

Variation in biomass production, moisture content, and specific gravity in some North American willows (*Salix* L.)

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Biomass production and quality in seedlings and coppices of *Salix amygdaloides* Anders., *S. eriocephala* Michx., *S. exigua* Nutt., and *S. lucida* Muhl. were investigated in a full-sib family test. Between 65 and 77% of the variation in plant biomass was due to species, while less than 5% was due to families. Approximately 39% of the variation in moisture content and 37% of the variation in specific gravity was due to species differences, while only 3 and 14%, respectively, was due to families. *Salix eriocephala* produced the highest yields, with an average 1-year coppice production of almost 1 kg/plant (dry matter) and had the lowest moisture content and highest specific gravity of the four species. There was a strong positive correlation between seedling and coppice productivity for all species, with *S. eriocephala* and *S. lucida* producing the most vigorous regrowth from coppice.

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On a étudié la production de biomasse et la qualité des plants et taillis de *Salix amygdaloides* Anders., *S. eriocephala* Michx., *S. exigua* Nutt. et *S. lucida* Muhl. au moyen d'essais sur des familles complètes. On a trouvé que 65 à 77% de la variation de la biomasse des plantes était attribuable à l'espèce, alors que moins de 5% était attribuable à la famille. Environ 39% de la variation du taux d'humidité et 37% de la variation de la gravité spécifique étaient causés par les différences d'espèce, alors que seulement 3 et 14%, respectivement, étaient attribuables à la famille. La *S. eriocephala* a donné le plus haut rendement avec une production annuelle moyenne de taillis de presque 1 kg/plante (matière sèche) et le taux d'humidité le plus faible avec la gravité spécifique la plus élevée des quatre espèces. On a constaté une forte corrélation positive entre la productivité des plants et celles des taillis pour toutes les espèces, *S. eriocephala* et *S. lucida* produisant la plus vigoureuse repousse à partir des taillis.

Introduction

Interest in the use of willows (*Salix* spp.) as a source of short-rotation woody biomass for energy and chemicals has been developing in Europe since the 1970s (Siren 1981), and more recently in North America (Zsuffa 1982; Dyer 1983). There are more than 500 willow species worldwide, of which approximately 100 are native to North America (Argus 1986), but only *S. nigra* Marsh. from the Mississippi River valley has been commercially exploited (Randall 1973). Most of the recent research interest in American *Salix* has focused on taxonomic treatments (Argus 1986; Dorn 1976) within this very large and phylogenetically complex genus, and on interspecific hybridization and reproductive barriers (Mosseier 1987; Argus 1974). The high productivity of willows on sites and in climates unsuited to the use of conventional forest tree species may provide the basis for a new commercial interest in this genus, especially in light of emerging conversion technologies such as wood liquefaction, gasification, anaerobic digestion, and fermentation (Ranney *et al.* 1987).

Very little is known about variation within and between willow species in growth performance and physical properties such as specific gravity and moisture content, which are important factors in assessing biomass quality (Ranney *et al.* 1987). The main objectives of the present study were (i) to quantify oven-dry biomass production, wood specific gravity, and moisture content in several of the more important willows native to North America; (ii) to determine if there

are important differences in these parameters within and between these species; (iii) to determine which species appear most promising as sources of biomass; and (iv) to determine the phenotypic correlation between seedling productivity and that of coppice growth in each species.

Methods and materials

The full-sib families described in this investigation were produced during the course of a study on interspecific hybridization and reproductive barriers between some of the more important willows native to North America (Mosseier 1987). The parent plants used in making these controlled crosses were collected from natural wetland populations in southern Ontario. Close genetic relatedness of parents used in individual crosses was minimized by collecting parents from small, isolated populations associated with different drainage systems. Gene flow via seed dispersal and insect-disseminated pollen between river systems would be restricted by distance, topography, and high forest cover.

A field test consisting of 38 full-sib families (including both intra- and inter-specific families) was established in August 1984 in a well-prepared nursery compartment at the Ontario Tree Improvement and Forest Biomass Institute near Maple, Ontario (latitude 44°, longitude 80°). The seedlings were established in a randomized complete block design consisting of six blocks with one 4-tree plot per family per block, and the test was surrounded by a triple border row. The seedlings were spaced at 1 × 1 m to allow for mechanical weed control during the year of establishment. The nursery site was located on a well-drained, silty-clay loam upland site on former agricultural land. The site was fertile but too dry for optimal growth of willows. Supplemental irrigation was regularly applied during extended dry periods from June to August during the first 2 years of seedling growth. After coppicing, the test was irrigated infrequently (only during severe dry periods).

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TABLE 1. Expected mean squares (EMS) for each source of variation in the nested factorial ANOVA for oven-dry biomass production, percent moisture content, and specific gravity

Source of variation	df	EMS	Denominator for F -test
B_i	5	$\sigma_s^2 + 4\sigma_{B \times F}^2 + 20\sigma_{B \times S}^2 + 80\sigma_B^2$	
S_j	3	$\sigma_s^2 + 4\sigma_{B \times F}^2 + 24\sigma_F^2 + 20\sigma_{B \times S}^2 + 120\sigma_S^2$	MS_X
$B \times S_{ij}$	15	$\sigma_s^2 + 4\sigma_{B \times F}^2 + 20\sigma_{B \times S}^2$	$MS_{B \times F}$
$F_{k(j)}$	16	$\sigma_s^2 + 4\sigma_{B \times F}^2 + 24\sigma_F^2$	$MS_{B \times F}$
$B \times F_{ik(j)}$ (experimental error)	80	$\sigma_s^2 + 4\sigma_{B \times F}^2$	MS_S
$S_{(ijk)l}$ (sampling error)	360	σ_s^2	

NOTE: The value MS_X to test for the species effect was constructed according to Hicks (1982, pp. 221-223), as $MS_{BS} + MS_F - MS_{BF}$.

TABLE 2. Oven-dry biomass production for 2.5-year-old seedlings and 1-year-old coppices of *S. amygdaloides*, *S. eriocephala*, *S. exigua*, and *S. lucida*

	Biomass production (kg)		
	Mean \pm SE	Range	CV ^a
<i>Salix eriocephala</i>			
Seedlings	1.36 \pm 0.05	0.40-3.26	38.6
Coppices	0.98 \pm 0.04	0.06-2.43	41.4
<i>Salix exigua</i>			
Seedlings	0.65 \pm 0.03	0.13-1.60	46.6
Coppices	0.19 \pm 0.01	0.04-0.63	59.1
<i>Salix lucida</i>			
Seedlings	0.50 \pm 0.02	0.13-1.28	45.3
Coppices	0.23 \pm 0.01	0.01-0.66	55.4
<i>Salix amygdaloides</i>			
Seedlings	0.26 \pm 0.02	0.01-0.83	55.1
Coppices	0.12 \pm 0.01	0.01-0.50	68.1

^aCoefficient of variation.

Five full-sib families each of *S. amygdaloides* Anders., *S. eriocephala* Michx., *S. exigua* Nutt., and *S. lucida* Muhl. were selected for an analysis of biomass quality and yield. The seedlings were harvested in January 1987 after approximately two and a half growing seasons in the field, and again after 1 year of coppice growth, in December 1987. The aboveground (leafless) biomass of each seedling was measured on an electronic weight scale, while the coppiced plants were weighed on a mechanical scale to the nearest 0.01 kg. Three of the dominant, upright stems were randomly selected from each seedling or coppice and a stem section approximately 20 cm in length was removed from each shoot centroid (balance point) for moisture content and specific gravity determinations.

The 20-cm stem sections (wood plus bark) were weighed to the nearest 0.001 g, immersed in a cylinder of water placed on a balance to obtain their green volume by weighing the water displaced, dried at 105 \pm 5°C for 24 h, and then reweighed to obtain the moisture content and specific gravity. Specific gravity was calculated by dividing the oven-dry weight of each stem section by its green volume (Panshin and de Zeeuw 1980). Oven-dry biomass production was obtained by multiplying the green weight of each plant by the average moisture content of the three stem sections.

The following linear model describes the nested factorial design

TABLE 3. Percent moisture content and specific gravity of 1-year old coppice shoots of *S. amygdaloides*, *S. eriocephala*, *S. exigua*, and *S. lucida*

	Mean \pm SE	Range	CV ^a
<i>Salix eriocephala</i>			
% moisture content	91.6 \pm 0.60	80.3-113.1	7.2
Specific gravity	0.457 \pm 0.002	0.404-0.538	5.5
<i>Salix exigua</i>			
% moisture content	100.1 \pm 0.73	84.3-127.2	8.0
Specific gravity	0.430 \pm 0.002	0.385-0.465	4.5
<i>Salix lucida</i>			
% moisture content	106.3 \pm 0.98	88.6-148.2	9.9
Specific gravity	0.394 \pm 0.002	0.293-0.443	5.1
<i>Salix amygdaloides</i>			
% moisture content	106.5 \pm 0.80	89.8-138.1	8.1
Specific gravity	0.421 \pm 0.002	0.367-0.464	4.7

^aCoefficient of variation.

used in analysis of variance (ANOVA) of oven-dry biomass production, moisture content, and specific gravity:

$$Y_{ijkl} = u + B_i + S_j + B \times S_{ij} + F_{k(j)} + B \times F_{ik(j)} + S_{(ijk)l}$$

where

Y_{ijkl} = the response of the l th seedling of the k th full-sib family nested within the j th species in the i th block

u = the overall mean

B_i = the effect of the i th block, $i = 1, \dots, 6$

S_j = the effect of the j th species, $j = 1, \dots, 4$

$B \times S_{ij}$ = the effect of the block \times species interaction

$F_{k(j)}$ = the effect of the k th family nested within the j th species, $k = 1, \dots, 5$

$B \times F_{ik(j)}$ = plot variance or experimental error

$S_{(ijk)l}$ = the within-plot (sampling) error, $l = 1, \dots, 4$

All factors in this model were considered to be random. Species were not selected with respect to the traits being analysed, because this study represents the first investigation of the biomass characteristics of these species. The expected mean squares (EMS) used in determining tests for significance (see Anderson and McLean 1974, pp. 52-62) appear in Table 1. According to the EMS, no exact test for significance is available for the effect of species, and therefore a pseudo F -test was constructed according to methods presented in Hicks (1982, pp. 221-223). The error term in the present design is referred to as a sampling error (Steel and

TABLE 4. ANOVA for biomass production in seedlings and 1-year-old coppices and for specific gravity and moisture content in coppice shoots of *S. amygdaloides*, *S. eriocephala*, *S. exigua*, and *S. lucida*

Source of variation	df	Biomass				Coppices			
		Seedlings		Coppices		Specific gravity		Moisture content	
		MS	VC ^a	MS	VC	MS	VC	MS	VC
Blocks	5	0.36	0.8	0.33	1.3	0.0029	2.0	0.0335	1.8
Species	3	26.29***	65.6	19.06***	77.2	0.0706***	37.4	0.5468***	39.3
Blocks × species	15	0.14 ns	0	0.11 ns	0.7	0.0005 ns	0	0.0162 ns	1.4
Family/species	16	0.53***	4.9	0.18*	2.1	0.0056***	13.7	0.0196 ns	3.4
Experimental error ^b	80	0.14	5.1	0.08	4.2	0.0008	1.6	0.0117	9.3
Plot error	360 ^c	0.08	23.5	0.03	14.3	0.0007	45.2	0.0065	44.7

NOTE: Level of statistical significance is indicated as follows: *, 0.01 < P < 0.05; ***, P < 0.001; ns, P > 0.05.

^aComponents of variation as a percentage.

^bExperimental error = B × F(S).

^cBecause of missing values, actual degrees of freedom (df) are 351 for seedling biomass, 333 for coppice biomass, 349 for coppice specific gravity, and 350 for coppice moisture content.

Torrie 1980) because it accounts only for variation between seedlings within a plot and thus underestimates the true experimental error. The same linear model was used to test for the significance of differences in wood moisture content and specific gravity, both of which were based on the average value from the three stem sections taken per seedling.

All statistical analyses were carried out on programs developed by the SAS Institute (SAS Institute Inc. 1987). ANOVA was carried out within the general linear model in SAS, using type III sums of squares for the F-tests, and the components of variance were calculated. The phenotypic correlation between biomass production in 2-year old seedlings and that in 1-year old coppices was estimated as an indication of the effect of coppicing on biomass production.

Results and discussion

Biomass production

The values for oven-dry biomass production in seedlings and coppices and for the specific gravity and moisture content of 1-year old coppice shoots are summarized in Tables 2 and 3, respectively, for five full-sib families of *S. amygdaloides*, *S. eriocephala*, *S. exigua*, and *S. lucida*. The ANOVA for these data is presented in Table 4. On the well-drained site used in this investigation, families of *S. eriocephala* produced the highest biomass yields, exceeding the production of the other species by several times. In southern Ontario, *S. eriocephala* and *S. exigua* were most often associated with moist but better-drained sites on floodplains and along fast-flowing streams, while *S. amygdaloides* and *S. lucida* were most commonly associated with poorly drained or permanently inundated wetlands. The relatively low biomass yields of the latter two species in comparison with that of *S. eriocephala* probably reflected a poorer adaptability to the drier site upon which they were tested.

Regrowth from coppice (after 1 year) expressed as a percentage of growth achieved in 2.5 growing seasons as seedlings was 72% for *S. eriocephala*, 29% for *S. exigua*, and 46% for both *S. lucida* and *S. amygdaloides*, demonstrating the beneficial effects of biomass production from coppice regrowth and the variation between species in this trait.

The three species contrasts selected for (orthogonal) comparison are presented in Table 5. The contrasts between *S. eriocephala* and *S. exigua* and between *S. amygdaloides* and *S. lucida* compare biomass production between species

TABLE 5. F-statistics for orthogonal contrasts between *S. eriocephala* (ERIO) and *S. exigua* (INT), *S. lucida* (LUC) and *S. amygdaloides* (SAM), and *S. eriocephala* and *S. lucida*

Species contrast	Biomass production		% moisture content ^a	Specific gravity ^a
	Seedlings	Coppices		
ERIO vs. INT	33.9***	104.6***	69.6**	3.7 ns
LUC vs. SAM	20.7**	24.2**	0.003 ns	19.7**
ERIO vs. LUC	54.4***	74.3***	38.2***	29.5***

NOTE: Levels of statistical significance are indicated as follows: **, 0.001 < P < 0.01; ***, P < 0.001; ns, P > 0.05.

^aOne-year old coppice shoots.

that coexist in similar habitats but have very different growth habits (presence versus absence of root shoots, and tree forming versus shrub forming, respectively), whereas the contrast between *S. eriocephala* and *S. lucida* compares species with different habitat preferences (better-drained versus inundated sites, respectively) but similar growth habit and prolific coppice production.

The differences observed in biomass production in contrasts between *S. eriocephala* and *S. exigua* (Table 5) may be partly related to differences in biomass partitioning between aboveground and belowground plant parts in these species. Species of the taxonomic section *Longifoliae* (to which *S. exigua* belongs) are unique within the genus *Salix* for their ability to produce new stems from their extensive lateral root systems (G. W. Argus, personal communication).² Because the root systems of these species provide an important mode of reproduction, they may accumulate proportionately more biomass in root growth during the early stages of their development than species that do not form such root shoots. *Salix exigua* is also believed to have its evolutionary origins in Mexico and the arid regions of the southwestern United States, where it is still found in moist areas in predominantly arid climates (Dorn 1976). Observations of other species suggest that species and provenances within species adapted to drier conditions tend to allocate more of their total biomass to roots than to stems and leaves (Cannell *et al.* 1978; Bongarten and Teskey 1987). Stems

²Dr. G.W. Argus, Vascular Plant Section, National Museum of Natural Sciences, Ottawa, Ont., Canada K1A 0M8.

arising from lateral roots also made it more difficult to accurately assess the aboveground biomass production of individual plants of *S. exigua*. Although stem production from lateral roots was minimal because of the tight spacing and shading within the test site, biomass production in this species was probably underestimated to some extent, as some stems could not be accurately assigned to the proper parent plant and therefore were not included in yield measurements.

The ability to produce stems from roots in *S. exigua* may hold special promise for very short (1-year) harvesting cycles, particularly on nutrient-rich floodplains. The ability to regenerate via root shoots may also mitigate the effect of diseases of the root collar area resulting from the continuous damage caused by repeated coppicing. Deterioration in the root collar area from repeated coppicing appears to affect coppice production in poplars (C. S. Papadopol, personal communication),³ and may also affect willows unless harvesting machinery that avoids such damage can be designed. Recent attempts to transfer this trait from *S. exigua* to *S. eriocephala* through interspecific hybridization have been unsuccessful. This trait appears to be recessive in the F_1 hybrids, and hybrid sterility has thus far restricted artificial hybridization attempts with these hybrids (Mosseler 1987).

The significant differences in seedling biomass yields observed between *S. amygdaloides* and *S. lucida* (Table 5) may be partly explained by the tree-forming habit and decreased leaf surface area of the former species in the juvenile phase of its growth, compared with the much larger leaf surface area typical of shrub willows. The shrub-forming willows are characterized by a more rapid accumulation of biomass early in their life cycle compared with that in the tree-forming species, because of the profuse branching habit of the former. *Salix amygdaloides* also performed poorly in comparison with the other species during regrowth from coppice. Casual observations of coppice production in other tree-forming willows suggest that this relatively poor biomass production following coppicing may be an inherent feature of the tree willows. All four species suffered to some extent from infections by *Melampsora* spp. leaf rust, but only *S. amygdaloides* suffered severe midseason defoliation from such infections, which no doubt also contributed to growth losses in this species.

Despite the much higher biomass production of *S. eriocephala* in comparison with *S. lucida* in this trial (Tables 2 and 5), observations of natural populations indicate that the latter species is highly productive on poorly drained sites. Although, the productive potential of *S. lucida* was probably not realized on such a well-drained test site, the higher moisture content and lower specific gravity observed in coppice shoots of *S. lucida* reduce the quality and yield of biomass compared with that of *S. eriocephala*.

Differences in seedling and coppice biomass yields between full-sib families within each species (Table 4) are interpreted as indications that a significant part of this variation is genetic in origin and may be improved through selective breeding. The potential for such improvement needs to be established through site trials in which genotypes are clonally replicated. Such trials have been established at several sites in Ontario and New York, and are currently being evaluated.

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TABLE 6. Phenotypic correlation coefficients for biomass production between seedlings and coppices for different families within species and for each species

Family	<i>Salix</i>	<i>Salix</i>	<i>Salix</i>	<i>Salix</i>
	<i>amygdaloides</i>	<i>eriocephala</i>	<i>exigua</i>	<i>lucida</i>
1	0.83	0.80	0.80	0.83
2	0.90	0.65	0.71	0.88
3	0.71	0.85	0.65	0.80
4	0.89	0.84	0.72	0.73
5	0.92	0.77	0.48	0.89

NOTE: Estimates are based on 24 seedlings per full-sib family.

Table 6 presents the estimated phenotypic correlation coefficients for biomass production before and after the initial harvest for the five families assessed within each species. As might be expected, these estimates were quite high, but they also showed considerable variation between families. A one-way ANOVA did not reveal any significant differences in this correlation between species. The high variability within species suggested that coppicing ability may also be improved through selective breeding and that an initial screening for good coppicing ability may be based on seedling growth performance.

Moisture content and specific gravity

The average moisture content and specific gravity values for coppice shoots presented in Table 3 have a similar range to values of clones of European species investigated by Deka (1987) and Kristin (1985). The ANOVA (Table 4) and species contrasts (Table 5) for these traits reveal significant differences between species in specific gravity and moisture content, indicating that these traits can be improved through species selection. For instance, there is an average difference of 16% in both moisture content and specific gravity between *S. eriocephala* and *S. lucida* (Table 3). Significant differences ($P < 0.001$) between families within species were observed for specific gravity but not for moisture content, indicating that clonal selection within species (between families) may be useful in improving specific gravity. Moisture content within families was highly variable and large differences between plants within families were observed. As individual genotypes were not replicated (as clones) within the test site, the significance of these differences could not be properly assessed. However, Sennerby-Forsse (1985) found significant differences in moisture content and specific gravity between clones of *S. viminalis* L., and the relative differences between clones appeared to be reasonably stable over time.

The lack of uniformity in a composite material, such as willow coppice shoots, that includes both wood and bark presents some problems for the analysis of genetic differences between species, families, and clones. Because wood and bark are very different in their structure and chemical composition, measurements of wood-quality parameters in such a composite material will be influenced by the proportion of wood to bark. A weak negative correlation was observed in the coppice shoots when moisture content and specific gravity were plotted against stem section volume (which in this experiment was related to stem section diameter because all sections were approximately 20 cm in length). Moisture content, specific gravity, and chemical composition will vary with shoot diameter as a result of differences in the wood to bark ratio. Bark contributed

between 37 and 43% of the dry weight of 1-year-old willow shoots in clones analysed by Krigstin (1985) and between 25 and 38% in clones analysed by Sennerby-Forsse (1985), and most of the variability among clones was attributable to stem diameter (Krigstin 1985). For this reason, future analyses of biomass quality traits should account for the inherent variability of this composite material. It may be more appropriate to analyse variation in biomass quality traits through analysis of covariance, in which either shoot diameter or the bark to wood ratio itself are used as covariates for the adjustment of variation in physical and chemical characteristics. Multivariate analysis also provides an alternative approach to solving the problems presented by the analysis of such composite materials. These approaches were not taken in the present investigation because stem section diameter was not measured.

Components of variance

Reliable comparisons of genetic variances or heritabilities of traits within these species would require much larger samples of progeny and extensive testing over many environments to determine whether genotype \times environment interactions are important (Dudley and Moll 1969). In *Populus deltoides* Bartr., wood properties such as specific gravity are influenced by environmental conditions (Farmer 1970), but clone \times site interactions are generally small and not statistically significant (Farmer and Wilcox 1968; Randall and Cooper 1973). The components of variance (Table 4) provide some indication of the potential for genetic improvement through selection and breeding. Between 65 and 77% of the variation in biomass production in both seedlings and coppices was due to species. A large portion of the variation in moisture content and specific gravity (39.3 and 37.4%, respectively) was also due to species, which emphasizes the importance of species selection in influencing these traits. In a genus with more than 500 species available, species testing and selection deserve a major emphasis in the initial stages of genetic improvement efforts. Because of the limitations of experimental design, only a very small but statistically significant portion of variation was attributable to families. Large within-family variation and large error terms in the analyses of moisture content and specific gravity were mainly responsible for this outcome. Variation due to block \times species and block \times family interactions was negligible, and variation due to sampling error provided a reasonably good estimate of the experimental error.

Conclusion

In terms of numbers of species, the genus *Salix* provides one of the largest unexploited gene pools for the production of woody biomass, particularly in the harsher climatic zones of the northern hemisphere. Our results indicate that species testing and selection will result in major gains in biomass yield and quality. Although willows are most commonly associated with poorly drained sites, our observations of natural and experimental populations suggest that an understanding of the adaptive ranges of different species with respect to water relations will be an important factor in maximizing their productivity.

The biomass produced by *S. eriocephala*, especially from coppice regrowth, was superior in amount and quality to that of the other species tested. This species deserves special attention in selection and breeding efforts to genetically

improve biomass yield and quality. The results of this experiment suggest that biomass yields of 15–20 t dry weight \cdot ha⁻¹ \cdot a⁻¹ can be expected from unselected material planted at a spacing of 1.0 \times 0.5 m and harvested on rotations of 1–3 years. Although differences between seedlings (genotypes) could not be tested in this experiment, the large within-family variation observed also suggests that the results could be substantially improved through clonal selection.

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