is the first biological prerequisite to stand establishment. The ability of hybrid poplars to form adventitious roots is crucial to the commercial deployment of intensively cultured poplar plantations. Heilman et al. (1994b) expressed one key to the success of such trees as the ability of specific poplar hybrid (*Populus trichocarpa* x *P. deltoides*) roots to develop and grow rapidly from cuttings. Thus, hybrid poplar vegetative propagation is an effective means of quickly establishing a plantation with minimal costs (Dickmann and Stuart 1983, Heilman 1999, Wright 1976, Wright 1962).

There are two types of hybrid poplar propagules. One type of propagule is the dormant unrooted hardwood cutting (Riemenschneider and Bauer 1997, Maisenhelder 1960, Wilcox and Farmer 1968). Another type of propagule is the rooted hardwood cutting (Hansen et al. 1983). Rooted stock are subject to injury and possibly deformation of the root system during planting (Smith et al. 1997), although with poplars the potential for deformation is limited due to the thickness and strength of roots left on the cutting. The reduction of root systems results in decreased growth in the new individual (Luxova 1984), just as root system enhancement potentially increases growth (Heilman et al. 1994b, Raven et al. 1992). Rooted cuttings also require more resources during preparation and planting. However, relative rates of growth and survival are much higher for rooted than for unrooted stock. Therefore, choice of propagule is situation dependent.

The Genus *Populus*

General Characteristics

The genus *Populus* belongs to the family Salicaceae (the willow family). *Populus* spp. are hereafter referred to as poplars. Generally species are diploid with two sets of 19 chromosomes ($2n = 38$), but triploid trees exist ($3n = 57$). Dickmann (2001) reported that the

physical size of the *Populus* genome is very small. For example, the maize genome is six times larger and the loblolly pine genome is forty times larger than *Populus*. The relatively less complex genome and favorable traits such as fast growth rates, ease of propagation, and crossability among certain sections make poplars favorable for study (Dickmann 2001, Dickmann and Stuart 1983, Eckenwalder 1996, Schreiner 1971).

Poplars are deciduous, with leaf senescence occurring in autumn (yellow to pale gold leaf color) and new leaves emerging in the spring of the year. Leaves are alternate and simple, with broad variation in size and shape. Poplars are dioecious. Individual trees are male or female, bearing pollen or producing seed, respectively. Male to female ratios are 1:1 (Farmer 1964, Kaul and Kaul 1984, Schreiner 1971). Flowers are borne on pendant catkins. Male and female catkins emerge prior to leaf flush in the spring. Female flowers are wind pollinated. Post-pollination events include fertilization, formation of capsules within catkins, capsule ripening, seed maturation, and wind disseminated seed dispersal. In addition to sexual reproduction, vegetative reproduction is common among poplars. An ortet is the original seed derived parent and a ramet is an individual clonal offspring of an ortet. Thus, ramets are exact genetic replicas of ortets (Dickmann 2001, Dickmann and Stuart 1983, Eckenwalder 1996, Kaul 1995, Schreiner 1971). Clones (Shull 1912a, Shull 1912b) are initially vegetatively propagated from ortets and may be further propagated from ramets in a clonal orchard. Poplars are fast growing and relatively short-lived. Stem form is generally tall and straight. Poplar wood properties are desirable for many uses. Dickmann (2001, pages 14 – 15) stated that:

It[poplar wood] is light in weight, soft, light in color (except for a dark-colored heartwood or wetwood core), straight-grained, and, because it is diffuse porous, uniform in texture. The wood is used for pulp and paper, veneer, excelsior, composition boards (especially oriented-strandboard, also known as OSB), lumber, and energy.

Taxonomy

Six taxonomically unique sections within the *Populus* genus exist, with approximately thirty species having worldwide natural distribution in the northern hemisphere (Dickmann 2001, Eckenwalder 1996). The six sections include: *Abaso* (Mexican poplar), *Aigeiros* (cottonwoods and black poplar), *Leucoides* (swamp poplars), *Populus* (aspens and white poplars), *Tacamahaca* (balsam poplars), and *Turanga* (Afro-Asian

poplars). Sections *Aigeiros*, *Populus*, and *Tacamahaca* are most important for tree improvement and plantation culture (Heilman 1999, Ronald 1982). This dissertation focuses on the use of two species (*Populus deltoides* and *P. nigra*) within section *Aigeiros* and two species (*P. maximowiczii* and *P. trichocarpa*) within section *Tacamahaca*. These four species are genetically distinct from each other (Rajora and Zsuffa 1990). Most economically important clones in the North Central United States are from the sections *Aigeiros* and *Tacamahaca* (Dickmann 2001, Dickmann and Stuart 1983, Eckenwalder 1996). A brief description of these four species is given below.

Section Aigeiros. Populus deltoides Bartr. ex Marsh, eastern cottonwood, is naturally distributed in eastern North America. The North American range of *P. deltoides* includes the eastern half of the United States and southern Canada. *P. deltoides* grows over a range of sites from bottomlands and riparian corridors to old fields and disturbed upland sites. *P. deltoides* is the only species in this dissertation research program that is native to the North Central United States. Therefore, *P. deltoides* is more resistant to local races of *Septoria* canker than other species in the study. The major drawback of *P. deltoides* is that it roots relatively erratically from unrooted dormant hardwood cuttings. Yet *P. deltoides* expresses the highest growth rates of any tree species in North America. Heilman (1999) stated that 90% of poplar hybrids have *P. deltoides* parentage. Traditional breeding programs of the North Central region have used *P. deltoides* germplasm from the southern forest region of the United States to northern Minnesota and parts of Canada (Dickmann 2001, Dickmann and Stuart 1983, Eckenwalder 1996).

Section Aigeiros. P. nigra L., European black poplar, is naturally distributed in Europe, Asia, and North Africa. *P. nigra* grows over a range of sites from wastelands and riverbanks to other disturbed areas. *P. nigra* is perhaps the oldest species to be manipulated. In contrast to approximately one half century of breeding in the United States, Europeans began breeding *P. nigra* and other species almost two centuries ago. This species introduces greater rooting ability than *P. deltoides*, yet *P. nigra* bears limited defense against *Septoria* canker and other cankers. Growth rates of *P. nigra* are not as vigorous as *P. deltoides*, but when grown on adequate soils can be relatively comparable. Original *P. nigra* germplasm utilized in North Central breeding programs came from Europe. However, current germplasm

is distributed worldwide (Dickmann 2001, Dickmann and Stuart 1983, Eckenwalder 1996, Netzer et al. 2002).

Section Tacamahaca. *P. maximowiczii* A. Henry, Japanese poplar, is naturally distributed in northeast Asia and Japan. *P. maximowiczii*, like *P. nigra*, grows over a range of sites from wastelands and riverbanks to other disturbed areas. *P. maximowiczii* is a species from Asia that has adapted well in the United States. It also has a long history of being used in breeding programs. *P. maximowiczii* may have the best rooting ability of the species studied herein and also experiences phenomenal growth rates (in fact, early records indicate that these trees grew large enough to be used for sea-bearing dugout canoes). *P. maximowiczii* is susceptible to *Septoria* canker. Original *P. maximowiczii* germplasm in North Central breeding programs came from Japan and other Asian countries. Current germplasm is mostly from Canada, but distribution is worldwide (Dickmann 2001, Dickmann and Stuart 1983, Eckenwalder 1996, Netzer et al. 2002).

Section Tacamahaca. *P. trichocarpa* Torr. & Gray, western black cottonwood, is naturally distributed in northwestern North America. The North American range of *P. trichocarpa* is throughout the Pacific coastal states and western Canadian provinces from Alaska to California. Isolated patches of *P. trichocarpa* have been found east of the Rocky Mountains. *P. trichocarpa* grows in low elevation, moist bottomland, riverine, and alluvial sites. *P. trichocarpa* is the only species utilized in this research program that is native to the Northwest United States. More than half of the breeding efforts of the Northwest focus on *P. trichocarpa*. The main justification for including this species in this research program is because of its excellent rooting ability. The major drawback with *P. trichocarpa* is that it is highly susceptible to *Septoria* canker when grown in the North Central United States. *P. trichocarpa* expresses very rapid growth rates in plantation culture in the absence of canker problems. Traditional breeding programs of the North Central region have primarily used *P. trichocarpa* germplasm from Idaho, Washington, and Oregon, but sources extend from Alaska to southern California (Dickmann 2001, Dickmann and Stuart 1983, Eckenwalder 1996, McCamant and Black 2000, Netzer et al. 2002).

Breeding and Genetics

Breeding and selecting improved hybrid poplar genotypes have been conducted in North America since the beginning of the 20th century (Stout and Schreiner 1933). Poplars

are excellent candidates for genetic improvement because of their ease of propagation, relatively short generation time, and broad range of genetic variation (Farmer 1970, Orlovic et al. 1998, Schreiner 1971, Sokal et al. 1986, Stout and Schreiner 1933). Gains from selection are proportional to variation (Falconer and Mackay 1989, Fehr 1991). Realized selection gains in poplar breeding warrant further development (Riemenschneider et al. 2001). For example, Wilcox and Farmer (1967) reported high heritabilities estimated on an individual plant basis (0.20 – 0.97) and clone-mean basis (0.58 – 0.99). They used these heritability estimates to predict gain from selection of four plant characters (plant height, stem diameter, number of branches, rust incidence score). As an example of realized selection gains, Wilcox and Farmer (1967) estimated an increase in the mean height of selected trees of 1.2 feet if they were to use a 10% selection intensity. Correlations among traits limit expected gains from selection (Wilcox and Farmer 1967). Thus, it is increasingly more important to develop breeding programs incorporating multiple traits, in addition to testing across multiple years and environments (Eriksson 1991). Significant genotype x environment interactions result in a decision to select generalist genotypes that perform well over a broad geographic range or to select specific genotypes within designated breeding zones (Orlovic et al. 1998).

The overarching goal of poplar genetic improvement is to produce superior clones. These clones should exhibit regional adaptability in terms of maximum wood produced in the shortest amount of time and adequate pest resistance (Schreiner 1971, Stout and Schreiner 1933). Hybrids that are clonally propagated take advantage of heterosis resulting from additive and dominance genetic effects (Ronald 1982). Selecting improved clones that outperform their parents enhances the probability of success of genetic improvement programs.

Intersectional hybridization is successful between *Populus* sections *Aigeiros* and *Tacamahaca* (Eckenwalder 1984). Such hybridization is important because the genus provides the genetic diversity needed for clonal improvement (Schreiner 1971). Stout and Schreiner (1933) reported that 56% of elite plant parents resulting from breeding trials are from these sections (*Aigeiros* 29%, *Tacamahaca* 27%).

In summary, hybrid poplar breeding programs have been successful due to broad genetic variation, crossability among species within different sections, and ease of

propagation. Clonal propagation of poplars in terms of processing and planting unrooted dormant cuttings is relatively easy compared with other forest species. The research detailed in subsequent sections of this dissertation focuses on evaluating the variation in rooting ability among poplar clones. The clones belong to five taxonomic groups consisting of pure species and hybrids of the four species described in the *Taxonomy* section above. Although these five groups are not pedigrees in the strict genetics and plant breeding sense, the designation “pedigree” is used for “taxonomic group” throughout the dissertation for convenience.

CHAPTER 2. LITERATURE REVIEW

Inheritance and Correlation of Growth Parameters

Numerous studies describe growth and productivity of hybrid poplar at various stages of development, ranging from two weeks up to rotation age (>10 years). Given the broad amount of genetic variation and relative propagation ease of hybrid poplar, many studies provide results from tests estimating heritability of and correlation among belowground and aboveground traits. This section provides a brief review of key studies describing the inheritance and correlation of such growth parameters.

Mohn and Randall (1971) provided heritability and correlation estimates from a clonal test of six year old *Populus deltoides*. Broad-sense heritabilities for height ranged from 0.32 – 0.51 and for diameter ranged from 0.20 – 0.35. Significant phenotypic correlations ($\alpha = 0.05$) between fifth year heights and earlier measurements ranged from 0.31 – 0.81, and those between sixth year diameter and earlier measurements ranged from 0.53 – 0.81.

Riemenschneider et al. (1994) evaluated genotypic variation of *Populus trichocarpa* collections from British Columbia and northern Idaho. They reported significant clonal effects and high broad-sense heritabilities in both populations for 14 traits relating to height, phenology, leaf morphology, and resistance to damaging agents. Heritabilities ranged from 0.10 (stem lesions – northern Idaho) to 0.94 (extent of *Melampsora* rust). Almost all traits were significantly correlated with tree height at age two years. Rogers et al. (1989) studied genetic variation within ten natural populations of *Populus trichocarpa* located in the Pacific Northwest. They found that nearly 25% of height and diameter variation after three growing seasons was attributable to clones. Heritabilities were measured on a narrow-sense basis and therefore were more conservative than most poplar studies. They estimated narrow-sense heritabilities of 0.13 and 0.10 for diameter and height at age three years, respectively. In addition, they reported significant phenotypic correlations involving seven aboveground traits relating to leaves, branches, and volume.

Riemenschneider et al. (1992) studied genetic variation of 153 *Populus balsamifera* L. clones originating from 21 populations occurring naturally in the Lake States. They concluded that clones accounted for most of the variation in all traits relating to height, phenology, leaf morphology, and resistance to damaging agents. Broad-sense heritabilities ranged from 0.14 (stem lesions) to 0.65 (days to bud set). Correlations among all traits and

tree height at age two years were significant at the 0.01 probability level. In a related study, Riemenschneider and McMahon (1993) concluded that genetic differentiation among Lake States *P. balsamifera* exists. They grouped the aforementioned 21 populations into the following three clusters: northwestern, central, and southeastern. The populations differed with respect to phenology and growth, and branching patterns. Farmer et al. (1988) evaluated the variation of *P. balsamifera* clones in order to estimate heritability and the magnitude of C effects. They reported that after three years growth, C effects were negligible and clones accounted for nearly 50%, 24%, and 71% of total variation in height, shoot growth rate, and foliation date, respectively. Broad-sense heritabilities across these parameters ranged from 0.16 – 0.74.

Wu and Stettler (1994) studied growth and development in F_2 and backcross (B_1) families with *Populus trichocarpa* and *P. deltoides* parental germplasm. *P. deltoides* was used as the recurrent parent in the backcross program. Clones accounted for a large portion of variation in stem, branch, and leaf characters for both families. Heritabilities in the F_2 family ranged from 0.43 (branches) to 0.91 (leaves). Likewise, heritabilities in the B_1 family ranged from 0.52 (stem) to 0.92 (leaves). Wu and Stettler (1998) used the parents and selected clones from the F_2 family described above in a study evaluating phenotypic plasticity at two contrasting sites. One site represented a coastal environment typical of western Oregon and the other site represented an interior environment. They found high broad-sense heritabilities at both sites for traits relating to leaves, branches, and canopy structure. Heritabilities at the coastal site ranged from 0.44 (leaf shape) to 0.78 (leaf width of the current terminal shoot). Heritabilities at the interior site ranged from 0.28 (leaf shape) to 0.70 (leaf length of the current terminal shoot). Wu (1994) extensively evaluated two hybrid poplar pedigrees to determine patterns of genetic variance among 58 different morphological traits relating to leaf, branch, main stem, and whole tree geometry. The results are too extensive to describe here, but clones accounted for approximately 70 – 99% of the variation among the 58 traits. Wu et al. (1992) studied the inheritance patterns in two interspecific populations of hybrid poplar (*Populus deltoides* x *P. simonii* Carrière ‘DS’ and *P. deltoides* x *P. nigra* ‘DN’). Similar to the studies above, clonal variation dominated the system in both populations. Clones of the DS pedigree accounted for 92%, 95%, and 96% of the variation in height,

diameter, and volume, respectively, at age six years. DN clones accounted for 95%, 93%, and 92% of the variation in height, diameter, and volume, respectively.

Anatomy of Rooting

The anatomy of rooting from dormant cuttings is well studied. Sledge (1930) defined two regions of cambial activity throughout the cutting. He found two opposing gradients of cambial activity in four species studied (apple - *Malus* spp., *Forsythia* spp., California privet - *Ligustrum ovalifolium* Aureum, sycamore - *Platanus occidentalis* L.). The first region is located above the uppermost bud of the cutting. The second region of cambial activity is located at the base of the cutting. In both instances, the spread of cambial activity decreases in a direction toward the middle of the cutting. Similar results are reported for poplar. Luxova (1984) observed fewer cells expressing cambial activity in middle regions of poplar cuttings compared with apical and basal regions. Ying and Bagley (1977, *P. deltoides*) and Ernst and Fechner (1981, narrowleaf cottonwood, *P. angustifolia* E. James) reported root development of cuttings made from apical portions of the parent shoot to be located exclusively at the base of the cutting. Likewise, Farmer et al. (1989) defined a zone on the basal 3 cm of the cutting where induced root primordia are present. Bagley and Sutton (2002) stated that eastern provenances of *P. deltoides* root predominantly from the base of the cutting.

There are two distinct rooting ontogenies of dormant cuttings (Girouard 1967, Haissig 1974, Luxova 1984, Schier and Campbell 1976). The first rooting ontogeny is lateral roots that develop from induced primordia differentiating from primary roots as a result of response to external stimuli or from latent root primordia located in the cambium of the stem. Induced root primordia originate near vascular tissues within the cambium, phloem, and pericycle (Haissig 1974). Smith and Wareing (1974) found sites of initiation near secondary phloem along the boundary of medullary rays. Similarly, Girouard (1967) reported initiation near the outside of the vascular system in interfascicular parenchyma cells. Sources cited within Girouard (1967) listed sites of initiation for *Populus* species within the *Aegeiros* section just outside the cambium near primary rays (Braun 1963) and for *P. nigra* and *P. trichocarpa* opposite medullary rays (van der Lek 1924).

Asynchronous latent root primordia initiate acropetally during stages of active cell division and cell expansion of the poplar stem. Thus, older primordia are located toward the

base of the stem. Individual primordia retain independence from adjacent primordia (Luxova 1985, Luxova and Lux 1981a, Luxova and Lux 1981b). The primordia form in early July and are active throughout the growing season (Brown 1935, Luxova 1984, Smith and Wareing 1974). Luxova and Lux (1981b) described differentiation of root primordia near biseriate, occasionally multiseriate, rays. They explained that division of ray cells triggers division in a group of adjacent phloem cells. The cell group enlarges as cambial activity increases and more cells divide. This group of cells becomes the root primordium. Once the primordium is formed, periclinal and anticlinal cell divisions begin growth in a direction perpendicular to the length of the stem. Growth divisions support periclinal zoning of the primordial distal region. Zonation includes ground meristem and procambium in the interior of the primordium, and root cap initials in the exterior regions. The base of the primordium begins acropetal formation of vascular connection with the root apex as differentiation of the distal region takes place. Thus, differentiation proceeds until vascular connection between the stem and the root is complete. At this point, the root procambium previously formed begins continuous acropetal differentiation following connected stem tracheids (Luxova 1985, Luxova and Lux 1981a, Luxova and Lux 1981b). Dormancy of the root primordia follows cessation of vascular cambium activity during winter months (Brown 1935, Luxova and Lux 1981b). Root initiation from latent root primordia depends on age of the primordia, presence of vegetative buds, and stratification (Smith and Wareing 1974).

The second rooting ontogeny is adventitious roots that develop from callus at the base of the cutting in response to wounding. Callus cells are undifferentiated and capable of division (Haissig 1974). The adventitious callus roots complement the lateral roots and provide an uptake system while the permanent root system is becoming established (Luxova 1984). Differentiation of adventitious root primordia in callus occurs in many other tree species such as: loblolly pine (*Pinus taeda* L.), white pine (*Pinus strobus* L.), and jack pine (*Pinus banksiana* Lamb.) (Gupta and Durzan 1986, Minocha 1980, Montain et al. 1983).

Genetics of Rooting

There is an information shortage about the genetics of hybrid poplar rooting (Haissig and Davis 1994, Haissig et al. 1992, Pregitzer and Friend 1996). Less is known of genetic and environmental covariances between root and shoot developmental systems (Riemenschneider et al. 1996). It is difficult to acquire new knowledge of genetic control of

rooting in poplars because not all species root equally well (Cunningham 1953, Farmer et al. 1989, Zalesny et al. 2000). Methods supporting heritability estimates of rooting ability are laborious, yet possible. The traditional approach for estimating heritability in hybrid poplar programs is to conduct replicated clonal tests at multiple locations (Wilcox and Farmer 1968, Ying and Bagley 1977). Heritability estimates and estimated selection gain are predicted using data from these clonal tests.

Wilcox and Farmer (1967, 1968) conducted early rooting experiments of *P. deltoides* cuttings based on root weight, root number, and root length and found significant broad sense heritabilities for all characteristics (0.36 – 0.58, 0.44 – 0.56, 0.33 – 0.52, respectively). They attributed most clonal variation of rooting ability to two primary factors. First, clonal differences were a result of inherent variability due to specific genotype (e.g. heritability / parent-offspring resemblance). Second, clonal differences were a result of C-effects (e.g. differences due to unique physiological / morphological characters unique to their ortet because of positional effects and environmental preconditioning). Wilcox and Farmer were some of the first researchers of *P. deltoides* to conclude that variation in rooting ability is under fairly strong genetic control and is thus responsive to selection.

Ying and Bagley (1977) estimated high broad sense heritability ($H > 0.80$) for root number in *P. deltoides*. They conducted a greenhouse study and a field study testing for differences in rooting ability of provenances, families, and clones. Both studies showed broad clonal variation in mean number of roots per cutting (greenhouse: 0.0 – 22.5, field: 0.4 – 17.8). Clones of Nebraska and Minnesota – Wisconsin origin produced the largest root numbers. Thus, these researchers concluded that gains from selection for clonal rooting ability can be realized given the high amount of variation.

Riemenschneider and Bauer (1997) found significant differences in clonal rooting ability of *P. trichocarpa*. Clone effects were significant for all rooting characters. Despite lower broad sense heritabilities than previous studies reported (Wilcox and Farmer 1968, Wilcox and Farmer 1967, Ying and Bagley 1977), the broad sense heritabilities of this study were significant at the 0.01 level (root dry weight: 0.20 – 0.33, root number: 0.15 – 0.18, total root length: 0.23 – 0.28). Riemenschneider and Bauer (1997, page 197) attributed this discrepancy to:

1. Ancestry and diversity of experimental populations

2. Method of accounting for C-effects, if any

3. Computational formulations.

They concluded that since clones differed significantly for all rooting characters regardless of sample time, rooting is subject to improvement through selection. In addition, measures of rooting were correlated. This indicated that a few easily measured dependent variables could be isolated that explain most of the variation in rooting (e.g. they could reduce the number of variables measured and still find significant information). In essence, rooting is highly subject to genetic gain from selection as it is almost always heritable (Riemenschneider and Bauer 1997, Wilcox and Farmer 1967, Wilcox and Farmer 1968, Ying and Bagley 1977).

Other studies also found high genetic variation in the rooting ability of poplar cuttings. Cunningham (1953) reported that percentage of cuttings that rooted in a population of 30 *P. deltoides* clones and 30 hybrid clones ranged from 3% to 100%. Farmer et al. (1989) evaluated variance in rooting ability within four provenances of *P. balsamifera*. They conducted two tests and found highly significant clonal effects for mean number of roots per cutting. Root number ranged from 0 – 22 and 3 – 20 in the greenhouse and field test, respectively. The reported range of estimated broad sense heritabilities for root number was 0.15 – 0.80. Ernst and Fechner (1981) used cuttings of *P. angustifolia* to test for variation in rooting ability. They detected significant variation among 75 native sources with respect to mean number of roots per cutting (0.22 – 19.5) and mean root length (0 – 45 mm). The results of these studies corroborated those reported in preceding paragraphs. Rooting ability of poplars is highly variable, and the extensive genotypic variation could result in substantial realized selection gains.

Moreover, high and unpredictable variation makes it very difficult to predict how clones will perform across sites. Prediction is especially difficult because genotype x environment interactions affect rooting (Haissig et al. 1992, Heilman et al. 1994a). Yet attempts to map chromosomes by relating molecular markers to quantitative trait loci (QTL) for other parameters have been successful (Han et al. 1994, Wu et al. 1998). With such technologies, genetic control of rooting may be understood better and selection gain increased. Strauss et al. (1992) expressed reservations for long-term utilization of marker-assisted selection (MAS). Nevertheless, Wu et al. (1998) used QTL's to estimate the relative efficiency of MAS for aboveground traits. Likewise, markers have been used to estimate

genetic composition of seed orchard trees (El-Kassaby et al. 1988, Smith and Adams 1983, Szmidt 1987). Similar MAS may be conducted for genetic analysis of root initiation and development. Furthermore, Wu (1994) used such methods to evaluate the genetics and selection gain of hybrid poplar individual tree geometry. Such quantitative measures of evaluation and prediction may also be used to predict selection gain relating to improved rooting ability, but have presently not been thoroughly explored.

Traditional quantitative genetics provide a needed source of information regarding the genetic basis of rooting. Yet molecular genetics combined with quantitative genetics ("molecular breeding") provides new information, which further enhances knowledge acquisition (Bradshaw 1996, Larkin et al. 1989). The addition of molecular genetic analysis provides information beyond the family and clone level (Adams et al. 1988, Davis et al. 1991, Heinze 1997, Neale and Williams 1991). Thus, there is no longer a need to solely analyze progeny means and other statistics, as described above, to evaluate genetic systems. The addition of molecular genetic analysis seeks to acquire information regarding the following (Bradshaw 1996, page 185):

1. The chromosomal location of each quantitative trait locus (QTL) affecting the trait.
2. The magnitude of effect of each QTL on the observed phenotype.
3. The mode of gene action at each QTL (additive, dominant/recessive, overdominant).
4. The effect of interactions among different QTL's (epistasis).
5. The parental source of beneficial QTL alleles.

As a result, Bradshaw et al. (1994) created an F₂-pedigree linkage map in an Inter-American hybrid (*P. deltoides* x *P. trichocarpa*). Adventitious rooting is one of the traits segregating in this F₂ population that was mapped. This map along with markers could potentially be used to directly clone genes responsible for adventitious root initiation in *Populus*.

The quantitative inheritance of adventitious rooting in hybrid poplar is a very complex system that cannot adequately be evaluated with traditional clonal tests. There is a lack of knowledge regarding the genetic system of rooting because of its complexity and the laborious task of excavating roots in quantitative studies. Yet the addition of molecular tools such as QTL mapping and MAS support a greater understanding of the controls of

adventitious rooting. Future research devoted to adventitious rooting should take advantage of “molecular breeding” along with traditional methods of analysis (Bradshaw 1996).

Factors Affecting Rooting

Physiology

The physiological status of the cutting is important for rooting success since root initiation and early growth are dependent upon endogenous resources (Tschaplinski and Blake 1989). Mobilization of carbohydrates (starch and sugar) and hormone translocation within the cutting and developing parts control the extent to which the young plant grows (Davies 1988, Maynard 1993, van Overbeek et al. 1946). Davies and Hartmann (1988) listed three factors necessary for adventitious rooting. The first factor is the differentiation of cells into root primordia, which is addressed in the anatomy section above. The second factor is accumulation and partitioning of carbohydrates, along with changes in nutrient levels (an energy source), as substrates are needed for root initiation and growth. The third factor is the balance of rooting promoters and inhibitors such as hormones and rooting cofactors.

Carbohydrate content of cuttings is associated with rooting success (Haissig 1982). Carbohydrates are involved in a continuous feedback system containing sources and sinks. The sources are primarily photosynthetic organs that provide photosynthates to the sinks. Excess reserves, mostly carbohydrates, are stored in the sinks until they are used for growth and respiration (Nguyen et al. 1990, Tschaplinski and Blake 1989). Carbohydrate sources in the cutting consist of free reducing sugars (glucose, fructose, sucrose, and other soluble carbohydrates), storage carbohydrates (starch and other insoluble carbohydrates), and cell wall polysaccharides (Davies 1988). Efficiency of utilization of soluble carbohydrates accounts for variation in rooting success (Tschaplinski and Blake 1989). Fege and Brown (1984) and Fege (1983) tested the distribution of carbohydrates in dormant *Populus* cuttings collected from September to May. They found that cuttings made from the more apical regions of the parent shoot exhibited higher sugar and starch concentrations and greater seasonal variation of carbohydrate distribution. Yet cuttings made from basal portions of the parent shoot had greater quantities of carbohydrates due to the larger size of the cuttings. Interconversions between sugars and from starch to sugars resulted in similar levels of total carbohydrates during dormancy.

Kosola et al. (2002) also found fairly stable starch concentrations over time in fine roots of *Populus x canadensis* Moench. They concluded that a dynamic pool of starch was present, regardless of increasing root age or long-term defoliation. Nguyen et al. (1990) tested allocation of starch and sugar within shoot and root systems of two hybrid poplar clones. Both clones allocated major amounts of starch and sugar to the root systems during the onset of dormancy, although starch concentration was 10 times higher in one clone than the other.

Transport of assimilates throughout the cutting during photosynthesis governs the potential for new root and shoot development. Okoro and Grace (1976) studied the levels of carbohydrates (starch and sugar) and rates of photosynthesis in *Populus tremula* L. and *P. x euramericana* Dode cuttings. Overall, *P. tremula* exhibited very poor rooting, which may have been due to lack of preformed root initials, rather than carbohydrate assimilation. In contrast, *P. x euramericana* cuttings showed an initial high carbohydrate content. During growth of the root and shoot, the carbohydrate content decreased throughout the cutting as reserves were being mobilized to roots, shoots, and leaves. Dickson (1979) studied xylem translocation of amino acids in *Populus deltoides*. He found that sugars were translocated to the roots from the leaves via phloem, converted to amino acids in the roots, and then translocated back to the leaves via the xylem.

Carbon and nitrogen allocation is important for success of the cuttings during and directly following establishment. Scarascia-Mugnozza et al. (1999) evaluated seasonal carbon allocation patterns from branches in *Populus* and found that elevated carbon allocation to the root system enhanced success under water and nutrient stress. In addition, older leaves shift more assimilates (~50%) to the base of the stem and root system (Scarascia-Mugnozza et al. 1999). The onset of leaf senescence marks a shift toward increased translocation of photosynthate to the lower stem and roots (Isebrands and Nelson 1983). Carbon and nitrogen storage in the lower stem increases the potential for successful root and shoot development. In addition, storage of carbon and nitrogen in the root systems supports rapid growth of coppiced plants in a field setting following break of dormancy in the spring (Dickmann et al. 1996). Scarascia-Mugnozza et al. (1999, page 1430) summarized results of their work and that of Wareing and Patrick (1975) as follows:

Photosynthate allocation patterns within a plant are determined by factors related to source activity, namely photosynthetic production, environmental conditions, and age of organs; by sink strength, the ability of a given sink to compete for resources within the plant; and by the proximity of the sink to the source and the nature of vascular connections between them.

Nitrate is an important nitrogen source for the developing cutting. Dickson (1979) conjectured that nitrate is reduced in the roots and shoots of *Populus deltoides*. Excess nitrate in the roots is transported to the leaves, where it is utilized or further transported to other sinks. Black et al. (2002) studied the differences in root and shoot localization of nitrate reduction and assimilation in a *Populus tremula* x *P. alba* L. hybrid. Their results corroborated those of Dickson (1979). They found that tissue nitrate concentration was greater in the roots than in the shoots and leaves. However, enzymes that catalyze nitrate assimilation were much higher in the leaves than shoots or roots. Therefore, they concluded that nitrogen acquired in the roots was transported to the leaves and quickly assimilated.

The interaction of hormones, along with rooting cofactors, affects the rooting ability of cuttings. Five general classes of hormones are recognized: auxin, cytokinin, gibberellic acid, abscisic acid, and ethylene. The interrelationships among these hormones governs many physiological activities within the developing cutting (Moore 1991).

Auxin is the most important hormone for rooting. Indoleacetic acid (IAA) is the most common endogenous auxin. Naphthaleneacetic acid (NAA) and indolebutyric acid (IBA), structural analogues of IAA, are the most common synthetic auxins. Auxins stimulate cell elongation and cell division. Thus, they are crucial for the development of preformed root primordia and the initiation of adventitious roots (Haissig 1972). Auxins also inhibit lateral bud break in stems (Farmer 1966, Moore 1991). Plüss et al. (1989) observed increased rooting of *Populus tremula* cuttings with increased levels of IAA. The number of adventitious roots per cutting increased from 1 – 30 with IAA concentrations of 30 – 1425 μ M, respectively. Likewise, Farmer (1966) reported large increases in percentage of cuttings rooted with IBA treatment versus no treatment. Despite one tree with unusual rooting, the range in percentage of cuttings that rooted in those subjected to IBA treatment was 25 – 97%. The range in percentage in those cuttings without IBA treatment was 2 – 92%.

Rooting cofactors (synergists) often enhance rooting when present with auxin. Haissig and Riemenschneider (1992) tested the effects of auxin on rooting of jack pine (*Pinus banksiana*) cuttings. They concluded that an undefined, nonauxin endogenous root-

forming stimulus was present. This cofactor acted additively with auxin, as the treatments did not interact. Therefore, a cofactor along with auxin may be needed for optimal rooting. Gorter (1969) found two auxin-synergists that increased the number of roots from 10 to 50 in dwarf bean (*Phaseolus vulgaris* L.) cuttings. The time of year when cuttings are collected and associated auxin levels also affect rooting. Anand and Heberlein (1975) tested the effects of seasonal variation in auxin concentration on the rooting of fig (*Ficus infectoria* Roxb.) cuttings. They concluded that two auxin-induced rooting phases exist: the first rooting phase is from the onset of spring growth and cambial activity (March) through August and consists of high auxin-sensitivity that leads to increased rooting with auxin application; the second rooting phase is from September through January and consists of low auxin-sensitivity that fails to promote rooting with auxin application. Haissig (1972) tested the effects of endogenous auxin and exogenous gibberellic acid on root primordia development of brittle willow (*Salix fragilis* L.) cuttings. He found that the age of root primordia also affects the extent of auxin induction of roots. Auxin influence and age of primordia were inversely related.

Cytokinin is also very important for rooting. Cytokinins are mostly known for promotion of cell division and cell expansion in the leaves and shoots, although their role in callus formation is also documented. Cytokinins also inhibit senescence (Moore 1991). Cytokinin is often associated with auxin in cell differentiation and tissue development. High auxin:cytokinin levels generally result in favorable rooting (Blakesley 1994). Auxin:cytokinin levels are positively related to temperature (Kester 1970). Decreased transport of cytokinin to the leaves from the roots under cold temperatures is a factor controlling leaf responses to these conditions (Kacperska and Szaniawski 1993). Tromp (1996) conjectured that a negative feedback mechanism between the roots and shoots controls growth such that at cooler temperatures the amount of cytokinin transported from the roots to the shoots decreases. Transport of cytokinin in xylem sap from roots to shoots also decreases as a result of root hypoxia (Neuman et al. 1990). Cytokinin is generally believed to inhibit rooting due to its inhibition of root primordia in stem cuttings (Hartmann et al. 1997, Haissig 1972). Okoro and Grace (1978) studied the effect of cytokinin activity on rooting of *Populus tremula* and *P. x euramericana* cuttings. Cytokinin activity decreased in both species during initial root and shoot growth, which suggests that cytokinin was

transported to growing regions. *Populus tremula* always had greater cytokinin activity in the upper and lower portion of cuttings than *P. x euramericana*. They attributed the unfavorable rooting of *P. tremula* to high levels of cytokinin. However, cytokinin levels may increase as rooting progresses because some endogenous cytokinins are synthesized in the roots. Hansen and Kristensen (1990) found increased cytokinin levels in the shoot as root number increased in Madagascar jasmine (*Stephanotis floribunda* Brongn.) cuttings. They attributed the onset of axillary bud growth to the transport of cytokinin from the roots to the shoots.

Gibberellic acid (GA) promotes stem elongation and cell division, in addition to converting starch to sugar for energy (Moore 1991). GA also impacts rooting of cuttings because of its inhibition on root primordia development (Haissig 1972). Brian et al. (1960) tested the effects of GA application on the rooting ability of garden pea (*Pisum sativum* L.) and dwarf bean (*Phaseolus vulgaris*) cuttings. They applied GA to both ends of the cutting and observed a reduction of root growth with basal GA application. Their results indicated that the inhibition of rooting was the result of a direct local effect of GA.

Absciscic acid (ABA) is a hormone often associated with inhibition of plant growth. However, studies have shown that ABA acts additively with auxins to promote rooting of cuttings (Basu et al. 1970). In addition, ABA enhances bud dormancy, leaf senescence, and leaf abscission (Moore 1991). Following synthesis in roots in response to stress, ABA is translocated to the leaves where it reduces stomatal conductance and photosynthesis (Smit et al. 1990). This stress may reduce the amount of cytokinins produced in the roots, which support leaf growth. Smit et al. (1990) studied the effects of root hypoxia on leaf growth of a *Populus trichocarpa* x *P. deltoides* hybrid. They found that ABA inhibited growth and cytokinin (zeatin riboside) promoted growth. Their conclusions indicated transport of a stimulus in the transpiration stream may be a prerequisite for the reduction in leaf growth. Therefore, roots under hypoxic conditions decreased growth and produced greater levels of ABA. The ABA moved through the transpiration stream to the leaves, where it caused a growth reduction. Conditions of hypoxia consist of a reduction of oxygen (O₂) and an increase of carbon dioxide (CO₂) in the root zone. Smit and Stachowiak (1988) tested the effects of hypoxia and elevated CO₂ on water flux through the root system of a *Populus trichocarpa* x *P. deltoides* hybrid. They concluded that hypoxia and elevated CO₂ reduced water flux, which increased water use efficiency. They believed internal aeration and rapid

root turnover in the root system, along with reduced stomatal conductance and transpiration in the shoot system, were necessary for survival under hypoxic conditions. Studies testing the effect of elevated CO₂ on root growth corroborated these results. Bosac et al. (1995) reported that elevated CO₂ increased root length of a *Populus deltoides* x *P. nigra* hybrid. Root dry weight of the hybrid exposed to ambient levels of CO₂ for 68 days was 5.02 g and that with exposure to elevated levels of CO₂ was 6.71 g. Liu and Dickmann (1996) reported that two hybrid poplar clones subjected to hypoxic conditions showed an ability to adjust to the lack of oxygen in the root zone. They reported a delay and stabilization of photosynthetic capacity as a result of increased adventitious rooting and decreased cytokinin supply to the leaves.

The effect of ethylene on root and shoot growth of cuttings is not well documented. Ethylene is the only hormone that is a gas. Ethylene inhibits root, stem, and leaf elongation, along with influencing senescence of plant tissues (Moore 1991).

Propagation

Propagation conditions used with unrooted hybrid poplar cuttings are critical to the success of their rooting. Poor care and handling during propagation can limit root development in otherwise good-rooting clones. Careful propagation methods can support root growth in poor-rooting clones. Propagation of cuttings involves the following three stages: processing, storage, and pre-planting treatments.

The size and age of cuttings are important considerations during processing. Cuttings ranging from 20 to 30 cm in length and 8 to 10 mm in diameter are currently recommended. Allen and McComb (1956) reported that the percentage of cuttings rooted increased from 20 – 42 – 66 % with cuttings of 15 cm, 25 cm, and 46 cm lengths, respectively. Advantages due to cutting diameter were minimal in their study, yet increased vigor was associated with larger diameter cuttings. Dickmann et al. (1980) conducted two studies testing for cutting diameter differences with respect to survival and growth of six hybrid poplar clones. They found in both studies that survival percentage and shoot growth increased with increasing cutting diameter. Furthermore, a standard practice in poplar culture is that cuttings should be made from one year old shoots. In general, cuttings of woody plants made from older shoots express declining success (Browne et al. 1997a, 1997b, Davies and Hartmann 1988, Geneve 1993). Allen and McComb (1956) tested the rooting ability of *Populus deltoides* using cuttings that ranged in age from one to four years. They reported that the percentage of

cuttings rooted and the number of roots per cutting decreased as cutting age increased. Houle and Babeux (1993) used cuttings collected from trees of different ages to test for temporal variation in the rooting ability of *Populus balsamifera*. The range in percentage of cuttings rooted of the young clone was 59.3 – 100%. The range in percentage of cuttings rooted for the old clones was 7 – 100%.

The original position on the stool plant from which cuttings are made is another consideration during processing. There is a general trend of increasing survival and root growth from cuttings originating closer to the base of the original stool plant (Hansen and Kristensen 1990, Hartman et al. 1997). Bloomberg (1959) tested for differences in root number and root length among four regions of the original stool plant. The four regions were the top quarter of the shoot, middle two quarters of the shoot, and the bottom quarter of the shoot. Root number and root length increased from the apex to the base of the original parent shoot. Thus, he concluded that cuttings made from the bottom quarter of the original shoot should be used to increase performance of *Populus trichocarpa* cuttings. Similarly, O'Rourke (1944) used four cuttings from each parent shoot of highbush blueberry (*Vaccinium corymbosum* L.) to test whether or not parent shoot position had an effect on rooting ability of cuttings. He concluded the percentage of rooting per cutting increased from cuttings made closer to the base of the parent shoot. The rooting percentages ranged from 6% (apex) to 66% (base). Fege and Brown (1984) evaluated carbohydrate distribution in dormant hybrid poplar cuttings and found higher levels associated with cuttings made from basal portions of the original stool plant. Higher contents of total carbohydrates are often associated with increased survival and root system production.

The time of year when cuttings are collected is another consideration during processing (Nanda and Anand 1970). Cuttings need a chilling period and rest stage in order to break bud dormancy properly (Kester 1970). Chandler and Thielges (1973) tested the effects of chilling period duration from 0 – 90 days on breaking bud dormancy in *Populus deltoides*. They concluded that chilling periods are required for the break of bud dormancy. The time of bud break following exposure to warm temperatures and duration of chilling period are inversely related. Cunningham and Farmer (1984) assessed the performance of cuttings made at different stages of dormancy from fall to spring. They evaluated the relationship of dormancy status to rooting ability in *Populus balsamifera* cuttings. They

concluded cuttings made after December, following break of bud dormancy, had greater rooting potential than those collected before chilling requirements had been met. The range of percentage of cuttings rooted and root number per cutting for October collections through April collections was 43 – 88% and 1.6 – 4.0, respectively. Allen and McComb (1956) reported that cuttings from shoots collected in March outperformed those collected in November and December. The percentage of cuttings rooted was 61%, 32%, and 97% for November, December, and March collections, respectively. Farmer (1966) reported that *P. deltoides* cuttings collected in February expressed higher percentages of cuttings rooted than those collected in December, January, or March. Furthermore, collection of cuttings too late in the growing season reduces their growth potential. Houle and Babeux (1993), in subarctic Quebec, collected *Populus tremuloides* monthly from May (before bud break) through October in order to test for temporal variation in the species' rooting ability. They found that cuttings collected before bud break (May) or shortly thereafter had higher percentages of root production, and higher root number and length than those collected later in the growing season.

Cuttings of woody perennial species can be stored in polyethylene bags just above freezing for about one year without significant reduction in growth potential (Snyder and Hess 1956). Likewise, hybrid poplar cuttings should be stored for less than six months at temperatures between 3 °C and 7 °C. Longer time periods require storage at subfreezing temperatures. Phipps et al. (1983) tested for differences in root and shoot growth in three hybrid poplar clones after one year storage at -7 °C. They concluded that after long-term storage at subfreezing temperatures, cuttings should be subjected to a warming period of at least two weeks at 3 °C, then soaked in water until root emergence. Humidity levels during storage are also important. Shugert (1989) suggests storing cuttings at 90% humidity.

The most common pre-planting treatment is to soak cuttings in water for a specified time period until roots begin to initiate. Soaking cuttings is especially important if soil moisture levels are low during or directly following planting. Hansen and Phipps (1983) and Phipps et al. (1983) conducted extensive tests of soaking effects on early survival and growth of hybrid poplar cuttings. Soaked cuttings outperformed those not soaked for percentage of cuttings flushed and shoot length. The optimal duration of soaking for their set of clones was 9 – 11 days in water temperature of 16 °C. Yet they pointed out that duration was clone

specific, and therefore it was best to soak until the point of root emergence. Phipps et al. (1983) also concluded that soaking 20 cm cuttings in 15 cm of water improved root length and root dry weight over soaking cuttings at a depth of 3 cm. Allen and McComb (1956) planted *Populus deltoides* cuttings in five different soil moisture regimes ranging from below field capacity to saturated. They found that the percentage of cuttings rooted (0 – 80%) and the number of roots per cutting (2 – 20) increased with increasing soil moisture up to the point of saturation. Hansen (1986) conducted tests over four years to evaluate planting date effects on survival and growth of hybrid poplar cuttings. In these studies he also compared treatments of soaking and not soaking and found a 10% increase in height growth with soaking. Petersen and Phipps (1976) tested for differences in soaking and not soaking treatments on survival and growth of three hybrid poplar clones. They concluded that soaking increased survival and shoot growth compared with not soaking. Likewise, Bloomberg (1963) reported increased root number, root length, and root dry weight with increased cutting moisture content.

Another pre-planting treatment is to immerse the base of cuttings in an auxin solution, either indoleacetic acid (IAA) or indole-n-butyric acid (IBA). Auxin is a major root-inducing hormone. Allen and McComb (1956) tested rooting ability of *Populus deltoides* as a result of IAA and IBA treatment and found that cuttings treated with IBA expressed greater number and size of roots per cutting than with IAA treatments. Overall, both auxin treatments increased the percentage of cuttings rooted and the number of roots per cutting over untreated controls. A detailed description of auxin effects on rooting is described in the physiology section above.

Root production increases when floral buds are removed before planting from cuttings made from young scions of older trees that are capable of flowering (Davies 1988). Farmer (1966) removed all flower buds from *Populus deltoides* cuttings and observed twice as many roots per cutting. He reported that debudded cuttings averaged 2.1 roots per cutting and cuttings with flower buds averaged 0.9 roots per cutting. Howard (1968) removed buds of plum (*Prunus cerasifera* Ehrh. cv. 'Myrobalan B') and apple (*Malus domestica* Borkh. cv. 'M.26') and observed higher percentage of cuttings rooted. Debudded and intact cuttings of Myrobalan B and M.26 expressed percentages of cuttings rooted of 0% versus 35%, and 29% versus 46%, respectively.

Soil

Heterogeneity of soils is an important consideration for the establishment of hybrid poplar plantations. Soil types with different chemical and physical properties often cause variable rooting responses (Heilman et al. 1994a, Hilton and Mason 1971). The effects of chemical and physical soil properties on plant growth are too extensive to be addressed in this dissertation. However, this section is provided to highlight those soil physical properties most likely to influence or impact the rooting ability of cuttings used in this study. One major difference between our plantation grown system and others across natural forest stands is that mechanical cultivation in the plantation can change the physical properties of the soil in the plow layer (Fehrenbacher et al. 1969). But this does not negate the need for consideration of soil physical properties. Soil strength, aeration, and soil moisture content are discussed below. Wiersum (1957, page 75) pointed out that it is difficult to separate the effects of these properties, as "...a dense soil is usually poorly aerated and may often contain an excess of moisture." Soil temperature also affects rooting. The final sub-section of this chapter is devoted to soil (and air) temperature effects.

Soil strength affects root growth across variable sites. Roots penetrate and deform soils during elongation. Soil strength is a measure of the ability of the soil to resist such deformation (Barley et al. 1965). Bulk density and particle size affect soil strength. Rocks and other impenetrable structures will decrease rooting potential and restrict rooting to cracks and other furrows (Wiersum 1980). Zimmerman and Kardos (1961) found significant negative correlations ($\alpha = 0.01$) between root weight and soil bulk density in soybean (*Glycine max* L.) ($r = -0.4939$) and sudangrass (*Sorghum Sudanese* Stapf.) ($r = -0.4582$). They also qualitatively documented limited penetration of roots into soils at higher bulk densities. Barley et al. (1965) reported similar findings from a study testing rooting ability of wheat (*Triticum sp.*) at three different bulk densities. They estimated an overall decrease in total root length per plant from 9.4 – 6.1 cm with increasing bulk densities from 1.5 – 1.7 g/cm³. Likewise, number of emerging roots decreased from 10.5 – 8.8 with increasing bulk densities. Aubertin and Kardos (1965a) studied the effect of pore size and rigidity of a growth medium on rooting of corn (*Zea mays* L.). When relating their results to growth in natural conditions they concluded that the roots did not grow into existing pore spaces but rather into soil particles. Thus, the roots created their own path through the soil. High levels

of soil strength impede such penetration. Wiersum (1957) concluded that roots grow into soil consisting of original pores that are smaller than the diameter of the root, as long as soil strength does not reach an impenetrable threshold.

Aeration is another consideration of root growth in heterogeneous soils. Low oxygen (O_2) availability impacts root growth because of its effect on respiration (Grable 1966). Roots developing in aerated soils are relatively longer and generally have more root hairs than those growing in low O_2 conditions. Gilman et al. (1987) evaluated the effects of soil compaction and reduced O_2 levels on the root growth of honey locust (*Gleditsia triacanthos* L.). They reported that the treatment combining compaction with reduced aeration resulted in root growth located near the soil surface and significantly ($\alpha = 0.01$) less total root length compared with treatments of only compaction or reduced aeration and the control with neither compaction nor reduced aeration. Without compaction, the total root length of the reduced aeration treatment (30.8 m) was less than that of normal aeration (36 m), yet these means were not statistically different. Aubertin and Kardos (1965b) studied the effect of aeration levels and rigidity of a growth medium on rooting of corn (*Zea mays*). They tested the following four aeration levels: 2.5% O_2 , 5% O_2 , 10% O_2 , and 21% O_2 . Root growth was consistently best at 10% O_2 and worst at 2.5% O_2 . Number of roots ranged from 174 – 909, total root length ranged from 189.4 – 757.4 cm, measured root volume ranged from 0.32 – 0.86 cc, and total root weight ranged from 11.6 – 36.8 mg.

Soil moisture content and water availability are key issues affecting root growth across variable sites. Successful rooting requires an acceptable balance between moisture content and water availability. Too much water causes conditions of poor aeration, which will reduce growth (Wiersum 1980). Lack of water will lead to desiccation and death. However, some *Populus* species exhibit drought resistance following development of a root system (Harvey and van den Driessche 1999, Strong and Hansen 1991). Tschaplinski et al. (1998) tested the drought resistance of two interspecific clones of poplar hybrids (*Populus deltoides* x *P. nigra* 'DN') and (*P. trichocarpa* x *P. deltoides* 'TD'). The DN clone exhibited higher levels of drought resistance than the TD clone. The DN clone allocated more carbon to the roots during periods of drought, in addition to sustaining efficient stomatal regulation. The larger root system of the DN clone was able to occupy more soil space and thus capture higher levels of available water. Rhodenbaugh and Pallardy (1993) tested three hybrid poplar

clones in their ability to grow in soils lacking and containing adequate water. Although none of the clones significantly outperformed any of the others in dry soil, they all exhibited the trend of increasing root and shoot growth with increasing soil moisture. The range of root length was 161.3 – 660.3 cm and 31.7 – 86.1 cm for moist and dry soils, respectively. The range of leaf dry weight was 0.32 – 0.93 g and 0.12 – 0.16 g for moist and dry soils, respectively.

Regardless of drought resistance mechanisms, the movement of water through the soil is very important. Movement of water is inversely related to clay content of the soil (Fehrenbacher et al. 1969, Weaver and Crist 1922). Thus, high permeability in sandy soils leads to low amounts of available water (Fehrenbacher et al. 1973). Permeability is a key issue because available soil water depends on extent and depth of the root system and unrooted cuttings must quickly develop roots to avoid desiccation. Macropores, generally defined as passageways in the soil that facilitate water drainage, can be advantageous or disadvantageous in plantation settings. Earthworm burrows, structural pores following cultivation, and cracks between soil structural units are the most common macropores in plantations. Macropores allow water to enter dense soils, improve soil aeration, and serve as sites for root growth. Yet macropores may provide too much drainage that can guide water away from surface soil, leaving this layer unwetted (Aubertin 1971). Furthermore, soils with heavy clay content get very hard and become virtually impenetrable during periodic drought conditions. The ability of the suberized root tips to grow along planes of weaknesses becomes increasingly important under these conditions (Stolzy and Barley 1968), especially when supplemental irrigation is not feasible. Pregitzer et al. (1993) tested the rooting response of trees growing in a mixed hardwood forest to water and nitrogen applied for 20 and 40 days and found the increase of available water over the 40 day duration resulted in an increase in root production. Newman (1966b) studied root growth of flax (*Linum usitatissimum* L.) at different soil water potentials. He found rooting increased at higher soil moisture content.

Temperature

Soil and air temperature affect the success of rooting from dormant cuttings, as root metabolism, which is temperature-driven, governs root growth and uptake (Wiersum 1980). Proper temperatures facilitate activity within root primordia, which support lateral and

adventitious root development (Luxova 1984). Landhäusser et al. (2001) and Wan et al. (1999) tested temperature effects on *Populus tremuloides* Michx. and concluded that root growth was inhibited at and below 5 °C. Landhäusser et al. (2002) and Wan et al. (1999) reported that the combination of cold soil temperatures and warm air temperatures may cause reduced vigor due to the lack of ability to conduct water fast enough to meet transpirational demands of the leaves and shoots. Furthermore, temperatures that are too cold reduce cell division and associated root initiation. Rooting decreases because the rate of metabolism within the cutting is not sufficient. In addition, temperatures that are too warm inhibit growth due to accelerated respiration levels that deplete stored reserves within the cutting.

DesRochers et al. (2002) evaluated coarse and fine root respiration in *Populus tremuloides* and observed increased respiration levels at higher soil temperatures. Respiration has a temperature coefficient (Q_{10}) of about two, which means that the amount of carbon dioxide (CO_2) given off doubles for every 10 °C increase in temperature. Q_{10} levels near four are reported for *Populus tremuloides* (DesRochers et al. 2002). Respiration is necessary for rooting since the cutting must release energy to facilitate growth. Yet excessive respiration levels usually result in desiccation and death of the cutting (Kester 1970, Preece 1993).

Photosynthesis is a process that complements respiration. During photosynthesis light energy, water, and CO_2 are converted into chemical products such as sugars, fats, and proteins the cutting needs in order to grow and develop. Two reactions occur in this process. First, light energy is converted to chemical energy in a photochemical reaction. Second, chemical energy is converted into the usable products mentioned above via a dark reaction. Yet, unlike photosynthesis, respiration will continue at night (Raven et al. 1992). Excessive night temperatures will cause the cutting to deplete its reserves more rapidly (Preece 1993). The success of the cutting depends on the balance between respiration and photosynthesis (Kester 1970).

Generally accepted air temperature thresholds for optimum root growth include 18 – 32 °C day and 5 – 15 °C night (Dykeman 1976, Hartmann et al. 1997, Preece 1993). Although rooting takes place at soil temperatures below 10 °C (Domisch et al. 2001, Fennell et al. 1990, Landhäusser et al. 2002, Pavel and Fereres 1998), successful rooting is sustained at soil temperatures above this threshold (Hansen 1986, Jenkinson 1980, Landhäusser et al.

2001, Wan et al. 1999). Kester (1970) states that the 24-hour minimum temperatures very often govern rooting.

Root growth from cuttings involves preinitiation, initiation, and development (Haissig and Davis 1994). Dykeman (1976) and Preece (1993) stated that root initiation is a function of root primordia formation and rate of cell division. Root development includes cell elongation, differentiation, and cell division. They conjectured that two optimum temperatures govern total root growth. According to this model, root growth requires a brief period of warm temperatures for initiation followed by a sustained period of cooler temperatures for elongation. Dykeman (1976, page 202) cited another study (Versluys 1927) where the highest level of root initiation was at 27 °C and subsequent root elongation took place best at 17 °C. Dykeman (1976) tested the rooting ability of *Chrysanthemum* cuttings, which can withstand higher temperatures. He grew the cuttings in humid air and applied the following four temperature treatments: 1) 22 °C and 35 °C; 2) 30 °C and 35 °C; 3) 25 °C and 30 °C; and 4) 25 °C, 30 °C, and 35 °C until emergence, then 25 °C. He concluded the optimal temperature for root initiation, quick emergence, and greater number of roots per cutting was 30 °C. Subsequent root elongation, diameter growth, root hair development, and secondary branching occurred at 25 °C. Roots developed at 35 °C but quickly dessicated and died. Cuttings subjected to 22 °C survived but were smaller and fewer in number. Hilton and Mason (1971) reported another pattern of root growth. They observed that root responses of mugo pine (*Pinus mugho* Turra) lagged 2 – 5 days behind temperature extremes.

Rooting Study Methods

Rooting is one of the most biologically and economically important plant traits. Without roots plants die and when plants die money is lost. Four common root functions are identified: anchorage, absorption, storage, and conduction (Esau 1977, Kolek 1974, Raven et al. 1992). Roots act as a source of nutrients and as a sink of carbon and nutrients (Black et al. 1998, Tschaplinski and Blake 1994). Despite their obvious necessity to the plant, root systems have not been studied as much as aboveground growth parameters due to limited efficiency of sampling procedures (Carlson 1965, Friend et al. 1991, Lauenroth and Whitman 1971). Belowground growth is relatively less explored because of extensive commitments of time, money, and resources necessary for statistically sound experimentation. Primary factors affecting efficiency of rooting study methods include, but are not limited to, root width, root

length, root surface area, root structure, soil texture, soil moisture, and soil temperature (Yorke 1968). Given these constraints, it is often necessary to conduct rooting trials in a greenhouse. Extending such results to field performance is difficult, but attempts have been made (Cook and Millar 1946). Traditional rooting study methods and common rooting parameters studied are described below.

Destructive Sampling

The most common destructive sampling method of young root systems is excavating, washing, and collecting roots. Excavation is often conducted with a spade or spade-like tool. Riemenschneider and Bauer (1997) and Zalesny et al. (2000) used common garden spades to excavate hybrid poplar cuttings. Blaser (1937) used an iron straight-edged tool to make a rectangular opening in the soil and then a beveled-edged hinged tool to remove the sample from the opening. Auger sampling is also conducted. Schuurman and Goedewaagen (1971) described a common soil corer consisting of a 15 cm cylinder connected to an auger shaft with a handle. Many revisions of this design exist. In addition, excavation is conducted using pinboards. A general pinboard method consists of digging a soil pit, inserting a pinboard into the soil profile, and cutting the soil away from the board (Oliveira et al. 2000).

Many studies have been developed to identify more efficient root washing methods. Lauenroth and Whitman (1971) used a system involving a set of sieves and a bucket. Roots are removed from soil particles after being washed through both sieves. McKell et al. (1961) used a root-flotation method where roots separate from soil particles onto a screen. Likewise, Heilman et al. (1994a) used a system of sieving, floating, and sorting fine and coarse roots of hybrid poplar. Fribourg (1953) used metal straps to secure soil samples between two trays. He then immersed the trays into a drum of water and placed them into a platform below overhead sprinklers. The washing process was finished after one hour under the sprinklers.

Mapping root systems *in situ* is also conducted (Yorke 1968). Bohm (1979) described excavating one side of the plant and carefully removing soil in a direction parallel to the roots to preserve the extent and distribution of the original root system. The root system is then photographed for characterization and permanent record (Shultz and Biswell 1955). Reicosky et al. (1970) used photographs for root length estimation of destructively sampled soybean plants. Collecting soil cores and separating roots is another method of testing the depth and distribution of root systems (Carlson 1965).

Improvements in computer systems and related technologies have supported digital image analysis systems that are more efficient, precise, and repeatable than manual methods of estimating dimensions and numbers (Bignami and Rossini 1996, Kaspar and Ewing 1997, Kershaw and Larsen 1992, Kokko et al. 1993, Stoermer 1996). The usual protocol for rooting studies is to excavate and wash the developing plant, dissect or leave the plant intact, capture an image (digitally via digital camera or desktop scanner, or on some type of high quality tape) of the desired growth parts, and estimate dimensions and numbers from the images with a properly calibrated computer software program. Images captured on high quality tape may need to be converted to digital format before subjecting them to image analysis. Grayscale images are preferred because thresholding is more efficient than with color images. Thresholding of color images requires adjustment of red, green, and blue channels and is much more subjective and time-consuming than grayscale thresholding. Most imaging programs have some type of data export function that establishes a hyperlink with common spreadsheet software. The data are automatically transferred from the imaging software to the spreadsheet (Richner et al. 2000, Russ 1995). A camera-based, digital image analysis system connected to a computer was used in this dissertation research.

Although inference from image analysis requires some caution (Onyango et al. 1997), image analysis systems have been used for a broad range of applications and continue to show exceptional promise in the plant sciences. Dickmann et al. (1996) used minirhizotron tubes to capture images of fine roots of two hybrid poplar clones. They used a computer-based image analysis system with the computer software program ROOTS to estimate number, length, condition (dead or alive), and color of roots. Coleman et al. (1996) also used ROOTS to collect data from images acquired using minirhizotron tubes. Heilman et al. (1994a) measured lengths of fine and coarse hybrid poplar roots with a computer-based, video digitizer. Wan et al. (1999) estimated root length of *Populus tremuloides* with a digital scanning system named Sigma Scan 3.0. Kaspar and Ewing (1997) used a computer software program named ROOTEDGE to estimate root length of corn (*Zea mays*), from images acquired with a desktop scanner. Compared with a manual line intersection method, their system took less time, required less worker training, and was less fatiguing to workers. Costa et al. (2001) also used a scanner-based image analysis system. They estimated root length of five agronomic species and one horticultural species using a computer software program

named WinRHIZO. Kokko et al. (1993) used a video camera to capture images of root systems in soil cores. They used a Tracor Northern 8502 image analyzer to estimate total root surface area and concluded that the method was very precise and repeatable.

Kershaw and Larsen (1992) used Optimas™, a camera-based, digital image analysis system, to capture and measure images of conifer needles. They reported Optimas™ had much lower variances between successive measurements of the same sample compared with a traditional leaf area meter. Vollenweider et al. (1994) and Dustin et al. (1994) described another camera-based image analysis system used to analyze anatomical sections in bark samples of beech (*Fagus sylvatica* L.). Their imaging software was Semper 6-Plus. They concluded their system was quick, easy, and yet very precise. Bignami and Rossini (1996) applied a non-destructive method of estimating leaf area index and plant size of woody plants. They took black and white photographs in the field, digitized the photographs, and estimated parameters with a Vidas Image Analyzer. Stoermer (1996) described an image analysis system used to identify diatoms in paleolimnology. He used a camera connected to a computer to acquire images, then used NIH Image software to conduct image analysis. Uozumi et al. (1993) used image analysis to classify celery embryos in plant somatic embryo culture. Szirmai et al. (1993) connected a microscope to a computer equipped with a frame grabber that would capture the image on a second monitor. Micronucleus frequency inside human lymphocytes was estimated.

Non-destructive Sampling

Measuring aboveground growth and relating it to root growth is a common non-destructive sampling technique. Shoot:root ratios are based on the premise that root growth is directly related to aboveground absorbing surface area (Bohm 1979, Carlson 1965). Injecting radioactive elements or minerals into the soil and testing for uptake is another method that does not involve direct observation (Bingham et al. 2000, Carlson 1965). The assumption of this technique is that root growth is directly related to surface area of uptake. Likewise, ground-penetrating radar is a non-invasive technique used to map root systems of trees across a given land area and variable soil conditions (Butnor et al. 2001, Hruska et al. 1999). Ground penetrating radar is efficient and repeated measurements are easy to conduct.

Observing roots growing in glass or Plexiglas chambers is another non-destructive sampling technique. This method is advantageous because root growth is observed and traced

throughout development (Bohm 1979, Carlson 1965, Kemp 1972). Growing plants in clear tubes is also conducted (Aubertin and Kardos 1964). The major disadvantage of these observational methods is that chamber size limits root growth and study duration and it is difficult to transfer results to field settings. Minirhizotrons allow for root observations in situ. Minirhizotrons are clear glass or plastic tubes inserted into the soil. Roots are observed at the tube-soil interface (Smit et al. 2000).

Rooting Parameters

Studies reporting rooting results with some of the parameters listed below were conducted nearly a century ago. Haissig and Davis (1994) refer to such studies about root weight (Loeb 1919a, Loeb 1919b), root length (Went 1929), and root number (Vöchting 1906). Recent studies report the use of computers equipped with image analysis software to determine root length, root number, and root surface area (Richner et al. 2000, Riemenschneider and Bauer 1997, see Chapter 3: Materials and Methods). The following literature sources contributed general information about the rooting parameters below: Atkinson (2000), Bohm (1979), Kemp (1976), Kemp (1972), Marsh (1971), Newman (1966a), Pinkas et al. (1964), Reicosky et al. (1970), Tennant (1975), Yorke (1968). Specific information is cited in the text.

Root Weight. Root weight is the most common parameter for rooting studies. Weight has been used often because of its ease of estimation before the advent of modern equipment. Weight is proportional to storage capacity and, therefore, is indicative of carbon allocation to the root system (Bengough et al. 2000). Root weight provides an estimate of root system size. Most shoot:root relation studies are based on dry weight, but other parameters may also be used (Bohm 1979).

Root Length. Root length is a very common rooting study parameter, except with extremely branched root systems. Root length provides an estimate of root system activity and size. Lengths are often measured directly. In addition, intersection methods are used to increase efficiency compared with direct measurement (Newman 1966a). For example, Reicosky et al. (1970) reported that a line intersect method is five times faster than directly measuring root length. Intersection methods estimate root length as the number of root intersections with vertical and horizontal lines of a grid.

Root Number. Root number is a common rooting study parameter. Root number provides an estimate of meristematic activity. Estimating numbers may be very efficient or very inefficient depending on the type of plant, age of plant, and experimental objectives. Oftentimes, root order is also considered.

Root Diameter. Root diameter measurements, though time consuming, are used fairly often. Root diameter provides an estimate of growth potential and response to soil conditions. A microscope or calipers are commonly used for root diameter determination. Root diameter is also estimated from root volume and length.

Root Surface Area. Root surface area is not a common parameter used for rooting studies because it is a function of other parameters (diameter and length, diameter and volume) and it is time consuming. Root surface area provides an estimate of root system size, growth potential, and response to soil conditions. Root surface areas are determined using photoelectric equipment (e.g. a leaf area meter) and various adsorption methods.

Root Volume. Root volume is a less common rooting study parameter because it is a function of other parameters. Root volume provides an estimate of root system size, growth potential, and response to soil conditions. Root volume is determined using diameter and length measurements and water displacement techniques.

CHAPTER 3: MATERIALS AND METHODS

General Information

Site Selection

Experimental plantings were established at Ames, Iowa; Waseca, Minnesota; and Westport, Minnesota (Fig. 1). Each site was chosen because of its inclusion in a *Populus* Regional Testing Program conducted in Minnesota, Iowa, Wisconsin, and Michigan since 1995 (Ames, IA; Westport, MN) and 2000 (Waseca, MN) (Riemenschneider et al. 2001). The sites were also chosen because they represent a latitudinal gradient from central Iowa to central Minnesota and a range of soil types typical of hybrid poplar plantations. Table 2 gives the soil classification and planting location of each test site.

Fig. 1. Location of experimental plantings and the stool bed planting of a multi-year experiment testing for clonal differences in rooting ability of hybrid poplar.

Table 2. Soil classification and planting location for each site in a multi-year experiment testing for clonal differences in rooting ability of hybrid poplar.

Site	Year	Soil classification	Planting location
Ames, IA	2001	Hanlon fine sandy loam	Iowa State University Moore Farm
Ames, IA	2002	Hanlon fine sandy loam ²	Iowa State University Moore Farm
Waseca, MN	2001 2002	Clarion loam (western half of planting) and Webster clay loam (eastern half of planting)	University of Minnesota Southern Research and Outreach Center
Westport, MN	2001 2002	Estherville sandy loam	Herman Rosholt Research Farm

² Based on the Story County, IA Soil Survey, four rows at the western edge of the 2002 planting may be established on Coland clay loam

Table 3. Clones within pedigrees and their origin in a multi-year experiment testing for clonal differences in rooting ability of hybrid poplar.

Pedigree	Clone	Origin
<i>P. deltoides</i> (D)	D110 D105 D117 D133	C. Mohn, University of Minnesota
(<i>P. trichocarpa</i> x <i>P. deltoides</i>) x <i>P. deltoides</i> (BC ₁)	NC13563 NC13570 NC13624 NC13649 NC13686 NC14042	D. Riemenschneider, US Forest Service
<i>P. deltoides</i> x <i>P. maximowiczii</i> (DM)	25 DM105 NC14103 NC14105 NC14106	V. Steenacker, Belgium C. Mohn, University of Minnesota and D. Riemenschneider, US Forest Service
<i>P. deltoides</i> x <i>P. nigra</i> (DN)	DN17 DN34 DN5 DN70	Euramerican hybrid, France Euramerican hybrid, experimental control (a.k.a. 'Eugenei') Euramerican hybrid, Netherlands Euramerican hybrid
<i>P. nigra</i> x <i>P. maximowiczii</i> (NM)	NM2 NM6	Germany Experimental control, Germany

Clone Selection

Clonal selections were made during December 2000 based on Regional Test Program data, prior experimental data, and availability of clonal stock. The 21 clones selected (Table 3) exhibited good growth potential and provided a broad range of rooting abilities. Material was collected from stool beds established at Hugo Sauer Nursery in Rhinelander, WI (Fig. 1). Effects of environmental preconditioning, C effects, that are often prevalent due to ramets coming from different locations within the stock plant (Farmer et al. 1989, Farmer et al. 1988, Farmer et al. 1986, Wilcox and Farmer 1968) were thought to be negligible since only one year old terminal shoots were used to make cuttings. The plot was tilled and Lorox was applied to the plot before the stool beds were planted during June 1999. The planting design was 15-tree clonal blocks at 0.6 x 0.6 m spacing. The spacing between blocks was 1.2 m. A mid-summer fertilizer application (10 – 10 – 10) was applied during July 1999, July 2000, and July 2001. Cuttings were replanted to replace 1999 mortality during June 2000 and to replace 2000 mortality during June 2001. Intensive site management took place on the stool bed during summer 1999, 2000, and 2001. Site management included hand weeding around individual trees and shallow tilling among rows in both directions. Insufficient soil moisture warranted irrigation. A nine foot woven wire fence protected the stool beds from deer and other potential outside impacts.

Stool bed material was originally cut back during January 2000. Cuttings (20 cm long) were prepared during December 2000/January 2001 and December 2001/January 2002. Cuttings that met the following quality standards were selected (Hansen et al. 1983, page 5):

1. No evidence of mechanical damage such as stripped bark, split or crushed ends, or broken or missing buds near the top of the cutting.
2. No signs of insect or disease infestation such as galls, lesions, eggs, borers, or fruiting bodies.
3. Green inner bark and no desiccated or shriveled outer bark.

A bud was left within the upper 5 cm of the cutting to be left above the soil during planting (Hansen et al. 1983, Hansen et al. 1993, Radwan et al. 1987). Cuttings were sealed and stored in the dark in polyethylene bags in a greenhouse cooler at 5 °C in Ames, IA until planting during spring 2001 and spring 2002.

Both plantings at Ames, IA and Waseca, MN were bidirectionally shallow tilled prior to planting. Both plantings at Westport, MN were shallow tilled in one direction during the preceding autumn. Cuttings were soaked in water for three days prior to planting in 2001 and 2002 (Phipps et al. 1983). There were three planting dates for each year x site combination (Table 4). Based on prior indication that soil temperature affects rooting (Zalesny et al. 2000), and recommendations to plant when soil temperature reaches 10 °C (Hansen et al. 1993, Hansen 1986), we attempted to begin planting when nighttime soil temperatures reached this threshold. However, this protocol was not maintained given erratic weather conditions, extremely fluctuating soil temperatures, and unrealistic logistics involved. Unrooted cuttings ranging in diameter (measured in the middle of the cutting) from 3 – 20 mm (mean = 8 mm) were planted using dibble bars to create a hole and then hand-packing soil around the cutting to reduce potential for air pockets (Hansen et al. 1983). Planting began at 0600 hours for each planting date. Planting and mapping took 2.5 – 4.5 hours, depending on weather conditions and number of people in the planting crew. A short-term rooting study testing for clonal differences in initial root development and a long-term study examining tree growth during establishment were planted. Site management following planting included shallow cultivation between rows and minimal hand weeding around individual trees. The plantings were not irrigated.

Table 4. Planting and harvesting dates across sites in a multi-year experiment testing for clonal differences in rooting ability of hybrid poplar.

Site	Date	Planting		Harvesting	
		2001	2002	2001	2002
Ames, IA	1	April 19	April 13	May 3	April 27
	2	April 24	April 20	May 8	May 4
	3	April 30	April 26	May 14	May 10
Waseca, MN	1	May 9	April 30	May 23	May 14
	2	May 16	May 16	May 30	May 30
	3	May 22	May 23	June 5	June 6
Westport, MN	1	May 10	April 29	May 24	May 13
	2	May 17	May 15	May 31	May 29
	3	May 21	May 22	June 4	June 5

Data Acquisition

Tree Data

Initial Root Development. Individual trees were harvested two weeks after planting. The harvesting procedure consisted of using a spade to dig a soil mass up to 65 cm in diameter and 40 cm deep around the developing cutting. A major potential source of error was loss of roots during excavation and washing (Friend et al. 1991). Yet we believe root loss was minimal since root systems were small and unbranched. Careful attention was placed on excavation. Four to six people excavated 252 cuttings in three to four hours each harvesting date. Following excavation the cuttings were washed and photographed with a computerized imaging system. Images were stored on high-resolution (High 8 format) video tape and subsequently converted to 8-bit grayscale TIFF (Tagged Image File Format) digital images. The TIFF images were analyzed with an image analysis system (Optimas™ 6.2, Optimas 1997) to determine dimensions and numbers. Leaves, stems, lateral roots, callus, and callus roots were dissected from each cutting, bagged, and oven dried to a constant weight at 70 °C for dry weight (mg) determination.

Tree growth. Tree height (cm) measured from the soil line to the apical bud was recorded each June and following leaf senescence each October.

Fig. 2 expresses plant-related dependent variables measured at each experimental stage.

Environmental Data

Environmental data were collected at 15 minute intervals throughout each growing season. HOBO® H8 Pro Series data loggers (Onset 1997) were used to record relative humidity, soil temperature, and ambient temperature. Appendix A illustrates the weather station design by Dr. A. Assibi Mahama (Iowa State University), adapted from earlier designs. Ed Bauer (US Forest Service, retired) and Adam Wiese (US Forest Service) are credited with the original design. Dr. Richard B. Hall (Iowa State University) and Ron Zalesny (Iowa State University) are credited with the first design revision.

Initial Root Development Analysis

Tree Growth Analysis

Fig. 2. Dependent variables at different stages of experimentation from an initial root development analysis and a tree growth analysis in a multi-year study testing for clonal differences in rooting ability of hybrid poplar.

Fig. 3. Field layout of a multi-year experiment testing for clonal differences in rooting ability of hybrid poplar. (A) Layout of initial root development study and tree growth study (B) Layout of tree growth study only, after rooting study trees have been harvested. Notice that randomization of dates is one of six possible arrangements. Blocks (twelve per date) run from the left to right and consist of 21 clones randomly arranged.

Experimental Design

Layout

The experimental design was randomized complete blocks with twelve blocks per planting date and one ramet per clone per block. Blocking occurred perpendicular to slope gradients, where possible (Lin et al. 1993, Nelson and Rawlings 1983). The initial root development study and tree growth study were planted adjacent to one another. Spacing was 1.2 x 2.4 m for each study, with 0.6 m between similar clones within a block until the root development study was harvested after two weeks growth (Fig. 3). Zavitkovski (1981) reported that at spacings up to 1.2 x 1.2 m, border effects up to 1.5 m exist for trees of age five and six years. Likewise, Hansen (1981) found border effects up to 3 m for three year old trees at 1.2 x 1.2 m spacing. Friend et al. (1991) report 4 m root spread for two year old trees at 1 x 1 m spacing. Therefore, we attempted to plant two border rows at each site. Spatial constraints limited the 2002 Westport, MN planting to one border row (clone NM2). However, two border rows (clones DN34 and NM2) were established at all other plantings.

Statistical Tests

The ten dependent variables evaluated in this study are listed below. Pearson correlation coefficients among all variables were estimated using PROC CORR of the Statistical Analysis System (SAS[®]) (SAS Institute Inc. 2000). I believe the rooting parameters examined very adequately explain most aspects of root system distribution from unrooted cuttings. Yorke (1968) explains that root distribution is a function of direction and extent of growth. Direction relates to growth movements and tropisms, which are not addressed in our study. However, extent of distribution, as it relates to root dry weight, is directly tested in the current study. Two components of extent are elongation and multiplication, which root length and root number, respectively, address.

1. ROOTDW	Lateral root dry weight (mg)
2. CALDW	Callus dry weight (mg)
3. TOPDW	Top dry weight (mg) = leaf dry weight + stem dry weight
4. TOTLFAR	Total leaf area (cm ²) = sum of individual leaf areas
5. MEANLFAR	Mean leaf area (cm ²) = total leaf area / leaf number
6. ROOTNUM	Root number

7. TOTRTL	Total root length (cm) = sum of individual root lengths
8. MEANRTL	Mean root length (cm) = total root length / root number
9. SRRATIO	Shoot:root ratio = top dry weight / root dry weight
10. HT	Tree height (cm) = tree height in June and October

Data were analyzed by analysis of variance according to SAS[®] (PROC GLM and PROC VARCOMP; SAS Institute Inc. 2000) on multiple year (Model I) and single year (Model II) bases assuming all random effects. Non-significant ($\alpha = 0.25$) interaction terms from the original all-effects model were pooled with the residual error term to increase precision of F-tests (Carmer et al. 1989, Carmer et al. 1969, Lorenzen and Anderson 1993). Each model and a description of its effects is given below. Tables 5 and 6 express the expected mean squares for Model I and Model II, respectively.

Planting date was originally used as an artificial classification variable that acted as a surrogate measure of soil and air temperature. Since these temperatures were recorded throughout the study, I felt it much more meaningful to use them in the analysis in lieu of planting date. Growing degree days (GDD) have been used in the plant sciences to predict growth, harvest dates, insect outbreaks, and other biological phenomena (Dunn et al. 1996, Eisensmith et al. 1980, Newman et al. 1968). GDD are defined as the average temperature in a 24-hour period minus a base temperature, where the base temperature equals a threshold that supports adequate plant growth. A commonly accepted base temperature in the North Central region is 10°C (Hansen 1986, Hansen et al. 1983, Jenkinson 1980, Wan et al. 1999). Our temperature data were converted to belowground and aboveground GDD and each combination of these values was used as a factor designated growing degree day ("G") in Model I and II.

Fisher's least significant difference (LSD) was used to compare means of main effects for both models. The LSD is an appropriate multiple comparison procedure because the factor levels are qualitative and, therefore, lack logical structure that is often associated with quantitative factor levels (Carmer et al. 1989, Nelson and Rawlings 1983, Petersen 1977). The LSD is often described as the multiple comparison procedure of choice (Carmer et al. 1989, Carmer and Walker 1985, Carmer and Walker 1982). The LSD controls comparison-wise error rate, which is defined as the probability of declaring difference

between any two means to be statistically significant when in fact it is not (Borders and Shiver 1989). Chew (1976) lists aspects of the LSD that make it desirable:

1. The LSD permits unequally replicated treatments,
2. The LSD can be used for interval estimation, and
3. The LSD is easy to apply.

Variance components were determined for both models using restricted maximum likelihood (REML) estimation in PROC VARCOMP of SAS® (SAS Institute Inc. 2000). These variance parameters were used to estimate broad-sense heritability (H), the percent of phenotypic variation among clones due to combined genetic effects, on an individual tree basis according to Fehr (1991), Hallauer and Miranda (1988), Wilcox and Farmer (1968), and Ying and Bagley (1977). The general form of the equation used to estimate H was:

$$\begin{aligned} H_{\text{general}} &= \sigma^2_{\text{genotypic}} / \sigma^2_{\text{phenotypic}} \\ &= \sigma^2_G / (\sigma^2_G + \sigma^2_{GE} + \sigma^2_E) \end{aligned}$$

Where: σ^2_G = genotypic variance attributed to genetic differences among clones

σ^2_{GE} = variance attributed to genotype x environment interaction

σ^2_E = environmental variance attributed to experimental error resulting from failure to treat each genotype similarly

Specific equations used to estimate H in this study are:

$$H_{\text{MODEL I}} = \sigma^2_C / [\sigma^2_C + (\sigma^2_{YC} + \sigma^2_{SC} + \sigma^2_{GC}) + \sigma^2_E]$$

$$H_{\text{MODEL II}} = \sigma^2_C / [\sigma^2_C + (\sigma^2_{SC} + \sigma^2_{GC}) + \sigma^2_E]$$

Where: σ^2_C = genotypic variance attributed to genetic differences among clones

σ^2_{YC} = variance attributed to year x clone interaction

σ^2_{SC} = variance attributed to site x clone interaction

σ^2_{GC} = variance attributed to growing degree day x clone interaction

σ^2_E = environmental variance attributed to experimental error

Regression analysis was used to evaluate soil and air temperature effects on rooting. Netzer and Hansen (1992) separated 37 poplar clones into two parentage groups and tested for group differences in tolerance to glyphosate. Likewise, Heilman et al. (1994b) separated 79 poplar clones into three parentage groups and tested for rooting differences among groups. For the regression analysis of this study, clones were grouped according to pedigree (Table 3), and growth functions were fit to the data. I believe recommendations based on pedigrees are most useful for researchers and producers since pedigrees have greater potential of long-term availability than specific clones.

Belowground GDD were used instead of aboveground GDD because soil temperature was much more stable than air temperature and I believe soil temperature has the most dramatic affect on rooting given the need for temperature-driven initiation of root primordia and utilization of stored reserves within the cutting. Least-squares regression analysis was used to examine the relationship between soil GDD and each rooting parameter. Linear and quadratic terms were fit to the data and the choice of appropriate model was determined according to significance of an F-test with the addition of the quadratic term (Neter et al. 1996). All quadratic terms were non-significant. Thus, simple linear regression models were fit to the data. MEANRTLГ was used in the analysis because of relatively higher coefficients of determination and because extent of root penetration into the soil is crucial for uptake of water and nutrients. Appendix B provides the simple linear models predicting ROOTDW, ROOTNUM, and TOTRTLГ for each pedigree, along with derived statistics. The analysis of MEANRTLГ is described in the text.

Principal component analyses according to SAS® (PROC PRINCOMP; SAS Institute Inc. 2000) were used to assess genotype x environment interactions on single-year and multi-year bases (Manly 1986).

Model I

$$Y_{ijklmn} = \mu + Y_i + S_j + YS_{ij} + G_{(ij)k} + B_{(ijk)l} + C_m + YC_{im} + SC_{jm} + GC_{(ij)km} + E_{(ijklm)n}$$

Where:

Y_{ijklmn} = response variable to be analyzed from n^{th} experimental unit

μ = overall mean

Y_i = main effect of i^{th} year (RANDOM)

S_j = main effect of j^{th} site (RANDOM)

YS_{ij} = effect of 2-way interaction between i^{th} year and j^{th} site

$G_{(ij)k}$ = main effect of k^{th} growing degree day estimation nested within i^{th} year and j^{th} site (RANDOM)

$B_{(ijk)l}$ = main effect of l^{th} block nested within i^{th} year and j^{th} site and k^{th} growing degree day estimation (RANDOM)

C_m = main effect of m^{th} clone (RANDOM)

YC_{im} = effect of 2-way interaction between i^{th} year and m^{th} clone

SC_{jm} = effect of 2-way interaction between j^{th} site and m^{th} clone

$GC_{(ij)km}$ = effect of 2-way interaction between k^{th} growing degree day estimation nested within i^{th} year and j^{th} site and m^{th} clone

$E_{(ijklm)n}$ = pooled experimental error associated with n^{th} experimental unit, NID ($0, \sigma^2$)

Table 5. Model I (multiple year analysis) degrees of freedom and expected mean squares in an experiment testing for clonal differences in rooting ability of hybrid poplar.

Source	df	Expected mean squares ² (EMS)
Y_i	1	$\sigma^2 + 12\sigma^2GC + 108\sigma^2YC + 21\sigma^2B + 252\sigma^2G + 756\sigma^2YS + 2268\sigma^2Y$
S_j	2	$\sigma^2 + 12\sigma^2GC + 72\sigma^2SC + 21\sigma^2B + 252\sigma^2G + 756\sigma^2YS + 1512\sigma^2S$
YS_{ij}	2	$\sigma^2 + 12\sigma^2GC + 21\sigma^2B + 252\sigma^2G + 756\sigma^2YS$
$G_{(ij)k}$	12	$\sigma^2 + 12\sigma^2GC + 21\sigma^2B + 252\sigma^2G$
$B_{(ijk)l}$	198	$\sigma^2 + 21\sigma^2B$
C_m	20	$\sigma^2 + 12\sigma^2GC + 72\sigma^2SC + 108\sigma^2YC + 216\sigma^2C$
YC_{im}	20	$\sigma^2 + 12\sigma^2GC + 108\sigma^2YC$
SC_{jm}	40	$\sigma^2 + 12\sigma^2GC + 72\sigma^2SC$
$GC_{(ij)km}$	280	$\sigma^2 + 12\sigma^2GC$
$E_{(ijklm)n}$	3960	σ^2
Total	4535	

² Degrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System³ (SAS[®]).

³ SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513

Model II

$$Y_{ijklm} = \mu + S_i + G_{(ij)} + B_{(ij)k} + C_l + SC_{il} + GC_{(ij)l} + E_{(ijkl)m}$$

Where:

Y_{ijklm} = response variable to be analyzed from m^{th} experimental unit

μ = overall mean

S_i = main effect of i^{th} site (RANDOM)

$G_{(ij)}$ = main effect of j^{th} growing degree day estimation nested within i^{th} site (RANDOM)

$B_{(ij)k}$ = main effect of k^{th} block nested within i^{th} site and j^{th} growing degree day estimation (RANDOM)

C_l = main effect of l^{th} clone (RANDOM)

SC_{il} = effect of 2-way interaction between i^{th} site and l^{th} clone

$GC_{(ij)l}$ = effect of 2-way interaction between j^{th} growing degree day estimation nested within i^{th} site and l^{th} clone

$E_{(ijkl)m}$ = pooled experimental error associated with m^{th} experimental unit, NID ($0, \sigma^2$)

Table 6. Model II (single year analysis) degrees of freedom and expected mean squares in an experiment testing for clonal differences in rooting ability of hybrid poplar.

Source	df	Expected mean squares ² (EMS)
S_i	2	$\sigma^2 + 12\sigma^2GC + 36\sigma^2SC + 21\sigma^2B + 252\sigma^2G + 756\sigma^2S$
$G_{(ij)}$	6	$\sigma^2 + 12\sigma^2GC + 21\sigma^2B + 252\sigma^2G$
$B_{(ij)k}$	99	$\sigma^2 + 21\sigma^2B$
C_l	20	$\sigma^2 + 12\sigma^2GC + 36\sigma^2SC + 108\sigma^2C$
SC_{il}	40	$\sigma^2 + 12\sigma^2GC + 36\sigma^2SC$
$GC_{(ij)l}$	120	$\sigma^2 + 12\sigma^2GC$
$E_{(ijkl)m}$	1980	σ^2
Total	2267	

² Degrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System³ (SAS[®]).

³ SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513

CHAPTER 4: RESULTS AND DISCUSSION

Abbreviations

Pedigrees

BC ₁	<i>(P. trichocarpa x P. deltoides) x P. deltoides</i>
D	<i>P. deltoides</i>
DM	<i>P. deltoides x P. maximowiczii</i>
DN	<i>P. deltoides x P. nigra</i>
NM	<i>P. nigra x P. maximowiczii</i>

Dependent Variables

ROOTDW	Lateral root dry weight (mg)
CALDW	Callus dry weight (mg)
TOPDW	Top dry weight (mg) = leaf dry weight + stem dry weight
TOTLFAR	Total leaf area (cm ²) = sum of individual leaf areas
MEANLFAR	Mean leaf area (cm ²) = total leaf area / leaf number
ROOTNUM	Root number
TOTRTLGL	Total root length (cm) = sum of individual root lengths
MEANRTLGL	Mean root length (cm) = total root length / root number
SRRATIO	Shoot:root ratio = top dry weight / root dry weight
HT	Tree height (cm) = tree height in June and October

Initial Root Development Analysis

Rootability

The percentage of cuttings that rooted during 14 days of growth was highly variable, ranging across years and sites from 21.8% (D105) to 86.1% (NM6) (Fig. 4). The NM (81%) and DM (66%) pedigrees exhibited the greatest mean percentage of rooting, followed by the DN (61%) and BC₁ (57%) pedigrees. The D (33%) pedigree produced the lowest mean percentage of rooting. Overall, clonal variation within the DM, DN, and NM pedigrees was low, except for the low rooting of clone 25 in the DM pedigree. Clones of the BC₁ and D pedigrees exhibited greater variation in rooting percent. Rooting of the six BC₁ clones ranged from 38% (NC13570) to 73.1% (NC13563). Rooting of the four D clones ranged from 21.8% (D105) to 47.2% (D133).

Fig. 4. Percentage of dormant, unrooted hybrid poplar cuttings that rooted after 14 days of growth in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone.

The percentage of cuttings that rooted within years and sites ranged from 8% (D105, Ames 2001) to 100% (NM6, Ames 2002) (Fig. 5). Most clones rooted best in the Ames 2002 planting date. However, NC13570 rooted best at Westport both years. The percentage rooted generally increased from Ames to Waseca to Westport in 2001, but decreased from Ames to Waseca to Westport in 2002. Clonal rooting ability was highly variable across years and sites, which indicates that genotype x environment interactions were present. Clones of the DM, DN, and NM pedigrees showed much less variation than clones of the D and BC₁ pedigrees.

The variation in rooting success within the BC₁ pedigree is an expression of the broad genetic variation resulting from backcross breeding. Depending on recombination, genotypes of the first generation following backcrossing may have almost all alleles from the recurrent parent or half of the alleles from the recurrent parent and half of the alleles from the donor parent. Thus, I conjecture that clones such as NC13563 that exhibit very high rooting percentages have acquired alleles associated with rooting from the donor parent. Likewise, clones such as NC13570 that have poor rooting most likely have more alleles from the *Populus deltoides* parent, which is known for excellent growth rates and disease resistance, but has poor rooting ability.

Establishment success of cuttings is related to rooting ability such that increased initial rooting supports higher rates of establishment and subsequent survival. Therefore, rooting may be used as an initial selection criterion for clonal performance. These results corroborate those of Riemenschneider and Bauer (1997) and Tschaplinski and Blake (1989) who also related root initiation and growth with early production. However, the rooting percent among clones in this study is lower than other poplar studies reported. Farmer et al. (1989) cite that 53 of 100 clones belonging to four provenances of *Populus balsamifera* exhibited 100% rooting, while only two clones had less than 50% rooting. The range in provenance means was 88 – 94%. Cunningham and Farmer (1984) tested whether *P. balsamifera* cuttings collected at different times of the year affected rooting. They report rooting ranging from 13 – 100%, with an overall mean of 70%. The primary reason for lower rooting percentages in our study is that the cuttings were planted in three contrasting field sites, where they were subjected to changing environmental conditions such as soil and air temperature, soil moisture, solar radiation, wind, and soil properties such as texture and

Fig. 5. Percentage of dormant, unrooted hybrid poplar cuttings that rooted after 14 days of growth at 3 sites and over 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with 2 pedigrees in A.) and 3 pedigrees in B.). Standard error bars represent one standard error of the mean, $n=36$ cuttings for each clone.

fertility. In contrast, the studies described in the preceding paragraphs were conducted under near-ideal conditions in growth chambers or greenhouses, where environmental conditions were controlled. However, controlled conditions do not always produce greater rooting success. Farmer (1966) made cuttings from ten open-grown ortets and observed lower rooting than in our present study. Rooting of his *Populus deltoides* cuttings ranged from 21 – 63%.

Moreover, another reason for lower rooting percentages in our study may be the shorter time of growth. Farmer (1966), Cunningham and Farmer (1984) and Farmer et al. (1989) grew their cuttings for 28 days before harvesting. I used a 14-day harvesting schedule because I did not want the root systems to get too large given error associated with loss of roots during excavation and the high amount of time it takes to harvest each cutting. June survival of trees across years and sites in this study (see *Tree Growth Analysis* section below) ranged from 72% (D105) – 100% (NM6) (Fig. 22). Thus, when using June survival as a surrogate measure of rooting, results of this study are as good or better than others reported.

Trait Correlations

Clone-mean correlations ranged from -0.10 to 0.89 (Table 7). Correlations among all traits were highly significant (CALDW-SRRATIO ($P=0.0094$); ROOTNUM-SRRATIO ($P=0.0013$); all others ($P<0.0001$)). The correlation between MEANRTL and SRRATIO was the only non-significant correlation ($P=0.9155$) among traits. Belowground traits were more highly correlated with other belowground traits than with aboveground traits. The interrelationships among traits suggests that a few dependent variables can be used to explain the variation in rooting ability among genotypes. Our results corroborate those of Riemenschneider and Bauer (1997), who also found very high correlations among root dry weight, root length, and root number. Analyses of variance below compare the variation of all traits across years.

Multiple Year Evaluation (Model I)

Genotypic Effects. Clones varied greatly in ROOTDW, TOPDW, and SRRATIO, accounting for high amounts of variation in each of these traits (Table 8). The percent of total variation in ROOTDW, TOPDW, and SRRATIO was 8, 27, and 5%, respectively. Broad-sense heritability estimates are 0.09, 0.31, and 0.06 for ROOTDW, TOPDW, and SRRATIO, respectively. These estimates are lower than those previously reported. However, most

Table 7. Clone-mean correlations² (*r*) among above- and below-ground growth traits in an experiment testing for differences in rooting ability among 21 hybrid poplar clones across two years (2001, 2002) and three sites (Ames, IA; Waseca, MN; Westport, MN). Significant *P*-values are in bold. Descriptions of traits are in the text.

	CT-DW	ROOT-DW	CAL-DW	TOP-DW	TOT-LFAR	MEAN-LFAR	ROOT-NUM	TOT-RTL	MEAN-RTL	SR-RATIO
CTDW		0.24 <0.0001	0.22 <0.0001	0.60 <0.0001	0.46 <0.0001	0.45 <0.0001	0.24 <0.0001	0.20 <0.0001	0.22 <0.0001	0.16 <0.0001
ROOTDW			0.13 <0.0001	0.38 <0.0001	0.41 <0.0001	0.40 <0.0001	0.80 <0.0001	0.89 <0.0001	0.61 <0.0001	-0.10 <0.0001
CALDW				0.29 <0.0001	0.24 <0.0001	0.19 <0.0001	0.11 <0.0001	0.11 <0.0001	0.14 <0.0001	0.04 0.0094
TOPDW					0.86 <0.0001	0.77 <0.0001	0.40 <0.0001	0.36 <0.0001	0.41 <0.0001	0.24 <0.0001
TOTLFAR						0.88 <0.0001	0.44 <0.0001	0.41 <0.0001	0.42 <0.0001	0.15 <0.0001
MEANLFAR							0.44 <0.0001	0.41 <0.0001	0.43 <0.0001	0.16 <0.0001
ROOTNUM								0.87 <0.0001	0.52 <0.0001	-0.05 0.0013
TOTRTL									0.67 <0.0001	-0.09 <0.0001
MEANRTL										-0.002 0.9155
SRRATIO										

²Pearson correlation coefficients generated using "PROC CORR" of the Statistical Analysis System (SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

previous studies estimated heritability based on smaller sample sizes and growth in an environmentally controlled setting (Farmer et al. 1988, Riemenschneider and Bauer 1997, Wilcox and Farmer 1968).

Analyses of variance indicate that clones differed significantly with respect to ROOTDW, TOPDW, and SRRATIO ($P < 0.0001$) (Table 8). ROOTDW ranged from 1 (D105) to 11.5 mg (NC13563) (Fig. 6). NC13563 and NC13649 exhibited at least twice as much ROOTDW as all other clones. DN and NM clones expressed less variation than those of other pedigrees. The BC₁ pedigree expressed the most variation among clones (1.9 – 11.5 mg). TOPDW ranged from 32.3 (D105) to 145.8 mg (NM6) (Fig. 7). Trends in TOPDW differed from those observed with ROOTDW. The DM pedigree almost doubled and the NM pedigree more than doubled the aboveground production of all other pedigrees. Clonal variation within pedigrees was low except for DM.

Table 8. Analysis of variance, variance components, and derived statistics in an experiment testing for differences in root dry weight (mg), top dry weight (mg), and shoot:root ratio among 21 hybrid poplar clones across two years (2001, 2002) and three sites (Ames, IA; Waseca, MN; Westport, MN). Significant *P*-values are in bold. G= soil growing degree days associated with planting date.

Source of variation	df ^z	Mean square	F variance-ratio	P-value	Variance component ^y	Percent of total variation	Heritability ^x
ROOTDW							
Year (Y)	1	0.60	0.03	0.8858	0	0	$\sigma^2_G = 58.36$
Site (S)	2	40.98	1.83	0.3504	14.8	1.94	$\sigma^2_P = 642.24$
YS	2	22.16	1.16	0.3459	0	0	H= 0.09
G	12	19.09	7.86	<0.0001	65.1	8.55	
Block/YSG	198	1.36	2.57	<0.0001	39.5	5.18	
Clone (C)	20	14.78	6.77	<0.0001	58.4	7.66	
YC	20	1.90	1.77	0.0233	7.6	1.00	
SC	40	1.35	1.26	0.1451	3.9	0.51	
GC	280	1.07	2.04	<0.0001	45.5	5.97	
Error	3960	0.53			527.0	69.18	
Total	4535				762.0	100.00	
TOPDW							
Year (Y)	1	81.27	0.34	0.6130	0	0	$\sigma^2_G = 1.34$
Site (S)	2	63.69	0.28	0.7791	0	0	$\sigma^2_P = 4.32$
YS	2	223.96	2.19	0.1551	0.04	0.76	H= 0.31
G	12	102.49	14.12	<0.0001	0.38	7.67	
Block/YSG	198	6.84	2.46	<0.0001	0.19	3.92	
Clone (C)	20	309.70	14.71	<0.0001	1.34	27.11	
YC	20	20.14	6.29	<0.0001	0.16	3.17	
SC	40	4.13	1.29	0.1246	0.01	0.26	
GC	280	3.20	1.15	0.0471	0.04	0.71	
Error	3960	2.78			2.78	56.40	
Total	4535				4.93	100.00	
SRRATIO							
Year (Y)	1	175922	37.61	0.0425	61.96	0.63	$\sigma^2_G = 527.17$
Site (S)	2	162475	13.21	0.0020	79.00	0.80	$\sigma^2_P = 9502.68$
YS	2	4025	0.10	0.9048	0	0	H= 0.06
G	12	39881	3.03	0.0008	85.60	0.87	
Block/YSG	198	12359	1.41	0.0002	170.11	1.72	
Clone (C)	20	132397	7.15	<0.0001	527.17	5.33	
YC	20	10257	1.07	0.3833	6.05	0.06	
SC	40	17874	1.86	0.0021	114.87	1.16	
GC	280	9604	1.09	0.1457	68.09	0.69	
Error	3960	8787			8786.50	88.76	
Total	4535				9899.39	100.00	

^zDegrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System (SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

^yRestricted Maximum Likelihood (REML) estimates of variance components.

^xBroad-sense heritability estimated on an individual tree basis (H), with σ^2_G = genotypic variance attributed to combined genetic effects of clone (σ^2_C); and σ^2_P = variance attributed to phenotypic effects, where phenotype = genotype + (genotype x environment) + environment [$\sigma^2_C + (\sigma^2_{YC} + \sigma^2_{SC} + \sigma^2_{GC}) + \sigma^2_E$].

Fig. 6. Root dry weight (mg) of dormant, unrooted hybrid poplar cuttings after 14 days of growth across 3 sites and 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone.

Fig. 7. Top dry weight (mg) of dormant, unrooted hybrid poplar cuttings after 14 days of growth across 3 sites and 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone.

The allometric relationship between shoot growth and root growth is very important for developed trees with adequate root and shoot systems (Barlow 1960, Harris 1914). A feedback loop exists whereby roots simultaneously depend on the shoot for assimilate and provide the shoot with hormones (Wiersum 1980). The initial presence of leaf emergence before an adequate root system is developed may deplete the cutting of stored reserves and lead to death. Shoot:root ratios affect the water balance and distribution of photosynthate among plant parts within the developing tree (Pallardy and Kozlowski 1979). Likewise, shoot:root ratios affect transpiration rates (Parker 1949). With respect to these cuttings, allocation of resources to leaves and shoots takes place the prior year during bud formation on the parent shoot. The leaves are ready for expansion following bud break the next spring when the cutting is planted. In contrast, root initiation takes place *de novo* from preformed and induced primordia (and from callus, which is negligible here). Therefore, considering SRRATIO a comparison of resources apportioned to aboveground and belowground biomass production during the 14 days of growth is not correct. However, SRRATIO does provide insight into relative rooting variation among pedigrees. SRRATIO ranged from 11.12 (D) to 70.94 (NM) (Fig. 8). Thus, the D pedigree partitioned relatively more resources to root growth than the NM and DM pedigrees, but still exhibited greater leaf and shoot expansion relative to root growth. These results corroborate those of Drew and Bazzaz (1978) who tested for SRRATIO differences in three *P. deltoides* provenances. They found that the northern Wisconsin provenance apportioned more growth to aboveground parts and the two southern sources (Illinois, Louisiana) expressed more belowground growth. The D clones of this study are of northern origin (Minnesota). There was also broad variation among clones with respect to SRRATIO. Clonal allometric ratios ranged from 4.9 (NC13563) to 77.4 (DM105) (Fig. 9). The BC₁ pedigree expressed the most variation among clones (4.9 – 33.4). Clones of the D pedigree were more similar than those within any other pedigree. NC13563 had the lowest SRRATIO, greatest ROOTDW, ROOTNUM, TOTRTLG, and MEANRTLG, and did not maintain vigorous aboveground growth rates throughout the growing season. In contrast, NM2 and NM6 had exceptional early aboveground growth, sustained adequate root growth to support the increasing top demand, and exhibited the best height growth following one growing season. Allometric ratios of DN34 were between that of NC13563 and the NM clones. The conservative nature of DN34 allowed it to survive, but not to sustain aggressive

Fig. 8. Shoot:root ratio of dormant, unrooted hybrid poplar cuttings after 14 days of growth across 3 sites and 2 years in an experiment testing 5 pedigrees in their ability to develop roots and shoots. Standard errors and number of experimental units for each pedigree are as follows: BC1: SE=1.66, n=1296; D: SE=1.25, n=864; DM: SE=4.37, n=1080; DN: SE=2.47, n=864; NM: SE=7.18, n=432.

root or shoot growth. OCTHT of DN34 expressed this conservative nature, as NC13563 and the NM clones outperformed DN34 (Table 30; Fig. 28).

Furthermore, clones were significantly different with respect to ROOTNUM ($P<0.0001$), TOTRTLGL ($P<0.0001$), and MEANRTLGL ($P=0.0016$) (Table 9). ROOTNUM ranged from 0.7 (D105) to 6.7 (NC13563) (Fig. 10). ROOTNUM of NC13563 was almost twice as much as all other clones, except NC13649 (5.8), NM6 (4.7), and NC13686 (4.1). D133 (3.1) more than doubled the ROOTNUM of D110 (1.2) and D117 (1.2), and D133 more than tripled the ROOTNUM of D105 (0.7). The BC₁ pedigree expressed the most variation among clones (1.2 – 6.7). TOTRTLGL ranged from 1.2 (D105) to 15.5 cm (NC13563) (Fig. 11). Trends in TOTRTLGL were similar to those observed with ROOTDW and ROOTNUM. NC13563 and NC13649 (13.5) nearly doubled the TOTRTLGL of all other clones. NC13570 (2.4) and NC13624 (2.3) exhibited very poor root growth. D133 (6.1) had excellent root growth despite belonging to a poor-rooting pedigree. MEANRTLGL ranged

Fig. 9. Root:shoot ratio of dormant, unrooted hybrid poplar cuttings after 14 days of growth across 3 sites and 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone.

Table 9. Analysis of variance in an experiment testing for differences in root number, total root length (cm), and mean root length (cm) among 21 hybrid poplar clones across two years (2001, 2002) and three sites (Ames, IA; Waseca, MN; Westport, MN). Significant *P*-values are in bold. G = soil growing degree days associated with planting date.

Source of variation	df ²	Mean square	F variance-ratio	P-value
ROOTNUM				
Year (Y)	1	561.56	0.88	0.4390
Site (S)	2	548.34	0.91	0.5247
YS	2	607.25	1.07	0.3725
G	12	565.67	12.41	<0.0001
Block/YSG	198	29.86	2.55	<0.0001
Clone (C)	20	551.93	11.47	<0.0001
YC	20	55.27	2.02	0.0070
SC	40	20.27	0.74	0.8759
GC	280	27.42	2.34	<0.0001
Error	3960	11.70		
Total	4535			
TOTRTLG				
Year (Y)	1	428.21	0.20	0.6991
Site (S)	2	7994.96	3.63	0.2040
YS	2	2120.07	0.55	0.5911
G	12	3857.87	12.41	<0.0001
Block/YSG	198	192.02	2.40	<0.0001
Clone (C)	20	2888.50	8.29	<0.0001
YC	20	264.26	1.33	0.1592
SC	40	282.86	1.42	0.0551
GC	280	198.80	2.48	<0.0001
Error	3960	80.00		
Total	4535			
MEANRTL				
Year (Y)	1	12.19	0.31	0.6284
Site (S)	2	117.87	3.25	0.2390
YS	2	36.66	0.74	0.4978
G	12	49.56	14.91	<0.0001
Block/YSG	198	2.56	2.09	<0.0001
Clone (C)	20	22.23	4.60	0.0016
YC	20	5.27	2.65	0.0002
SC	40	1.55	0.78	0.8315
GC	280	1.99	1.63	<0.0001
Error	3960	1.22		
Total	4535			

²Degrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System (SAS® Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

Fig. 10. Root number of dormant, unrooted hybrid poplar cuttings after 14 days of growth across 3 sites and 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone.

Fig. 11. Total root length (cm) of dormant, unrooted hybrid poplar cuttings after 14 days of growth across 3 sites and 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone.

from 0.4 (D105) to 1.5 cm (NC13563) (Fig. 12). MEANRTLGL of NC13563 and NC13649 was at least 50% greater than all other clones except NM2 and NM6. Once again, clones of the BC₁ pedigree expressed the most variation (0.7 – 1.5).

Variation in root number may have been the result of differences among clones in their ability to develop preformed root primordia throughout the parent shoot during the preceding growing season. Good-rooting clones may have developed an abundance of preformed primordia, while poor-rooting clones may have relatively fewer preformed primordia. For example, the greater number of roots in specific clones of the BC₁ and NM pedigrees compared with the others may be due to an increased number of preformed primordia dispersed throughout the cutting. *P. deltoides* does not root well from dormant, unrooted cuttings. Other than D133, ROOTNUM of other D clones was well below the overall mean. Therefore, D clones may simply not have as many preformed primordia. Root initiation and growth from D cuttings may be the result of induced primordia, which emerge as a result of influence from environmental stimuli. This is reflected in the June survival rate of the D clones in the tree growth study (78%) (Figs. 22 – 23). About one month separated the harvest of short-term cuttings and measuring of long-term trees. The advantage of other pedigrees over the D clones in the initial root development analysis is much less at the end of June than during the initial rooting. Thus, I conjecture that rooting of the D pedigree was primarily from induced primordia that developed some time after 14 days, although there is no way of proving this given the methodology and primary objectives of this study. Poor root production from clone 25, NC13570, and NC13624 may also be the result of fewer root primordia throughout the cutting, despite greater root production from other clones within their pedigrees. I assume there is a high correlation between number of preformed primordia and root number, given significantly high correlations among all other belowground traits. Another consideration is the distribution of primordia along the parent shoot. In other words, there may be more primordia located near the base of the parent shoot than near the apex, and therefore rooting may be the result of where the cutting came from on the parent shoot. A general trend of increasing survival and root growth from cuttings originating closer to the base of the original stool plant has been reported (Bloomberg 1959, Hansen and Kristensen 1990, Hartman et al. 1997).

Fig. 12. Mean root length (cm) of dormant, unrooted hybrid poplar cuttings after 14 days of growth across 3 sites and 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone.

Variation in rooting may have also been the result of differences in utilization of soluble carbohydrates available in the cutting. NC13563 exhibited very high rooting, with low shoot:root ratios, yet height growth at the end of the season was average at best. Thus, NC13563 may continuously utilize more reserves for rooting and therefore reduce its ability to sustain vigorous growth rates following establishment. These results agree with Wu et al. (1998). They report that an inbred F₂ generation of poplar (*Populus trichocarpa* x *P. deltoides*) exhibited a broad amount of variation resulting in varying rooting success. Those genotypes that had the best rooting did not necessarily have the best growth rates. In addition, large cuttings made from the base of the parent shoot may have more available reserves than those made from the apex of the parent shoot. Thus, rooting may also be due to the quantity of available reserves in addition to how fast such reserves are utilized. Fege and Brown (1984) found greater quantities of carbohydrates in the cuttings made from the base portion of the parent shoot.

Analyses of variance also indicate that clones differed significantly for CALDW, TOTLFAR, and MEANLFAR ($P < 0.0001$) (Table 10). CALDW ranged from 0 (D105, NC13624) to 3.8 mg (NM2) (Fig. 13). CALDW had the most variation of all traits examined. Callus production of the D clones was limited. In contrast, NM clones produced a relatively high amount of callus. Nevertheless, trends in CALDW do not appear to be related to pedigree. Rather, callus production appears to be clone-specific. Only 15 callus roots were produced across all clones each season. Thus, adventitious rooting from callus was negligible in this study. Farmer et al. (1989) cite similar results from an experiment testing the genetic variance in rooting of *Populus balsamifera*. They conjectured that most roots emerged from preformed primordia, and a limited number of callus roots developed from the base of the cutting. The lack of callus and callus root formation in our study is most likely due to the short growing period (14 days) and soil temperatures that are not conducive to callus differentiation. I believe, based on the limited callus formation in this study and the lack of testing above 88 soil GDD per 14-day growing period, that a higher soil temperature optimum exists for callus root production than is necessary for lateral root initiation.

TOTLFAR ranged from 1.4 (D105) to 11.1 cm² (NM2) (Fig. 14). The NM and DM pedigrees exhibited greater TOTLFAR than other pedigrees. The NM clones nearly tripled the TOTLFAR of all other clones except those belonging to the DM pedigree. Clones within

Table 10. Analysis of variance in an experiment testing for differences in callus dry weight (mg), total leaf area (cm²), and mean leaf area (cm²) among 21 hybrid poplar clones across two years (2001, 2002) and three sites (Ames, IA; Waseca, MN; Westport, MN). Significant *P*-values are in bold. G= growing degree days associated with planting date.

Source of variation	df ²	Mean square	F variance-ratio	<i>P</i> -value
<i>CALDW</i>				
Year (Y)	1	0.452	5.06	0.0245
Site (S)	2	0.206	2.85	0.0581
YS	2	0.060	0.61	0.5605
G	12	0.099	3.79	<0.0001
Block/YSG	198	0.012	1.26	0.0089
Clone (C)	20	0.304	5.45	<0.0001
YC	20	0.044	2.99	<0.0001
SC	40	0.027	1.83	0.0026
GC	280	0.015	1.59	<0.0001
Error	3960	0.009		
Total	4535			
<i>TOTLFAR</i>				
Year (Y)	1	5774.01	11.46	0.0113
Site (S)	2	720.48	2.79	0.2525
YS	2	248.65	0.18	0.8377
G	12	1383.76	16.13	<0.0001
Block/YSG	198	67.14	2.63	<0.0001
Clone (C)	20	2013.62	6.51	<0.0001
YC	20	299.54	6.78	<0.0001
SC	40	53.93	1.22	0.1797
GC	280	44.15	1.73	<0.0001
Error	3960	25.50		
Total	4535			
<i>MEANLFAR</i>				
Year (Y)	1	58.53	2.10	0.2529
Site (S)	2	27.52	1.14	0.4658
YS	2	23.97	0.69	0.5182
G	12	34.50	16.04	<0.0001
Block/YSG	198	1.80	3.22	<0.0001
Clone (C)	20	58.68	11.91	<0.0001
YC	20	4.76	5.25	<0.0001
SC	40	1.07	1.18	0.2232
GC	280	0.91	1.62	<0.0001
Error	3960	0.56		
Total	4535			

²Degrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System (SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

Fig. 13. Callus dry weight (mg) of dormant, unrooted hybrid poplar cuttings after 14 days of growth across 3 sites and 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone.

Fig. 14. Total leaf area (cm²) of dormant, unrooted hybrid poplar cuttings after 14 days of growth across 3 sites and 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone.

pedigrees expressed fairly consistent leaf production. The DM pedigree had the most variation ($6.1 - 9.6 \text{ cm}^2$). MEANLFAR ranged from 0.2 (D105) to 1.9 cm^2 (NM6) (Fig. 15). NM and DM clones expressed the highest MEANLFAR. Other trends were similar to those shown for TOTLFAR.

Site Effects. Site effects were negligible for ROOTDW, TOPDW, and SRRATIO, accounting for no more than 2% of the variation in any of these traits (Table 8). The percent of total variation in ROOTDW, TOPDW, and SRRATIO was 2, 0, and 1%, respectively. Analyses of variance indicate that differences among sites were not significant with respect to ROOTDW ($P=0.3504$) and TOPDW ($P=0.7791$). However, there were significant differences among sites for SRRATIO ($P=0.0020$). According to Fisher's protected least significant difference ($\alpha=0.05$, $n=1512$ for each site, $LSD=6.7$), Ames (S:R=22.5) was significantly different from Waseca (S:R=39.8) and Westport (S:R=41.1). Waseca and Westport were not significantly different from each other. Site effects were also negligible for all remaining traits: ROOTNUM ($P=0.5247$), TOTRTLGL ($P=0.2040$), MEANRTLGL ($P=0.2390$), CALDW ($P=0.0581$), TOTLFAR ($P=0.2525$), and MEANLFAR ($P=0.4658$) (Tables 9 and 10).

Genotype x Environment Interactions. Growing degree days represent a means of classifying belowground and aboveground air temperature into heat units that affect plant growth. Year, site, and growing degree days define the environment in this analysis. Genotype x environment (G x E) interactions were highly variable across all traits. Analyses of variance indicate that the year x clone interaction was significant for ROOTDW ($P=0.0233$), TOPDW ($P<0.0001$), ROOTNUM ($P=0.0070$), MEANRTLGL ($P=0.0002$), CALDW ($P<0.0001$), TOTLFAR ($P<0.0001$), and MEANLFAR ($P<0.0001$) (Tables 8-10). The year x clone interaction was negligible with respect to SRRATIO ($P=0.3833$) and TOTRTLGL ($P=0.1592$) (Tables 8-9). The site x clone interaction was significant for SRRATIO ($P=0.0021$) and CALDW ($P=0.0026$), borderline significant for TOTRTLGL ($P=0.0551$), but negligible for ROOTDW ($P=0.1451$), TOPDW ($P=0.1246$), ROOTNUM ($P=0.8759$), MEANRTLGL ($P=0.8315$), TOTLFAR ($P=0.1797$), and MEANLFAR ($P=0.2232$) (Tables 8-10). The growing degree day x clone interaction was significant for ROOTDW ($P<0.0001$), ROOTNUM ($P<0.0001$), TOTRTLGL ($P<0.0001$), MEANRTLGL ($P<0.0001$), TOPDW ($P=0.0471$), CALDW ($P<0.0001$), TOTLFAR ($P<0.0001$), and

Fig. 15. Mean leaf area (cm²) of dormant, unrooted hybrid poplar cuttings after 14 days of growth across 3 sites and 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone.

MEANLFAR ($P < 0.0001$), but this interaction was negligible for and SRRATIO ($P = 0.1457$) (Tables 8-10). Clone-mean correlations among all sites with respect to ROOTDW, ROOTNUM, TOTRTLG, and MEANRTLG were uniformly significant ($P < 0.0001$) (Fig. 16). Correlations among sites for ROOTDW were the most variable, ranging from 0.81 between Ames and Waseca to 0.94 between Ames and Westport. Nevertheless, significance of correlations among all sites for each trait suggests stable clonal performance across sites. Principal component analyses corroborate our univariate interpretation of variance in the four rooting traits (Table 11). Principal component 1 loaded highly uniformly on all traits at each site, with associated eigenvalues accounting for at least 92% of the variation. The single year evaluation (MODEL II) below addresses these G x E interactions, along with genotypic and site effects, in more detail.

Single Year Evaluation (Model II)

Wilcox and Farmer (1968) found very high correlations among rooting parameters and concluded that each trait would be equally useful in testing the rooting ability of clones. Given the similar nature of and high correlations among traits examined in the multiple year evaluation (Model I) (Table 7), the single year evaluation (Model II) described below graphically examines effects based on ROOTDW, TOPDW, and SRRATIO. Using these traits as representatives of belowground and aboveground growth reduces redundancy in presentation of these data. Results of analyses of variance of all other traits are given.

Genotypic Effects. Clones varied greatly in ROOTDW, TOPDW, and SRRATIO for the 2001 and 2002 growing season. Clones accounted for high amounts of variation in each of these traits. The percent of total variation during 2001 of ROOTDW, TOPDW, and SRRATIO was 10, 31, and 6%, respectively (Table 12). Broad-sense heritability estimates in 2001 were 0.11, 0.32, and 0.06 for ROOTDW, TOPDW, and SRRATIO, respectively. Likewise, the percent of total variation during 2002 of ROOTDW, TOPDW, and SRRATIO was 7, 30, and 5%, respectively (Table 13). Broad-sense heritability estimates in 2002 were 0.09, 0.38, and 0.06 for ROOTDW, TOPDW, and SRRATIO, respectively.

Analyses of variance indicate that clones differed significantly in 2001 and 2002 with respect to ROOTDW, TOPDW, and SRRATIO ($P < 0.0001$) (Tables 12 and 13). ROOTDW in 2001 ranged from 0.4 (D117-Ames; D110-Westport) to 12.2 mg (NC13649-Waseca) (Table 14; Fig. 17). ROOTDW in 2002 ranged from 0.2 (NC13570-Waseca; clone 25-

Fig. 16. Clone-mean correlations among three sites (Ames, IA; Waseca, MN; Westport, MN) with respect to A.) root dry weight (mg), B.) root number, C.) total root length (cm), and D.) mean root length (cm) in an experiment testing 21 hybrid poplar clones in their ability to develop roots and shoots from dormant, unrooted cuttings ($n=21$). Correlations significant at $P<0.0001$ level.

Table 11. Eigenvectors and eigenvalues of principal component analyses of root dry weight (mg), root number, total root length (cm), and mean root length (cm) across two years and three sites in an experiment testing five hybrid poplar pedigrees in their ability to develop roots and shoots from dormant, unrooted cuttings.

<i>Root dry weight (mg)</i>	
Site	Eigenvector
	Principal component 1
Ames	0.5780
Waseca	0.5628
Westport	0.5909
Eigenvalue (Cumulative Percent)	2.75 (92%)
<i>Root number</i>	
Site	Eigenvector
	Principal component 1
Ames	0.5769
Waseca	0.5720
Westport	0.5831
Eigenvalue (Cumulative Percent)	2.86 (95%)
<i>Total root length (cm)</i>	
Site	Eigenvector
	Principal component 1
Ames	0.5750
Waseca	0.5722
Westport	0.5848
Eigenvalue (Cumulative Percent)	2.81 (94%)
<i>Mean root length (cm)</i>	
Site	Eigenvector
	Principal component 1
Ames	0.5777
Waseca	0.5793
Westport	0.5750
Eigenvalue (Cumulative Percent)	2.83 (94%)

Table 12. Analysis of variance, variance components, and derived statistics in an experiment testing for differences in root dry weight (mg), top dry weight (mg), and shoot:root ratio among 21 hybrid poplar clones across three sites (Ames, IA; Waseca, MN; Westport, MN) during the 2001 growing season. Significant *P*-values are in bold. G= soil growing degree days associated with planting date.

Source of variation	df ²	Mean square	F variance-ratio	<i>P</i> -value	Variance component ^y	Percent of total variation	Heritability ^x
ROOTDW							
Site (S)	2	0.39	0.30	0.7527	0	0.00	$\sigma^2_G = 75.56$
G	6	1.37	7.06	<0.0001	39.83	5.30	$\sigma^2_P = 704.73$
Block/SG	99	0.07	1.24	0.0567	6.84	0.91	H= 0.11
Clone (C)	20	0.92	17.09	<0.0001	75.56	10.06	
SC	40	0.05	0.45	0.9977	0	0.00	
GC	120	0.12	2.02	<0.0001	36.68	4.88	
Error	1980	0.06			592.50	78.85	
Total	2267				751.41	100.00	
TOPDW							
Site (S)	2	32.67	0.71	0.5301	0	0.00	$\sigma^2_G = 1.57$
G	6	46.86	11.52	<0.0001	0.16	3.05	$\sigma^2_P = 4.92$
Block/SG	99	4.11	1.22	0.0720	0.036	0.71	H= 0.32
Clone (C)	20	173.00	69.66	<0.0001	1.57	30.76	
SC	40	2.48	0.75	0.8532	0	0.00	
GC	120	3.32	0.99	0.5225	0	0.00	
Error	1980	3.36			3.34	65.48	
Total	2267				5.11	100.00	
SRRATIO							
Site (S)	2	100334	2.08	0.2027	68.87	1.09	$\sigma^2_G = 380.02$
G	6	47000	8.15	<0.0001	160.12	2.52	$\sigma^2_P = 6117.85$
Block/SG	99	4774	0.84	0.8629	0	0.00	H= 0.06
Clone (C)	20	48959	6.18	<0.0001	380.02	5.99	
SC	40	7918	1.19	0.2339	35.22	0.55	
GC	120	6650	1.18	0.0999	86.11	1.36	
Error	1980	5659			5616.50	88.49	
Total	2267				6346.84	100.00	

²Degrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System (SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

^yRestricted Maximum Likelihood (REML) estimates of variance components.

^xBroad-sense heritability estimated on an individual tree basis (H), with σ^2_G = genotypic variance attributed to combined genetic effects of clone (σ^2_C); and σ^2_P = variance attributed to phenotypic effects, where phenotype = genotype + (genotype x environment) + environment [$\sigma^2_C + (\sigma^2_{YC} + \sigma^2_{SC} + \sigma^2_{GC}) + \sigma^2_E$].

Table 13. Analysis of variance, variance components, and derived statistics in an experiment testing for differences in root dry weight (mg), top dry weight (mg), and shoot:root ratio among 21 hybrid poplar clones across three sites (Ames, IA; Waseca, MN; Westport, MN) during the 2002 growing season. Significant *P*-values are in bold. G= soil growing degree days associated with planting date.

Source of variation	df ²	Mean square	F variance-ratio	<i>P</i> -value	Variance component ³	Percent of total variation	Heritability ⁴
ROOTDW							
Site (S)	2	5.93	2.34	0.1726	44.93	5.73	$\sigma^2_G = 53.09$
G	6	2.45	8.26	<0.0001	87.35	11.14	$\sigma^2_P = 579.80$
Block/SG	99	0.20	4.28	<0.0001	72.09	9.19	H= 0.09
Clone (C)	20	0.75	4.27	<0.0001	53.09	6.77	
SC	40	0.18	1.77	0.0098	21.13	2.70	
GC	120	0.10	2.15	<0.0001	44.27	5.65	
Error	1980	0.05			461.30	58.83	
Total	2267				784.17	100.00	
TOPDW							
Site (S)	2	254.98	1.61	0.2750	0.13	2.67	$\sigma^2_G = 1.42$
G	6	158.12	14.49	<0.0001	0.58	12.19	$\sigma^2_P = 3.73$
Block/SG	99	9.57	4.35	<0.0001	0.35	7.32	H= 0.38
Clone (C)	20	156.83	45.30	<0.0001	1.42	29.63	
SC	40	3.46	0.98	0.5189	0	0.00	
GC	120	3.55	1.61	<0.0001	0.11	2.31	
Error	1980	2.20			2.20	45.87	
Total	2267				4.79	100.00	
SRRATIO							
Site (S)	2	66167	1.83	0.2296	39.72	0.30	$\sigma^2_G = 711.59$
G	6	32762	1.52	0.1804	44.72	0.34	$\sigma^2_P = 2848.83$
Block/SG	99	19944	1.67	<0.0001	382.36	2.87	H= 0.06
Clone (C)	20	93694	5.56	<0.0001	711.60	5.34	
SC	40	16841	1.25	0.1781	93.83	0.70	
GC	120	13464	1.13	0.1648	129.11	0.97	
Error	1980	11914			11914.30	89.48	
Total	2267				13315.62	100.00	

²Degrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System (SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

³Restricted Maximum Likelihood (REML) estimates of variance components.

⁴Broad-sense heritability estimated on an individual tree basis (H), with σ^2_G = genotypic variance attributed to combined genetic effects of clone (σ^2_C); and σ^2_P = variance attributed to phenotypic effects, where phenotype = genotype + (genotype x environment) + environment [$\sigma^2_C + (\sigma^2_{YC} + \sigma^2_{SC} + \sigma^2_{GC}) + \sigma^2_E$].

Table 14. Mean root dry weight (mg), mean top (stem + leaf) dry weight (mg), and mean shoot:root ratio per cutting after 14 days of growth in an experiment testing 21 hybrid poplar clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002).

Clone	2001				2002				Expt-wide
	Ames	Waseca	Westport	Across sites	Ames	Waseca	Westport	Across sites	
Root dry weight (mg)									
D105	0.8	0.7	0.6	0.7	2.4	0.4	0.8	1.2	1.0
D110	1.1	0.7	0.4	0.8	4.1	1.2	2.7	2.7	1.7
D117	0.4	1.4	0.9	0.9	6.8	3.0	2.9	4.2	2.6
D133	1.7	3.9	0.9	2.2	7.5	5.4	5.2	6.1	4.1
NC13563	12.1	9.4	11.1	10.9	24.4	7.9	4.3	12.2	11.5
NC13570	2.8	2.4	2.8	2.7	2.7	0.2	0.5	1.2	1.9
NC13624	2.9	1.4	1.4	1.9	2.8	1.0	1.7	1.8	1.9
NC13649	11.2	12.2	9.4	10.9	11.8	7.0	4.6	7.8	9.4
NC13686	7.5	4.1	7.0	6.2	9.8	2.7	1.9	4.8	5.5
NC14042	2.9	2.2	2.8	2.6	8.5	1.9	1.9	4.1	3.4
25	1.0	1.8	1.1	1.3	3.1	0.2	0.4	1.3	1.3
DM105	4.6	4.1	1.9	3.5	7.1	1.4	1.1	3.2	3.4
NC14103	4.9	3.4	1.6	3.3	3.4	1.0	1.8	2.0	2.7
NC14105	6.8	9.9	4.0	6.9	5.9	2.4	2.0	3.4	5.2
NC14106	8.1	3.7	4.0	5.2	8.2	2.3	2.3	4.3	4.8
DN17	3.4	5.0	2.7	3.7	7.2	2.0	2.2	3.8	3.8
DN34	3.1	3.8	0.9	2.6	7.3	2.5	2.7	4.2	3.4
DN5	5.3	5.7	4.5	5.2	11.7	5.0	5.0	7.2	6.2
DN70	5.9	7.6	4.1	5.9	7.7	5.2	2.4	5.1	5.5
NM2	5.4	5.7	4.4	5.2	8.8	5.7	2.9	5.8	5.5
NM6	5.3	7.1	4.1	5.5	9.2	7.4	3.0	6.5	6.0
Mean	4.6	4.6	3.4	4.2	7.6	3.1	2.5	4.4	4.3
Top dry weight (mg)									
D105	25.2	34.5	28.9	29.5	55.3	31.3	18.8	35.1	32.3
D110	22.2	34.8	41.8	32.9	46.3	27.6	32.1	35.3	34.1
D117	13.0	38.6	35.6	29.1	57.6	32.3	28.1	39.3	34.2
D133	27.2	41.0	35.9	34.7	52.5	48.7	32.8	44.7	39.7
NC13563	42.0	45.6	44.2	43.9	30.8	27.1	14.4	24.1	34.0
NC13570	46.4	65.8	73.0	61.7	58.2	37.4	36.2	43.9	52.8
NC13624	67.6	83.4	75.8	75.6	71.8	42.4	24.6	46.3	61.0
NC13649	58.7	68.7	67.1	64.8	42.5	36.6	24.6	34.6	49.7
NC13686	52.8	71.2	68.8	64.3	55.5	26.0	16.5	32.7	48.5
NC14042	63.6	68.6	77.4	69.8	99.6	43.8	40.4	61.3	65.6
25	103.8	152.9	133.7	130.1	101.2	69.7	80.0	83.6	106.9
DM105	114.7	119.6	107.5	113.9	146.4	108.0	96.2	116.9	115.4
NC14103	107.7	113.6	113.1	111.5	110.3	53.8	55.5	73.2	92.3
NC14105	150.2	161.9	132.9	148.3	141.6	116.3	101.4	119.8	134.1
NC14106	127.3	106.7	112.2	115.4	160.1	102.0	94.8	119.0	117.2
DN17	50.2	55.4	66.5	57.4	104.2	61.2	64.1	76.5	66.9
DN34	53.4	67.0	65.9	62.1	83.3	65.3	58.0	68.9	65.5
DN5	59.3	87.9	76.5	74.5	96.1	80.2	60.4	78.9	76.7

Table 14. (continued)

DN70	41.8	60.5	57.4	53.2	74.2	57.2	44.2	58.5	55.9
NM2	147.8	147.0	150.7	148.5	163.3	139.0	114.4	138.9	143.7
NM6	131.9	147.5	139.7	139.7	163.9	157.3	134.5	151.9	145.8
Mean	71.7	84.4	81.2	79.1	91.2	64.9	55.8	70.6	74.9
<i>Shoot:root ratio</i>									
D105	2.2	22.3	2.8	9.1	14.8	10.7	8.6	11.4	10.2
D110	2.2	11.4	12.4	8.7	7.4	7.1	15.1	9.9	9.3
D117	1.8	10.5	6.6	6.3	7.1	32.4	9.6	16.3	11.3
D133	4.1	20.8	11.0	12.0	19.7	15.5	10.8	15.3	13.7
NC13563	6.1	5.0	4.5	5.2	4.3	5.1	4.2	4.5	4.9
NC13570	4.1	16.3	41.3	20.6	36.2	25.6	19.1	27.0	23.8
NC13624	21.7	31.1	18.7	23.8	32.9	27.3	9.6	23.3	23.6
NC13649	6.4	13.7	9.8	10.0	8.7	3.2	20.4	10.7	10.4
NC13686	8.4	35.7	10.3	18.1	11.3	15.1	15.4	13.9	16.0
NC14042	14.8	32.3	44.0	30.4	18.6	63.5	27.2	36.4	33.4
25	28.4	77.4	93.7	66.5	40.8	54.2	116.6	70.5	68.5
DM105	22.9	60.0	108.7	63.8	51.8	106.0	115.0	91.0	77.4
NC14103	31.3	39.6	57.3	42.7	56.1	110.3	35.0	67.1	54.9
NC14105	24.1	66.9	50.3	47.1	81.9	125.9	65.9	91.2	69.2
NC14106	26.4	32.6	35.4	31.4	43.3	79.1	86.2	69.5	50.5
DN17	19.1	13.0	17.2	16.5	31.7	67.1	45.8	48.2	32.3
DN34	10.9	27.4	31.3	23.2	25.8	58.6	53.4	45.9	34.6
DN5	8.2	17.8	20.2	15.4	20.0	16.5	24.9	20.5	18.0
DN70	5.4	21.8	13.2	13.4	13.8	30.4	37.5	27.2	20.3
NM2	41.5	54.6	111.0	69.0	35.6	55.8	144.1	78.5	73.8
NM6	27.8	80.9	71.1	59.9	66.6	72.8	89.5	76.3	68.1
Mean	15.1	32.9	36.7	28.3	29.9	46.8	45.4	40.7	34.5

Fig. 17. Root dry weight (mg) of dormant, unrooted hybrid poplar cuttings after 14 days of growth at 3 sites and 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=36 cuttings for each clone.

Waseca) to 24.4 mg (NC13563-Ames) (Table 14; Fig. 17). NC13563 exhibited at least twice as much ROOTDW as all other clones, given very high productivity in Ames 2002. However, ROOTDW of NC13649 was comparable at all other sites and dates. DN and NM clones expressed less variation than those of other pedigrees. The DM pedigree expressed lower variation than the D and BC₁ pedigrees, despite poor root growth of clone 25. The BC₁ pedigree expressed the most variation among clones (1.4 – 12.2 mg-2001; 0.2 – 24.4 mg-2002). TOPDW in 2001 ranged from 13 (D117-Ames) to 161.9 mg (NC14105-Waseca) (Table 14; Fig. 18). TOPDW in 2002 ranged from 14.4 (NC13563-Westport) to 163.9 mg (NM6-Ames) (Table 14; Fig. 18). The DM and NM pedigrees exhibited the greatest TOPDW. NC13563 expressed TOPDW similar to D clones and allocated more resources to belowground biomass production than aboveground growth. SRRATIO was highly variable across clones. SRRATIO in 2001 ranged from 1.8 (D117-Ames) to 111 (NM2-Westport) (Table 14; Fig. 19). SRRATIO in 2002 ranged from 3.2 (NC13649-Waseca) to 144.1 (NM2-Westport) (Table 14; Fig. 19). SRRATIO was greatest in the DM and NM pedigrees and least in the D and BC₁ pedigrees. However, three BC₁ clones allocated a moderate amount of resources to the shoot and leaves compared with the roots. The SRRATIO of NC13570, NC13624, and NC14042 is double that of the other BC₁ clones. Analyses of variance indicate significant clone main effects ($P < 0.0001$) during 2001 and 2002 with respect to ROOTNUM, TOTRTLG, MEANRTLG, CALDW, TOTLFAR, and MEANLFAR (Tables 15 – 18).

Site Effects. Site effects were negligible for ROOTDW, TOPDW, and SRRATIO. Sites accounted for no more than 1% of variation in each of these traits during 2001 (Table 12) and no more than 6% during 2002 (Table 13). The percent of total variation in ROOTDW, TOPDW, and SRRATIO during 2001 was 0, 0, and 1%, respectively. The percent of total variation in ROOTDW, TOPDW, and SRRATIO during 2002 was 6, 3, and 0.3%, respectively. Analyses of variance indicate that sites were not significantly different in 2001 with respect to ROOTDW ($P = 0.7527$), TOPDW ($P = 0.5301$), and SRRATIO ($P = 0.2027$). Likewise, sites were not significantly different in 2002 with respect to ROOTDW ($P = 0.1726$), TOPDW ($P = 0.2750$), and SRRATIO ($P = 0.2296$). Site effects were also negligible for all remaining traits: ROOTNUM (2001: $P = 0.9338$; 2002: $P = 0.2847$), TOTRTLG (2001: $P = 0.6972$; 2002: $P = 0.2063$), MEANRTLG (2001: $P = 0.7017$;

Fig. 18. Top dry weight (mg) of dormant, unrooted hybrid poplar cuttings after 14 days of growth at 3 sites and 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=36 cuttings for each clone.

Fig. 19. Shoot:root ratio of dormant, unrooted hybrid poplar cuttings after 14 days of growth at 3 sites and 2 years in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=36 cuttings for each clone.

Table 15. Analysis of variance in an experiment testing for differences in root number, total root length (cm), and mean root length (cm) among 21 hybrid poplar clones across three sites (Ames, IA; Waseca, MN; Westport, MN) during the 2001 growing season. Significant *P*-values are in bold. G= soil growing degree days associated with planting date.

Source of variation	df ²	Mean square	F variance-ratio	<i>P</i> -value
ROOTNUM				
Site (S)	2	28.21	0.07	0.9338
G	6	411.62	15.30	<0.0001
Block/SG	99	16.86	1.62	0.0001
Clone (C)	20	264.88	16.82	<0.0001
SC	40	15.75	0.77	0.8264
GC	120	20.43	1.97	<0.0001
Error	1980			
Total	2267			
TOTRTL				
Site (S)	2	1314.17	0.39	0.6972
G	6	3545.73	14.99	<0.0001
Block/SG	99	105.30	1.32	0.0218
Clone (C)	20	1602.27	20.86	<0.0001
SC	40	76.81	0.36	0.9998
GC	120	211.15	2.64	<0.0001
Error	1980	79.92		
Total	2267			
MEANRTL				
Site (S)	2	22.50	0.38	0.7017
G	6	60.91	21.24	<0.0001
Block/SG	99	1.96	1.24	0.0572
Clone (C)	20	19.35	1.57	<0.0001
SC	40	1.28	15.13	0.9912
GC	120	2.49	0.51	0.0001
Error	1980	1.58		
Total	2267			

²Degrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System (SAS® Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

Table 16. Analysis of variance in an experiment testing for differences in callus dry weight (mg), total leaf area (cm²), and mean leaf area (cm²) among 21 hybrid poplar clones across three sites (Ames, IA; Waseca, MN; Westport, MN) during the 2001 growing season. Significant *P*-values are in bold. G= soil growing degree days associated with planting date.

Source of variation	df ^a	Mean square	F variance-ratio	P-value
<i>CALDW</i>				
Site (S)	2	0.22	1.50	0.2223
G	6	0.14	4.35	0.0002
Block/SG	99	0.01	1.02	0.4283
Clone (C)	20	0.26	10.70	<0.0001
SC	40	0.02	1.13	0.2971
GC	120	0.02	1.89	<0.0001
Error	1980	0.01		
Total	2267			
<i>TOTLFAR</i>				
Site (S)	2	350.18	0.55	0.6032
G	6	627.47	10.80	<0.0001
Block/SG	99	52.24	1.50	0.0012
Clone (C)	20	1718.22	33.74	<0.0001
SC	40	50.92	1.26	0.1742
GC	120	40.56	1.17	0.1081
Error	1980	34.72		
Total	2267			
<i>MEANLFAR</i>				
Site (S)	2	7.47	0.54	0.6074
G	6	13.66	9.99	<0.0001
Block/SG	99	1.24	1.80	<0.0001
Clone (C)	20	43.46	45.50	<0.0001
SC	40	0.96	1.17	0.2542
GC	120	0.82	1.18	0.0906
Error	1980	0.69		
Total	2267			

^aDegrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System (SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

Table 17. Analysis of variance in an experiment testing for differences in root number, total root length (cm), and mean root length (cm) among 21 hybrid poplar clones across three sites (Ames, IA; Waseca, MN; Westport, MN) during the 2002 growing season. Significant *P*-values are in bold. G= soil growing degree days associated with planting date.

Source of variation	df ¹	Mean square	F variance-ratio	<i>P</i> -value
ROOTNUM				
Site (S)	2	1127.37	1.56	0.2847
G	6	719.73	11.54	<0.0001
Block/SG	99	42.87	3.29	<0.0001
Clone (C)	20	342.32	9.11	<0.0001
SC	40	37.59	1.16	0.2712
GC	120	32.52	2.50	<0.0001
Error	1980	13.02		
Total	2267			
TOTRTL				
Site (S)	2	8800.86	2.04	0.2063
G	6	4170.02	10.36	<0.0001
Block/SG	99	278.74	3.48	<0.0001
Clone (C)	20	1550.49	4.39	<0.0001
SC	40	353.01	1.73	0.0121
GC	120	203.73	2.54	<0.0001
Error	1980	80.09		
Total	2267			
MEANRTL				
Site (S)	2	132.02	3.42	0.1007
G	6	38.21	9.90	<0.0001
Block/SG	99	3.15	3.64	<0.0001
Clone (C)	20	8.15	4.05	<0.0001
SC	40	2.01	1.28	0.1560
GC	120	1.57	1.82	<0.0001
Error	1980	0.87		
Total	2267			

¹Degrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System (SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

Table 18. Analysis of variance in an experiment testing for differences in callus dry weight (mg), total leaf area (cm²), and mean leaf area (cm²) among 21 hybrid poplar clones across three sites (Ames, IA; Waseca, MN; Westport, MN) during the 2002 growing season. Significant *P*-values are in bold. G= soil growing degree days associated with planting date.

Source of variation	df ²	Mean square	F variance-ratio	P-value
<i>CALDW</i>				
Site (S)	2	0.0447	0.78	0.4564
G	6	0.0538	2.61	0.0160
Block/SG	99	0.0115	1.66	<0.0001
Clone (C)	20	0.0858	6.99	<0.0001
SC	40	0.0123	1.34	0.1127
GC	120	0.0091	1.32	0.0130
Error	1980	0.0069		
Total	2267			
<i>TOTLFAR</i>				
Site (S)	2	618.95	0.29	0.7578
G	6	2140.05	18.46	<0.0001
Block/SG	99	82.04	5.04	<0.0001
Clone (C)	20	594.94	14.93	<0.0001
SC	40	39.84	0.79	0.7965
GC	120	50.17	3.08	<0.0001
Error	1980	16.29		
Total	2267			
<i>MEANLFAR</i>				
Site (S)	2	44.01	0.80	0.4930
G	6	55.34	18.48	<0.0001
Block/SG	99	2.37	5.49	<0.0001
Clone (C)	20	19.98	23.70	<0.0001
SC	40	0.84	0.80	0.7917
GC	120	1.06	2.45	<0.0001
Error	1980	0.43		
Total	2267			

²Degrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System (SAS® Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

2002: $P=0.1007$), CALDW (2001: $P=0.2223$; 2002: $P=0.4564$), TOTLFAR (2001: $P=0.6032$; 2002: $P=0.7578$), and MEANLFAR (2001: $P=0.6074$; 2002: $P=0.4930$) (Tables 15 – 18).

Genotype x Environment Interactions. Site and growing degree days define the environment in this analysis. Genotype x environment (G x E) interactions were highly variable across all traits. The site x clone interaction during 2001 was negligible for all traits: ROOTDW ($P=0.9977$), TOPDW ($P=0.8532$), SRRATIO ($P=0.2339$), ROOTNUM ($P=0.8264$), TOTRTLGL ($P=0.9998$), MEANRTLGL ($P=0.9912$), CALDW ($P=0.2971$), TOTLFAR ($P=0.1742$), and MEANLFAR ($P=0.2542$) (Tables 12, 15 – 16). The site x clone interaction during 2002 was significant for ROOTDW ($P=0.0098$) and TOTRTLGL ($P=0.0121$), but negligible for TOPDW ($P=0.5189$), SRRATIO ($P=0.1781$), ROOTNUM ($P=0.2712$), MEANRTLGL ($P=0.1560$), CALDW ($P=0.1127$), TOTLFAR ($P=0.7965$), and MEANLFAR ($P=0.7917$) (Tables 13, 17 – 18). There was a significant growing degree day x clone interaction during 2001 for ROOTDW ($P<0.0001$), ROOTNUM ($P<0.0001$), TOTRTLGL ($P<0.0001$), MEANRTLGL ($P=0.0001$), and CALDW ($P<0.0001$), but this interaction was negligible for TOPDW ($P=0.5225$), SRRATIO ($P=0.0999$), TOTLFAR ($P=0.1081$), and MEANLFAR ($P=0.0906$) (Tables 12, 15 – 16). In addition, a significant growing degree day x clone interaction during 2002 existed for ROOTDW ($P<0.0001$), TOPDW ($P<0.0001$), ROOTNUM ($P<0.0001$), TOTRTLGL ($P<0.0001$), MEANRTLGL ($P<0.0001$), CALDW ($P=0.0130$), TOTLFAR ($P<0.0001$), and MEANLFAR ($P<0.0001$), but this interaction was negligible for SRRATIO ($P=0.1648$) (Tables 13, 17 – 18).

Therefore, in 2001 G x E interactions governed belowground growth, but aboveground growth was less affected. In contrast, G x E interactions govern belowground and aboveground growth in 2002. Changes in rank and scale of genotypic production across sites define the G x E interactions. Table 14 and Figs. 17 – 19 express the changes in rank and scale. Fig. 20 expresses the clonal rank of the top five clones at each site in both years for ROOTDW. NC13563 illustrates the rank and scale change. NC13563 ranks first in Ames 2001, third in Waseca 2001, and first in Westport 2001. The magnitude of its superiority increases from 0.9 mg in Ames 2001 to 1.7 mg in Westport 2001. The greatest change in magnitude of scale occurs in Ames 2002 when NC13563 ranks first with a 12.6 mg advantage over the second best clone (NC13649). This advantage decreases to 0.5 mg in Waseca 2002. NC13563 ranked fourth in Westport 2002. A detailed evaluation of G x E

Fig. 20. Root dry weight (mg) of the best 5 clones at 3 sites and 2 years in an experiment testing 21 hybrid poplar clones in their ability to develop roots and shoots from dormant, unrooted cuttings. n=108 cuttings for each clone.

interactions was conducted given the very poor root growth at Westport 2002. Clonal performance at Westport 2002 suggested that clones may have responded differently to that site (Fig. 20). Principal component analyses supported this interpretation (Table 19). Principal component 1 loaded highly on ROOTDW, TOTRTLG, and MEANRTLG for all site x year combinations except for Westport 2002. Principal component 2 loaded highly on ROOTDW, TOTRTLG, and MEANRTLG at Westport 2002, but weakly on other year x site combinations. Principal component 1 loaded highly uniformly on ROOTNUM for each year x site combination. Therefore, I conclude that clonal performance was stable over all year x site combinations, except for Westport 2002 where root growth was relatively very poor. The lack of production from the Westport 2002 planting was most likely due to residual herbicide impact. Prior application of herbicide to the site was not known before planting.

I believe soil temperature and moisture (as expressed by precipitation events) were major factors promoting and inhibiting root growth at all sites. Since harvest took place 14 days after planting, the cuttings were not subjected to long-term environmental effects. Initial growth most likely depended on the existence of preformed root primordia throughout the cutting, reserves of carbohydrates stored in the cutting, and how the cutting responded to environmental stimuli such as soil temperature and moisture. Evaluation of the G x E interactions was difficult since I did not know exactly when during the 14 days of growth the roots initiated and emerged from the cuttings. However, assessment of the influence (or impact) of thermal units and moisture on the development of the newly planted cutting provided crucial information to the understanding of root initiation and development across variable environmental and geographic thresholds. The analysis below focuses on the link between accumulation of heat units, moisture, and rooting ability of the cuttings.

Soil Temperature and Moisture Evaluation

Belowground growing degree days (GDD) accumulated over each 14-day growing period ranged from 0 – 88. Despite our initial hypothesis that GDD increases with increasing planting date, belowground and aboveground temperatures were very erratic throughout the study. Minimum soil temperatures at a depth of 20 cm often varied up to 4 °C in a 24-hour period (Appendix C). The differential between aboveground GDD and belowground GDD was highly variable at each site early in the growing season but stabilized as soil temperatures below 20 cm increased. A trend relating root production with the

Table 19. Eigenvectors and eigenvalues of principal component analyses of root dry weight (mg), root number, total root length (cm), and mean root length (cm) across two years and three sites in an experiment testing five hybrid poplar pedigrees in their ability to develop roots and shoots from dormant, unrooted cuttings.

<i>Root dry weight (mg)</i>		
Site / year	Eigenvector	Eigenvector
	Principal component 1	Principal component 2
Ames 2001	0.4175	-0.4402
Waseca 2001	0.4123	-0.1897
Westport 2001	0.4306	-0.3594
Ames 2002	0.4228	0.0499
Waseca 2002	0.4201	0.3700
Westport 2002	0.3391	0.7083
Eigenvalue (Cumulative Percent)	4.50 (75%)	0.85 (89%)
<i>Root number</i>		
Site / year	Eigenvector	Eigenvector
	Principal component 1	Principal component 2
Ames 2001	0.3970	0.4940
Waseca 2001	0.4179	0.1473
Westport 2001	0.4067	0.4838
Ames 2002	0.4222	-0.1465
Waseca 2002	0.4075	-0.4543
Westport 2002	0.3976	-0.5218
Eigenvalue (Cumulative Percent)	4.90 (82%)	0.58 (91%)
<i>Total root length (cm)</i>		
Site / year	Eigenvector	Eigenvector
	Principal component 1	Principal component 2
Ames 2001	0.4243	-0.3818
Waseca 2001	0.4273	-0.0967
Westport 2001	0.4208	-0.3914
Ames 2002	0.4207	-0.0719
Waseca 2002	0.4162	0.3633
Westport 2002	0.3317	0.7447
Eigenvalue (Cumulative Percent)	4.70 (78%)	0.80 (92%)
<i>Mean root length (cm)</i>		
Site / year	Eigenvector	Eigenvector
	Principal component 1	Principal component 2
Ames 2001	0.4427	-0.3073
Waseca 2001	0.4512	-0.2353
Westport 2001	0.4405	-0.3801
Ames 2002	0.3672	0.3530
Waseca 2002	0.4380	0.1588
Westport 2002	0.2823	0.7456
Eigenvalue (Cumulative Percent)	4.17 (69%)	0.91 (85%)

$GDD_{aboveground} - GDD_{belowground}$ differential was not evident. However, the differential may be very important for phenological events such as bud break. Further testing of the differential between aboveground GDD and belowground GDD under controlled environments is warranted. Appendix D illustrates the temperature difference between aboveground GDD and belowground GDD across Julian dates for both growing seasons.

My original hypothesis was that increasing belowground GDD would promote rooting until reaching an upper threshold associated with inhibition of root initiation. Dykeman (1976) cites that rooting from cuttings of *Chrysanthemum* had two optimum temperatures for total growth. A high temperature was required for optimal initiation and a relatively lower temperature was required for optimal elongation and development. I tested this hypothesis but my pedigrees showed no such trends in root initiation and growth.

I hypothesized that pedigree responses to the accumulation of thermal units would differ. I also believed that responses across rooting traits would be similar as high positive correlations among parameters were estimated. Least-squares regression models indicated very similar pedigree responses and near-identical predictive functions for each rooting trait (Table 20; Fig. 21; Appendix B). Simple linear models predicting MEANRTL_G for each pedigree fit the data moderately well (Fig. 21). Table 20 expresses regression coefficients and derived statistics for MEANRTL_G, which increased with increasing soil GDD for all pedigrees. Root growth did not stabilize within the limits of these data, which suggests that temperature limits inhibiting rooting were not reached.

I believe the interaction of soil temperature and moisture governed rooting of these clones. Plots of maximum and minimum soil temperatures, along with belowground GDD and precipitation events, indicated that a minimum of 4 days with at least 4 GDD are needed in order for cuttings to produce greater than average root dry weight, root number, and total root length (Appendix D). Cuttings subjected to less than four days with four GDD per day, regardless of soil moisture, did not exhibit comparable root production. However, cuttings subjected to belowground GDD satisfying this threshold also required adequate soil moisture in order to increase root initiation and growth. MEANRTL_G of the Ames 2001 planting date 2 was very low, despite having 12 days with four or more GDD and 10 days with five or more GDD (Table 21). This growing period had very low precipitation at the start. In contrast, cuttings of the Ames 2002 planting date 1 exhibited the second highest

Table 20. Regression equation coefficients and derived statistics for mean root length (cm) (MEANRTL_G) per cutting of five hybrid poplar pedigrees in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002). Pedigrees are: BC₁=(*Populus trichocarpa* x *Populus deltoides*) x *P. deltoides*; D=*P. deltoides*; DM=*P. deltoides* x *Populus maximowiczii*; DN=*P. deltoides* x *Populus nigra*; NM=*P. nigra* x *P. maximowiczii*.

Pedigree	<i>MEANRTL_G = a + b(Soil Growing Degree Days)</i>						
	n	R ²	P-value _b	a	b	P _{min} ^z	P _{max}
BC ₁	1296	0.37	0.0132	0.9854	0.0128	0.99	2.11
D	864	0.29	0.0318	0.9420	0.0108	0.94	1.89
DM	1080	0.33	0.0202	0.9254	0.0103	0.93	1.83
DN	864	0.33	0.0192	1.0613	0.0110	1.06	2.03
NM	432	0.44	0.0048	0.8328	0.0148	0.83	2.14

^zP_{min} = Predicted minimum MEANRTL_G; P_{max} = Predicted maximum MEANRTL_G

MEANRTL_G yet only had four days above the 4 and 5 GDD thresholds. Precipitation was also low during this growing period. However, the precipitation was dispersed throughout the 14 days. Many other planting dates with low to moderate precipitation had above-average MEANRTL_G when precipitation was dispersed (Table 21). For example, cuttings of the 2002 Westport date 3 planting only received 0.7 cm of precipitation during 14 days of growth. Yet MEANRTL_G was tied for the fifth best overall. There was one case where it appeared too much moisture may have inhibited rooting. The 2001 Waseca date 2 planting had 8 days with >4 GDD and 7 days with >5 GDD, along with total precipitation of 8.3 cm (Table 21). These values indicate conditions for enhanced rooting were met. However, evaluation of precipitation events shows almost all of the precipitation came in the middle of the growing period concurrently with decreasing soil temperatures (Appendix D). Thus, it appears dispersed precipitation events and daily belowground GDD accumulation at or above 4 for at least 4 days lead to greater root initiation and growth of these hybrid poplar cuttings.

Although performance was similar across pedigrees, some variation existed (Appendix E). Evaluation of the number of days with greater than 4 or 5 GDD and total precipitation showed that the D pedigree performed differently from the hybrid pedigrees with respect to MEANRTL_G. Planting dates expressing the highest MEANRTL_G of the D clones were associated with lower belowground GDD and lower precipitation compared with

Fig. 21. Mean root length (cm) versus soil growing degree days of five hybrid poplar pedigrees (listed in the figure) in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings. Each point, except for that of 33 GDD and 69 GDD (which represent 2n due to similar GDD at two site x planting date combinations) represents the mean of the following number (n) of cuttings: A.) 72, B.) 48, C.) 60, D.) 48, and E.) 24.

Fig. 21. Continued.

Fig. 21. Continued.

those of the hybrid pedigrees. For example, the 2002 Ames planting date 2 had zero days above four GDD yet the MEANRTLGL for D clones ranked fourth. In addition, the 2002 Westport planting date 2 had four days with greater than four GDD per day and three days with greater than five GDD per day, along with very low precipitation (0.5 cm), yet MEANRTLGL ranked fifth. Similar trends were apparent for other year x site x planting date combinations (Appendix E). Nevertheless, dispersed precipitation events throughout the growing period were important for the D pedigree.

Table 21. MEANRTLГ (cm), number of days with >4 and >5 growing degree days (GDD), and total precipitation across years, sites, and planting dates in an experiment testing five hybrid poplar pedigrees in their ability to develop roots and shoots from dormant, unrooted cuttings. MEANRTLГ is estimated across pedigrees, n=252 cuttings. Pedigrees are: BC₁=(*Populus trichocarpa* x *Populus deltoides*) x *P. deltoides*; D=*P. deltoides*; DM=*P. deltoides* x *Populus maximowiczii*; DN=*P. deltoides* x *Populus nigra*; NM=*P. nigra* x *P. maximowiczii*.

Rank	Year	Site	Planting date	MEAN-RTLГ (cm)	Number of days with >4 GDD	Number of days with >5 GDD	Total precip (cm)	Comments
1	2001	Ames	3	2.1	14	13	8.8	High precipitation randomly distributed throughout growth period.
2	2002	Ames	1	1.7	4	4	2.7	Low precipitation randomly distributed throughout growth period.
3	2002	Ames	3	1.6	5	4	5.3	High precipitation randomly distributed throughout growth period.
4	2001	Waseca	3	1.3	8	5	3.6	Moderate precipitation at beginning; very low precipitation throughout final nine days.
5	2001	Waseca	1	1.1	10	8	6.6	High precipitation at beginning and end; high soil temperatures.
5	2002	Westport	3	1.1	11	10	0.7	Low precipitation randomly distributed throughout growth period; high soil temperatures.
6	2002	Waseca	3	1.0	14	13	8.3	High precipitation randomly distributed throughout growth period; excess at end.
7	2001	Westport	2	0.9	7	6	5.2	High precipitation randomly distributed throughout growth period.
7	2002	Ames	2	0.9	0	0	7.3	High precipitation; inadequate soil temperatures.
8	2001	Westport	3	0.8	7	6	5.0	Low precipitation at end, very low soil temperatures at beginning.
8	2001	Westport	1	0.8	11	9	3.4	Low precipitation at beginning; high soil temperatures.
9	2001	Ames	1	0.7	8	6	4.4	Low precipitation at beginning and end; nothing in the middle.
9	2001	Waseca	2	0.7	8	7	8.3	High precipitation in middle (too much at one time?); low precipitation at beginning and end.
9	2002	Waseca	2	0.7	7	7	1.8	Low precipitation at beginning; moderate precipitation during final five days.
9	2001	Ames	2	0.7	12	10	5.6	Low precipitation at beginning.
10	2002	Westport	2	0.6	4	3	0.5	Low precipitation; inadequate throughout growing period; low soil temperatures at beginning.
11	2002	Westport	1	0.4	0	0	5.9	High precipitation; inadequate soil temperatures.
12	2002	Waseca	1	0.3	0	0	2.5	Low precipitation; inadequate soil temperatures.

Performance Relative to Commercial Standards

Although more than two commercial clones were used in this study, NM6 and DN34 were used as commercial standards. NM6 is currently the most popular commercial clone in the Lake States, and DN34 is a popular commercial clone that has also been extensively studied. The primary objective of the analysis of clones relative to NM6 and DN34 was to test whether other clones exhibited better root initiation and growth than the standards in an attempt to identify promising genotypes for further clonal testing and inclusion in future research studies. ROOTDW and TOPDW were used for this evaluation since traits were highly significantly correlated and these two parameters represent growth of other associated traits.

Performance Relative to NM6. Five clones exhibited greater ROOTDW than NM6 during the 2001 growing season (Table 22). NC13649, NC13563, NC14105, NC13686, and DN70 expressed 199, 198, 126, 112, and 107% greater ROOTDW than NM6, respectively. Three clones outperformed NM6 during the 2002 growing season. NC13563, NC13649, and DN5 had 187, 120, and 111% of growth of NM6, respectively. Three clones produced more ROOTDW across years than NM6. NC13563, NC13649, and DN5 exhibited 192, 156, and 103% growth relative to NM6. The percent advantage of the best clone's ROOTDW over NM6 at each year and site ranged from 107 (Waseca 2002) – 271% (Westport 2001) (Table 23). Likewise, the percent advantage of ROOTDW of the best three clones over NM6 at each year and site ranged from 100 (Waseca 2002) – 224% (Westport 2001). Two clones exhibited greater TOPDW than NM6 during the 2001 growing season (Table 24). NC14105 and NM2 each expressed 106% greater TOPDW than NM6. No clones outperformed NM6 during the 2002 growing season or when TOPDW is averaged across years. The percentage of the best clone's TOPDW of NM6 at each year and site ranged from 85 (Westport 2002) – 114% (Ames 2001) (Table 25). Likewise, the percent of the TOPDW of the best three clones compared to NM6 at each year and site ranged from 77 (Waseca 2002; Westport 2002) – 108% (Ames 2001).

NC13563, NC13649, and NC14105 are very promising for future use based on initial rooting. Clone NM6 ranked in the upper 25% in terms of rooting and was the best in terms of shoot and leaf production, which supports the conclusion that this clone should continue to be utilized.

Table 22. Relative growth of 19 hybrid poplar clones to commercial standards NM6 and DN34 with respect to root dry weight (mg) after 14 days of growth in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002). Greater relative growth is highlighted in bold.

Clone	<i>Percentage root dry weight relative to commercial standard</i>					
	NM6			DN34		
	2001	2002	Across years	2001	2002	Across years
D105	13.0	18.3	15.9	27.6	28.3	28.0
D110	13.9	40.8	28.5	29.3	63.2	50.2
D117	16.6	65.2	42.9	35.2	100.9	75.8
D133	39.3	93.1	68.4	83.2	144.0	120.8
NC13563	197.5	187.4	192.0	417.8	290.0	338.8
NC13570	48.4	17.7	31.8	102.4	27.4	56.1
NC13624	34.1	28.1	30.9	72.0	43.6	54.5
NC13649	199.1	119.8	156.1	421.1	185.4	275.5
NC13686	112.4	73.9	91.5	237.9	114.3	161.5
NC14042	47.3	63.3	55.9	100.0	98.0	98.7
25	23.6	19.3	21.3	49.9	29.9	37.6
DM105	64.1	49.2	56.1	135.6	76.2	98.9
NC14103	60.3	31.5	44.7	127.6	48.7	78.9
NC14105	125.5	53.1	86.3	265.5	82.1	152.2
NC14106	95.4	65.9	79.4	201.9	102.0	140.2
DN17	67.4	58.4	62.5	142.6	90.4	110.4
DN34	47.5	63.8	56.3	100.0	100.0	100.0
DN5	93.7	111.2	103.2	198.3	172.0	182.1
DN70	106.8	78.3	91.4	226.0	121.1	161.2
NM2	93.7	89.0	91.1	198.3	137.7	160.8
NM6	100.0	100.0	100.0	211.4	155.7	177.0

Table 23. Root dry weight (mg) of commercial standards NM6 and DN34 and 19 other hybrid poplar clones after 14 days of growth in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002).

	<i>Root dry weight (mg)</i>								
	2001				2002				
	Ames	Waseca	Westport	Across sites	Ames	Waseca	Westport	Across sites	Across years
Control mean (NM6)	5.3	7.1	4.1	5.5	9.2	7.4	3.0	6.5	6.0
Best clone mean	12.1	12.2	11.1	10.9	24.4	7.9	5.2	12.2	11.5
Mean of best 3 clones	10.5	10.5	9.2	9.6	15.9	7.4	5.0	9.1	9.0
Percent of best clone (%)	228.3	171.8	270.7	198.2	265.2	106.8	173.3	187.7	191.7
Percent of best 3 clones (%)	197.5	148.0	223.8	174.0	173.3	100.2	165.2	139.4	150.4
Control mean (DN34)	3.1	3.8	0.9	2.6	7.3	2.5	2.7	4.2	3.4
Best clone mean	12.1	12.2	11.1	10.9	24.4	7.9	5.2	12.2	11.5
Mean of best 5 clones	9.1	9.3	7.3	8.2	13.4	6.7	4.4	8.2	8.2
Percent of best clone (%)	390.3	321.1	1233.3	419.2	334.2	316.0	192.6	290.5	338.2
Percent of best 5 clones (%)	294.5	243.6	809.9	313.7	183.3	266.7	164.1	194.3	239.9

Table 24. Relative growth of 19 hybrid poplar clones to commercial standards NM6 and DN34 with respect to top (stem + leaf) dry weight (mg) after 14 days of growth in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002). Greater relative growth is highlighted in bold.

Clone	<i>Percentage top dry weight relative to commercial standard</i>					
	NM6			DN34		
	2001	2002	Across years	2001	2002	Across years
D105	21.2	23.1	22.2	47.6	51.0	49.4
D110	23.6	23.3	23.4	53.0	51.3	52.1
D117	20.8	25.9	23.5	46.8	57.1	52.2
D133	24.8	29.4	27.2	55.9	64.8	60.6
NC13563	31.4	15.9	23.3	70.7	35.0	51.9
NC13570	44.2	28.9	36.2	99.4	63.8	80.7
NC13624	54.1	30.5	41.8	121.8	67.2	93.1
NC13649	46.4	22.8	34.1	104.4	50.2	75.9
NC13686	46.0	21.5	33.2	103.5	47.4	74.0
NC14042	50.0	40.3	45.0	112.5	88.9	100.1
25	93.2	55.1	73.3	209.6	121.4	163.2
DM105	81.6	76.9	79.1	183.5	169.6	176.2
NC14103	79.8	48.2	63.3	179.5	106.2	141.0
NC14105	106.2	78.8	91.9	238.9	173.8	204.7
NC14106	82.6	78.3	80.4	185.8	172.7	178.9
DN17	41.1	50.4	45.9	92.4	111.0	102.2
DN34	44.5	45.3	44.9	100.0	100.0	100.0
DN5	53.4	51.9	52.6	120.0	114.5	117.1
DN70	38.1	38.5	38.3	85.7	84.9	85.3
NM2	106.3	91.4	98.6	239.1	201.6	219.4
NM6	100.0	100.0	100.0	225.0	220.5	222.6

Table 25. Top (stem + leaf) dry weight (mg) of commercial standards NM6 and DN34 and 19 other hybrid poplar clones after 14 days of growth in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002).

	<i>Top dry weight (mg)</i>								
	2001				2002				
	Ames	Waseca	Westport	Across sites	Ames	Waseca	Westport	Across sites	Across years
Control mean (NM6)	131.9	147.5	139.7	139.7	163.9	157.3	134.5	151.9	145.8
Best clone mean	150.2	161.9	150.7	148.5	163.3	139.0	114.4	138.9	143.7
Mean of best 3 clones	141.8	149.1	139.1	142.3	156.6	121.1	104.0	125.9	131.6
Percent of best clone (%)	113.9	109.8	107.9	106.3	99.6	88.4	85.1	91.4	98.5
Percent of best 3 clones (%)	107.5	101.1	99.5	101.9	95.5	77.0	77.4	82.9	90.3
Control mean (DN34)	53.4	67.0	65.9	62.1	83.3	65.3	58.0	68.9	65.5
Best clone mean	150.2	161.9	150.7	148.5	163.3	139.0	114.4	138.9	143.7
Mean of best 5 clones	129.5	136.1	128.5	131.3	144.3	109.1	97.4	115.6	123.4
Percent of best clone (%)	281.4	241.7	228.6	239.1	196.1	212.9	197.2	201.7	219.4
Percent of best 5 clones (%)	242.7	203.2	194.9	211.3	173.4	167.1	167.9	167.9	188.5

Performance Relative to DN34. DN34 was consistently outperformed throughout the study. Thirteen clones exhibited greater ROOTDW than DN34 during the 2001 growing season (Table 22). Ten clones outperformed DN34 during the 2002 growing season. Eleven clones produced more ROOTDW across years than DN34. The percent advantage of the best clone's ROOTDW over DN34 at each year and site ranged from 193 (Westport 2002) – 1233% (Westport 2001) (Table 23). Likewise, the percent advantage of the ROOTDW of the best five clones over DN34 at each year and site ranged from 164 (Westport 2002) – 810% (Westport 2001). Twelve clones exhibited greater TOPDW than DN34 during the 2001 growing season (Table 24). Nine clones exhibited greater TOPDW than DN34 during the 2002 growing season. Ten clones produced more TOPDW across years than DN34. The percent advantage of the best clone's TOPDW over DN34 at each year and site ranged from 196 (Ames 2002) – 281% (Ames 2001) (Table 25). Likewise, the percent advantage of the TOPDW of the best five clones over DN34 at each year and site ranged from 167 (Waseca 2002) – 243% (Ames 2001).

DN34 should have limited use in future testing, given poor short-term growth. Some clones from all pedigrees outperformed DN34, which suggests that selection within any of them can provide clones that exhibit greater belowground and aboveground growth for similar short-term research studies.

Tree Growth Analysis

Survivability

June Survival. The percentage of trees alive during June, approximately one month after planting, across years and sites ranged from 72% (D105) to 100% (NM6) (Fig. 22). The NM (99%) pedigree exhibited the greatest overall survival rate. The DN and DM pedigrees each expressed a survival rate of 92%. The BC₁ pedigree was very close with 88% survival. The D (78%) pedigree expressed the lowest survival rate. The survival rate was most variable within the BC₁ pedigree, where survival rates ranged from 82% (NC14042) to 94% (NC13649). The percentage of cuttings that rooted within years and sites ranged from 42% (D117, Ames 2001) to 100% (20 occurrences of year x site x clone combinations) (Fig. 23). The best survival rate was from the Waseca 2001 planting. However, Ames 2002 also experienced a June survival rate greater than 90% across clones. NM6 had the highest

Fig. 22. Percentage of hybrid poplar trees alive during June and October after being planted as dormant, unrooted hybrid poplar cuttings in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone. Data are pooled across two years (2001, 2002).

Fig. 23. Percentage of hybrid poplar trees alive during June at 3 sites (Ames, IA; Waseca, MN; Westport, MN) and 2 years (2001, 2002) after being planted as dormant, unrooted hybrid poplar cuttings in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=36 cuttings for each clone.

survival rate (100%) for every year x site combination. Ames 2001 and Westport 2002 expressed very low survival rates compared with other year x site combinations for almost all clones.

October Survival. There was limited mortality throughout the remainder of the growing seasons. Clonal survival rates decreased about 10% from June to October. The percentage of trees alive following one growing season across years and sites ranged from 56% (D105) to 98% (NM6) (Fig. 22). The survival rate of the NM pedigree was 96%. The DN and DM pedigrees remained similar with survival rates of 83% and 82%, respectively. The BC₁ pedigree ranked fourth with a survival rate of 76%, and the D pedigree had the lowest survival rate with 66%. Survival rates were variable within all pedigrees except for NM, which only had a 4% difference between clones. The percentage of cuttings that rooted within years and sites ranged from 31% (D105, Westport 2001) to 100% (NC14106, Waseca 2002; NM2, Waseca 2002; NM6, Ames 2002; NM6, Waseca 2002) (Fig. 24). The best survival rate was from the Waseca 2001 planting. However, Waseca 2002 also experienced a relatively high survival rate. NM6 had the highest survival rate (>94%) for every year x site combination. There was a lack of survival across clones in Westport 2001. The rapid decrease in survival rate at Westport 2001 from June to October suggests a non-genetic impact. The most likely cause of mortality is lack of proper site management or low soil fertility. The site was mowed and tilled in early August 2001, but significant mortality was noticed at that time. In addition, despite inadequate site management, there were many noticeable areas with lack of weed competition or abrupt changes in species composition.

Trait Correlations

June height was positively correlated with October height ($r=0.60$, $P<0.0001$) (Table 26). Correlations between tree height with ROOTNUM and with MEANRTLGL were similar to those previously reported (Riemenschneider and Bauer 1997). Clone-mean correlations among June and October height with all initial root development traits ranged from 0.01 to 0.23. Correlations among most traits were significantly correlated: OCTHT-ROOTDW ($P=0.0026$), OCTHT-TOTRTLGL ($P=0.0004$), OCTHT-MEANRTLGL ($P=0.0026$), OCTHT-SRRATIO ($P=0.0055$), and all others ($P<0.0001$). The JUNEHT-SRRATIO ($P=0.5295$) and OCTHT-CALDW ($P=0.0636$) correlations were non-significant. Although highly significant,

Fig. 24. Percentage of hybrid poplar trees alive during October at 3 sites (Ames, IA; Waseca, MN; Westport, MN) and 2 years (2001, 2002) after being planted as dormant, unrooted hybrid poplar cuttings in an experiment testing 21 clones in their ability to develop roots and shoots. The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=36 cuttings for each clone.

Table 26. Phenotypic correlations² (*r*) among June and October height of sister trees not harvested and above- and below-ground growth traits of short-term trees harvested after 14 days of growth in an experiment testing for differences in root ability among 21 hybrid poplar clones across two years (2001, 2002) and three sites (Ames, IA; Waseca, MN; Westport, MN). Significant *P*-values are in bold. Descriptions of traits are in the text.

	OCT-HT	CT-DW	ROOT-DW	CAL-DW	TOP-DW	TOT-LFAR	MEAN-LFAR	ROOT-NUM	TOT-RTLG	MEAN-RTLG	SR-RATIO
JUNE-HT	0.60	0.14	0.14	0.06	0.23	0.15	0.19	0.15	0.14	0.15	0.01
	<0.0001	<0.0001	<0.0001	0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.5295
OCT-HT		0.14	0.04	0.03	0.11	0.07	0.09	0.07	0.05	0.04	0.04
		<0.0001	0.0026	0.0636	<0.0001	<0.0001	<0.0001	<0.0001	0.0004	0.0026	0.0055

²Pearson correlation coefficients generated using "PROC CORR" of the Statistical Analysis System (SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

correlations among traits were fairly small with most below 0.15. However, the significance of the correlations supports the potential for early selection from short-term rooting trials.

Multiple Year Evaluation (Model I)

Genotypic Effects. Clones varied greatly in JUNEHT and OCTHT, accounting for high amounts of variation in each of these traits (Table 27). The percent of total variation in JUNEHT and OCTHT was 10% and 8%, respectively. Broad-sense heritability estimates are 0.18 and 0.10 for JUNEHT and OCTHT, respectively.

Analyses of variance indicate that clones differed significantly with respect to JUNEHT and OCTHT ($P < 0.0001$ for both). JUNEHT ranged from 8.3 (D105) to 23.9 cm (NM6) (Fig. 25). Clones NM2 and NM6 exhibited the greatest JUNEHT. Overall, D clones were not as productive as those from the other pedigrees. This lack of productivity was mostly attributed to poor growth of D105 and D117. The BC₁ pedigree expressed the greatest variation among clones (9.8 – 15.2 cm). OCTHT ranged from 33 (D117) to 82.7 cm (NM2) (Fig. 26). Variation in height among clones was greater with OCTHT than with JUNEHT. Discrepancies among clones within pedigrees became evident following an entire growing season as the more-productive clones outcompeted less vigorous ones for available resources. In addition to the NM clones, NC14105 and NC13649 exhibited excellent height growth relative to the rest of the clones. Another separation among clones was that of the DN

Table 27. Analysis of variance, variance components, and derived statistics in an experiment testing for differences in tree height (cm) among 21 hybrid poplar clones across two years (2001, 2002) and three sites (Ames, IA; Waseca, MN; Westport, MN). Significant *P*-values are in bold. G = soil growing degree days associated with planting date.

Source of variation	df ²	Mean square	F variance-ratio	P-value	Variance component ³	Percent of total variation	Heritability ⁴
JUNE HEIGHT							
Year (Y)	1	9829	0.32	0.6279	0	0	$\sigma^2_G = 12.00$
Site (S)	2	52327	1.71	0.3684	18.9	15.37	$\sigma^2_P = 65.50$
YS	2	30533	23.26	<0.0001	29.7	24.15	H = 0.18
G	12	1314	8.54	<0.0001	4.6	3.74	
Block/YSG	198	141	2.81	<0.0001	4.3	3.50	
Clone (C)	20	2877	10.45	<0.0001	12.0	9.76	
YC	20	194	3.06	<0.0001	1.2	0.98	
SC	40	145	2.28	<0.0001	1.1	0.89	
GC	280	64	1.27	0.0023	1.1	0.89	
Error	3960	50			50.1	40.73	
Total	4535				123	100.00	
OCTOBER HEIGHT							
Year (Y)	1	446315	3.74	0.1840	144.8	6.25	$\sigma^2_G = 176.9$
Site (S)	2	136077	1.19	0.4582	13.9	0.60	$\sigma^2_P = 1861.9$
YS	2	115168	4.24	0.0405	117.6	5.07	H = 0.10
G	12	27186	6.12	<0.0001	91.8	3.96	
Block/YSG	198	3402	2.18	<0.0001	87.7	3.78	
Clone (C)	20	45054	7.19	0.0001	176.9	7.63	
YC	20	6849	2.62	0.0003	39.9	1.72	
SC	40	2033	0.78	0.8312	0	0.00	
GC	280	2616	1.67	<0.0001	81.8	3.53	
Error	3960	1563			1563.3	67.45	
Total	4535				2317.7	100.00	

²Degrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System (SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

³Restricted Maximum Likelihood (REML) estimates of variance components.

⁴Broad-sense heritability estimated on an individual tree basis (H), with $\sigma^2_G =$ genotypic variance attributed to combined genetic effects of clone (σ^2_C); and $\sigma^2_P =$ variance attributed to phenotypic effects, where phenotype = genotype + (genotype x environment) + environment [$\sigma^2_C + (\sigma^2_{YC} + \sigma^2_{SC} + \sigma^2_{GC}) + \sigma^2_E$].

Fig. 25. June height (cm) in an experiment testing for differences in tree height among 21 hybrid poplar clones across two years (2001, 2002) and three sites (Ames, IA; Waseca, MN; Westport, MN). The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone.

Fig. 26. October height (cm) in an experiment testing for differences in tree height among 21 hybrid poplar clones across two years (2001, 2002) and three sites (Ames, IA; Waseca, MN; Westport, MN). The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=216 cuttings for each clone.

pedigree. DN5 and DN70 continued to be productive, while DN17 and DN34 exhibited decreased productivity.

Site Effects. Site effects were negligible for JUNEHT and OCTHT. The percent of total variation in JUNEHT and OCTHT was 15 and 1%, respectively (Table 27). Analyses of variance indicate that sites were not significantly different for JUNEHT ($P=0.3684$) and OCTHT ($P=0.4582$).

Genotype x Environment Interactions. Genotype x environment (G x E) interactions were highly significant for both traits. Analyses of variance indicate that the year x clone interaction was significant for JUNEHT ($P<0.0001$) and OCTHT ($P=0.0003$) (Table 27). The site x clone interaction was significant for JUNEHT ($P<0.0001$), but negligible for OCTHT ($P=0.8312$). Thus, G x E interactions were highly significant. The single year evaluation (MODEL II) below addresses these G x E interactions, along with genotypic and site effects, in more detail.

Single Year Evaluation (Model II)

Genotypic Effects. Clones varied greatly in JUNEHT and OCTHT for the 2001 and 2002 growing seasons, accounting for high amounts of variation in both traits. The percent of total variation during 2001 in JUNEHT and OCTHT was 18 and 8%, respectively (Table 28). Broad-sense heritability estimates for 2001 JUNEHT and OCTHT are 0.20 and 0.10, respectively. Likewise, the percent of total variation during 2002 in JUNEHT and OCTHT was 7 and 11%, respectively (Table 29). Broad-sense heritability estimates for JUNEHT and OCTHT are 0.20 and 0.11, respectively.

Analyses of variance indicate that clones differed significantly in 2001 and 2002 for JUNEHT and OCTHT ($P<0.0001$) (Tables 28 and 29). JUNEHT in 2001 ranged from 5.2 (D117-Ames) to 25.7 cm (NM6-Ames) (Table 30, Fig. 27). JUNEHT in 2002 ranged from 4.6 (NC13570-Westport; clone 25-Westport) to 40.3 cm (NM6-Ames). JUNEHT was greatest in Ames 2002 for all clones (27 cm). Most clones exhibited at least twice as much height in Ames 2002 than any other plantings (Fig. 27). In addition, Ames 2001 was the second highest planting with respect to JUNEHT (13.6 cm). This Ames advantage was most likely due to increased site potential, warmer air and soil temperatures, and excellent site management leading up to the June measurements. OCTHT in 2001 ranged from 10.2 (D117-Westport) to 91.5 cm (NM2-Ames) (Table 30, Fig. 28). OCTHT in 2002 ranged from

Table 28. Analysis of variance, variance components, and derived statistics in an experiment testing for differences in tree height (cm) among 21 hybrid poplar clones across three sites (Ames, IA; Waseca, MN; Westport, MN) during the 2001 growing season. Significant *P*-values are in bold. G= soil growing degree days associated with planting date.

Source of variation	df ²	Mean square	F variance-ratio	P-value	Variance component ³	Percent of total variation	Heritability ⁴
JUNE HEIGHT							
Site (S)	2	1649	1.42	0.3122	0.6	0.84	$\sigma^2_{G^*}$ 13.0
G	6	1157	15.90	<0.0001	4.4	6.18	$\sigma^2_{P^*}$ 65.8
Block/SG	99	60	1.16	0.1340	0.4	0.56	H= 0.20
Clone (C)	20	1476	20.97	<0.0001	13.0	18.26	
SC	40	70	1.09	0.3509	0.2	0.28	
GC	120	65	1.25	0.0370	1.0	1.40	
Error	1980	52			51.6	72.47	
Total	2267				71.2	100.00	
OCTOBER HEIGHT							
Site (S)	2	209261	4.38	0.0659	219.0	11.56	$\sigma^2_{G^*}$ 150.0
G	6	47297	20.49	<0.0001	181.3	9.57	$\sigma^2_{P^*}$ 1466.6
Block/SG	99	1829	1.45	0.0031	27.1	1.43	H= 0.10
Clone (C)	20	18452	8.32	<0.0001	150.0	7.92	
SC	40	2218	1.27	0.1652	13.2	0.70	
GC	120	1751	1.39	0.0044	40.7	2.15	
Error	1980	1263			1262.7	66.67	
Total	2267				1894.0	100.00	

²Degrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System (SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

³Restricted Maximum Likelihood (REML) estimates of variance components.

⁴Broad-sense heritability estimated on an individual tree basis (H), with $\sigma^2_{G^*}$ = genotypic variance attributed to combined genetic effects of clone (σ^2_C); and $\sigma^2_{P^*}$ = variance attributed to phenotypic effects, where phenotype = genotype + (genotype x environment) + environment [$\sigma^2_C + (\sigma^2_{SC} + \sigma^2_{GC}) + \sigma^2_E$].

Table 29. Analysis of variance, variance components, and derived statistics in an experiment testing for differences in tree height (cm) among 21 hybrid poplar clones across three sites (Ames, IA; Waseca, MN; Westport, MN) during the 2002 growing season. Significant *P*-values are in bold. G= soil growing degree days associated with planting date.

Source of variation	df ²	Mean square	F variance-ratio	P-value	Variance component ³	Percent of total variation	Heritability ⁴
JUNE HEIGHT							
Site (S)	2	81459	52.12	<0.0001	105.7	57.38	$\sigma^2_G = 13.4$
G	6	1470	6.36	<0.0001	4.9	2.66	$\sigma^2_P = 65.4$
Block/SG	99	222	4.56	<0.0001	8.2	4.45	H = 0.20
Clone (C)	20	1595	10.56	<0.0001	13.4	7.27	
SC	40	151	2.59	<0.0001	2.6	1.41	
GC	120	58	1.20	0.0744	0.8	0.43	
Error	1980	49			48.6	26.38	
Total	2267				184.2	100.00	
OCTOBER HEIGHT							
Site (S)	2	39886	3.90	0.0511	39.2	1.60	$\sigma^2_G = 258.3$
G	6	7074	1.28	0.2749	6.1	0.25	$\sigma^2_P = 2256.8$
Block/SG	99	4975	2.67	<0.0001	148.2	6.05	H = 0.11
Clone (C)	20	33474	6.01	<0.0001	258.3	10.54	
SC	40	5573	2.29	0.0003	87.2	3.56	
GC	120	2432	1.31	0.0169	47.4	1.93	
Error	1980	1864			1863.9	76.07	
Total	2267				2450.3	100.00	

²Degrees of freedom and Type III expected mean squares generated using the "RANDOM" statement in "PROC GLM" of the Statistical Analysis System (SAS[®] Version 8.1, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513).

³Restricted Maximum Likelihood (REML) estimates of variance components.

⁴Broad-sense heritability estimated on an individual tree basis (H), with σ^2_G = genotypic variance attributed to combined genetic effects of clone (σ^2_C); and σ^2_P = variance attributed to phenotypic effects, where phenotype = genotype + (genotype x environment) + environment [$\sigma^2_C + (\sigma^2_{SC} + \sigma^2_{GC}) + \sigma^2_E$].

Table 30. Mean tree height (cm) measured in June and October in an experiment testing 21 hybrid poplar clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002).

Clone	2001				2002				Exptl-wide
	Ames	Waseca	Westport	Across sites	Ames	Waseca	Westport	Across sites	
June height (cm)									
D105	6.9	8.1	5.3	6.7	18.8	6.0	4.9	9.9	8.3
D110	8.4	7.7	7.8	8.0	25.3	9.4	9.1	14.6	11.3
D117	5.2	7.3	7.5	6.6	20.3	6.5	6.3	11.0	8.8
D133	12.7	8.5	8.6	9.9	22.8	10.3	8.3	13.8	11.9
NC13563	12.8	10.3	8.4	10.5	22.7	8.7	6.2	12.5	11.5
NC13570	8.2	9.9	8.6	8.9	20.9	6.7	4.6	10.7	9.8
NC13624	12.0	11.7	10.2	11.3	25.8	8.6	7.9	14.1	12.7
NC13649	14.7	11.9	13.9	13.5	27.8	11.4	11.7	17.0	15.2
NC13686	15.1	13.6	11.2	13.3	29.0	8.4	7.3	14.9	14.1
NC14042	9.1	8.5	7.1	8.2	22.2	6.4	5.3	11.3	9.8
25	13.9	13.9	13.3	13.7	22.9	8.6	4.6	12.0	12.9
DM105	13.9	13.0	12.2	13.0	30.1	8.8	5.7	14.9	14.0
NC14103	16.7	13.7	11.7	14.0	28.0	6.7	5.5	13.4	13.7
NC14105	17.9	17.7	13.2	16.3	34.2	10.8	9.2	18.1	17.2
NC14106	16.4	12.6	12.1	13.7	32.6	12.3	9.4	18.1	15.9
DN17	11.9	10.4	9.1	10.5	26.8	7.3	7.3	13.8	12.1
DN34	13.0	10.7	8.3	10.7	23.2	9.9	7.5	13.5	12.1
DN5	14.8	11.8	11.1	12.5	31.1	12.8	9.8	17.9	15.2
DN70	15.7	10.9	10.3	12.3	25.5	10.6	9.7	15.3	13.8
NM2	20.9	15.3	15.2	17.1	35.6	16.4	15.9	22.6	19.9
NM6	25.7	22.0	19.1	22.3	40.3	18.6	17.4	25.4	23.9
Mean	13.6	11.9	10.7	12.1	27.0	9.8	8.3	15.0	13.5
October height (cm)									
D105	29.2	39.6	13.7	27.5	60.9	34.3	42.6	46.0	36.7
D110	41.3	29.6	16.9	29.3	71.0	75.1	56.6	67.6	48.4
D117	18.3	34.4	10.2	20.9	55.3	28.2	51.9	45.1	33.0
D133	53.6	36.2	20.4	36.7	52.2	49.9	58.3	53.5	45.1
NC13563	63.2	54.4	18.2	45.3	58.0	54.3	56.9	56.4	50.8
NC13570	34.9	39.2	19.0	31.0	64.4	38.0	34.3	45.6	38.3
NC13624	51.2	46.1	22.8	40.0	76.3	68.3	47.1	63.9	51.9
NC13649	64.2	64.3	37.3	55.3	84.5	74.7	88.0	82.4	68.8
NC13686	63.5	80.7	30.1	58.1	76.2	59.0	39.4	58.2	58.1
NC14042	37.0	29.9	10.3	25.7	67.5	35.8	41.1	48.1	36.9
25	64.3	60.7	32.6	52.5	73.0	54.8	54.0	60.6	56.6
DM105	55.7	55.7	28.1	46.5	83.4	44.1	48.2	58.6	52.5
NC14103	64.9	65.7	28.5	53.0	83.5	48.4	62.5	64.8	58.9
NC14105	75.5	77.2	39.4	64.1	103.5	75.7	100.4	93.2	78.6
NC14106	56.1	49.4	31.3	45.6	77.6	70.2	88.0	73.6	62.1
DN17	43.3	59.5	20.8	41.2	65.7	33.1	40.8	46.5	43.8
DN34	49.5	48.2	16.9	38.2	48.6	43.4	56.1	49.4	43.8
DN5	62.1	55.5	26.0	47.9	80.0	65.1	69.1	71.4	59.6

Table 30. (continued)

DN70	76.9	67.3	29.0	57.7	65.1	60.8	91.6	72.5	65.1
NM2	91.5	52.3	36.4	60.1	78.2	114.3	123.3	105.3	82.7
NM6	74.0	79.3	42.3	65.2	93.7	87.0	102.8	94.5	79.8
Mean	55.7	53.6	25.2	44.8	72.3	57.8	64.4	64.9	54.8

28.2 (D117-Waseca) to 123.3 cm (NM2-Westport). OCTHT was greatest in Ames 2002 for all clones (72.3 cm). Yet the height advantage of Ames 2002 observed in JUNEHT was diminished at the end of the growing season. Westport 2002 was the second most productive planting (64.4 cm). The Westport 2001 planting was the least productive, with OCTHT of 25.2 cm. This productivity was less than half of other plantings. These results indicate a lack of productive potential on this plot, which corroborates the results of the survivability analysis above. The 2001 Westport planting was located not more than 200 m from the 2002 planting, yet productivity and survival were drastically reduced in the 2001 planting. The excellent height growth of D110 in Ames 2002 and Waseca 2002 supports results of previous research that the D pedigree exhibits excellent growth once established. Root growth was not very good for D110 in the short-term rooting study, yet it outperformed many other good-rooting clones after one growing season.

Site Effects. Site effects were negligible with respect to OCTHT, but differences in JUNEHT during 2002 existed. Sites accounted for 1% and 12% of variation in JUNEHT and OCTHT during 2001, respectively (Table 28). Sites accounted for 57% and 2% of variation in JUNEHT and OCTHT during 2002, respectively (Table 29). Analyses of variance indicate that sites were not significantly different in 2001 with respect to JUNEHT ($P=0.3122$) and OCTHT ($P=0.0659$). Likewise, sites were not significantly different in 2002 with respect to OCTHT ($P=0.0511$). However, sites differed significantly for JUNEHT in 2002. According to Fisher's protected least significant difference ($\alpha=0.05$, $n=756$ for each site, $LSD=0.7$), Ames (27 cm) was significantly different from Waseca (9.8 cm) and Westport (8.3 cm). In addition, Waseca and Westport were significantly different from each other.

Genotype x Environment Interactions. Genotype x environment (G x E) interactions were highly variable across both traits. The site x clone interaction during 2001 was

Fig. 27. June height (cm) in an experiment testing for differences in tree height among 21 hybrid poplar clones during two years (2001, 2002) at three sites (Ames, IA; Waseca, MN; Westport, MN). The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=36 cuttings for each clone.

Fig. 28. October height (cm) in an experiment testing for differences in tree height among 21 hybrid poplar clones during two years (2001, 2002) at three sites (Ames, IA; Waseca, MN; Westport, MN). The clones belong to five pedigrees (listed in the figure), with D and BC₁ pedigrees in A.) and DM, DN, and NM pedigrees in B.). Standard error bars represent one standard error of the mean, n=36 cuttings for each clone.

negligible for JUNEHT ($P=0.3509$) and OCTHT ($P=0.1652$) (Table 28). The site x clone interaction during 2002 was significant for JUNEHT ($P<0.0001$) and OCTHT ($P=0.0003$) (Table 29). There was a significant growing degree day x clone interaction in 2001 for JUNEHT ($P=0.0370$) and OCTHT ($P=0.0044$) (Table 28). In addition, a significant growing degree day x clone interaction during 2002 existed for OCTHT ($P=0.0169$), but this interaction was negligible for JUNEHT ($P=0.0744$) (Table 29).

The significant G x E interactions are similar to those reported elsewhere. Genotypic adaptability and stability influenced height growth across sites throughout the growing season and lead to changes in rank and scale. The extreme growth of trees during June in Ames 2002 likely lead to the highly significant G x E interactions during that year. In addition, inconsistent site management across sites most likely contributed to G x E interactions. Weed competition in Ames 2002 was minimal until the beginning of July and then increased as the growing season progressed. Weed competition was minimal in Waseca 2002 throughout the entire growing season. Furthermore, weed competition in Westport 2002 was inconsistent throughout the planting due to areas of residual herbicide in the soil and lack of weed control in areas that were not previously sprayed with herbicide.

Performance Relative to Commercial Standards

There were two objectives of the analysis of clones relative to NM6 and DN34. First, I tested whether other clones exhibited better height growth than the standards in an attempt to identify promising genotypes for further testing and broad-scale deployment. Second, I tested the productivity of commercial standards to see if they should be replaced.

Performance Relative to NM6. No clones exhibited greater JUNEHT than NM6 during the 2001 and 2002 growing season (Table 31). NM2 expressed the second highest JUNEHT in both seasons. The percentage of NM6 JUNEHT for NM2 was 77 and 89% for 2001 and 2002, respectively. The best clone JUNEHT as a percentage of NM6 JUNEHT at each year and site ranged from 80 (Westport 2001) to 92% (Westport 2002) (Table 32). Likewise, the mean of the best three clones as a percentage of NM6 JUNEHT at each year and site ranged from 71 (Waseca 2001) to 85% (Ames 2002). No clones exhibited greater OCTHT than NM6 during the 2001 growing season (Table 33). NM2 expressed 111% and 104% greater OCTHT than NM6 in 2002 and across years, respectively. NC14105 expressed 99% percent of NM6 OCTHT during both growing seasons and across years. The percentage

Table 31. Relative growth of 19 hybrid poplar clones to commercial standards NM6 and DN34 with respect to tree height (cm) measured in June in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002). Greater relative growth is highlighted in bold.

Clone	<i>Percentage tree height relative to commercial standard</i>					
	NM6			DN34		
	2001	2002	Across years	2001	2002	Across years
D105	30.2	39.0	34.8	63.0	73.4	68.8
D110	35.7	57.4	47.1	74.3	108.0	93.1
D117	29.8	43.4	37.0	62.1	81.6	73.0
D133	44.5	54.4	49.7	92.8	102.4	98.1
NC13563	47.2	49.3	48.2	98.3	92.7	95.2
NC13570	39.9	42.3	41.1	83.1	79.6	81.1
NC13624	50.7	55.6	53.2	105.7	104.5	105.0
NC13649	60.5	66.8	63.7	126.2	125.7	125.9
NC13686	59.7	58.7	59.0	124.4	110.4	116.6
NC14042	36.8	44.5	40.8	76.8	83.6	80.6
25	61.5	47.4	53.9	128.2	89.1	106.4
DM105	58.4	58.6	58.4	121.7	110.2	115.3
NC14103	62.9	52.8	57.4	131.2	99.4	113.4
NC14105	72.9	71.1	71.8	151.9	133.8	141.8
NC14106	61.4	71.2	66.5	127.9	133.9	131.3
DN17	46.9	54.4	50.8	97.7	102.4	100.3
DN34	47.9	53.2	50.6	100.0	100.0	100.0
DN5	56.3	70.5	63.7	117.3	132.7	125.9
DN70	55.1	60.2	57.7	114.7	113.3	113.9
NM2	76.9	89.0	83.2	160.3	167.5	164.3
NM6	100.0	100.0	100.0	208.2	188.4	197.1

Table 32. Tree height (cm) measured in June of commercial standards NM6 and DN34 and 19 other hybrid poplar clones in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002).

	<i>Tree height (cm)</i>									
	2001					2002				
	Ames	Waseca	Westport	Across sites		Ames	Waseca	Westport	Across sites	Across years
Control mean (NM6)	25.7	22.0	19.1	22.3		40.3	18.6	17.4	25.4	23.9
Best clone mean	20.9	17.7	15.2	17.1		35.6	16.4	15.9	22.6	19.9
Mean of best 3 clones	18.5	15.6	14.2	15.8		34.1	13.8	12.5	19.6	17.6
Percent of best clone (%)	81.3	80.5	79.7	77.0		88.2	87.8	91.8	88.9	83.4
Percent of best 3 clones (%)	71.8	71.2	74.1	71.0		84.6	74.2	71.9	77.0	74.0
Control mean (DN34)	13.0	10.7	8.3	10.7		23.2	9.9	7.5	13.5	12.1
Best clone mean	20.9	17.7	15.2	17.1		35.6	16.4	15.9	22.6	19.9
Mean of best 5 clones	17.5	14.8	13.6	15.0		32.7	12.7	11.3	18.7	16.7
Percent of best clone (%)	160.4	165.4	183.0	160.5		153.4	165.7	212.9	167.4	164.3
Percent of best 5 clones (%)	134.2	138.8	163.1	140.1		141.1	129.1	151.0	138.6	137.8

Table 33. Relative growth of 19 hybrid poplar clones to commercial standards NM6 and DN34 with respect to tree height (cm) measured in **October** in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002). Greater relative growth is highlighted in bold.

Clone	<i>Percentage tree height relative to commercial standard</i>					
	NM6			DN34		
	2001	2002	Across years	2001	2002	Across years
D105	42.2	48.6	46.0	72.0	93.0	83.8
D110	44.9	71.5	60.7	76.6	136.8	110.5
D117	32.1	47.8	41.4	54.8	91.4	75.4
D133	56.3	56.6	56.5	96.2	108.2	103.0
NC13563	69.4	59.7	63.7	118.5	114.2	116.1
NC13570	47.6	48.2	48.0	81.2	92.2	87.4
NC13624	61.4	67.6	65.1	104.8	129.3	118.6
NC13649	84.8	87.2	86.3	144.7	166.8	157.2
NC13686	89.1	61.6	72.9	152.1	117.8	132.7
NC14042	39.4	50.9	46.3	67.3	97.4	84.3
25	80.5	64.1	70.9	137.5	122.7	129.1
DM105	71.3	62.0	65.8	121.7	118.5	119.9
NC14103	81.4	68.6	73.9	138.9	131.2	134.5
NC14105	98.3	98.6	98.5	167.7	188.7	179.5
NC14106	69.9	83.1	77.8	119.3	159.1	141.7
DN17	63.1	49.2	54.9	107.8	94.2	100.1
DN34	58.6	52.2	54.9	100.0	100.0	100.0
DN5	73.4	75.5	74.7	125.3	144.5	136.1
DN70	88.6	76.7	81.6	151.1	146.8	148.7
NM2	92.1	111.4	103.6	157.3	213.1	188.7
NM6	100.0	100.0	100.0	170.6	191.3	182.3

of the best clone OCTHT of NM6 OCTHT at each year and site ranged from 93 (Westport 2001) to 131% (Waseca 2002) (Table 34). Likewise, the percent of the OCTHT of the best three clones compared to NM6 at each year and site ranged from 89 (Westport 2001) to 110% (Ames 2001).

NC14105 is promising for future use, given its potential for high rooting and good height growth relative to NM6. NM6 nearly outperformed all other clones tested and should continue to be utilized.

Performance Relative to DN34. DN34 was consistently outperformed throughout the study. Twelve clones exhibited greater JUNEHT than DN34 during the 2001 growing season (Table 31). Thirteen clones outperformed DN34 during the 2002 growing season and across years. The percent advantage of the best clone JUNEHT over DN34 JUNEHT at each year and site ranged from 153 (Ames 2002) to 213% (Westport 2002) (Table 32). Likewise, the percent advantage of the JUNEHT of the best five clones over DN34 at each year and site ranged from 129 (Waseca 2002) to 163% (Westport 2001). Fourteen clones exhibited greater OCTHT than DN34 during the 2001 growing season (Table 33). Fifteen clones produced greater OCTHT than DN34 during the 2002 growing season. Sixteen clones exhibited more OCTHT across years than DN34. The percent advantage of the best clone OCTHT over DN34 at each year and site ranged from 168 (Waseca 2001) to 263% (Waseca 2002) (Table 34). Likewise, the percent advantage of the OCTHT of the best five clones over DN34 at each year and site ranged from 148 (Waseca 2001) to 209% (Westport 2001).

DN34 should not be used for future testing and plantation deployment, given poor height growth. Some clones from all pedigrees outperformed DN34, which suggests that selection within any of them can provide clones that exhibit greater belowground and aboveground growth.

Table 34. Tree height (cm) measured in October of commercial standards NM6 and DN34 and 19 other hybrid poplar clones in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002).

	<i>Tree height (cm)</i>								
	2001				2002				
	Ames	Waseca	Westport	Across sites	Ames	Waseca	Westport	Across sites	Across years
Control mean (NM6)	74.0	79.3	42.3	65.2	93.7	87.0	102.8	94.5	79.8
Best clone mean	91.5	80.7	39.4	64.1	103.5	114.3	123.3	105.3	82.7
Mean of best 3 clones	81.3	75.1	37.7	60.7	90.5	88.3	105.1	93.6	76.7
Percent of best clone (%)	123.7	101.7	93.3	98.3	110.5	131.4	119.9	111.4	103.6
Percent of best 3 clones (%)	109.9	94.7	89.3	93.2	96.6	101.6	102.2	99.1	96.1
Control mean (DN34)	49.5	48.2	16.9	38.2	48.6	43.4	56.1	49.4	43.8
Best clone mean	91.5	80.7	39.4	64.1	103.5	114.3	123.3	105.3	82.7
Mean of best 5 clones	76.6	71.0	35.4	59.0	87.0	82.0	98.3	86.4	71.5
Percent of best clone (%)	185.1	167.5	233.0	167.8	213.1	263.2	219.7	213.2	188.9
Percent of best 5 clones (%)	154.8	147.5	209.3	154.7	179.0	188.8	175.1	175.0	163.3

CHAPTER 5: CONCLUSIONS

Summary

Initial Root Development Analysis

1. The percentage of cuttings rooted during 14 days of growth was highly variable, ranging across years and sites from 21.8 – 86.1%. Rooting percentages within years and sites ranged from 8 – 100%. The differences in rooting success are most likely due to broad variation among and within pedigrees. The *Populus nigra* x *Populus maximowiczii* (NM) and the *Populus deltoides* (D) pedigree exhibited the highest and lowest rooting percentages, respectively. The rooting percentages observed were lower than those previously reported. However, cuttings in the current study were planted in three contrasting field sites across two years, where they were subjected to changing environmental conditions such as soil and air temperature, soil moisture, solar radiation, wind, and soil properties such as texture and fertility. In contrast, most previous rooting studies were conducted under near-ideal conditions in growth chambers or greenhouses. Another explanation for lower rooting percentages in the current study is that the growing period (14 days) was much shorter than other studies (28 days).
2. Phenotypic correlations among traits were highly significant, which suggests that a few dependent variables can be used to explain most of the variation in rooting ability among genotypes. Thus, we can decrease the number of variables evaluated without significant loss of biological information.
3. Clones accounted for high amounts of variation in all traits. Broad-sense heritability estimates for root dry weight ranged from 0.09 – 0.11 across years and within each year, and for top dry weight ranged from 0.31 – 0.38 across years and within each year. These estimates are lower than those previously reported. The wide variation among pedigrees and clones, in addition to wide variation among years and sites, contributed to lower heritability estimates.
4. Clones within the (*Populus trichocarpa* x *P. deltoides*) x *P. deltoides* (BC₁) pedigree exhibited the greatest root dry weight across years and sites, although clones within this pedigree varied greatly. NM and *P. deltoides* x *P. maximowiczii* (DM) clones produced more stem and leaf growth than those of other pedigrees. Resources

apportioned to aboveground and belowground biomass production varied greatly among pedigrees. Although roots of the cuttings are differentiated *de novo* and leaf primordia are formed prior to planting, analysis of shoot:root ratios showed distinct contrasts among pedigrees and clones in their resource allocation to the initiation and early growth of new roots. Pedigree shoot:root ratios ranged from 11 – 71, and clonal ratios ranged from 5 – 77.

5. Callus and callus root differentiation were negligible in this study, with only 15 callus roots produced in each year of planting.
6. Genotype x environment interactions were highly significant for most traits, with belowground growing degree days (GDD) accounting for the majority of environmental variation. Clone-mean correlations across years indicated that root dry weight, root number, total root length, and mean root length were relatively stable across sites. Principal component analysis corroborated this univariate interpretation of the variance in rooting. Principal component 1 loaded highly uniformly on all traits at each site, with associated eigenvalues accounting for at least 92% of the variation. Changes in rank and scale of genotypic production across sites indicated G x E interactions within each year. Clonal performance at Westport 2002 suggested that clones may have responded differently to that site. Principal component analyses supported this interpretation, with principal component 1 loading highly on root dry weight, total root length, and mean root length for all site x year combinations except for Westport 2002. Principal component 2 loaded highly on these rooting traits at Westport 2002, but weakly on all other year x site combinations. Thus, clonal performance was stable over all year x site combinations, except for Westport 2002 where root growth was relatively very poor.
7. Rooting increased with increasing belowground GDD for all pedigrees. Least-squares regression models indicated very similar pedigree responses and near-identical predictive functions for each rooting trait. Root growth did not stabilize within the limits of belowground GDD observed, which suggests that temperature limits inhibiting rooting were not met.
8. The interaction of soil temperature and moisture seems likely to have governed rooting of these clones. A minimum of four days with at least four GDD per day,

along with appropriate soil moisture, were needed in order to sustain high levels of rooting. Cuttings subjected to less than four days with four GDD per day, regardless of soil moisture, did not exhibit comparable root production. Precipitation dispersed throughout the growing period also supported increased rooting.

9. The D pedigree performed differently than all other pedigrees with respect to mean root length. Planting dates expressing the highest mean root length of the D clones were associated with lower belowground GDD and lower precipitation compared with those of the hybrid pedigrees.
10. Evaluation of belowground and aboveground performance relative to commercial standards showed that experimental clones exhibit a lot of potential for further experimentation and possibly large-scale testing. Commercial clone NM6 performed well relative to most clones tested, while commercial clone DN34 performed very poorly. Thus, NM6 should continue to be used in experimental studies. Although DN34 has a long history of use in research, these results suggest that utilization of this clone in future studies should be limited.

Tree Growth Analysis

1. The survival percentage of pedigrees during June ranged from 72 – 100%, and that of pedigrees during October ranged from 66 – 96%. Clonal survival rates decreased about 10% from June to October. Tree heights in June and October were highly correlated with traits from the initial root development analysis, which suggests that there is potential for early selection in short-term rooting trials.
2. Multiple-year and single-year analyses indicated that clones varied with respect to June and October height, yet height was less variable than rooting responses. G x E interactions governed height across years and within each year.
3. Evaluation of June and October height relative to commercial standards showed that many experimental clones are very promising for future testing and plantation deployment. NM6 nearly outperformed all other clones tested and should continue to be utilized. In contrast, the production of DN34 was very poor relative to most other clones tested. DN34 should not be used for future testing and plantation deployment, given lack of vigorous growth. Some clones from all pedigrees tested outperformed

DN34, which suggests that selection within any of them can provide clones that exhibit greater belowground and aboveground growth than DN34.

Recommendations for Future Research

1. The broad variation in the rooting ability of the BC₁ pedigree suggests that further testing and selection within this group could be very beneficial for identifying good-rooting clones. Testing the rooting of BC₁ clones under controlled environments may show broader variation in root initiation and growth than that observed in the current study, which may lead to a better understanding of temperature dependent rooting ontogenies and physiologies.
2. I speculated that variation in root number may have been the result of differences among clones in their ability to develop preformed primordia throughout the parent shoot during the preceding growing season. Good-rooting clones may have developed an abundance of preformed primordia, while poor-rooting clones may have relatively fewer preformed primordia. Thus, future research could study the rooting ability of a range of clones to test whether the existence of such primordia contributes to greater root number per cutting. I believe the number of preformed primordia and root number are highly correlated, given the significance of correlations among belowground traits. However, induced primordia may also lead to higher numbers of roots.
3. Testing the effects of the differential between aboveground GDD and belowground GDD on root and top growth is warranted. Although the results of this study were inconclusive with respect to the effects of the aboveground GDD to belowground GDD differential on root production and growth, controlled environment studies that maintain constant but different temperatures aboveground and belowground should be conducted. Testing the aboveground and belowground growth of cuttings under varying temperature regimes may lead to the identification of specific temperature optima for each, based on the clone being used. Likewise, such tests could be used to identify the optimal moisture necessary for growth.
4. Future testing of higher belowground temperatures than those observed in this study are warranted to observe temperatures that are necessary for the production of callus and callus roots. In addition, sequential harvesting may lead to the identification of

the time period under a given belowground temperature regime that is necessary for callus root production.

5. Additional testing for specific genotype x environment interactions across regional scales is needed to improve the reliability of locally based clonal recommendations.
6. Significant correlations among rooting traits and height in June and October suggest that future testing of such correlations may lead to better prediction of clonal response across variable environments. Correlations among rooting traits and second- and third-year growth should be estimated.

APPENDIX A. WEATHER STATION DESIGN

Figure 29. HOBO® weather station design.

Figure 30. HOBO® weather station design with measurements.

**APPENDIX B. REGRESSION ANALYSIS OF ROOTING
PARAMETERS ON SOIL GROWING DEGREE
DAYS**

Figure 31. Root dry weight versus soil growing degree days of five hybrid poplar pedigrees (listed in the figure) in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings. Each point, except for that of 33 GDD and 69 GDD (which represent 2n due to similar GDD at two site x planting date combinations) represents the mean of the following number (n) of cuttings: A.) 72, B.) 48, C.) 60, D.) 48, and E.) 24.

Figure 31. Continued.

Figure 31. Continued.

Table 35. Regression equation coefficients and derived statistics for root dry weight (ROOTDW) per cutting of five hybrid poplar pedigrees in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002). Pedigrees are: BC₁=(*P. trichocarpa* x *P. deltoides*) x *P. deltoides*; D=*P. deltoides*; DM=*P. deltoides* x *P. maximowiczii*; DN=*P. deltoides* x *P. nigra*; NM=*P. nigra* x *P. maximowiczii*.

Pedigree	n	R^2	P -value _b	$ROOTDW = a + b(\text{Soil Growing Degree Days})$			
				a	b	$P_{\min}^z$	$P_{\max}$
BC ₁	1296	0.36	0.0144	3.1955	0.1017	3.20	12.15
D	864	0.33	0.0208	2.3274	0.0637	2.33	7.93
DM	1080	0.22	0.0636	2.0761	0.0500	2.08	6.48
DN	864	0.39	0.0093	3.2464	0.0668	3.25	9.12
NM	432	0.36	0.0147	1.4931	0.0932	1.49	9.69

^z $P_{\min}$ = Predicted minimum ROOTDW; $P_{\max}$ = Predicted maximum ROOTDW

Figure 32. Root number versus soil growing degree days of five hybrid poplar pedigrees (listed in the figure) in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings. Each point, except for that of 33 GDD and 69 GDD (which represent 2n due to similar GDD at two site x planting date combinations) represents the mean of the following number (n) of cuttings: A.) 72, B.) 48, C.) 60, D.) 48, and E.) 24.

Figure 32. Continued.

Figure 32. Continued.

Table 36. Regression equation coefficients and derived statistics for root number (ROOTNUM) per cutting of five hybrid poplar pedigrees in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002). Pedigrees are: BC₁=(*P. trichocarpa* x *P. deltoides*) x *P. deltoides*; D=*P. deltoides*; DM=*P. deltoides* x *P. maximowiczii*; DN=*P. deltoides* x *P. nigra*; NM=*P. nigra* x *P. maximowiczii*.

Pedigree	<i>ROOTNUM = a + b(Soil Growing Degree Days)</i>						
	n	<i>R</i> ²	<i>P</i> -value _b	a	b	<i>P</i> _{min} ^z	<i>P</i> _{max}
BC ₁	1296	0.32	0.0221	3.5042	0.0426	3.50	7.25
D	864	0.12	0.1822	2.7505	0.0195	2.75	4.47
DM	1080	0.16	0.1278	2.9681	0.0125	2.97	4.07
DN	864	0.40	0.0083	2.4205	0.0348	2.42	5.48
NM	432	0.29	0.0299	2.7445	0.0383	2.74	6.11

^z*P*_{min} = Predicted minimum ROOTNUM; *P*_{max} = Predicted maximum ROOTNUM

Figure 33. Total root length versus soil growing degree days of five hybrid poplar pedigrees (listed in the figure) in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings. Each point, except for that of 33 GDD and 69 GDD (which represent 2n due to similar GDD at two site x planting date combinations) represents the mean of the following number (n) of cuttings: A.) 72, B.) 48, C.) 60, D.) 48, and E.) 24.

Figure 33. Continued.

Figure 33. Continued.

Table 37. Regression equation coefficients and derived statistics for total root length (TOTRTLG) per cutting of five hybrid poplar pedigrees in an experiment testing clones in their ability to develop roots and shoots from dormant, unrooted cuttings when planted across three sites (Ames, IA; Waseca, MN; Westport, MN) and two growing seasons (2001, 2002). Pedigrees are: BC₁=(*P. trichocarpa* x *P. deltoides*) x *P. deltoides*; D=*P. deltoides*; DM=*P. deltoides* x *P. maximowiczii*; DN=*P. deltoides* x *P. nigra*; NM=*P. nigra* x *P. maximowiczii*.

Pedigree	TOTRTLG = a + b(Soil Growing Degree Days)						
	n	R ²	P-value _b	a	b	P _{min} ^z	P _{max}
BC ₁	1296	0.29	0.0311	4.5716	0.1324	4.57	16.22
D	864	0.23	0.0612	3.0964	0.0705	3.10	9.30
DM	1080	0.19	0.0931	3.1973	0.0504	3.20	7.63
DN	864	0.42	0.0067	3.0284	0.0947	3.03	11.36
NM	432	0.42	0.0070	2.2528	0.1209	2.25	12.89

^zP_{min} = Predicted minimum TOTRTLG; P_{max} = Predicted maximum TOTRTLG

APPENDIX C. TEMPERATURE AND PRECIPITATION DATA

Table 38. Temperature and precipitation data across sites and years.

Year	Site	Planting Date	Julian Day	Soil Max ^z	Soil Min ^z	Soil GDD ^y	Air Max ^z	Air Min ^z	Air GDD ^y	Precip ^x
2001	Ames	1	109	11.59	8.85	0.22	23.49	5.77	4.63	0.00
			110	14.52	11.16	2.84	29.25	13.57	11.41	0.18
			111	14.13	13.53	3.83	19.27	7.30	3.29	0.05
			112	13.36	11.87	2.62	26.28	8.83	7.56	1.85
			113	13.31	10.36	1.84	13.88	0.32	0.00	0.00
			114	11.90	9.37	0.64	21.75	1.46	1.61	0.18
			115	13.86	10.55	2.21	25.29	2.55	3.92	0.00
			116	15.48	12.33	3.91	31.30	6.84	9.07	0.00
			117	16.93	13.79	5.36	29.64	6.98	8.31	0.00
			118	17.63	15.33	6.48	28.97	12.97	10.97	0.00
			119	18.50	16.16	7.33	29.91	13.85	11.88	0.00
			120	17.68	16.07	6.88	22.19	11.03	6.61	0.66
			121	17.99	15.44	6.72	30.51	11.15	10.83	0.46
			122	17.43	15.37	6.40	17.99	12.11	5.05	0.99
						57.25			95.13	4.37
2001	Ames	2	114	11.90	9.37	0.64	21.75	1.46	1.61	0.18
			115	13.86	10.55	2.21	25.29	2.55	3.92	0.00
			116	15.48	12.33	3.91	31.30	6.84	9.07	0.00
			117	16.93	13.79	5.36	29.64	6.98	8.31	0.00
			118	17.63	15.33	6.48	28.97	12.97	10.97	0.00
			119	18.50	16.16	7.33	29.91	13.85	11.88	0.00
			120	17.68	16.07	6.88	22.19	11.03	6.61	0.66
			121	17.99	15.44	6.72	30.51	11.15	10.83	0.46
			122	17.43	15.37	6.40	17.99	12.11	5.05	0.99
			123	15.42	14.53	4.98	17.89	10.31	4.10	2.11
			124	14.91	14.29	4.60	16.20	11.33	3.77	0.30
			125	14.31	13.69	4.00	17.37	10.67	4.02	0.38
			126	15.37	14.09	4.73	23.24	9.09	6.17	0.56
			127	15.18	13.96	4.57	21.53	7.11	4.32	0.00
						68.78			90.62	5.64
2001	Ames	3	120	17.68	16.07	6.88	22.19	11.03	6.61	0.66
			121	17.99	15.44	6.72	30.51	11.15	11.84	0.46
			122	17.43	15.37	6.40	17.99	12.11	4.76	0.99
			123	15.42	14.53	4.98	17.89	10.31	4.10	2.11
			124	14.91	14.29	4.60	16.20	11.33	3.44	0.30
			125	14.31	13.69	4.00	17.37	10.67	4.07	0.38
			126	15.37	14.09	4.73	23.24	9.09	5.94	0.56
			127	15.18	13.96	4.57	21.53	7.11	4.32	0.00
			128	16.21	13.33	4.77	26.49	9.27	7.88	0.00
			129	18.09	14.80	6.45	31.07	9.35	10.21	0.18
			130	19.09	16.76	7.93	28.26	9.45	8.86	2.49
			131	17.73	16.19	6.96	22.85	4.80	3.83	0.00
			132	17.19	15.26	6.23	22.64	4.67	3.66	0.00
			133	16.38	15.04	5.71	16.04	11.02	3.53	0.66
						80.90			83.03	8.79

^xMaximum and minimum soil temperature and air temperature (°C).^ySoil and air growing degree days estimated as [(max temperature + min temperature) / 2] - 10, where 10 equals the base temperature (°C).^zPrecipitation measured in cm.

Table 38. Continued.

Year	Site	Planting Date	Julian Day	Soil Max	Soil Min	Soil GDD	Air Max	Air Min	Air GDD	Precip
2001	Waseca	1	129	14.43	12.79	3.61	27.10	12.17	9.64	0.00
			130	13.67	12.72	3.20	19.74	8.49	4.12	0.61
			131	14.00	12.17	3.09	18.96	3.06	1.01	0.69
			132	14.62	11.65	3.14	22.25	3.05	2.65	0.00
			133	15.15	12.98	4.07	20.94	11.12	6.03	0.00
			134	17.52	13.61	5.57	34.84	12.25	13.55	0.00
			135	19.73	16.77	8.25	34.46	12.57	13.52	0.00
			136	19.74	17.65	8.70	29.18	10.95	10.07	0.00
			137	19.01	17.15	8.08	27.74	7.87	7.81	0.00
			138	19.46	16.55	8.01	27.96	9.16	8.56	0.00
			139	19.42	17.01	8.22	28.42	9.32	8.87	0.00
			140	18.35	15.81	7.08	16.92	8.63	2.78	0.10
			141	15.76	13.81	4.79	15.15	6.33	0.74	5.11
			142	13.76	11.66	2.71	9.39	3.39	0.00	0.08
			78.48						89.32	6.58
2001	Waseca	2	136	19.74	17.65	8.70	29.18	10.95	10.07	0.00
			137	19.01	17.15	8.08	27.74	7.87	7.81	0.00
			138	19.46	16.55	8.01	27.96	9.16	8.56	0.00
			139	19.42	17.01	8.22	28.42	9.32	8.87	0.00
			140	18.35	15.81	7.08	16.92	8.63	2.78	0.10
			141	15.76	13.81	4.79	15.15	6.33	0.74	5.11
			142	13.76	11.66	2.71	9.39	3.39	0.00	0.08
			143	12.11	10.92	1.52	11.78	3.56	0.00	0.48
			144	12.27	11.02	1.65	13.65	6.87	0.26	0.28
			145	12.44	11.65	2.05	13.14	9.35	1.25	0.18
			146	13.62	11.85	2.74	16.81	6.28	1.55	2.11
			147	14.49	12.26	3.38	20.47	6.98	3.73	0.00
			148	15.87	12.86	4.37	24.04	7.02	5.53	0.00
			149	16.62	14.15	5.39	23.91	7.67	5.79	0.00
			68.64						56.91	8.33
2001	Waseca	3	142	13.76	11.66	2.71	9.39	3.39	0.00	0.08
			143	12.11	10.92	1.52	11.78	3.56	0.00	0.48
			144	12.27	11.02	1.65	13.65	6.87	0.26	0.28
			145	12.44	11.65	2.05	13.14	9.35	1.25	0.18
			146	13.62	11.85	2.74	16.81	6.28	1.55	2.11
			147	14.49	12.26	3.38	20.47	6.98	3.73	0.00
			148	15.87	12.86	4.37	24.04	7.02	5.53	0.00
			149	16.62	14.15	5.39	23.91	7.67	5.79	0.00
			150	16.70	14.75	5.73	21.37	7.48	4.43	0.00
			151	15.37	14.25	4.81	18.10	5.83	1.97	0.00
			152	14.38	13.49	3.94	16.24	7.53	1.89	0.00
			153	14.74	12.97	3.86	19.72	6.11	2.92	0.46
			154	16.06	13.10	4.58	19.97	6.51	3.24	0.00
			155	15.58	13.99	4.79	19.13	7.93	3.53	0.00
			51.47						36.06	3.58

Table 38. Continued.

Year	Site	Planting Date	Julian Day	Soil Max	Soil Min	Soil GDD	Air Max	Air Min	Air GDD	Precip
2001	Westport	1	130	14.71	12.74	3.73	21.20	7.44	4.32	0.00
			131	15.46	12.10	3.78	20.09	1.55	0.82	0.00
			132	17.03	11.95	4.49	24.32	2.98	3.65	0.00
			133	18.71	13.49	6.10	27.51	5.54	6.53	0.00
			134	21.00	15.95	8.48	36.97	12.61	14.79	0.00
			135	22.19	18.27	10.23	36.31	9.60	12.96	0.00
			136	20.38	17.96	9.17	25.12	10.05	7.59	0.00
			137	20.63	17.31	8.97	23.41	5.87	4.64	0.13
			138	21.99	16.74	9.37	28.48	5.87	7.18	0.00
			139	19.27	17.17	8.22	21.54	11.64	6.59	0.00
			140	18.40	14.24	6.32	22.87	5.59	4.23	0.56
			141	14.17	11.46	2.82	12.85	5.01	0.00	0.41
			142	11.42	8.97	0.20	7.49	2.28	0.00	0.25
			143	10.74	8.42	0.00	12.38	2.48	0.00	2.03
						81.86			73.28	3.38
2001	Westport	2	137	20.63	17.31	8.97	23.41	5.87	4.64	0.13
			138	21.99	16.74	9.37	28.48	5.87	7.18	0.00
			139	19.27	17.17	8.22	21.54	11.64	6.59	0.00
			140	18.40	14.24	6.32	22.87	5.59	4.23	0.56
			141	14.17	11.46	2.82	12.85	5.01	0.00	0.41
			142	11.42	8.97	0.20	7.49	2.28	0.00	0.25
			143	10.74	8.42	0.00	12.38	2.48	0.00	2.03
			144	12.21	9.26	0.73	18.43	4.94	1.69	0.03
			145	12.66	10.58	1.62	19.63	9.09	4.36	0.10
			146	12.57	11.46	2.02	14.71	8.99	1.85	0.36
			147	13.99	11.58	2.79	18.14	6.11	2.13	1.14
			148	16.60	12.05	4.33	25.19	5.62	5.41	0.18
			149	17.95	13.39	5.67	24.34	5.96	5.15	0.00
			150	17.88	14.18	6.03	22.60	6.25	4.43	0.00
						59.07			47.64	5.18
2001	Westport	3	141	14.17	11.46	2.82	12.85	5.01	0.00	0.41
			142	11.42	8.97	0.20	7.49	2.28	0.00	0.25
			143	10.74	8.42	0.00	12.38	2.48	0.00	2.03
			144	12.21	9.26	0.73	18.43	4.94	1.69	0.03
			145	12.66	10.58	1.62	19.63	9.09	4.36	0.10
			146	12.57	11.46	2.02	14.71	8.99	1.85	0.36
			147	13.99	11.58	2.79	18.14	6.11	2.13	1.14
			148	16.60	12.05	4.33	25.19	5.62	5.41	0.18
			149	17.95	13.39	5.67	24.34	5.96	5.15	0.00
			150	17.88	14.18	6.03	22.60	6.25	4.43	0.00
			151	17.08	15.06	6.07	20.19	10.66	5.43	0.00
			152	16.78	13.92	5.35	19.43	7.68	3.56	0.48
			153	17.29	13.26	5.28	22.47	4.71	3.59	0.00
			154	19.48	14.04	6.76	22.59	5.52	4.06	0.00
						49.65			41.63	4.98

Table 38. Continued.

Year	Site	Planting Date	Julian Day	Soil Max	Soil Min	Soil GDD	Air Max	Air Min	Air GDD	Precip
2002	Ames	1	103	10.09	8.66	0.00	17.45	4.00	0.73	0.00
			104	11.87	7.51	0.00	27.40	8.44	7.92	0.00
			105	14.79	11.24	3.02	32.92	13.69	13.31	0.00
			106	16.22	14.32	5.27	29.60	10.70	10.15	0.43
			107	16.29	14.71	5.50	26.44	10.23	8.34	0.00
			108	16.86	15.28	6.07	31.79	7.32	9.56	0.05
			109	15.95	14.21	5.08	15.44	6.30	0.87	0.00
			110	14.17	12.31	3.24	13.60	3.17	0.00	1.42
			111	12.27	9.77	1.02	5.77	0.53	0.00	0.46
			112	10.82	9.09	0.00	12.82	1.75	0.00	0.00
			113	12.68	9.84	1.26	24.05	5.60	4.83	0.00
			114	12.56	11.35	1.96	15.09	2.84	0.00	0.30
			115	11.76	10.16	0.96	14.16	-2.19	0.00	0.00
			116	11.67	9.93	0.80	14.78	2.01	0.00	0.00
			34.17						55.69	
2002	Ames	2	110	14.17	12.31	3.24	13.60	3.17	0.00	1.42
			111	12.27	9.77	1.02	5.77	0.53	0.00	0.46
			112	10.82	9.09	0.00	12.82	1.75	0.00	0.00
			113	12.68	9.84	1.26	24.05	5.60	4.83	0.00
			114	12.56	11.35	1.96	15.09	2.84	0.00	0.30
			115	11.76	10.16	0.96	14.16	-2.19	0.00	0.00
			116	11.67	9.93	0.80	14.78	2.01	0.00	0.00
			117	11.31	9.87	0.59	12.33	2.94	0.00	3.84
			118	9.85	8.88	0.00	7.76	1.64	0.00	0.03
			119	11.24	8.35	0.00	21.00	2.79	1.90	0.00
			120	11.08	10.34	0.71	15.84	5.18	0.51	0.08
			121	11.57	10.37	0.97	16.42	2.52	0.00	1.14
			122	11.14	9.58	0.36	15.80	-1.20	0.00	0.03
			123	12.45	9.56	1.01	21.57	-1.49	0.04	0.00
			12.87						7.27	
2002	Ames	3	116	11.67	9.93	0.80	14.78	2.01	0.00	0.00
			117	11.31	9.87	0.59	12.33	2.94	0.00	3.84
			118	9.85	8.88	0.00	7.76	1.64	0.00	0.03
			119	11.24	8.35	0.00	21.00	2.79	1.90	0.00
			120	11.08	10.34	0.71	15.84	5.18	0.51	0.08
			121	11.57	10.37	0.97	16.42	2.52	0.00	1.14
			122	11.14	9.58	0.36	15.80	-1.20	0.00	0.03
			123	12.45	9.56	1.01	21.57	-1.49	0.04	0.00
			124	13.42	11.20	2.31	22.32	4.62	3.47	0.00
			125	15.00	12.07	3.54	28.92	7.32	8.12	0.18
			126	16.93	14.39	5.66	29.46	10.16	9.81	0.00
			127	16.50	15.31	5.91	23.91	9.00	6.46	0.00
			128	17.64	15.56	6.60	29.20	7.15	8.18	0.00
			129	16.70	15.10	5.90	15.45	1.92	0.00	0.00
			34.35						38.48	

Table 38. Continued.

Year	Site	Planting Date	Julian Day	Soil Max	Soil Min	Soil GDD	Air Max	Air Min	Air GDD	Precip
2002	Waseca	1	120	9.82	6.96	0.00	19.60	0.82	0.21	0.00
			121	8.93	7.51	0.00	12.33	-2.77	0.00	0.00
			122	7.95	6.57	0.00	11.83	-5.35	0.00	0.10
			123	9.44	5.81	0.00	19.70	-4.40	0.00	0.00
			124	11.05	8.57	0.00	18.83	-1.43	0.00	0.00
			125	12.09	8.54	0.32	26.30	-1.38	2.46	0.00
			126	11.98	10.56	1.27	14.70	3.73	0.00	0.58
			127	10.51	9.15	0.00	11.96	3.70	0.00	0.03
			128	10.98	9.07	0.03	21.57	3.48	2.53	0.66
			129	9.89	7.43	0.00	9.11	-0.61	0.00	0.08
			130	10.39	6.76	0.00	18.78	-0.30	0.00	0.00
			131	9.78	8.03	0.00	12.36	5.15	0.00	0.03
			132	8.41	7.44	0.00	9.78	0.25	0.00	1.04
			133	10.33	7.00	0.00	19.78	1.89	0.84	0.00
						1.61			6.03	2.51
2002	Waseca	2	136	14.20	12.30	3.25	18.24	2.74	0.49	0.00
			137	13.87	11.20	2.54	16.24	0.69	0.00	0.00
			138	13.83	11.03	2.43	17.34	-1.17	0.00	0.00
			139	13.82	10.92	2.37	17.54	0.19	0.00	0.00
			140	13.88	10.95	2.42	17.98	0.37	0.00	0.00
			141	14.27	11.41	2.84	20.85	4.39	2.62	0.00
			142	14.54	12.29	3.42	25.08	8.71	6.90	0.00
			143	16.10	14.22	5.16	20.74	6.83	3.79	0.00
			144	16.26	13.51	4.89	19.83	6.76	3.30	0.00
			145	15.60	13.86	4.73	21.86	8.24	5.05	0.41
			146	16.07	14.00	5.04	26.35	11.67	9.01	0.03
			147	17.64	14.55	6.10	27.29	13.11	10.20	0.18
			148	16.79	15.65	6.22	26.74	12.13	9.44	0.28
			149	18.73	15.37	7.05	29.57	12.27	10.92	0.94
						58.43			61.70	1.83
2002	Waseca	3	143	16.10	14.22	5.16	20.74	6.83	3.79	0.00
			144	16.26	13.51	4.89	19.83	6.76	3.30	0.00
			145	15.60	13.86	4.73	21.86	8.24	5.05	0.41
			146	16.07	14.00	5.04	26.35	11.67	9.01	0.03
			147	17.64	14.55	6.10	27.29	13.11	10.20	0.18
			148	16.79	15.65	6.22	26.74	12.13	9.44	0.28
			149	18.73	15.37	7.05	29.57	12.27	10.92	0.94
			150	20.54	17.07	8.81	33.55	12.95	13.25	0.08
			151	20.40	18.20	9.30	30.26	11.89	11.08	0.00
			152	20.51	18.17	9.34	31.33	13.83	12.58	0.03
			153	19.13	16.21	7.67	23.14	11.12	7.13	0.10
			154	16.19	14.61	5.40	15.84	11.15	3.50	4.37
			155	14.59	13.27	3.93	12.97	5.44	0.00	1.45
			156	16.54	12.79	4.67	25.26	5.34	5.30	0.41
						88.29			104.53	8.26

Table 38. Continued.

Year	Site	Planting Date	Julian Day	Soil Max	Soil Min	Soil GDD	Air Max	Air Min	Air GDD	Precip
2002	Westport	1	119	8.71	3.55	0.00	16.91	-2.38	0.00	0.00
			120	9.16	5.05	0.00	17.31	-1.10	0.00	0.00
			121	9.40	5.58	0.00	14.19	-5.39	0.00	0.00
			122	8.92	4.36	0.00	12.15	-5.34	0.00	0.00
			123	9.89	4.72	0.00	20.82	-0.38	0.22	0.00
			124	10.33	7.31	0.00	14.95	-0.28	0.00	0.10
			125	9.19	6.27	0.00	20.09	1.34	0.72	0.10
			126	10.13	6.75	0.00	16.72	3.04	0.00	0.03
			127	9.72	7.22	0.00	11.67	3.33	0.00	2.84
			128	7.78	5.83	0.00	7.22	2.78	0.00	1.52
			129	6.39	4.72	0.00	8.06	1.67	0.00	0.03
			130	7.50	4.17	0.00	12.50	2.50	0.00	0.00
			131	8.33	5.28	0.00	13.89	4.44	0.00	1.32
			132	8.33	6.67	0.00	12.22	3.61	0.00	0.00
						0.00			0.94	5.94
2002	Westport	2	135	12.22	8.61	0.41	23.61	4.17	3.89	0.05
			136	12.69	9.14	0.91	16.26	-1.59	0.00	0.00
			137	13.20	7.88	0.54	15.80	-1.79	0.00	0.00
			138	13.67	8.30	0.98	15.48	-1.89	0.00	0.00
			139	14.13	8.67	1.40	16.06	-2.27	0.00	0.00
			140	15.63	9.20	2.42	18.78	-2.49	0.00	0.00
			141	15.38	10.57	2.98	21.67	2.34	2.01	0.00
			142	14.06	12.02	3.04	22.52	7.68	5.10	0.00
			143	13.54	10.54	2.04	12.79	-1.65	0.00	0.00
			144	15.27	9.34	2.31	16.74	-1.87	0.00	0.00
			145	16.74	12.04	4.39	22.66	4.04	3.35	0.00
			146	16.63	12.52	4.58	23.23	3.97	3.60	0.00
			147	19.55	13.35	6.45	28.56	8.80	8.68	0.00
			148	17.56	15.67	6.62	24.21	10.64	7.43	0.46
						39.06			34.05	0.51
2002	Westport	3	142	14.06	12.02	3.04	22.52	7.68	5.10	0.00
			143	13.54	10.54	2.04	12.79	-1.65	0.00	0.00
			144	15.27	9.34	2.31	16.74	-1.87	0.00	0.00
			145	16.74	12.04	4.39	22.66	4.04	3.35	0.00
			146	16.63	12.52	4.58	23.23	3.97	3.60	0.00
			147	19.55	13.35	6.45	28.56	8.80	8.68	0.00
			148	17.56	15.67	6.62	24.21	10.64	7.43	0.46
			149	20.13	15.25	7.69	30.81	13.33	12.07	0.15
			150	21.95	16.34	9.15	33.76	12.49	13.13	0.00
			151	23.25	17.60	10.43	31.52	12.69	12.11	0.00
			152	23.34	18.76	11.05	29.12	11.47	10.30	0.00
			153	19.62	16.04	7.83	20.67	7.76	4.22	0.08
			154	15.98	13.17	4.58	10.91	7.64	0.00	0.00
			155	17.39	12.64	5.02	23.12	8.14	5.63	0.00
						85.15			85.60	0.69

**APPENDIX D. PLOTS OF TEMPERATURE AND PRECIPITATION
DATA ACROSS JULIAN DATES**

Figure 34. Maximum and minimum soil temperature, belowground growing degree days (GDD), precipitation events (denoted with arrows), and the differential between aboveground GDD and belowground GDD across Julian dates. Each black bar on the top of the figure represents a planting date, with the mean root length of 252 cuttings listed above it. The data represent the following site x year combinations: A.) Ames 2001, B.) Ames 2002, C.) Waseca 2001, D.) Waseca 2002, E.) Westport 2001, and F.) Westport 2002.

B

Figure 34. Continued.

C

Figure 34. Continued.

D

Figure 34. Continued.

Figure 34. Continued.

Figure 34. Continued.

**APPENDIX E. TABLES RANKING EACH YEAR X SITE X
PLANTING DATE COMBINATION WITH RESPECT
TO MEAN ROOT LENGTH, NUMBER OF DAYS
WITH >4 AND >5 GROWING DEGREE DAYS, AND
PRECIPITATION FOR EACH PEDIGREE**

Table 39. MEANRTL_G (cm), number of days with >4 and >5 growing degree days (GDD), and total precipitation across years, sites, and planting dates in an experiment testing five hybrid poplar pedigrees in their ability to develop roots and shoots from dormant, unrooted cuttings. MEANRTL_G is estimated for the BC₁ [(*P. trichocarpa* x *P. deltoides*) x *P. deltoides*] pedigree, n=72 cuttings.

Pooled rank ^a	Year	Site	Planting date	MEAN-RTL _G (cm)	Number of days with >4 GDD	Number of days with >5 GDD	Total precip (cm)	Comments
1	2001	Ames	3	2.7	14	13	8.8	High precipitation dispersed throughout growth period.
3	2002	Ames	3	1.6	5	4	5.3	High precipitation dispersed throughout growth period.
2	2002	Ames	1	1.6	4	4	2.7	Low precipitation dispersed throughout growth period.
4	2001	Waseca	3	1.5	8	5	3.6	Moderate precipitation at beginning; very low precipitation throughout final nine days.
7	2001	Westport	2	1.2	7	6	5.2	High precipitation dispersed throughout growth period.
5	2002	Westport	3	1.0	11	10	0.7	Low precipitation dispersed throughout growth period; high soil temperatures.
8	2001	Westport	1	0.9	11	9	3.4	Low precipitation at beginning; high soil temperatures.
8	2001	Westport	3	0.9	7	6	5.0	Low precipitation at end, very low soil temperatures at beginning.
9	2001	Waseca	2	0.9	8	7	8.3	High precipitation in middle (too much at one time?); low precipitation at beginning and end.
6	2002	Waseca	3	0.9	14	13	8.3	High precipitation dispersed throughout growth period; excess at end.
7	2002	Ames	2	0.9	0	0	7.3	High precipitation; inadequate soil temperatures.
5	2001	Waseca	1	0.8	10	8	6.6	High precipitation at beginning and end; high soil temperatures.
9	2002	Waseca	2	0.7	7	7	1.8	Low precipitation at beginning; moderate precipitation during final five days.
9	2001	Ames	1	0.7	8	6	4.4	Low precipitation at beginning and end; nothing in the middle.
9	2001	Ames	2	0.6	12	10	5.6	Low precipitation at beginning.
11	2002	Westport	1	0.6	0	0	5.9	High precipitation; inadequate soil temperatures.
10	2002	Westport	2	0.5	4	3	0.5	Low precipitation; inadequate throughout growing period; low soil temperatures at beginning.
12	2002	Waseca	1	0.2	0	0	2.5	Low precipitation; inadequate soil temperatures.

^aMEANRTL_G rank pooled across all pedigrees.

Table 40. MEANRTLГ (cm), number of days with >4 and >5 growing degree days (GDD), and total precipitation across years, sites, and planting dates in an experiment testing five hybrid poplar pedigrees in their ability to develop roots and shoots from dormant, unrooted cuttings. MEANRTLГ is estimated for the D (*P. deltoides*) pedigree, n=48 cuttings.

Pooled rank ^a	Year	Site	Planting date	MEAN-RTLГ (cm)	Number of days with >4 GDD	Number of days with >5 GDD	Total precip (cm)	Comments
2	2002	Ames	1	1.3	4	4	2.7	Low precipitation dispersed throughout growth period.
3	2002	Ames	3	1.1	5	4	5.3	High precipitation dispersed throughout growth period.
5	2002	Westport	3	1.1	11	10	0.7	Low precipitation dispersed throughout growth period; high soil temperatures.
6	2002	Waseca	3	0.9	14	13	8.3	High precipitation dispersed throughout growth period; excess at end.
7	2002	Ames	2	0.8	0	0	7.3	High precipitation; inadequate soil temperatures.
10	2002	Westport	2	0.7	4	3	0.5	Low precipitation; inadequate throughout growing period; low soil temperatures at beginning.
4	2001	Waseca	3	0.6	8	5	3.6	Moderate precipitation at beginning; very low precipitation throughout final nine days.
1	2001	Ames	3	0.6	14	13	8.8	High precipitation dispersed throughout growth period.
7	2001	Westport	2	0.5	7	6	5.2	High precipitation dispersed throughout growth period.
9	2002	Waseca	2	0.5	7	7	1.8	Low precipitation at beginning; moderate precipitation during final five days.
9	2001	Waseca	2	0.4	8	7	8.3	High precipitation in middle (too much at one time?); low precipitation at beginning and end.
5	2001	Waseca	1	0.4	10	8	6.6	High precipitation at beginning and end; high soil temperatures.
9	2001	Ames	2	0.4	12	10	5.6	Low precipitation at beginning.
8	2001	Westport	3	0.2	7	6	5.0	Low precipitation at end, very low soil temperatures at beginning.
11	2002	Westport	1	0.1	0	0	5.9	High precipitation; inadequate soil temperatures.
8	2001	Westport	1	0.1	11	9	3.4	Low precipitation at beginning; high soil temperatures.
9	2001	Ames	1	0.1	8	6	4.4	Low precipitation at beginning and end; nothing in the middle.
12	2002	Waseca	1	0.1	0	0	2.5	Low precipitation; inadequate soil temperatures.

^aMEANRTLГ rank pooled across all pedigrees.

Table 41. MEANRTLГ (cm), number of days with >4 and >5 growing degree days (GDD), and total precipitation across years, sites, and planting dates in an experiment testing five hybrid poplar pedigrees in their ability to develop roots and shoots from dormant, unrooted cuttings. MEANRTLГ is estimated for the DM (*P. deltoides* x *P. maximowiczii*) pedigree, n=60 cuttings.

Pooled rank ^a	Year	Site	Planting date	MEAN-RTLГ (cm)	Number of days with >4 GDD	Number of days with >5 GDD	Total precip (cm)	Comments
1	2001	Ames	3	2.0	14	13	8.8	High precipitation dispersed throughout growth period.
2	2002	Ames	1	1.9	4	4	2.7	Low precipitation dispersed throughout growth period.
5	2001	Waseca	1	1.7	10	8	6.6	High precipitation at beginning and end; high soil temperatures.
3	2002	Ames	3	1.6	5	4	5.3	High precipitation dispersed throughout growth period.
4	2001	Waseca	3	1.2	8	5	3.6	Moderate precipitation at beginning; very low precipitation throughout final nine days.
9	2001	Ames	1	1.2	8	6	4.4	Low precipitation at beginning and end; nothing in the middle.
8	2001	Westport	3	0.9	7	6	5.0	Low precipitation at end, very low soil temperatures at beginning.
9	2001	Ames	2	0.9	12	10	5.6	Low precipitation at beginning.
8	2001	Westport	1	0.9	11	9	3.4	Low precipitation at beginning; high soil temperatures.
6	2002	Waseca	3	0.9	14	13	8.3	High precipitation dispersed throughout growth period; excess at end.
7	2001	Westport	2	0.9	7	6	5.2	High precipitation dispersed throughout growth period.
5	2002	Westport	3	0.8	11	10	0.7	Low precipitation dispersed throughout growth period; high soil temperatures.
10	2002	Westport	2	0.7	4	3	0.5	Low precipitation; inadequate throughout growing period; low soil temperatures at beginning.
9	2001	Waseca	2	0.7	8	7	8.3	High precipitation in middle (too much at one time?); low precipitation at beginning and end.
7	2002	Ames	2	0.6	0	0	7.3	High precipitation; inadequate soil temperatures.
9	2002	Waseca	2	0.6	7	7	1.8	Low precipitation at beginning; moderate precipitation during final five days.
12	2002	Waseca	1	0.5	0	0	2.5	Low precipitation; inadequate soil temperatures.
11	2002	Westport	1	0.4	0	0	5.9	High precipitation; inadequate soil temperatures.

^aMEANRTLГ rank pooled across all pedigrees.

Table 42. MEANRTLГ (cm), number of days with >4 and >5 growing degree days (GDD), and total precipitation across years, sites, and planting dates in an experiment testing five hybrid poplar pedigrees in their ability to develop roots and shoots from dormant, unrooted cuttings. MEANRTLГ is estimated for the DN (*P. deltoides* x *P. nigra*) pedigree, n=48 cuttings.

Pooled rank ^a	Year	Site	Planting date	MEAN-RTLГ (cm)	Number of days with >4 GDD	Number of days with >5 GDD	Total precip (cm)	Comments
1	2001	Ames	3	2.2	14	13	8.8	High precipitation dispersed throughout growth period.
3	2002	Ames	3	2.0	5	4	5.3	High precipitation dispersed throughout growth period.
4	2001	Waseca	3	1.9	8	5	3.6	Moderate precipitation at beginning; very low precipitation throughout final nine days.
2	2002	Ames	1	1.8	4	4	2.7	Low precipitation dispersed throughout growth period.
7	2002	Ames	2	1.4	0	0	7.3	High precipitation; inadequate soil temperatures.
5	2002	Westport	3	1.3	11	10	0.7	Low precipitation dispersed throughout growth period; high soil temperatures.
5	2001	Waseca	1	1.2	10	8	6.6	High precipitation at beginning and end; high soil temperatures.
6	2002	Waseca	3	1.0	14	13	8.3	High precipitation dispersed throughout growth period; excess at end.
9	2002	Waseca	2	0.9	7	7	1.8	Low precipitation at beginning; moderate precipitation during final five days.
7	2001	Westport	2	0.9	7	6	5.2	High precipitation dispersed throughout growth period.
8	2001	Westport	3	0.9	7	6	5.0	Low precipitation at end, very low soil temperatures at beginning.
9	2001	Ames	1	0.7	8	6	4.4	Low precipitation at beginning and end; nothing in the middle.
8	2001	Westport	1	0.6	11	9	3.4	Low precipitation at beginning; high soil temperatures.
10	2002	Westport	2	0.6	4	3	0.5	Low precipitation; inadequate throughout growing period; low soil temperatures at beginning.
9	2001	Waseca	2	0.6	8	7	8.3	High precipitation in middle (too much at one time?); low precipitation at beginning and end.
9	2001	Ames	2	0.5	12	10	5.6	Low precipitation at beginning.
11	2002	Westport	1	0.2	0	0	5.9	High precipitation; inadequate soil temperatures.
12	2002	Waseca	1	0.2	0	0	2.5	Low precipitation; inadequate soil temperatures.

^aMEANRTLГ rank pooled across all pedigrees.

Table 43. MEANRTLГ (cm), number of days with >4 and >5 growing degree days (GDD), and total precipitation across years, sites, and planting dates in an experiment testing five hybrid poplar pedigrees in their ability to develop roots and shoots from dormant, unrooted cuttings. MEANRTLГ is estimated for the NM (*P. nigra* x *P. maximowiczii*) pedigree, n=24 cuttings.

Pooled rank ²	Year	Site	Planting date	MEAN-RTLГ (cm)	Number of days with >4 GDD	Number of days with >5 GDD	Total precip (cm)	Comments
1	2001	Ames	3	3.2	14	13	8.8	High precipitation dispersed throughout growth period.
2	2002	Ames	1	2.1	4	4	2.7	Low precipitation dispersed throughout growth period.
6	2002	Waseca	3	1.8	14	13	8.3	High precipitation dispersed throughout growth period; excess at end.
5	2001	Waseca	1	1.8	10	8	6.6	High precipitation at beginning and end; high soil temperatures.
9	2001	Ames	2	1.7	12	10	5.6	Low precipitation at beginning.
8	2001	Westport	1	1.6	11	9	3.4	Low precipitation at beginning; high soil temperatures.
5	2002	Westport	3	1.5	11	10	0.7	Low precipitation dispersed throughout growth period; high soil temperatures.
3	2002	Ames	3	1.5	5	4	5.3	High precipitation dispersed throughout growth period.
4	2001	Waseca	3	1.5	8	5	3.6	Moderate precipitation at beginning; very low precipitation throughout final nine days.
7	2001	Westport	2	1.3	7	6	5.2	High precipitation dispersed throughout growth period.
9	2001	Waseca	2	1.2	8	7	8.3	High precipitation in middle (too much at one time?); low precipitation at beginning and end.
9	2001	Ames	1	1.1	8	6	4.4	Low precipitation at beginning and end; nothing in the middle.
9	2002	Waseca	2	1.0	7	7	1.8	Low precipitation at beginning; moderate precipitation during final five days.
7	2002	Ames	2	1.0	0	0	7.3	High precipitation; inadequate soil temperatures.
8	2001	Westport	3	0.9	7	6	5.0	Low precipitation at end, very low soil temperatures at beginning.
10	2002	Westport	2	0.7	4	3	0.5	Low precipitation; inadequate throughout growing period; low soil temperatures at beginning.
11	2002	Westport	1	0.5	0	0	5.9	High precipitation; inadequate soil temperatures.
12	2002	Waseca	1	0.4	0	0	2.5	Low precipitation; inadequate soil temperatures.

²MEANRTLГ rank pooled across all pedigrees.

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BIOGRAPHICAL SKETCH

I was born June 8, 1977 in Rhinelander, Wisconsin. I was a Rotary International Youth Exchange student to Germany in 1993-1994. My early awards include the National Science Merit Award in biology (1993), Wisconsin All-State Academic Scholar (1995), and Karen Krull-Haissig Scholarship (1995).

I received the Bachelor of Science in Natural Resources and Environmental Studies from the University of Minnesota-Twin Cities in 1999, with minors in Forest Resources and German. During my undergraduate work, I served four clubs (Forestry, Environmental Studies, German, & Campus Ambassadors) and was inducted into four honor societies (Xi Sigma Pi, Gamma Sigma Delta, Phi Kappa Phi, & Golden Key). I was also an avid member of the Society of American Foresters. I was the recipient of the A.G. Roan Scholarship for Conservation Ethic in 1998.

I began my professional career working for Dr. Don E. Riemenschneider and Mr. Edmund O. Bauer of the USDA Forest Service, North Central Research Station, Forestry Sciences Laboratory in Rhinelander, Wisconsin, during June 1995. In 1998, I received the USDA Forest Service Health and Safety Certificate of Merit Award for the writing of a comprehensive nursery safety management plan, and in 1999 co-received the Forestry Sciences Laboratory Safety Award for writing a standing health and safety hazard analysis.

I was awarded the Sande McNabb Excellence Fellowship from Iowa State University in August 1999. I served as a research assistant for Dr. Richard B. Hall in the Department of Natural Resource Ecology and Management (formerly the Forestry Department) at Iowa State University. In 2000, I was inducted into Sigma Xi, The Scientific Research Society and the ISU chapter of Gamma Sigma Delta. I received ISU Graduate College Awards, including the Premium for Academic Excellence Award (1999-2000) and the ABD Scholarship (Spring, Summer, & Fall 2002, Spring 2003). I also received a Grant-in-Aid of Research from Sigma Xi, The Scientific Research Society (2003).