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# Biomass and Genotype × Environment Interactions of *Populus* Energy Crops in the Midwestern United States

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**Abstract** Using *Populus* feedstocks for biofuels, bioenergy, and bioproducts is becoming economically feasible as global fossil fuel prices increase. Maximizing *Populus* biomass production across regional landscapes largely depends on understanding genotype × environment interactions, given broad genetic variation at strategic (genomic group) and operational (clone) levels. A regional network of *Populus* field tests was established in the Midwest USA in 1995, 1997, and 2000 to assess relative productivity of 187 clones grown at Westport, Minnesota (45.7° N, 95.2° W); Waseca, Minnesota (only 2000; 44.1° N, 93.5° W); Arlington, Wisconsin (43.3° N, 89.4° W); and Ames, Iowa (42.0° N, 93.6° W). We evaluated biomass potential throughout plantation development and identified clones with yield substantially greater than commercial controls (Eugenei, NM6). For each site, biomass ranges (Mg ha$^{-1}$ year$^{-1}$) of the best six clones were: Westport: 2.3 to 3.9 (5 years), 8.0 to 10.1 (8 years), and 8.9 to 11.3 (10 years); Waseca: 10.4 to 13.4 (7 years); Arlington: 5.1 to 7.1 (3 years), 14.8 to 20.9 (6 years), and 16.1 to 21.1 (8 years); and Ames: 4.3 to 5.3 (4 years), 11.1 to 20.9 (7 years), and 14.3 to 24.5 (9 years). Mean biomass of the best three clones was 1.4 to 2.7 times greater than controls as trees developed at Westport (1995, 1997) and Waseca 2000. Genotype × environment interactions governed biomass production, with clone–mean rank correlations across sites ranging from 0.29 to 0.81. We identified generalist genotypes (e.g. Crandon, NC14105, NM2) with elevated biomass across the region and specialists (e.g. 7300501, 80X01015, and NC14103) with exceptional biomass at specific locations.

**Keywords** Bioenergy · Feedstock development · Hybrid poplar · Productivity · Tree improvement

**Abbreviations**

DBH diameter at breast height
LSD least significant difference
STE standard error

## Introduction

There is a global need to reduce consumption of non-renewable resources to maintain economical and eco-

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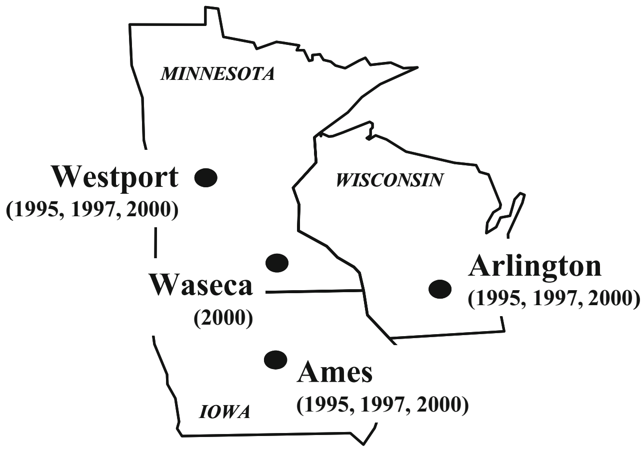


**Fig. 1** Regional network of *Populus* field tests established in 1995, 1997, and 2000 at Westport, Minnesota (45.7° N, 95.2° W), Waseca, Minnesota (44.1° N, 93.5° W), Arlington, Wisconsin (43.3° N, 89.4° W), and Ames, Iowa (42.0° N, 93.6° W) to assess productivity and regional adaptability of 187 genotypes

**Table 1** Monthly mean temperature and precipitation (1999–2008) at Westport and Waseca, Minnesota; Arlington, Wisconsin; and Ames, Iowa

| Month | Westport | Waseca | Arlington | Ames |
|---|---|---|---|---|
| Temperature (°C) | | | | |
| March | −7 | −4 | −1 | 3 |
| April | 13 | 15 | 16 | 19 |
| May | 23 | 24 | 24 | 27 |
| June | 31 | 33 | 32 | 35 |
| July | 36 | 37 | 36 | 38 |
| August | 34 | 34 | 34 | 36 |
| September | 27 | 28 | 28 | 30 |
| October | 15 | 17 | 18 | 20 |
| Precipitation (mm) | | | | |
| March | 28 | 55 | 41 | 44 |
| April | 67 | 85 | 92 | 96 |
| May | 82 | 115 | 122 | 133 |
| June | 107 | 130 | 134 | 113 |
| July | 91 | 103 | 97 | 112 |
| August | 72 | 115 | 105 | 104 |
| September | 85 | 93 | 77 | 72 |
| October | 59 | 56 | 54 | 53 |
| Total | 591 | 752 | 722 | 727 |

logical sustainability [19, 40]. Short rotation woody crops such as intensively grown *Populus* are an important component of the renewable energy supply chain. Increased fossil fuel prices in recent years have made feedstock production and management of *Populus* energy crops more economically viable than in previous years [22, 41]. More specifically, record oil, natural gas, and transportation fuel prices have made *Populus* a suitable potential alternative for the production of ethanol (cellulosics for biofuels) and electricity (biomass for bioenergy). These trees also provide associated ecological services such as carbon sequestration [2, 10, 14], contaminant remediation [47, 48], and soil stabilization [39, 44]. Additional advantages of *Populus* energy crops are that biomass can be stored on the stump and harvested throughout the year [11] and that trees have energy output:energy input ratios of up to 55:1 [23, 26].

*Populus* tree improvement programs in the United States began in the 1920s (Northeast) and 1930s (Midwest) [43]. Since then, more than 100,000 *Populus* offspring have been produced in the Midwest [48]. *Populus* species and hybrids are ideal for genetic improvement because they are fast-growing, relatively easy to propagate vegetatively, and have a broad range of genetic variation [4, 16, 33]. Given that most genetic diversity of *Populus* is at the genus level [38], there is successful intra- and inter-sectional hybridization within and between some of the six taxonomic sections, especially *Aigeiros* Duby and *Tacamahaca* Spach [6, 53]. Fifty-six percent of elite parents from the original *Populus* tree improvement programs was from these sections (29% *Aigeiros*; 27% *Tacamahaca*) [43], while *Aigeiros* and *Tacamahaca* parents constitute over 90% of recent breeding efforts in the Midwest [11, 28, 34]. Eastern cottonwood (*P. deltoides* Bartr. ex Marsh), western black cottonwood (*P. trichocarpa* Torr. & Gray), European black poplar (*P. nigra* L.), and Japanese poplar (*P. suaveolens* Fischer subsp. *maximowiczii* A. Henry) are the four species most commonly used in current Midwest *Populus* breeding.

Maximizing *Populus* biomass production across regional landscapes largely depends on understanding genotype × environment interactions, given broad genetic variation at strategic (genomic group) and operational (clone) levels. There is a lack of reported information about biomass of current experimental *Populus* genotypes in the Midwest, yet such data are needed to strengthen decisions on deploying clones for energy and other uses. The most recent reports were from 6-year-old trees of the 1995 plantings assessed in the current manuscript [34], as well as rotation-age trees from older clones that are mostly outdated and not being considered for further deployment [15, 30]. Therefore, the objective of the current study was to evaluate biomass potential throughout plantation development (2 to 10 years) from a regional network of *Populus* field tests established at four sites in the Midwest USA during 1995, 1997, and 2000. We also sought to identify clones with yield substantially greater than commercial controls (Eugenei, NM6).

**Table 2** *Populus* genomic groups and clones established in 1995, 1997, and 2000 in a regional network of field tests at Westport and Waseca (2000 only), Minnesota; Arlington, Wisconsin; and Ames, Iowa to assess productivity and regional adaptability of the 187 genotypes

| Genomic group | Year | Clone |
|---|---|---|
| *P. deltoides* | 1995 | 7300501, 8000105, 171-1, 180-1, 192-2, 193-5, 220-5, 252-4, 42-7, 51-2, C910502, C910506, C910508, C910510, C910613, C910706, C910809, C910903, C916500, C917900, D1, D3, D5, D7, D9, D10, D11, D101, D102, D104, D105, D106, D108, D109, D110, D112, D114, D120, D121, Ohio Red |
| | 1997 | 32-5, 61-2, 61-4, 61-8, 62-4, 63-1, 66-9, C912500, C916001, C916013, C916021, C916201, C916304, C916306, C916323, C916325, C916413, C918012, CHILI.2-01, CHILI.2-02, D103, D107, D111, D113, D117, D118, D119, D122, D123, D124, D125, D126, D129, D130, D132, D133, D134, D135, D137, D139, D141, D144, D147, M2-9, M3-4, M7-3 |
| | 2000 | 5910100, 7300500, 7300502, 7302801, 8000104, C910401, C916000, C916101, C916305, C916400, C916401, C918001 |
| *P. nigra* | 1997 | 22SNOP01 |
| | 2000 | 21SNOP12 |
| *P. deltoides* × *P. deltoides* | 1995 | 119.16, 80X00601, 80X00603, 80X01132 |
| | 1997 | 11428.03, 12111911, 80X01038, 80X01059, 80X01107, 80X01109, 80X01110, 80X01112, 91X01-02, 91X02-01, 91X02-02, 91X04-01, 91X04-02, 91X04-04, 91X04-05, GB123602, GB250205 |
| | 2000 | 80X00605, 80X01015, C9425R3, C9425R5, C9425S11 |
| *P. deltoides* × *P. nigra* | 1995 | Eugenei, 117.53 |
| | 1997 | Eugenei |
| | 2000 | Eugenei |
| *P. deltoides* × *P. suaveolens* subsp. *maximowiczii* | 1995 | 25, 113.64, 313.23, 313.55, MWH2, MWH12, MWH14, MWH17 |
| | 1997 | 202.37, MWH3, MWH5, MWH7, MWH10, MWH11, MWH13, MWH15, NC14103, NC14104, NC14105, NC14106, NC14107 |
| *P. nigra* × *P. suaveolens* subsp. *maximowiczii* | 1995 | NM6 |
| | 1997 | NM6 |
| | 2000 | NM6, NM2 |
| *P. alba* × *P. alba* | 1995 | 12XAA9005, 8XAA9004 |
| *P. alba* × *P. grandidentata* | 1995 | Crandon |
| *P. alba* × (*P. alba* × *P. grandidentata)* | 1995 | 11XAAG9102 |
| (*P. trichocarpa* × *P. deltoides*) × *P. deltoides* | 2000 | NC13377, NC13451, NC13544, NC13548, NC13552, NC13559, NC13563, NC13570, NC13609, NC13624, NC13649, NC13652, NC13668, NC13670, NC13672, NC13680, NC13684, NC13685, NC13724, NC13747, NC13749, NC13800, NC13801, NC13807, NC13845, NC13863, NC13992, NC13999, NC14002, NC14015, NC14018, NC14042 |

Sections (bold) and authorities for the aforementioned species are: ***Aigeiros* Duby**—*P. deltoides* Bartr. ex Marsh, *P. nigra* L.; ***Tacamahaca* Spach**—*P. suaveolens* Fischer subsp. *maximowiczii* A. Henry, *P. trichocarpa* Torr. & Gray; ***Populus* L.**—*P. alba* L., *P. grandidentata* Michx. Clones Eugenei and NM6 were included as commercial controls

## Materials and Methods

### Site Description

A regional network of field tests was developed in the Midwest USA in 1995, 1997, and 2000 to assess productivity and regional adaptability of experimental and commercial *Populus* genotypes. Trees were established at Westport, Minnesota (45.7° N, 95.2° W); Waseca, Minnesota (44.1° N, 93.5° W; 2000 only); Arlington, Wisconsin (43.3° N, 89.4° W); and Ames, Iowa (42.0° N, 93.6° W) to test across a latitudinal gradient within the region (Fig. 1). Soils exhibited 0% to 3% slopes; predominant soil types were: Estherville loam at Westport (sandy, mixed, mesic Typic Hapludolls), Nicollet clay loam at Waseca (fine-loamy, mixed, superactive, mesic Aquic Hapludolls), Huntsville silt loam at Arlington (fine-silty, mixed, superactive, mesic Cumulic Hapludolls), and Coland clay loam at Ames (fine-loamy, mixed, mesic, Cumulic Haplaquolls). Table 1 is a summary of historical monthly mean temperature and precipitation from March through October at each site.

### Clone Selection and Experimental Design

A total of 185 experimental genotypes belonging to ten genomic groups were chosen from Midwest breeding programs at Iowa State University, US Forest Service

**Table 3** Aboveground biomass (Mg ha$^{-1}$ year$^{-1}$; ± one standard error; STE) of *Populus* clones established in 1995 at Westport, Minnesota; Arlington, Wisconsin; and Ames, Iowa to assess productivity and regional adaptability of the 59 clones

| Clone | Westport | | Arlington | | Ames | |
|---|---|---|---|---|---|---|
| | Mean 10 years | STE | Mean 8 years | STE | Mean 9 years | STE |
| 25 | 7.42 | 0.70 | 8.18 | 4.07 | 7.99 | 1.40 |
| 113.64 | 8.43 | 0.62 | 13.53 | 1.82 | 7.00 | 1.62 |
| 117.53 | 6.66 | 0.70 | 6.02 | 1.29 | 6.32 | 1.14 |
| 119.16 | 5.24 | 0.65 | 4.54 | 2.04 | 11.17 | 1.40 |
| 313.23 | 7.67 | 0.44 | 14.40 | 0.93 | 4.02 | 0.93 |
| 313.55 | 8.64 | 0.42 | 12.90 | 1.23 | 7.38 | 0.78 |
| 7300501 | 5.76 | 1.31 | 17.47 | 1.36 | 24.52 | 1.14 |
| 8000105 | na | na | 11.76 | 1.36 | 14.28 | 0.99 |
| 11XAAG9102 | 8.81 | 0.58 | 7.02 | 1.82 | 15.47 | 1.62 |
| 12XAA9005 | 7.53 | 0.48 | 7.67 | 1.29 | 7.49 | 2.80 |
| 171-1 | 6.55 | 0.65 | 11.84 | 2.35 | 6.25 | 1.25 |
| 180-1 | 5.30 | 0.42 | 6.60 | 0.99 | 6.75 | 0.89 |
| 192-2 | 6.36 | 0.41 | 5.73 | 1.18 | 3.09 | 0.93 |
| 193-5 | 6.49 | 0.42 | 6.77 | 1.13 | 3.29 | 0.93 |
| 220-5 | 5.46 | 0.83 | 17.80 | 1.44 | 15.17 | 1.25 |
| 252-4 | 8.77 | 0.65 | 14.61 | 1.29 | 11.26 | 1.06 |
| 42-7 | 5.79 | 0.58 | 13.30 | 1.54 | 13.03 | 0.99 |
| 51-2 | 6.39 | 0.65 | 14.07 | 1.36 | 8.19 | 1.25 |
| 80X00601 | 3.94 | 1.07 | 21.09 | 1.29 | 12.13 | 1.25 |
| 80X00603 | 4.11 | 1.31 | 12.78 | 1.66 | 15.11 | 0.99 |
| 80X01132 | na | na | 12.76 | 1.36 | 13.45 | 0.81 |
| 8XAA9004 | 10.41 | 0.62 | 13.03 | 2.04 | 14.49 | 1.62 |
| C910502 | 5.54 | 0.48 | 14.20 | 1.54 | 3.76 | 1.40 |
| C910506 | 6.12 | 0.41 | 9.22 | 1.13 | 5.58 | 0.75 |
| C910508 | 6.21 | 0.58 | 9.88 | 1.29 | 3.61 | 1.25 |
| C910510 | 4.85 | 0.45 | 7.35 | 0.99 | 3.22 | 0.81 |
| C910613 | 5.46 | 0.56 | 10.26 | 1.66 | 3.38 | 1.62 |
| C910706 | 6.33 | 0.41 | 6.05 | 1.36 | 3.09 | 1.40 |
| C910809 | 5.64 | 0.53 | 10.99 | 1.29 | 5.30 | 1.25 |
| C910903 | 4.69 | 0.65 | 8.72 | 1.29 | 4.55 | 1.25 |
| C916500 | 5.87 | 0.58 | 9.45 | 1.29 | 4.96 | 1.06 |
| C917900 | 3.31 | 0.62 | 9.70 | 1.44 | 4.46 | 1.14 |
| Crandon | 8.18 | 0.44 | 17.81 | 0.91 | 11.34 | 0.85 |
| D1 | 4.70 | 0.65 | 8.14 | 1.54 | 5.16 | 1.40 |
| D10 | 4.00 | 0.58 | 3.77 | 1.54 | 2.35 | 2.80 |
| D101 | 5.13 | 0.58 | 5.83 | 1.44 | 5.00 | 0.99 |
| D102 | 6.09 | 0.58 | 4.64 | 2.04 | 3.51 | 1.98 |
| D104 | 7.04 | 0.41 | 6.87 | 1.05 | 5.31 | 0.81 |
| D105 | 7.47 | 0.44 | 16.05 | 0.91 | 8.65 | 0.75 |
| D106 | 8.94 | 0.62 | na | na | 4.56 | 0.78 |
| D108 | 5.64 | 0.42 | 14.30 | 0.93 | 8.13 | 0.78 |
| D109 | 6.57 | 0.46 | 15.65 | 0.91 | 8.83 | 0.81 |
| D11 | 5.54 | 0.75 | 3.91 | 2.04 | 2.67 | 1.62 |
| D110 | 5.34 | 0.58 | 8.23 | 1.18 | 6.46 | 0.93 |
| D112 | 6.46 | 0.62 | 13.40 | 1.36 | 9.03 | 1.06 |
| D114 | 9.46 | 0.48 | 10.17 | 1.82 | 6.01 | 0.78 |
| D120 | 5.16 | 0.58 | 13.26 | 1.36 | 4.21 | 1.06 |
| D121 | 9.77 | 0.58 | 8.31 | 1.29 | 5.28 | 1.14 |
| D3 | 5.01 | 0.58 | 7.15 | 1.66 | 6.47 | 1.98 |
| D5 | 3.94 | 0.42 | 10.15 | 0.93 | 4.44 | 0.93 |
| D7 | 5.99 | 0.58 | 6.86 | 1.36 | 6.53 | 1.14 |
| D9 | 7.26 | 0.92 | na | na | 3.37 | 1.25 |
| Eugenei | 7.08 | 0.42 | 9.01 | 0.91 | 7.87 | 0.85 |
| MWH12 | 4.25 | 0.46 | 7.43 | 1.36 | 2.39 | 1.98 |
| MWH14 | 9.30 | 0.70 | 7.67 | 1.36 | 4.41 | 1.40 |
| MWH17 | 4.92 | 0.62 | 7.22 | 1.66 | na | na |
| MWH2 | 4.63 | 0.53 | 7.08 | 2.35 | na | na |
| NM6 | 11.30 | 0.58 | 16.73 | 1.44 | 7.86 | 1.25 |
| OhioRed | 6.70 | 0.70 | 14.35 | 1.54 | 10.96 | 1.06 |

Estimates assume 100% stocking. $n$=2 to 20 trees

*na* not available

Northern Research Station, University of Illinois, and University of Minnesota and were selected based on growth, disease/insect resistance, and rooting data from greenhouse, nursery, and field experiments. Trees were established in 1995 (57 clones), 1997 (77), and 2000 (51; Table 2). Clones Eugenei (also known as DN34 and NC5326) and NM6 were included in all tests as commercial controls. In this paper we use the *Populus* section names as specified by Eckenwalder [7], as well as the current classification of *P. maximowiczii* as a subspecies of *P. suaveolens* [4, 7].

For the 1995 and 1997 trials, cuttings from stool beds at Ames and Grand Rapids, Minnesota (47.2° N, 93.5° W) were grown for 1 year in nurseries at these locations. Primary whips were harvested during dormancy at 20 cm above the soil surface, and the remaining stem and root systems were excavated. Each connected stem and root system was processed into rooted cuttings with 20 cm tops containing at least three primary buds, as well as root systems containing three to seven lateral roots initiated from a developing taproot surrounding the original cutting. Rooted cuttings were also used in 2000, except for clones belonging to the (*P. trichocarpa* × *P. deltoides*) × *P. deltoides* genomic group that were planted as unrooted cuttings because rooted stock was unavailable. For these, shoots were collected during dormancy from stool beds established at Hugo Sauer Nursery in Rhinelander and the nursery in

**Table 4** Aboveground biomass (Mg $ha^{-1}$ $year^{-1}$; ± one standard error; STE) of *Populus* clones established in 1997 at Westport, Minnesota; Arlington, Wisconsin; and Ames, Iowa to assess productivity and regional adaptability of the 79 clones

| Clone | Westport | | Arlington | | Ames | |
|---|---|---|---|---|---|---|
| | Mean 8 years | STE | Mean 6 years | STE | Mean 7 years | STE |
| 202.37 | 6.74 | 0.67 | 13.84 | 0.91 | 11.04 | 0.79 |
| 11428.03 | 7.64 | 0.63 | 10.66 | 0.91 | 8.31 | 0.75 |
| 12111911 | 6.21 | 0.60 | 8.97 | 1.01 | 4.23 | 0.75 |
| 22SNOP01 | 5.62 | 0.60 | 11.45 | 0.95 | 5.48 | 0.90 |
| 32-5 | 4.80 | 0.60 | 10.84 | 0.91 | 4.32 | 0.75 |
| 61-2 | 6.24 | 0.63 | 11.70 | 0.91 | 4.24 | 0.84 |
| 61-4 | 6.10 | 0.60 | 10.67 | 0.95 | 7.52 | 0.79 |
| 61-8 | 4.90 | 0.60 | 10.58 | 0.91 | 4.62 | 0.90 |
| 62-4 | 5.47 | 0.63 | 11.78 | 0.91 | 4.07 | 0.79 |
| 63-1 | 4.55 | 0.60 | 5.92 | 1.08 | 5.54 | 0.75 |
| 66-9 | 9.19 | 0.72 | 11.95 | 0.91 | 10.91 | 0.75 |
| 80X01038 | 5.40 | 0.77 | 10.99 | 0.95 | 14.78 | 0.84 |
| 80X01059 | na | na | 13.77 | 0.95 | 9.78 | 0.79 |
| 80X01107 | 4.23 | 1.90 | 14.50 | 0.95 | 9.63 | 0.84 |
| 80X01109 | na | na | 14.22 | 0.95 | 7.85 | 0.90 |
| 80X01110 | na | na | 12.23 | 1.17 | 6.05 | 0.97 |
| 80X01112 | 4.32 | 1.90 | 13.19 | 1.01 | 13.69 | 0.79 |
| 91X01-02 | 4.56 | 0.72 | 17.23 | 0.91 | 7.13 | 0.84 |
| 91X02-01 | 6.07 | 0.72 | 10.01 | 0.91 | 3.46 | 0.90 |
| 91X02-02 | na | na | 13.86 | 0.95 | 8.75 | 0.79 |
| 91X04-01 | 3.02 | 1.34 | 15.29 | 0.91 | 11.11 | 0.75 |
| 91X04-02 | na | na | 14.15 | 1.01 | 20.86 | 0.75 |
| 91X04-04 | 6.23 | 0.72 | 17.09 | 1.01 | 16.48 | 0.79 |
| 91X04-05 | 6.38 | 0.67 | 20.90 | 0.91 | 19.25 | 0.75 |
| C912500 | 6.52 | 0.77 | 11.24 | 0.95 | 10.31 | 0.84 |
| C916001 | 5.02 | 0.67 | 8.86 | 0.91 | 3.12 | 0.84 |
| C916013 | 4.76 | 0.60 | 5.79 | 0.91 | 3.58 | 0.79 |
| C916021 | 6.79 | 0.63 | 14.79 | 1.01 | 5.25 | 0.79 |
| C916201 | 8.89 | 0.85 | 11.44 | 1.01 | 5.72 | 1.37 |
| C916304 | 4.04 | 0.67 | 5.40 | 0.95 | 2.23 | 0.84 |
| C916306 | 5.65 | 0.60 | 7.07 | 0.91 | 3.53 | 0.75 |
| C916323 | 6.35 | 0.63 | 10.73 | 1.01 | 5.32 | 0.75 |
| C916325 | 4.12 | 0.60 | 6.07 | 0.91 | 2.99 | 0.75 |
| C916413 | 4.10 | 0.63 | 7.43 | 0.91 | 4.10 | 0.79 |
| C918012 | 4.95 | 0.60 | 6.60 | 0.95 | 2.15 | 0.79 |
| CHILI_2-01 | 5.14 | 0.60 | 10.11 | 0.91 | 6.09 | 0.79 |
| CHILI_2-02 | 6.57 | 0.60 | 14.51 | 0.91 | 9.40 | 0.79 |
| D103 | 3.96 | 0.60 | 3.22 | 1.01 | 1.36 | 0.75 |
| D107 | 8.30 | 0.60 | 12.26 | 0.91 | 4.20 | 0.75 |
| D111 | 4.78 | 0.60 | 6.60 | 0.95 | 4.16 | 0.75 |
| D113 | 5.81 | 0.63 | 13.05 | 0.95 | 7.04 | 0.90 |
| D117 | 4.60 | 0.60 | 10.35 | 0.91 | 4.31 | 0.75 |
| D118 | 4.94 | 0.60 | 4.41 | 0.91 | 3.94 | 0.75 |
| D119 | 6.33 | 0.60 | 6.76 | 0.95 | 4.55 | 0.75 |
| D122 | 5.66 | 0.63 | 7.62 | 0.95 | 3.48 | 0.90 |

**Table 4** (continued)

| Clone | Westport | | Arlington | | Ames | |
|---|---|---|---|---|---|---|
| | Mean 8 years | STE | Mean 6 years | STE | Mean 7 years | STE |
| D123 | 5.99 | 0.60 | 6.76 | 0.95 | 4.68 | 0.79 |
| D124 | 6.58 | 0.67 | 14.46 | 0.91 | 11.02 | 0.84 |
| D125 | 7.54 | 0.60 | 13.22 | 0.91 | 4.81 | 0.75 |
| D126 | 5.51 | 0.63 | 8.30 | 0.95 | 3.85 | 0.84 |
| D129 | 5.26 | 0.63 | 7.06 | 0.95 | 4.32 | 0.75 |
| D130 | 4.69 | 0.67 | 3.20 | 0.91 | 2.35 | 0.84 |
| D132 | 4.25 | 0.63 | 5.88 | 0.91 | 3.85 | 1.06 |
| D133 | 6.58 | 0.60 | 12.06 | 0.91 | 4.07 | 0.75 |
| D134 | 7.06 | 0.60 | 8.93 | 0.91 | 7.22 | 0.75 |
| D135 | 4.16 | 0.67 | 4.24 | 1.17 | 2.24 | 0.97 |
| D137 | 5.39 | 0.77 | 6.56 | 0.95 | 4.31 | 0.79 |
| D139 | 4.10 | 0.60 | 4.29 | 0.95 | 2.98 | 0.90 |
| D141 | 3.17 | 0.60 | 5.12 | 0.91 | 2.30 | 0.84 |
| D144 | 3.45 | 0.63 | 3.79 | 0.95 | 1.00 | 0.84 |
| D147 | 5.05 | 0.60 | 8.70 | 0.91 | 3.63 | 0.79 |
| Eugenei | 4.80 | 0.67 | 7.19 | 1.01 | 4.84 | 0.79 |
| GB123602 | 5.20 | 0.77 | 13.99 | 1.08 | 6.68 | 0.90 |
| GB250205 | 4.10 | 0.77 | 9.34 | 1.01 | 5.30 | 1.06 |
| M2-9 | 4.57 | 0.72 | 6.93 | 1.01 | 4.07 | 0.79 |
| M3-4 | 3.58 | 0.95 | 5.77 | 1.08 | 3.91 | 0.75 |
| M7-3 | 2.61 | 0.67 | 5.72 | 0.95 | 3.36 | 0.75 |
| MWH10 | 3.34 | 0.60 | 6.34 | 0.95 | 3.61 | 0.79 |
| MWH11 | 0.97 | 1.34 | 4.39 | 0.95 | 2.71 | 0.84 |
| MWH13 | 3.17 | 1.34 | 5.05 | 1.01 | 2.58 | 0.97 |
| MWH15 | 4.10 | 0.60 | 7.92 | 1.01 | 5.50 | 0.75 |
| MWH3 | 2.24 | 0.67 | 2.08 | 1.08 | 1.79 | 1.06 |
| MWH5 | 4.03 | 0.67 | 8.66 | 0.91 | 3.46 | 0.79 |
| MWH7 | 2.95 | 0.63 | 9.40 | 1.01 | 3.63 | 0.79 |
| NC14103 | 8.17 | 0.63 | 10.40 | 0.95 | 6.56 | 0.75 |
| NC14104 | 7.95 | 0.63 | 12.43 | 0.91 | 5.34 | 0.75 |
| NC14105 | 10.06 | 0.63 | 16.36 | 0.95 | 8.43 | 0.79 |
| NC14106 | 6.31 | 0.63 | 9.08 | 0.91 | 4.74 | 0.79 |
| NC14107 | 4.10 | 0.67 | 8.95 | 1.08 | 2.32 | 1.37 |
| NM6 | 6.61 | 0.60 | 8.84 | 0.91 | 6.27 | 0.97 |

Estimates assume 100% stocking. $n$=2 to ten trees
*na* not available

Grand Rapids. Unrooted cuttings, 30 cm long, were prepared during January and February of 2000, with cuts made to position at least one primary bud not more than 2.54 cm from the top of each cutting. Eugenei and NM6 were planted as both rooted and unrooted cuttings in 2000 and were, therefore, designated differently in the analyses. Regardless of planting year, all cuttings were stored at 5°C until being planted within 1 week of delivery at each site. Unrooted cuttings were soaked in water to a height of 15 cm for 3 days before planting. Prior to planting, the soils were either tilled or disked to a depth of at least 30 cm. Following planting, mechanical and hand weeding were performed as necessary to ensure maximum tree survival.

In 1995, trees were planted in a randomized incomplete block design with ten blocks, 59 clones, and two trees per clone at a spacing of 3.05×3.05 m (1,075 trees $ha^{-1}$). Incomplete blocks were used because

**Table 5** Aboveground biomass (Mg $ha^{-1}$ $year^{-1}$; ± one standard error; STE) of *Populus* clones established in 2000 at Westport and Waseca, Minnesota; Arlington, Wisconsin; and Ames, Iowa to assess productivity and regional adaptability of the 53 clones

| Clone[a] | Westport | | Waseca | | Arlington | | Ames | |
|---|---|---|---|---|---|---|---|---|
| | Mean 5 years | STE | Mean 7 years | STE | Mean 3 years | STE | Mean 4 years | STE |
| 5910100 | 0.84 | 0.28 | 8.16 | 0.74 | 5.12 | 0.51 | 4.55 | 0.56 |
| 7300500 | na | na | 8.34 | 0.74 | 2.77 | 0.42 | 4.32 | 0.59 |
| 7300502 | na | na | 6.73 | 0.88 | 2.30 | 0.42 | 4.02 | 0.59 |
| 7302801 | na | na | 11.87 | 0.74 | 4.52 | 0.42 | 4.72 | 0.79 |
| 8000104 | na | na | 10.01 | 0.77 | 5.63 | 0.42 | 3.78 | 0.56 |
| 21SNOP12 | na | na | 6.22 | 0.74 | 1.33 | 0.42 | 3.19 | 0.62 |
| 80X00605 | na | na | 7.82 | 0.74 | 2.80 | 0.42 | 5.32 | 0.56 |
| 80X01015 | 0.76 | 0.46 | 8.41 | 0.74 | 4.51 | 0.42 | 4.25 | 0.59 |
| C910401 | na | na | 13.37 | 0.74 | 4.52 | 0.42 | 5.10 | 0.62 |
| C916000 | 2.35 | 0.25 | 12.66 | 0.74 | 3.73 | 0.42 | 1.58 | 0.66 |
| C916101 | 3.87 | 0.40 | 9.91 | 0.82 | 2.92 | 0.42 | 2.61 | 0.62 |
| C916305 | 1.23 | 0.25 | 8.99 | 0.74 | 2.02 | 0.42 | 1.02 | 0.72 |
| C916400 | 1.79 | 0.25 | 9.06 | 0.74 | 3.20 | 0.42 | 4.32 | 0.62 |
| C916401 | 1.43 | 0.25 | 8.96 | 0.74 | 3.49 | 0.42 | 1.61 | 1.01 |
| C918001 | 1.33 | 0.25 | 7.43 | 0.74 | 3.08 | 0.42 | 1.46 | 0.72 |
| C9425R3 | na | na | 13.36 | 0.74 | 7.09 | 0.42 | 4.83 | 0.66 |
| C9425R5 | na | na | 9.53 | 0.74 | 6.15 | 0.42 | 2.52 | 0.62 |
| C9425S11 | na | na | 4.41 | 0.77 | 1.16 | 0.55 | 3.29 | 0.79 |
| $Eugenei_{unrooted}$ | 2.19 | 0.26 | 7.06 | 0.74 | 2.45 | 0.42 | 2.17 | 0.59 |
| $Eugenei_{rooted}$ | 2.27 | 0.26 | 4.83 | 0.74 | 2.46 | 0.42 | 2.21 | 0.59 |
| NC13377 | 1.70 | 0.25 | 5.40 | 0.77 | 3.21 | 0.42 | 2.01 | 0.79 |
| NC13451 | na | na | 3.11 | 0.95 | 2.50 | 0.45 | 0.85 | 1.01 |
| NC13544 | 0.69 | 0.32 | 2.02 | 0.74 | 1.85 | 0.42 | 0.85 | 0.66 |
| NC13548 | 0.94 | 0.35 | 5.24 | 0.88 | 4.07 | 0.45 | 1.63 | 0.62 |
| NC13552 | 0.71 | 0.35 | 3.83 | 0.82 | 2.86 | 0.45 | 1.23 | 1.24 |
| NC13559 | 1.05 | 0.35 | 4.18 | 0.74 | 2.57 | 0.45 | 1.52 | 0.72 |
| NC13563 | 2.17 | 0.28 | 7.87 | 0.77 | 2.72 | 0.45 | 1.93 | 0.66 |
| NC13570 | 0.65 | 0.79 | 2.87 | 0.88 | 3.69 | 0.47 | 1.31 | 0.72 |
| NC13609 | 0.70 | 0.30 | 2.89 | 0.74 | 2.13 | 0.42 | 0.83 | 0.59 |
| NC13624 | 0.92 | 0.56 | 4.60 | 1.04 | 3.82 | 0.45 | 1.53 | 0.59 |
| NC13649 | 0.59 | 0.40 | 6.25 | 0.95 | 2.40 | 0.55 | 3.20 | 0.72 |
| NC13652 | 0.95 | 0.30 | 3.57 | 0.74 | 2.29 | 0.42 | 1.80 | 0.56 |
| NC13668 | 0.60 | 0.40 | 1.32 | 0.74 | 1.12 | 0.45 | 0.76 | 1.76 |
| NC13670 | 0.64 | 0.30 | 2.40 | 0.82 | 2.70 | 0.42 | 1.02 | 0.59 |
| NC13672 | 0.86 | 0.40 | 3.60 | 0.77 | 2.82 | 0.45 | 1.47 | 0.62 |
| NC13680 | 0.90 | 0.28 | 3.02 | 0.77 | 1.56 | 0.42 | 0.87 | 0.66 |
| NC13684 | na | na | 1.05 | 1.34 | 2.58 | 0.45 | 1.20 | 0.72 |
| NC13685 | 0.84 | 0.35 | 3.67 | 0.77 | 2.42 | 0.45 | 1.17 | 0.72 |
| NC13724 | 0.80 | 0.79 | 2.27 | 1.34 | 4.63 | 0.47 | 0.97 | 1.01 |
| NC13747 | 0.68 | 0.56 | 2.76 | 0.95 | 2.81 | 0.45 | 0.80 | 1.01 |
| NC13749 | 0.58 | 0.56 | 1.78 | 1.04 | 1.78 | 0.45 | 0.96 | 0.79 |
| NC13800 | 0.75 | 0.28 | 2.65 | 0.74 | 3.34 | 0.45 | 0.81 | 0.72 |
| NC13801 | 0.79 | 0.35 | 4.64 | 0.74 | 3.06 | 0.47 | 1.30 | 0.79 |
| NC13807 | 1.04 | 0.25 | 6.73 | 0.74 | 3.32 | 0.45 | 2.90 | 0.66 |
| NC13845 | 0.76 | 0.32 | 3.52 | 0.82 | 2.63 | 0.45 | 1.52 | 0.79 |

**Table 5** (continued)

| Clone[a] | Westport | | Waseca | | Arlington | | Ames | |
|---|---|---|---|---|---|---|---|---|
| | Mean 5 years | STE | Mean 7 years | STE | Mean 3 years | STE | Mean 4 years | STE |
| NC13863 | 0.79 | 0.35 | 2.52 | 1.04 | 2.90 | 0.45 | 1.51 | 0.66 |
| NC13992 | 1.87 | 0.40 | 9.32 | 0.77 | 3.96 | 0.51 | 1.80 | 0.66 |
| NC13999 | 0.68 | 0.46 | 2.33 | 1.16 | 2.22 | 0.45 | 2.33 | 0.88 |
| NC14002 | 1.94 | 0.40 | 9.32 | 0.82 | 5.22 | 0.60 | 1.82 | 0.79 |
| NC14015 | na | na | 3.78 | 0.82 | 3.08 | 0.55 | 3.46 | 0.79 |
| NC14018 | 1.71 | 0.30 | 6.93 | 0.74 | 3.11 | 0.47 | 0.99 | 0.88 |
| NC14042 | na | na | 2.10 | 0.88 | 3.05 | 0.42 | 1.53 | 0.79 |
| NM2 | 3.93 | 0.32 | 10.44 | 0.74 | 5.63 | 0.42 | 3.06 | 0.56 |
| $NM6_{unrooted}$ | 3.59 | 0.26 | 13.22 | 0.74 | 2.47 | 0.31 | 2.51 | 0.62 |
| $NM6_{rooted}$ | 3.75 | 0.26 | 10.13 | 0.77 | na | na | 3.05 | 0.56 |

Estimates assume 100% stocking. $n$=2 to ten trees

*na* not available

[a] Clones Eugenei and NM6 were planted as both unrooted and rooted stock

of a limited number of ramets for certain genotypes; these clones were established in five blocks rather than ten. While clones were assigned to blocks at random, all blocks were of identical size. In 1997 and 2000, all trees were planted in a randomized complete block design with five blocks, 79 (1997) or 53 (2000) clones, and two trees per clone at a spacing of 3.05×3.05 m.

Clones were arranged in randomized blocks in all years to minimize effects of any potential environmental gradients. Border rows were established to reduce potential border effects [12, 52]. At least two border rows of clonal mixtures were established on the perimeter of the Arlington and Ames plantings in all years, while at Westport spatial constraints always limited the border to one row, and at Waseca the number of border rows ranged from 1 to 5.

## Data Collection and Analysis

Diameter at breast height (DBH) was measured to the nearest 0.1 cm yearly on all trees from 1995 to 2000, and the data from 6-year-old trees from the 1995 field tests were reported by Riemenschneider et al. [34]. Given a substantial reduction in funding from 2001 to the present as a result of the end of the US Department of Energy's Biofuels Feedstock Development Program [5], yearly measurements at all sites have not been possible since 2001. Nevertheless, diameter data collected from all field tests at later stages of plantation development have been recorded. Specifically, DBH was measured at Westport from 1999 to 2004 in the older plantations, providing data at 5 to 10 (1995) and 3 to 8 years of age (1997); 5-year diameter was also recorded in 2004 at the Westport 2000 site. Diameter measurements of 2- to 7-year-old trees were collected at Waseca from 2001 to 2006. Diameter was recorded at Arlington in 2002, providing data at 8 (1995), 6 (1997), and 3 years old (2000), while measurements of trees at ages 9 (1995), 7 (1997), and 4 years (2000) were collected at Ames in 2003.

All diameter data were used to estimate woody biomass from a model developed following destructive aboveground harvests of multiple genotypes across numerous sites in the Midwest ($r^2$=0.98, $P$<0.0001, $n$=152) [13]. This model was most recently used by Zalesny and Zalesny [46], Netzer et al. [30], and Riemenschneider et al. [34]:

$$\text{Woody biomass} = \left[6.16 - (2.23 \times \text{DBH}) + \left(0.353 \times \text{DBH}^2\right)\right]$$

Individual tree biomass data from the model were multiplied by the stocking rate of 1,075 trees $ha^{-1}$ (3.05×3.05 m spacing, assuming 100% survival) and their product was divided by the age of the trees to calculate biomass per unit land area per year (i.e. Mg $ha^{-1}$ $year^{-1}$), which were the data compared in all of the analyses. The survival rate likely overestimated the calculations; however, it is important to assess total biomass potential and it is nearly impossible to completely eliminate bias when inferring large-plot biomass from experimental-plot yields. Phenotypic correlations ($r_P$) among sites for biomass were determined using Pearson's correlation coefficients [PROC CORR; 35].

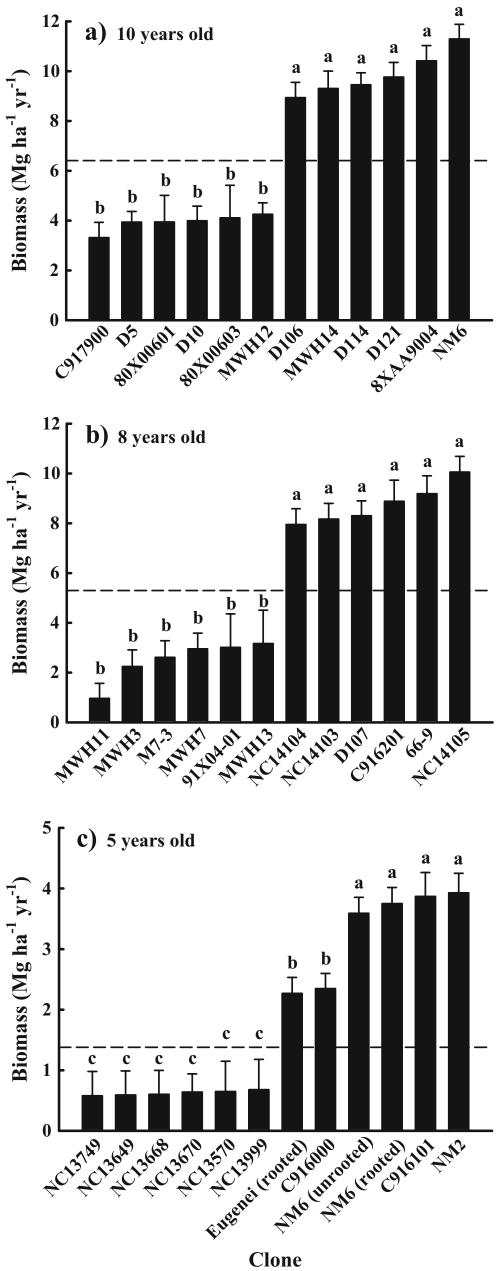


**Fig. 2** Biomass of the six best and six worst *Populus* clones grown at Westport, Minnesota. Fifty-nine, 79, and 53 clones were established in 1995 (**a**), 1997 (**b**), and 2000 (**c**), respectively. Each *bar* represents the mean of two to 20 trees with one standard error. *Bars labeled with different letters* were different at $P<0.05$. The *dashed line* represents the overall mean. Clones Eugenei and NM6 were planted as both unrooted and rooted stock in 2000

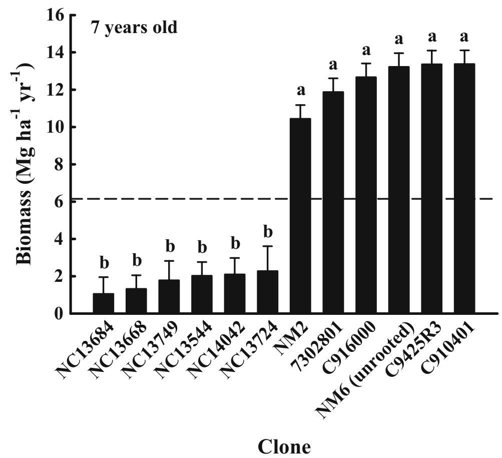


**Fig. 3** Biomass of the six best and six worst *Populus* clones grown at Waseca, Minnesota. Fifty-three clones were established in 2000. Each *bar* represents the mean of three to ten trees with one standard error. *Bars labeled with different letters* were different at $P<0.05$. The *dashed line* represents the overall mean. Clone NM6 was planted as both unrooted and rooted stock

Despite the randomized block design described above, widely varying numbers of trees for combinations of clone and site required the use of a completely random design analysis structure. Independent yearly data were analyzed using analyses of variance [PROC MIXED; 35] assuming a completely random design with a clone main effect. Means were considered different at probability values of $P<0.05$, according to Fisher's protected least significant difference (LSD). In addition, the Kruskal–Wallis Test (an analysis of variance on ranks) was used to test for differences in genotypic biomass ranks using both the completely random design for each combination of site and planting year, as well as the randomized block design for differences in biomass ranks throughout plantation development. A Bonferroni adjustment ($\alpha'$) of $[\alpha/(k\{k-1\}/2)]$ ($\alpha$=0.05 and $k$=number of clones tested) was used to limit the experiment-wise error rate to $\alpha\leq 0.05$. Significant effects were differentiated according to Fisher's protected LSD using $\alpha'<0.0001$ in lieu of $\alpha$=0.05.

## Results

### Biomass

There was broad clonal variation in biomass across sites and planting years ($P<0.0001$), which ranged from 0.58±0.56 (NC13749; Westport, 5 years) to 24.52±1.14 Mg ha$^{-1}$ year$^{-1}$ (7300501; Ames, 9 years). Tables 3, 4, and 5 depict the biomass of individual clones established at each site in 1995 (Table 3), 1997 (Table 4), and 2000 (Table 5). Clone NM6 had the greatest biomass for 10-year-old trees at Westport that was 3.4 times more than C917900 with the least (Fig. 2). Although Eugenei had above-average biomass (7.08±0.42 Mg ha$^{-1}$ year$^{-1}$), 15 experimental clones outperformed it. The best clones of 8-year-old trees at Westport had a tenfold increase in biomass over the worst genotypes (Fig. 2). The biomass of clone NC14105 was twice that of the mean. Clone NM6 exhibited above-

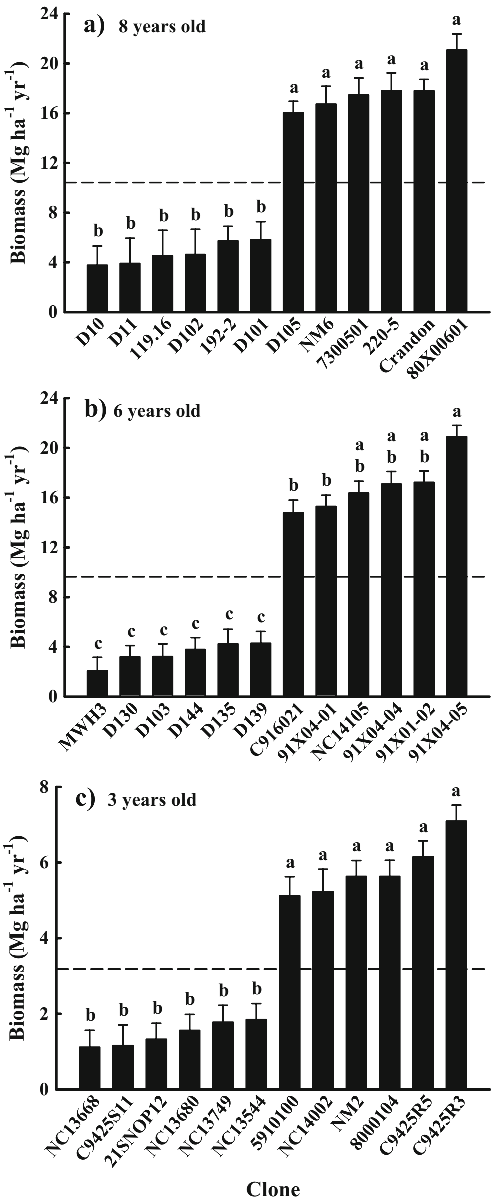


**Fig. 4** Biomass of the six best and six worst *Populus* clones grown at Arlington, Wisconsin. Fifty-nine, 79, and 53 clones were established in 1995 (**a**), 1997 (**b**), and 2000 (**c**), respectively. Each *bar* represents the mean of ten to 20 trees with one standard error. *Bars labeled with different letters* were different at $P<0.05$. The *dashed line* represents the overall mean

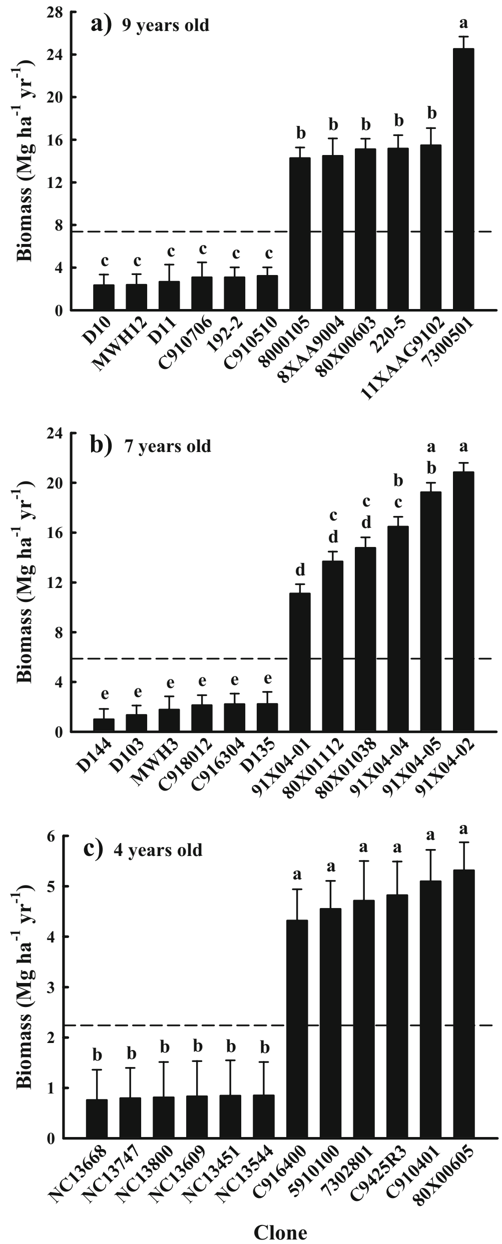


**Fig. 5** Biomass of the six best and six worst *Populus* clones grown at Ames, Iowa. Fifty-nine, 79, and 53 clones were established in 1995 (**a**), 1997 (**b**), and 2000 (**c**), respectively. Each *bar* represents the mean of two to 14 trees with one standard error. *Bars labeled with different letters* were different at $P<0.05$. The *dashed line* represents the overall mean

average biomass (6.61±0.60 Mg ha$^{-1}$ year$^{-1}$) and was ranked 12th, while 42 genotypes outperformed Eugenei that was below average (4.80±0.67 Mg ha$^{-1}$ year$^{-1}$). The best clones exhibited nearly seven times more biomass than the worst genotypes of 5-year-old trees at Westport, and both commercial genotypes were among the top clones (Fig. 2). Although not entirely depicted in Fig. 2, trees planted as unrooted and rooted cuttings of Eugenei and NM6 were in this group; Eugenei planted as unrooted stock ranked seventh.

Clone C910401 had the greatest biomass for 7-year-old trees at Waseca that was 12.7 times more than NC13684 with the least (Fig. 3). Clone NM6 planted as unrooted cuttings ranked third, while its rooted counterpart ranked seventh with 10.13±0.77 Mg ha$^{-1}$ year$^{-1}$. Although unrooted Eugenei had above-average biomass (7.06± 0.74 Mg ha$^{-1}$ year$^{-1}$), 26 experimental clones surpassed the productivity of rooted Eugenei that was below average (4.83±0.74 Mg ha$^{-1}$ year$^{-1}$).

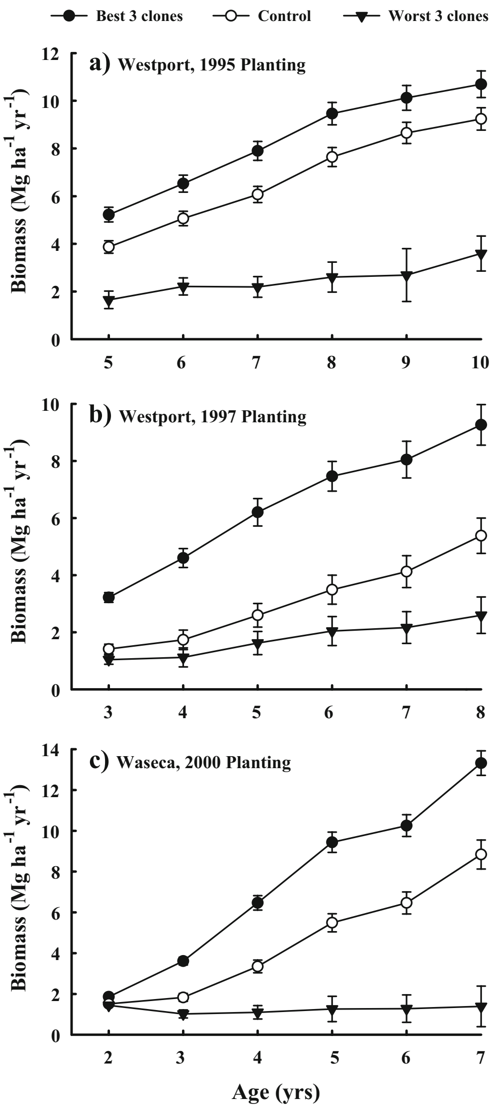


**Fig. 6** Mean biomass (± one standard error) of the three best and three worst *Populus* clones, as well as the mean of Eugenei and NM6 (control) throughout plantation development for trees established at Westport, Minnesota in 1995 (**a**) and 1997 (**b**) and Waseca, Minnesota in 2000 (**c**)

Clone 80X00601 had the greatest biomass for 8-year-old trees at Arlington that was 5.6 times more than D10 with the least biomass (Fig. 4). Although NM6 ranked fifth, Eugenei had below-average biomass (9.01±0.91 Mg ha$^{-1}$ year$^{-1}$) that 30 experimental clones surpassed. Clone 91X04-05 had ten times more biomass than MWH3 for 6-year-old trees at Arlington (Fig. 4). Both commercial clones exhibited below-average biomass; NM6 ranked 46th with 8.84±0.91 Mg ha$^{-1}$ year$^{-1}$ and Eugenei ranked 53rd with 7.19±1.01 Mg ha$^{-1}$ year$^{-1}$. The productivity of 3-year-old trees of clone C9425R3 was more than six times greater than that of NC13668 at Arlington (Fig. 4). Commercial genotypes had below-average biomass of 2.47±0.31, 2.46±0.42, and 2.45±0.42 Mg ha$^{-1}$ year$^{-1}$ for NM6$_{unrooted}$, Eugenei$_{rooted}$, and Eugenei$_{unrooted}$, respectively. Rooted cuttings of NM6 were not planted at Arlington in 2000.

Clonal variation for biomass was greatest in Iowa. For example, clone 7300501 had 10.4 times more biomass than the worst clone (D10) and 1.6 to 1.7 times more than the other top-ranking genotypes for 9-year-old trees at Ames (Fig. 5). Biomass was above average for Eugenei (7.87±0.85 Mg ha$^{-1}$ year$^{-1}$) and NM6 (7.86±1.25 Mg ha$^{-1}$ year$^{-1}$) that ranked 20th and 21st, respectively. Biomass among the best six clones was highly variable for 7-year-old trees at Ames, with a nearly twofold increase from 91X04-01 (ranked sixth) to 91X04-02 (first; Fig. 5). Clone 91X04-02 also had 20.9 times more biomass than D144. Although NM6 ranked 24th and had above-average biomass (6.27±0.97 Mg ha$^{-1}$ year$^{-1}$), Eugenei had below-average productivity (4.84±0.79 Mg ha$^{-1}$ year$^{-1}$) that 33 experimental clones surpassed. Clone 80X00605 had the greatest biomass for 4-year-old trees at Ames that was nearly seven times more than NC13668 with the least (Fig. 5). Biomass of NM6 established with rooted (3.05±0.56 Mg ha$^{-1}$ year$^{-1}$) and unrooted (2.51±0.62 Mg ha$^{-1}$ year$^{-1}$) cuttings was above average, while that of Eugenei was slightly below average (2.21±0.59 Mg ha$^{-1}$ year$^{-1}$ rooted; 2.17±0.59 Mg ha$^{-1}$ year$^{-1}$ unrooted).

Mean biomass of the best three clones established at Westport (1995, 1997) and Waseca 2000 increased more dramatically than that of the worst three genotypes (Fig. 6). The shape of the 1995 and 2000 curves was similar for the top clones and commercial controls given that clone NM6 was ranked first and third, respectively. The best three clones from Westport 1995 had up to 1.4-times greater biomass than the mean of the controls during years 5 to 10, reaching a 16% increase at 10 years (Fig. 6). Similarly, the best clones exhibited 2.9 to 3.8 times more biomass than the worst clones, reaching 198% more at 10 years. During development, the best clones from Westport 1997 had up to 2.7 and 4.1 times more biomass than controls and worst genotypes, respectively, as well as much greater biomass than the controls (72% more) and worst clones (256%) at 8 years (Fig. 6). The best three clones from Waseca 2000 exhibited up to two-times greater biomass than the mean of the controls during years 2 to 7, reaching a 51% increase at 7 years (Fig. 6). The advantage of the best clones over the worst clones was less stable, ranging from 1.3 to 9.6 times more biomass and reaching 858% more at 7 years.

## Genotype × Environment Interactions

Phenotypic correlations among sites for biomass of trees established in 1995, 1997, and 2000 were all positive and significant ($P<0.05$), except for that between Westport

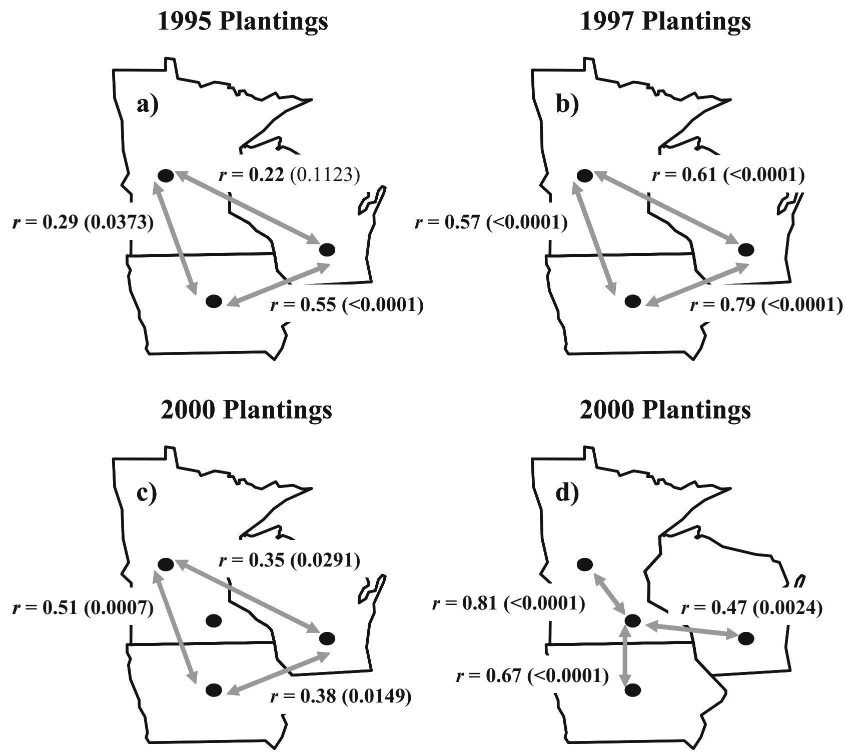


**Fig. 7** Phenotypic correlations among Westport, Minnesota (45.7° N, 95.2° W); Waseca, Minnesota (2000 only; 44.1° N, 93.5° W); Arlington, Wisconsin (43.3° N, 89.4° W); and Ames, Iowa (42.0° N, 93.6° W) for biomass of *Populus* established in 1995 (**a**; 53 clones), 1997 (**b**; 74 clones), and 2000 (**c**, **d**; 40 clones). Probability values are listed in *parentheses*

and Arlington in 1995 (Fig. 7). The remaining correlations ranged from 0.29 between Westport and Ames in 1995 to 0.81 between Westport and Waseca in 2000. General trends across sites and plantings were non-existent, thereby resulting in the need to assess changes in clonal rank and magnitude of biomass production for each combination of site and year. Table 6 summarizes such changes for select generalist and specialist clones that were exemplary in their respective adaptability classes. For example, clone 252-4 had stable ranks across all sites established in 1995, while D121 was well-adapted to Westport but poorly suited for Arlington and Ames. Likewise, D124 consistently ranked high across all three sites planted in 1997, yet 80X01038 was only productive in Ames. Similar examples exist for the 2000 planting (Table 6). In addition, changes in genotypic ranks throughout plantation development were used to highlight genotype × environment interactions. Table 7 depicts such rank changes for Westport (1995, 1997) and Waseca 2000. As an example, rank changes of exemplary clones from Westport 1997 were classified into three groups: (1) NC14105 exhibited stable ranks from 3 to 8 years; (2) 91X01-02 had decreasing ranks that resulted in a loss of 45 positions between the third and eighth years; and (3) D134 had increasing ranks that resulted in a gain of 11 positions between the third and fifth years followed by stable ranks until year 8. Additional examples are numerous (Table 7).

## Discussion

These results are the best potential biomass data currently available and, as such, will be important for resource managers, researchers, and policy makers needing to make informed decisions on *Populus* energy crop production in the Midwest USA. It should be noted, however, that there is a need to confirm these results with large-scale clonal yield trials throughout the region. Biomass potential was highly variable across clones and sites, regardless of plantation age. In general, experimental clones significantly outperformed commercial clone Eugenei, while NM6 had comparable biomass in most of the plantings. Trees at Arlington and Ames had the greatest biomass, with some clones exhibiting more than 20 Mg ha$^{-1}$ year$^{-1}$ at the end of the rotation. Although from clonal trials rather than yield trials, this estimated biomass was nearly twice that of the commonly reported upper limit of productivity ranging from 9 to 13 Mg ha$^{-1}$ year$^{-1}$ in the Midwest [13, 30, 34] and was indicative of the potential benefit of matching specific clones with locations to maximize productivity. Evaluation of phenotypic correlations and genotype × environment interactions also revealed that biomass of certain clones was stable across sites, which is an advantage for those seeking to deploy a limited number of genotypes adapted to heterogeneous conditions within the region. Overall, variability in biomass potential was due to a combination of broad

**Table 6** Genotypic rank based on aboveground biomass of *Populus* clones that exhibited similar productivity (generalists) at Westport, Minnesota; Arlington, Wisconsin; Ames, Iowa; and Waseca, Minnesota (2000 only) or that were better-adapted to a specific site or pair of sites (specialists)

| Adaptability | Clone[a] | Westport | Arlington | Ames | Waseca |
|---|---|---|---|---|---|
| *1995 Planting* | | | | | |
| Generalist | 8XAA9004 | 2 | 12 | 6 | |
| | 252-4 | 7 | 7 | 12 | |
| | C910506 | 29 | 31 | 32 | |
| | Crandon | 11 | 2 | 11 | |
| | D10 | 54 | 57 | 57 | |
| Specialist | 7300501 | 33 | 5 | 1 | |
| | 11XAAG9102 | 9 | 41 | 2 | |
| | 80X00603 | 55 | 17 | 3 | |
| | D121 | 3 | 35 | 36 | |
| | NM6 | 1 | 4 | 22 | |
| *1997 Planting* | | | | | |
| Generalist | 22SNOP01 | 28 | 34 | 28 | |
| | CHILI.2-02 | 13 | 6 | 11 | |
| | D124 | 11 | 10 | 6 | |
| | MWH13 | 69 | 71 | 70 | |
| | NC14105 | 1 | 4 | 12 | |
| Specialist | 66-9 | 3 | 25 | 7 | |
| | 80X01038 | 37 | 31 | 4 | |
| | 91X01-02 | 50 | 2 | 22 | |
| | 91X04-05 | 26 | 1 | 2 | |
| | NC14103 | 4 | 36 | 20 | |
| *2000 Planting* | | | | | |
| Generalist | 7302801 | na | 7 | 6 | 5 |
| | C910401 | na | 6 | 3 | 1 |
| | C9425R3 | na | 3 | 2 | 3 |
| | NC13807 | 20 | 17 | 21 | 24 |
| | NM2 | 1 | 9 | 12 | 6 |
| Specialist | 7300500 | na | 36 | 7 | 19 |
| | 80X01015 | 30 | 5 | 5 | 13 |
| | C916000 | 5 | 15 | 32 | 2 |
| | NC13724 | 23 | 11 | 45 | 50 |
| | $NM6_{unrooted}$ | 3 | 40 | 19 | 4 |

Fifty-nine, 79, and 53 clones were established at each site in 1995, 1997, and 2000, respectively

*na* not available

[a] Clones listed were exemplary in their respective adaptability classes

genetic variation among clones, changing environmental conditions, and genotypic responses to conditions at contrasting field sites.

There is broad genetic variation among *Populus* species [7, 17, 33], which substantially affects biomass production and other economically and ecologically important traits. There are about 30 *Populus* species worldwide belonging to six taxonomic sections: *Aigeiros*, *Tacamahaca*, *Populus* L., *Abaso* Eckenwalder, *Turanga* Bunge, and *Leucoides* Spach [4, 7]. Six species were tested as open-pollinated collections or used as parents in intra- and inter-sectional crosses in the current study (Table 2). Hybrids have been developed and tested to take advantage of heterosis and increase the potential transfer of favorable traits [17, 18, 36]. The most important species for biomass production in the Midwest belong to sections *Aigeiros*, *Tacamahaca*, and *Populus* [24], with the majority of inter-sectional hybrids being those between *Aigeiros* and *Tacamahaca* [6, 53]. In the current study, *P. deltoides* × *P. suaveolens* subsp. *max-*

**Table 7** Genotypic rank based on aboveground biomass of *Populus* clones throughout plantation development for trees established at Westport, Minnesota (1995, 1997) and Waseca, Minnesota (2000)

| Westport, 1995 Planting | | | | | | | Westport, 1997 Planting | | | | | | | Waseca, 2000 Planting | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Clone | Tree age (years) | | | | | | Clone | Tree age (years) | | | | | | Clone | Tree age (years) | | | | | |
| | 5 | 6 | 7 | 8 | 9 | 10 | | 3 | 4 | 5 | 6 | 7 | 8 | | 2 | 3 | 4 | 5 | 6 | 7 |
| 252-4 | 1 | 2 | 3 | 4 | 4 | 5 | NC14105 | 1 | 2 | 1 | 1 | 1 | 1 | C916000 | 1 | 7 | 7 | 6 | 3 | 2 |
| D121 | 2 | 1 | 2 | 3 | 3 | 3 | NC14104 | 2 | 10 | 4 | 6 | 8 | 6 | C916400 | 2 | 15 | 10 | 10 | 8 | 12 |
| D109 | 3 | 5 | 7 | 13 | 16 | 20 | NC14103 | 3 | 1 | 5 | 3 | 3 | 2 | NC13807 | 3 | 13 | 18 | 24 | 26 | 28 |
| 25 | 4 | 7 | 6 | 15 | 15 | 14 | C916201 | 4 | 9 | 2 | 5 | 5 | 4 | NC13685 | 4 | 39 | 45 | 44 | 45 | 47 |
| 8XAA9004 | 5 | 3 | 1 | 1 | 2 | 2 | D125 | 5 | 4 | 7 | 7 | 6 | 8 | NC13570 | 5 | 34 | 49 | 52 | 56 | 53 |
| D114 | 6 | 6 | 5 | 5 | 5 | 4 | 91X01-02 | 6 | 8 | 21 | 38 | 44 | 51 | NC14107 | 6 | 28 | 37 | 38 | 41 | 39 |
| NM6 | 7 | 4 | 4 | 2 | 1 | 1 | D107 | 7 | 3 | 3 | 2 | 2 | 5 | 5910100 | 7 | 6 | 9 | 9 | 15 | 16 |
| 51-2 | 8 | 11 | 12 | 18 | 23 | 26 | 91X04-04 | 8 | 7 | 10 | 13 | 30 | 25 | NC13552 | 8 | 30 | 41 | 45 | 46 | 44 |
| 113.64 | 9 | 16 | 15 | 7 | 8 | 8 | CHILI.2-02 | 9 | 20 | 11 | 12 | 11 | 11 | NC13801 | 9 | 17 | 31 | 35 | 38 | 40 |
| 117.53 | 10 | 8 | 14 | 17 | 19 | 23 | NC14107 | 10 | 24 | 37 | 55 | 59 | 59 | C910401 | 10 | 1 | 2 | 2 | 1 | 1 |
| MWH14 | 16 | 13 | 9 | 6 | 6 | 6 | D134 | 20 | 12 | 9 | 9 | 9 | 9 | NC14105 | 22 | 5 | 6 | 5 | 6 | 6 |
| Crandon | 18 | 12 | 11 | 9 | 9 | 10 | D119 | 31 | 38 | 23 | 17 | 14 | 13 | C9425R3 | 50 | 3 | 3 | 3 | 2 | 3 |
| D106 | 20 | 20 | 16 | 14 | 7 | 7 | 12111911 | 35 | 23 | 24 | 14 | 16 | 17 | NM2 | 60 | 32 | 19 | 14 | 7 | 7 |

Ranks for the top ten clones and three additional genotypes that exhibited positive rank changes are shown for each combination of site and establishment year. Fifty-nine, 79, and 53 clones were established at each site in 1995, 1997, and 2000, respectively *imowiczii* (NC14103, NC14104, NC14105) and *P. nigra* × *P. suaveolens* subsp. *maximowiczii* (NM2, NM6) $F_1$ hybrids, as well as a (*P. trichocarpa* × *P. deltoides*) × *P. deltoides* backcross ($BC_1$) hybrid (NC14002) had exceptional biomass. Similar examples of intrasectional hybrids exhibiting favorable biomass potential were from *P. deltoides* × *P. deltoides* (e.g. C9425R3, 91X04-02, 80X00605), *Populus alba* × *P. alba* (8XAA9004), and *P. alba* × *Populus grandidentata* (Crandon) $F_1$ hybrids, as well as the *P. alba* × (*P. alba* × *P. grandidentata*) $BC_1$ hybrid (11XAAG9102). The performance range of pure *P. deltoides* clones also expressed the broad variation among genotypes tested; many of these clones had top-ranking biomass (e.g. 7300501, C910401, 220-5). Overall, Midwest breeding programs at Iowa State University, US Forest Service Northern Research Station, University of Illinois, and University of Minnesota have focused substantial efforts on incorporating traits such as rooting ability from non-native species with growth potential, disease/insect resistance, and regional adaptability of native *P. deltoides* [50]. Current Midwest breeding efforts are at Iowa State University with focus on pure *P. deltoides*, their intraspecies hybrids, and *P. alba* hybrid aspen clones [11], as well as at University of Minnesota with *P. deltoides* × *P. nigra* $F_1$ hybrids [28].

The variability in soil and climatic conditions across sites likely affected biomass production. Soils within the testing network followed a general trend of having greater levels of sand and gravel in the north to more loam and clay in the south. Precipitation increased from north to south, while warmer temperatures resulted in extended growing seasons and greater numbers of growing degree days when moving southward (Table 1). Dispersed precipitation, sustained levels of adequate below- and aboveground temperatures, and the differential between daytime and nighttime temperatures have been vital for plantation establishment and development [51]. Although circumstances beyond the control of the original design precluded statistical testing of site effects in the current study, these locations and others within the region have exhibited significant differences for many traits, including those associated with biomass production. For example, Riemenschneider et al. [34] reported nearly 29% of variation in DBH of 6-year-old trees at these sites was attributable to location effects, which was the single greatest source of variation through years 1 to 5. In addition, Hansen [13] reported significant site differences among eight locations in Wisconsin, Minnesota, North Dakota, and South Dakota, USA, during regional testing of mid-rotation biomass of *P. deltoides* × *P. nigra* $F_1$ hybrids.

The response of individual genotypes to variability in soil and climatic conditions across the current regional network of field tests greatly influenced biomass potential throughout plantation development. Instability of phenotypic correlations, as well as dramatic changes in clonal biomass ranks and magnitude of differences in biomass potential corroborated previous studies reporting significant genotype × environment interactions for short-rotation *Populus* [29, 32]. From a genecology standpoint [9], minimal movements of genotypes beyond their zones of adaptability had the potential for substantial impacts on productivity. Although only 4° of latitude separate them, the gradients in daylength and temperature from Westport to Ames affected tree biomass and survival in the current study. Based on observations at all sites, most southern genotypes growing in Westport had a lack of cold hardiness and increased winter dieback, while many of the northern *Aigeiros* × *Tacamahaca* hybrids growing in Ames exhibited delayed bud break in the spring and early growth cessation in the autumn. Movement of genotypes across these latitudinal gradients also imposed observable pressures from *Septoria musiva* Peck (stem canker), *Melampsora medusae* Thüm (leaf rust), and *Chrysomela scripta* F. (cottonwood leaf beetle), with northern genotypes being affected in the south at a greater intensity than southern clones grown in the north. Riemenschneider et al. [34] reported similar results for 6-year-old trees in the 1995 plantings, while our assessments of silvicultural implications also agreed with those of Maisenhelder [25] who tested growth and pest resistance of pure *P. deltoides* versus hybrids growing in the lower Mississippi Valley, USA.

Regardless of environmental pressures, biomass of genomic groups followed a trend across the latitudinal gradient of testing; this was similar to the results of previous studies [8, 27, 45]. Qualitative comparisons of genomic groups at the strategic level of selection revealed that hybrids between *Aigeiros* and *Tacamahaca* clones exhibited the greatest biomass at northern sites, while *Aigeiros* × *Aigeiros* and *Populus* × *Populus* intrasectional hybrids had better biomass at southern sites than in the north. There was one exception to this trend: biomass for *P. deltoides* × *P. nigra* clones was better in northern sites despite belonging to an intrasectional *Aigeiros* × *Aigeiros* genomic group. As expected given the broad natural range of *P. deltoides* [4], biomass of pure *P. deltoides* clones and intraspecies hybrids was dependent upon where the specific genotypes were collected or developed. *P. deltoides* clones from the University of Minnesota performed better at upper latitudes, while those developed at the University of Illinois and Iowa State University had better biomass at lower latitudes.

Understanding genotype × environment interactions has been an essential component during testing of experimental clones that are selected for a variety of applications, including energy, fiber, and phytotechnologies [20, 49]. Overall, *Populus* breeding programs in the Midwest USA and other areas have prioritized regional fitness along with economically and ecologically important traits to commercialize genotypes that [42]: (1) allocate a large proportion of resources to harvestable biomass [13, 34]; (2) produce roots quickly from dormant hardwood cuttings [50, 51]; (3) immobilize, sequester, utilize, or volatilize contaminants for remediation of soils, sediments, and water [47, 48]; (4) resist or tolerate pest and pathogen attacks [3, 31]; (5) optimize the length of the growing season by increasing leaf retention and prolonging the production period [21]; (6) produce an increased epidermal cell number, cell size, or both for elevated levels of photosynthesis [1]; and (7) produce sylleptic branches for increased radial growth via greater photosynthetic tissue [4, 37]. Furthermore, given that more than 100,000 *Populus* offspring have been produced in the Midwest and that several hundred of those have made it to the clonal level of evaluation, there is an overwhelming need for further testing and subsequent deployment in a variety of applications. Practical implications from the current study will greatly contribute to advancement of such breeding. For example, these traditional tree improvement efforts enhanced biomass potential in the Midwest, with experimental genotypes exhibiting 1.4 to 2.7 times as much biomass as commercial clones throughout plantation development. A major decision for future testing is whether the performance of Eugenei is an adequate baseline for comparison, which did not seem to be valid in the current study. In addition, selection within both pure *P. deltoides* populations and hybrid genomic groups can increase biomass across the region. Given complex genotype × environment interactions, it is important to test, select, and deploy a combination of generalist genotypes (e.g. Crandon, NC14105, NM2) with elevated biomass across the region and specialists (e.g. 7300501, 80X01015, NC14103) with exceptional biomass at specific locations. Such deployment is important for all applications, especially plantations providing feedstocks for biofuels, bioenergy, and bioproducts.

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