ment of true fir in the Pacific Northwest. University of Washington, Seattle, WA. pp. 59–69 (1982). — KELLOGG, R. M. and WARREN, W. G.: Evaluating western hemlock stem characteristics in terms of lumber value. Wood Fiber Sci. **16**:583–597 (1984). — KING, J. N.: Selection of traits for growth, form, and wood quality in a population of coastal Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) from British Columbia. Ph.D. Thesis, University of Alberta, Edmonton, Alberta (1986). — KING, J. N., YEH, F. C. and HEAMAN, J. C.: Selection of growth and yield traits in controlled crosses of coastal Douglas-fir. Silvae Genet. **37**:158–164 (1988). — KING, J. N., YEH, F. C., HEAMAN, J. C. and DANCIK, B. P.: Selection of crown form traits in controlled crosses of coastal Douglas-fir. Silvae Genet. **41**:362–370 (1992). — LAMBETH, C. C.: Juvenile-mature correlations in Pinaceae with implications for early selection. Forest Sci. **26**:571–580 (1980). — MERRILL, R. E. and MOHN, C. A.: Heritability and genetic correlations for stem diameter and branch characteristics in white spruce. Can. J. For. Res. **15**:494–497 (1985). — NAMKOONG, G.: Introduction to quantitative genetics in forestry. Tech. Bull. No. 1588. USDA For. Serv., Washington, DC. (1979). — POLK, R. B.: Heritability of some first-order branching traits in *Pinus banksiana* LAMB. In: Proc. 8th Central States For. Tree Improv. Conf. pp. 33–39 (1972). — POYKKO, T.: Genetic variation in quality characters in Scots pine: an evaluation by means of the heritability concept. Silvae Fenn. **15**:135–140 (1982). — QUALM, R. (ed.): Northwest tree improvement cooperative report for local cooperative programs. NWTIC, Forest Sciences Lab., Corvallis, OR (1988). — RUETZ, W. F. et al.: The IUFRO *Abies procera* trial in the Federal Republic of Germany – field results at age 9 and 10 years. In: 1990 joint meeting of Western Forest Genetics Assoc. and IUFRO Working Parties S2.02–05, 06, 12, and 14 on Douglas-fir, contorta pine, Sitka spruce, and *Abies* breeding and genetic resources. 20 to 24 Aug. 1990, Olympia, WA. Weyerhaeuser Co., Tacoma, WA. pp. 2.276–2.289 (1990). — SCHERMANN, N., ADAMS, W. T., AITKEN, S. N. and BASTIEN, J.-CH.: Genetic parameters of stem form traits in a 9-year-old coastal Douglas-fir progeny test in Washington. Silvae Genet. **46**: 166–170 (1997). — SHELBOURNE, C. J. A.: Genetic improvement in different tree characteristics of radiata pine and the consequences for silviculture and utilization. Paper presented to FRI Symp. No. 12, Forest Res. Inst., Rotorua, New Zealand. 18 p. (1970). — SHELBOURNE, C. J. A.: Genotype-environment interaction: Its study and its implications to forest tree improvement. In: Proc. IUFRO Genetics-SABRAO joint symposia, Tokyo B-1(I), pp. 1–28 (1972). — SORENSEN, F. C., CAMBPELL, R. K. and FRANKLIN, J. F.: Geographic variation in growth and phenology of seedlings of the *Abies procera–A. magnifica* complex. For. Ecol. Manage. **36**:205–232 (1991). — STEEL, R. D. and TORRIE, J. H.: Principles and procedures of statistics, a biometrical approach. McGraw-Hill, Inc., New York. 633 pp. (1980). — STRICKLAND, R. K. and GODDARD, R. E.: Inheritance of branching and crown characteristics in slash pine. In: Proc. 8th South. Conf. on Forest Tree Improv., Savannah, GA. pp. 57–63 (1965). — USDA Forest Service: 1991 Annual Silvicultural Report. USDA Forest Service, Region 6, Portland, OR (1991). — XIE, C. Y. and YING, C. C.: Adaptedness of noble fir (*Abies procera* REHD.) beyond its northern limit. For. Sci. **40**:412–428 (1994). — Ying, C. C.: Effect of sites and provenances on 6th-year performance of noble fir in coastal British Columbia. Res. Note 112. B. C. Min. For., Victoria, BC (1992). — ZAVARIN, E., CRITCHFIELD, W. B. and SNAJBERK, K.: Geographic differentiation of monoterpenes from *Abies procera* and *Abies magnifica*. Biochem. Syst. Ecol. **6**:267–278 (1978). — ZOBEL, B. J. and TALBERT, J. T.: Applied forest tree improvement. John Wiley and Sons, New York (1984).

Genetic Variability in Anatomical, Physiological and Growth Characteristics of Hybrid Poplar (*Populus* x *euramericana* DODE (GUINIER)) and Eastern Cottonwood (*Populus deltoides* BARTR.) Clones

By S. ORLOVIĆ[1]), V. GUZINA[1]), B. KRSTIĆ[2]) and L. MERKULOV[2])

(Received 1st December 1997)

Summary

Anatomical and physiological parameters of rooted cuttings of eight black poplar clones (4 *Populus* x *euramericana* and 4 *Populus deltoides*) were evaluated in three field experiments on different soil types (humofluvisol, fluvisol f. loamy and fluvisol f. sandy). Measurements were taken on the thickness of assimilation tissues (palisade and spongy) on the cross section, and on net photosynthesis, dark respiration and leaf area. At the end of the vegetation period, the main plant growth elements were measured: diameter, height and biomass. The results showed a high interclonal variability for most parameters. Statistically significant differences among clones, regardless of site, indicated that the majority of study characters are controlled by genetic factors, specific to each clone. Most characteristics showed a statistically significant genotype x environmental interaction, as clone rankings at the three locations were not identical. The thickness of spongy tissue and plant height exhibited the highest genotype x environmental interaction, while the number of stomates per mm^2 of the adaxial surface of the leaf, leaf area, and biomass showed the least sensitivity to environmental change. Strong correlations were shown between the number of stomates on leaf adaxial surface and biomass, thickness of palisade layer and biomass, leaf area and with height and biomass respectively. Leaf area, also was strongly correlated with height. The results indicate that the stomata number adaxial, thickness of palisade tissue, net photosynthesis, and leaf area can be used in the selection of nursery stock for the desired characteristics, that will result in higher biomass production. Construction of high yielding hybrids with desirable anatomical features was considered to be feasible.

Key words: poplar clone, anatomy, physiology, variability, genotype x environment interaction.

FDC: 165.5; 161.2/.3; 164.5; 168; 232.13; 232.328.1; 532; 537; 561; 176.1 *Populus euramericana;* 176.1 *Populus deltoides.*

Introduction

The genus *Populus* L. is broadly distributed in Europe, North America, and Asia (CEULEMANS *et al.,* 1988). The ability of spontaneous and controlled intra- and interspecies hybridization within the genus has, enabled the creation of a high number of subspecies and transient forms, i.e. simple and complex hybrids. This has resulted in a great natural variability which enables *Populus* species to inhabit a variety of

[1]) Poplar Research Institute, Antona Čehova 13, P.O. Box 117, 21000 Novi Sad, Yugoslavia. Email: sasao@polj.ns.ac.yu

[2]) University of Novi Sad, Faculty of Natural Science, Institute of Biology, Novi Sad, Yugoslavia

forest sites, ranging from riparian to mesic. In addition to broad adaptibility which is significant for breeding, poplars are distinguished by extremly fast growth and are easy to vegetatively propagate (CAIN and ORMORD, 1984). From an economic aspect, the species in the section *Aigeiros* are very important in Yugoslavia. Although these species occupy a relatively small amount of hectares, their ability to rapidly produce fiber is a significant economic contribution.

The development of poplar research through the creation of new clones and enhancement of nursery production and plantation establishment techniques has been highly stimulated by a program Short Rotation Intensive Culture (SRIC) research program. This program is directed toward biomass production for energy and chemical and mechanical processing (ANDERSON *et al.,* 1983; FEGE, 1987; STETTLER *et al.,* 1988).

Poplars have showed the greatest potential for fast growth and biomass production compared to other tree species of the temperate climate. According to some authors, they can produce above 100 t of oven dry biomass per hectare over a for period of 20 years, (HERPKA, 1965). In consideration of a world wide shortage of timber for mechanical and chemical processing, and energy, the sudden interest for raising fast-growing tree species is not a mere chance. Therefore a number of poplar breeding programs have been directed to produce clones characterised by superior growth and resistance to pests and diseases of leaf and stem. A challenging problem faced by any breeder is to recognize genotypes with desirable properties as early as possible. Shortened periods of selection, also will reduce overall research expenses (CEULEMANS *et al.,* 1987). This type of research is complex as growth is exibited by diameter, height and biomass, which are quantitately inherited and a reflection of numerous anatomic properties, as well as physiological and biochemical processes. To date, numerous poplar clones have been created at Yugoslavian Poplar Research Institute, by hybridization and multiple selection. These genotypes are characterized by exceptional growth and other desirable properties, the most important of which is resistance to leaf and stem diseases. To accelerate the selection process, as well as to define critical parameters in the growth process, a long term research program on anatomic properties and physiological processes was designed at the Institute. The construction of a model tree (ideotype) after DICKMANN *et al.* (1994), is actually a method of summarizing the overall plant physiology. According to STETTLER *et al.* (1992), using a model tree is a possible method of producing cultivars for Short Rotation Intensive Culture Plantings. Previous studies have confirmed the relationship between some anatomical and physiological parameters with poplar yield and a very high degree of variability among poplar species (CEULEMANS *et al.,* 1984; ISEBRANDS *et al.,* 1988; BARIGAH *et al.,* 1994). This research points to a very high interspecies variability, as well as correlation of anatomic properties with growth elements. In a leaf anatomy analysis of poplar clones attention was focused on epidermal tissue, and especially to the number and size of stomates (ORLOVIĆ, 1993; ORLOVIĆ *et al.,* 1994). As stomates have an indispensable role in the exchange of gases during the processes of photosynthesis, as well as transpiration, it was hypothesized that these parameters can be used to recognize genotypes with fast growth. ORLOVIĆ and ĐOKOVIĆ (1991) concluded that there were statistically significant differences between the number and size (length and width) of stomates of different poplar species in the section *Aigeiros,* as well as that the number of stomates is lower on adaxial side compared to abaxial surface of the leaf. Additionally, ORLOVIĆ (1993) determined that the number of stomates is positively correlated with increased biomass production of one-year-old poplar clones. However, stomata number also can be affected by site conditions. GUZINA *et al.* (1995) showed that the differences between the numbers of stomates of the North American eastern cottonwood (*Populus delotides* BARTR.) and Euramerican hybrid poplar (*Populus* x *euramericana* (DODE) GUINIER) clones in the field experiment on three types of soil, were statistically different. Additionally, a genotype x environmental interaction (GE) was shown. In this paper we evaluate genetic variability in 9 anatomical, physiological and growth characteristics in *P.* x *euramericana* and *P. deltoides* clones for their importance in selection for fast growth.

Material and Method

In spring, 1995, three polyclonal field plantings of 8 black poplar clones were established in the nursery of the Yugoslavian Poplar Research Institute (45° 17' N, 19° 53' E, elevation 76 m) using cuttings. The planting contained four clones of the hybrid Euramerican poplar and four clones of eastern cottonwood. Each of these clones had been identified as having fast growth throughout the rotation cycle. Important characteristics of these clones are summarized in *table 1.* Each clones was represented by 50 ramets within a each blocks, planted in a single, row. The spacing was 1.2 m between rows and 0.25 m between ramets within a row. The first planting was established on humofluvisol (Location 1); the second planting on a loamy form of fluvisol (Location 2), and the third planting on a sandy form of fluvisol (Location 3). The soil types were according to the classification system of ŠKORIĆ *et al.* (1985). The study was conducted during and after the first growing season after planting. During the study's duration, the plantings were not fertilized and treated with insecticides of fungicides.

Various anatomical, physiological and growth parameters were evaluated to detect differences among the clones and planting sites.

Leaf anatomy

The anatomic structure of leaf cross sections from completely formed leaves fully exposed to light was analysed using temporary preparations made on a freezing microtome. The samples taken in mid summer, and ramets were selected randomly. The sample consisted of 5 leaves from 10 ramets from each block and location. The thickness of palisade and spongy mesophyll tissues were measured under a light microscope equipped with a micrometer in the eyepiece.

Stomata number

The samples were taken from the upper third of the tree upper height in the mid summer, and ramets were selected randomly. The sample consisted of 5 leaves from 10 ramets from each block and location. The number was determined by "collodion method" (WOLF, 1950). Leaf blades, on selected ramets was painted with colorless varnish between the second and the third veins on the adaxial and abaxial epidermis. After drying, varnish was removed by cellotape, which also removed a part of leaf epidermis. The specimen was mounted on a glass slide for microscopic evaluation of the stomates. The number of stomates per mm^2 was counted in four randomly chosen fields of view using an eyepiece micrometer.

Net photosynthesis and dark respiration

Net photosynthesis and dark respiration were measured on the sections of fully formed and exposed leaves. The sample was taken in the mid summer, and ramets were selected randomly. The sample consisted of 5 leaves from 10 ramets from each blocks and locations.

Table 1. – Taxonomy and characteristics of clones used in this study.

CLONES	TAXONOMY	SEX	CHARACTERISTICS	PLACE of ORIGIN
I-214	*Populus x euramericana* (Dode) Guinier	F	Fast growth and high susceptibility to *Dothichiza populea, Marssonina brunnea* and *Melampsora sp.*	Italy
Ostia	*Populus x euramericana* (Dode) Guinier	F	Fast growth and high susceptibility to *Dothichiza populea, Marssonina brunnea* and *Melampsora sp.*	Germany
M1	*Populus x euramericana* (Dode) Guinier	F	Fast growth and high susceptibility to *Dothichiza populea, Marssonina brunnea* and *Melampsora sp.*, high rooting ability by cuttings	Hungary
Robusta	*Populus x euramericana* (Dode) Guinier	M	Fast growth and low susceptibility to *Dothichiza populea, Marssonina brunnea* and *Melampsora sp.*	France
PE 19/66	*Populus deltoides* Bartr.	M	Fast growth, resistant to leaf diseases and *Dothichiza populea*, high rooting ability by cuttings	Italy
B-17	*Populus deltoides* Bartr.	Unknown	Fast growth, resistant to leaf diseases and *Dothichiza populea*	Yugoslavia
54/76-28	*Populus deltoides* Bartr.	Unknown	Fast growth, resistant to leaf diseases and *Dothichiza populea*	Yugoslavia
S6-7	*Populus deltoides* Bartr.	Unknown	Fast growth, practically immune to leaf diseases and *D. populea*	Yugoslavia

Net photosynthesis and dark respiration were determined polarographically by a Oxygen electrode (WALKER, 1989). Dark respiration intensity was determined by the quantity of absorbed oxygen (in the dark), and photosynthesis by the quantity of released oxygen, as expressed in mmol m^{-2} s^{-1}. Very fine parts of leaves (up to 0.5 mm) without veins (JONES and OSMOND, 1973) were used for the analysis. The leaf parts were placed in 1.5 ml of reaction medium consisting of: 50 mmol HEPES (N-2-hydroxy-ethyl pi-perazine-N-2-ethane sulphonic acid), pH 7.6 to 7.8 and 1 mmol $NaHCO_3$, at a constant temperature of 25 °C. The photosynthesis process was observed under complete saturation with white light supplied by quartz-iodide lamp (STANKOVIĆ and WALKER, 1977).

Leaf area

The samples was taken at the end of vegetative growing period, and ramets were selected randomly. The sample consisted of all leaves from 10 ramets from each block and location. Leaf area was measured by the apparatus LI 3000 (leaf portable areameter).

Diameter and height measurements

Diameter and height were measured on 20 ramets from each block and location after the first growing season. The ramets were selected randomly. Diameters were measured at the height of 10 cm above the root collar.

Biomass

Dry weight biomass was measured, as an indicator of productivity, by drying the entire ramet. The samples was taken at the end of the first growing season. The samples consisted of 10 randomly selected ramets from each block and location. The ramets were lifted and soil washed from roots. The ramets were dried at 105 °C. The heating and weighing were repeated for 2-hr periods until constant weight is obtained (BROWNING, 1967).

Statistical analyses

The data were subjected to various statistical analyses including: calculation of parameter means, coefficients of variation, analysis of variance (ANOVA), LSD tests and F tests. The analyses of variance were done with MSTAT ver. 1.2 program.

The following model used was:

$$Y_{ijkl} = \mu + \rho_i + \alpha_j + \beta_k + \gamma_i + (\alpha\beta)_{jk} + (\alpha\gamma)_{jl} + (\beta\gamma)_{kl} + (\alpha\beta\gamma)_{jkl} + \varepsilon_{ijkl}$$

where: Y = phenotypic mean; μ = mean, ρ_i = block effect; α_j = species effect; β_k = clone effect; γ_i = site effect; $(\alpha\beta)_{jk}$ = interaction effect between species and sites; $(\beta\gamma)_{kl}$ = interaction effect between clone and sites; $(\alpha\beta\gamma)_{jkl}$ = interaction effect among species, clones and sites; ε_{ijkl} = random error.

The source of variation were: block (r), species (A), clone (B), location (C), species x clone, species x location, clone x location and species x clone x location. F tests were used to determine if significant differences existed.

Table 2. – F values for investigation characters.

Source			Stomata number adaxial	Stomata number abaxial	Thickness of palisade tissue	Thickness of spongy mesophyll	Net photosynthesis	Dark respiration	Leaf area	Diameter	Height	Biomass
		df	F	F	F	F	F	F	F	F	F	F
Block	r	3	0.97^{ns}	0.52^{ns}	0.47^{ns}	1.92^{ns}	0.52^{ns}	0.34^{ns}	2.98^{ns}	2.33^{ns}	1.61^{ns}	1.44^{ns}
Species	A	1	809.02^{***}	77.81^{***}	1331.93^{***}	935.25^{***}	16.23^{***}	20.28^{***}	3389.89^{***}	136.36^{***}	151.79^{***}	937.02^{***}
Clone	B	7	56.39^{**}	211.33^{***}	206.46^{***}	151.22^{***}	20.19^{***}	29.97^{***}	1077.04^{***}	136.36^{***}	151.79^{***}	22.46^{***}
Locality	C	2	139.01^{***}	171.58^{***}	96.11^{***}	51.60^{***}	12.03^{***}	15.79^{***}	1465.32^{***}	163.44^{***}	278.67^{***}	266.82^{***}
Species x Clone		7	10.17^{***}	4.75^{**}	4205.23^{***}	461.09^{***}	15.71^{***}	14.49^{***}	694.34^{***}	87.47^{***}	142.94^{***}	97.18^{***}
Species x Locality		2	6.87^{**}	10.58^{***}	92.97^{***}	44.73^{***}	8.94^{***}	0.63^{ns}	17.08^{***}	9.11^{***}	27.07^{***}	7.17^{**}
Clone x Locality		14	7.44^{***}	12.47^{***}	120.55^{***}	211.90^{***}	4.70^{***}	1.63^{ns}	31.91^{***}	29.30^{***}	66.81^{***}	10.85^{***}
Species x Clone x Locality		14	14.53^{***}	14.35^{***}	246.96^{***}	28.96^{***}	4.83^{***}	4.02^{**}	21.49^{***}	30.44^{***}	4.35^{***}	5.53^{***}
Error		141										

Results

The analyses of variance revealed statistically significant differences between species, clones and locations (*Table 2*). In addition, all interactions species x clone, species x location, clone x locality, and species x clone x location were statistically significant. There were no statistically significant differences among the blocks.

Genotype x Environment Interaction

The analysis of variance (*Table 2*) revealed a highly significant interaction between clone and location for all parameters, indicating a large genotype x environment interaction. This is supported by the change in rank of the clones at each location for all parameters (*Tables 3, 4,* and *5*). The greatest quotient between variance genotype x environment and genetic variance (*Table 6*) characterized the thickness of spongy tissue and plant height (6.61 and 3.01). A very small quotient characterized the number of stomates per mm^2 of adaxial surface of the leaf, leaf area, and biomass (0.05, 0.12 and 0.11).

Leaf anatomy

The thickest palisade tissue occured in the eastern cottonwood clone, PE 19/66 at all locations (*Table 3*). Hybrid poplar clone Ostia had the thinnest palisade tissue at all locations. The coefficient of variation for thickness of palisade tissue ranging from 0.33 to 4.02. The LSD tests separated the clones into six groups of homogenity.

The greatest thickness of spongy tissue occured in the hybrid poplar clone Ostia at Location 1 and eastern cottonwood clone, PE 19/66 at Locations 2 and 3 (*Table 3*). The thinnest layer of this tissue was found in hybrid poplar clones I-214 at the first location and Robusta at the second and third locations. The intraclonal variation was low, i.e., low coefficient of variation (from 0.59 to 4.85). The LSD tests separated clones into five groups of homogenity.

Stomata number

The results show that the greatest number of stomates per leaf mm^2 on leaf adaxial side occured in one or both clones of eastern cottonwood (PE 19/66 and 54/76-28) in all plantings (*Table 3*). The lowest number of stomates was found in the clone I-214 at the first location, in the clone Robusta at the second location, and in the clones Ostia and M1 at the third location; all were hybrid poplar clones. The coefficient of variation for this parameter ranging from 1.21 to 10.76. The LSD tests separated clones into four groups of homogenity.

The highest number of stomates per mm^2 on leaf abaxial surface was found in the hybrid poplar clone I-214 at all locations (*Table 3*). The lowest number of stomates occured in the eastern cottonwood clones S6–7 at the first and the second locations and B-17 at the third location. The intraclonal variation was low, i.e., coefficient of variation ranging from 0.92 to 8.45. The LSD tests separated clones into several groups of homogenity.

Net photosynthesis and dark respiration

Net photosynthesis was most intensive in the hybrid poplar clone M1 at the first and second locations and I-214 at the third location (*Table 4*). The lowest net photosynthesis occured in the hybrid poplar clone Ostia at the first and third locations and in eastern cottonwood clone 54/76-28 at the second loca-

tion. The coefficient of variation for this parameter ranging from 1.04 to 9.10. The LSD tests separated clones into four groups of homogenity.

Dark respiration intensity was generally uniform at each locations (*Table 4*). The highest dark respiration intensity was in the hybrid poplar clone I-214 at all locations, and the lowest in the hybrid poplar clone Robusta at the first and second locations and eastern cottonwood clone B-17 at the third locations. If the clone Robusta is excluded, the highest respiration intensity of all study clones occurred at Locality 1. The intraclonal variation was low, i.e., coefficient of variation ranging from 1.73 to 11.85. The LSD tests separated clones into three groups of homogenity.

Leaf area

There was a large interclonal difference in leaf area (*Table 4*). Leaf area was greatly affect by location with the greatest number of clones having the largest leaf area at the first loca-

Table 3. – Means and LSD test for number of stomata, thickness of palisade tissue and spongy mesophyll of each clone.

Clone	Number of stomata adaxial				Number of stomata abaxial				Thickness of palisade tissue (μm)				Thickness of spongy mesophyll (μm)			
	Loc. I	Loc. 2	Loc. 3	LSD_{Clone}[1]	Loc. I	Loc. 2	Loc. 3	LSD_{Clone}	Loc. I	Loc. 2	Loc. 3	LSD_{Clone}	Loc. I	Loc. 2	Loc. 3	LSD_{Clone}
I-214	101.57	124.19	126.78	c	225.21	187.73	192.45	a	162.66	160.08	156.49	e	20.60	25.06	31.06	d
Ostia	114.45	79.23	105.15	d	182.20	158.40	171.48	d	154.09	148.54	152.09	f	36.90	34.34	23.78	b
M1	107.87	90.24	105.15	d	191.55	163.24	178.33	c	177.98	177.05	176.82	b	26.38	26.27	27.72	c
Robusta	128.33	77.00	111.77	d	184.02	156.80	160.87	de	169.92	168.05	169.86	c	21.57	21.30	22.85	e
PE 19/66	180.35	135.11	149.04	a	212.79	179.04	182.06	b	210.79	195.76	185.72	a	31.78	39.01	42.52	a
B-17	163.05	124.69	130.82	b	179.89	170.56	142.00	ef	185.38	188.55	170.90	a	30.74	24.65	25.73	c
54/76-28	145.71	140.75	147.38	b	170.03	152.49	161.40	f	161.56	166.14	167.34	d	31.24	30.77	30.94	b
S_{6-7}	142.41	131.37	141.54	b	160.40	151.79	168.30	f	158.68	156.63	160.27	e	24.96	27.37	38.10	b

[1]) LSD 0.05

Table 4. – Means and LSD test for net photosynthesis, dark respiration and leaf area of each clone.

Clone	Net photosynthesis (μmol $m^{-2}s^{-1}$),				Dark respiration (μmol $m^{-2}s^{-1}$),				Leaf area (m^2)			
	Loc. I	Loc. 2	Loc. 3	LSD_{Clone}	Loc. I	Loc. 2	Loc. 3	LSD_{Clone}	Loc. I	Loc. 2	Loc. 3	LSD_{Clone}
I-214	19.53	19.51	18.02	ab	8.70	7.57	7.07	a	1.65	1.49	1.05	c
Ostia	11.56	15.83	13.47	c	6.32	5.89	5.94	b	0.73	0.61	0.46	f
M1	22.95	21.70	17.06	a	6.43	6.14	5.42	b	1.13	0.91	0.62	e
Robusta	18.72	18.99	17.46	b	5.46	4.40	4.64	c	1.08	0.91	0.67	e
PE 19/66	22.21	15.65	13.86	b	5.85	5.38	6.39	b	1.88	1.50	1.39	a
B-17	14.94	14.73	16.23	c	6.02	6.05	4.15	bc	1.72	1.32	1.32	b
54/76-28	15.04	13.77	15.35	c	5.72	5.62	4.34	b	1.74	0.97	0.97	c
S_{6-7}	20.96	16.91	15.77	b	6.30	5.37	4.56	bc	1.14	0.75	0.75	d

Table 5. – Means and LSD tests for diameter, height and biomass of each clone.

Clone	Diameter (mm)				Height (m)				Biomass (g)			
	Loc. I	Loc. 2	Loc. 3	LSD_{Clone}	Loc. I	Loc. 2	Loc. 3	LSD_{Clone}	Loc. I	Loc. 2	Loc. 3	LSD_{Clone}
I-214	14.05	13.82	11.76	e	3.18	2.78	2.17	a	178.75	126.50	83.52	f
Ostia	14.05	13.10	13.17	e	1.91	1.88	1.89	c	111.25	102.00	73.13	g
M1	23.12	18.82	15.00	c	3.16	2.90	1.78	a	144.50	133.05	102.43	f
Robusta	13.57	13.07	12.39	e	1.94	2.18	1.64	c	188.00	157.25	124.25	e
PE 19/66	22.17	18.95	15.10	c	2.78	2.17	1.96	b	301.50	221.50	179.50	a
B-17	21.80	27.27	17.37	a	2.77	2.58	2.74	a	268.50	227.52	173.00	b
54/76-28	23.12	18.15	17.86	b	3.08	2.24	1.32	b	249.50	195.50	167.77	c
S_{6-7}	18.12	15.35	15.82	d	2.11	1.56	1.65	d	176.25	167.52	138.25	d

Table 6. – Quotient between the genotype x environment onteraction variance and the genetic variance.

Character	Stoma number adaxial	Stoma number abaxial	Palisade layer	Spongy mesophyll	Net photosynthesis	Dark respiration	Leaf area	Diameter	Height	Biomass
	0.05	0.62	0.60	6.61	0.35	0.92	0.12	0.84	3.01	0.11

tion. The eastern cottonwood clones, PE 19/66 at Locations 1 and 3 and B-17 at Location 2, had the largest leaf area at each respective location. The *P.* x *euramericana* clone Ostia had the smallest leaf area at all locations. The coefficient of variation for this parameter ranging from 0.33 to 7.73. The LSD tests separated clones into several groups of homogenity.

Diameter and height growth

The largest mean diameters were in the clones M1 (*P.* x *euramericana*) and 54/76-28 (*P. deltoides*) at the first location and eastern cottonwood clones, B-17 and 54/76-28 at the second and third locations, respectively (*Table 5*). The smallest diameters were in the hybrid poplar clones Robusta at Locations 1 and 2 and I-214 at Location 3. The intraclonal variation was low, i.e., coefficient of variation ranging from 1.62 to 7.84. The LSD tests separated clones into four intervals of homogenity.

Hybrid poplar clone I-214 had the greatest height growth at the first and second locations (*Table 5*). At the third location, the eastern cottonwood clone B-17 exibited the best height growth. Hybrid poplar clone Ostia was the shortest clone at the first location, while eastern cottonwood clones S6–7 and 54/76-28 had the shortest ramets at the third locations respectively. The coefficient of variation for this parameter ranging from 1.14 to 7.35. The LSD tests separated clones into three groups of homogenity.

Biomass

The eastern cottonwood clones PE 19/66 and B-17 had the greatest total dry biomass at the first and second locations, respectively (*Table 5*). Hybrid poplar clone Ostia had the lowest biomass at all locations. The interclonal variation of this parameter was low, as indicated by the low coefficient of variation (from 0.89 to 7.20). LSD tests separated clones in several intervals of homogenity.

Correlation analysis

Correlation coefficients between the analyzed characters are presented in *table 7*. The relationships between anatomical and physiological parameters and growth elements were especially important. Strong correlation was shown between the number of stomates on leaf adaxial surface and biomass, thickness of palisade layer and biomass, leaf area and and height and biomass, leaf area and height. Moderate correlation was shown between the stoma number adaxial and diameter, stoma number abaxial and height, net photosynthesis and height, and dark respiration and height.

Discussion

The most important tissue from the aspect of productivity is palisade tissue. Previous research indicated that this tissue with spongy tissue, were positively correlated with the biomass production (ORLOVIĆ, 1993). These two tissues constitute the

Table 7. – Correlation coefficient among investigation parameters.

	Stoma number adaxial	Stoma number abaxial	Thickness of palisade layer	Thickness of spongy mesophyll	Net photosynthesis	Dark respiration	Leaf area	Diameter	Height	Biomass
Stoma number adaxial		0.16^{ns}	0.45^{*}	0.40^{ns}	-0.11^{ns}	-0.08^{ns}	0.58^{**}	0.44^{*}	0.03^{ns}	0.68^{***}
Stoma number abaxial			0.30^{ns}	0.16^{ns}	0.33^{ns}	0.71^{***}	0.50^{*}	0.03^{ns}	0.42^{*}	0.18^{ns}
Thickness of palisade layer				0.17^{ns}	0.23^{ns}	$-0.11^{ns\,s}$	0.58^{**}	0.59^{ns}	0.32^{ns}	0.68^{***}
Thickness of spongy mesophyll					-0.47^{*}	-0.09^{ns}	0.08^{ns}	0.07^{ns}	-0.25^{ns}	0.11^{ns}
Net photosynthesis						0.23^{ns}	0.23^{ns}	0.10^{ns}	0.43^{*}	0.08^{ns}
Dark respiration							0.35^{ns}	-0.04^{ns}	0.51^{*}	-0.06^{ns}
Leaf area								0.54^{ns}	0.70^{***}	0.80^{***}
Diameter									0.52^{ns}	0.71^{***}
Height										0.42^{*}

internal photosynthetic area which, together with leaf area, comprise the total photosynthetic area. Clone PE 19/66, as well as clones I-214 and M1 of Euramerican poplar (*Populus* x *euramericana*) had the thickest palisade tissue at the first location on humofluvisol, which is the richest experimental location in humus. The clones of eastern cottonwood had a vast number of stomates on leaf adaxial and abaxial surfaces, in comparison with the hybrid poplar clones. This is understandable as transpiration through stomates must be conducted out by a very developed photosynthetically active tissue. These results are consistent with previous research on stomates on poplar leaves (CEULEMANS *et al.,* 1988; ORLOVIĆ and ĐOKOVIĆ, 1991; ORLOVIĆ, 1994).

Net photosynthesis was the most intensive in the clone M1 (*P.* x *euramericana*) and PE 19/66 (*P. deltoides*) at Location 1 while the hybrid clone I-214 and cottonwood clone B-17 showed the most intensive photosynthesis at Location 3. This is probably due to different clonal requirements for soil fertility and responses to environmental conditions, i.e., genotype x environment interaction.

The net photosynthesis of the clones of Euramerican poplar (M1 and I-214) was higher than that in the clones of Eastern cottonwood, can be explained by the effect of heterosis. The hybrid clone Ostia had the lowest intensity of photosynthesis compared to other clones of Euramerican poplar. Practical experience at the Yugoslavian Poplar Research Institute has shown that this clone is less productive compared to other hybrid clones. However, the clone Ostia is still important as it can tolerate somewhat drier sites. As for respiration intensity, the study confirms the existence of interclonal variability. The clones differed very slightly, but significantly, with respect to this parameter. Net respiration in this study was somewhat more intense than in reference data, probably resulting from the measurement of this parameter on older leaves. Leaf area is another significant physiological parameter that affects the quantity of absorbed energy, which is directly related to yield, is leaf area. As with net photosynthesis, the eastern cottonwood clones have larger leaf surfaces overall than hybrid poplars. Leaf area was the largest in high yielding clones of eastern cottonwood (PE 19/66), and Euramerican poplar (M1 and I-214). This phenomenon had already been observed in other clones of these species (ORLOVIĆ, 1993, 1996; BARIGAH *et al.,* 1994). This results was also showed by previous research of *P. trichocarpa* x *P. deltoides* hybrids with heterosis of hybrid genotypes regarding the formation of larger leaf area, faster closing of stomates in drought conditions, higher number of epidermal cells (HINCKLEY *et al.,* 1989). Interclonal differences in net photosynthesis and respiration, as well as in the size of leaf area, depended also on the locality in which the clones were raised.

Clones PE 19/66, 54/76-28, M1 and I-214 generally had greater diameter and height means that other clones of each respective species at the Locations 1 and 2. At the third location, the means were considerably lower with less difference among clones; the consequence of a relatively poorer soil. Clone PE 19/66 generally produced more biomass than the other eastern cottonwood clones across locations. In the hybrid poplars, however, Robusta is the best producer at all sites.

As the planting were established on three soil types, the adaptability of each clones was assessed. Most characteristics showed a statistically significant genotype x environment interaction. In addition, clonal rank at the three locations was not identical, reflecting the genotype x environment interaction for in all characteristics. The thickness of spongy tissue and plant height exhibited the highest interaction, while the number of stomates per mm^2 of the adaxial surface of the leaf, leaf area, and biomass showed the least sensitivity to environmental change. The results demonstrated that the genotype x environment interaction must be considered during selection as previously shown by LINDGREN (1984). Options for breeding include: 1. selection of genotypes that perform similarly on all sites, or 2. division of areas into several selection zones, with special breeding programs for each zone. The practical result is a combination of the above options through productional genotypes that are stable over a range of environments (*fide* RONNBERG-WASTLJUNG, 1996), and also developing high yielding clones matched to specific sites. In research on white willow (*Salix alba* L.) adaptability, KRSTINIĆ (1984) adopted a similar approach with success.

Previous research has shown the positive correlation between the number of stomates per mm^2 and growth elements (ORLOVIĆ, 1993; BARIGAH *et al.,* 1994; ORLOVIĆ *et al.,* 1995). Additionally, net photosynthesis has been positively correlated with growth elements in some cases (GORDON and PROMINTZ, 1976; CEULEMANS and IMPENS, 1983; ISEBRANDS *et al.,* 1988; CEULEMANS, 1990; ORLOVIĆ *et al.,* 1995). This positive correlation was much more frequent for poplars in comparison to agricultural crops. This difference was also the consequence of the character of yield, which is vegetative for poplars, and reproductive for agricultural crops (CEULEMANS and SAUGIER, 1991). In other studies, correlation involving net photosynthesis was absent, as this parameters was not measured throughout the vegetation period (FOOTE and SHAEDLE, 1974), or because other parameters important for yield, such as the size of leaf area and the content of photosynthetic pigments, were not monitored. The results of the research indicates that the stomata number adaxial, thickness of palisade tissue, and leaf area can be used in selection of nursery stock for the desired characteristics, i.e., for biomass production.

The results indicate that it is possible to create genotypes with an optimal structure of vegetative organs and level of physiological processes. These genotypes can serve as models for selection of high yielding, heterotic clones. The genetic control of these characters and the influence of environment will be determined through analyses of clonal plantations of half- and full sibling from subsequent breeding experiments on a variety of sites.

Literature

ANDERSON, H. W., PAPDOPOL, C. S. and ZSUFFA, L.: Wood energy plantations in temperature climates. For. Ecol. Manage. **6**: 281–306 (1983). — BARIGAH, T. S., SAUGIER, B., MOUSSEAU, M., GIUTTET, J. and CEULEMANS, R.: Photosynthesis, leaf area and productivity of 5 poplar clones during their establishment year. Ann. Sci. For. **51**: 613–625 (1994). — BROWNING, B. L.: Determination of water. In: Methods of Wood Chemistry. Vol. I: 59–71. A division of John Wiley & Sons (1967). — CAIN, N. P. and ORMORD, D. P.: Hybrid vigor as indicated by early growth characteristics of *Populus deltoides*, *P. nigra,* and *P.* x *euramericana.* Can. J. Bot. **62**: 1–8 (1984). — CEULEMANS, R.: Genetic variation in functional and structural productivity determinants in *Populus* spp. Dissertation, University of Antwerp, p. 104 (1990). — CEULEMANS, R. and IMPENS, I.: Photosynthetic, morphological, and biochemical gas exchange characteristics in relation to growth of young cuttings of *Populus* Clone. Advances in photosynthesis research. Proceedings of the VIth International Congress on Photosynthesis, Brussels, Belgium, August 1 to 6, Volume IV: 141–144 (1983). — CEULEMANS, R., IMPENS, I. and IMLER, R.: Stomatal conductance and stomatal behavior in *Populus* clones and hybrids. Can. J. Bot. **66**: 1404–1414 (1988). — CEULEMANS, R., IMPENS, I. and STEENACKERS, V.: Stomatal and anatomical leaf characteristics of ten *Populus* clones. Can. J. Bot. **62**: 513–518 (1984). — CEULEMANS, R., IMPENS, I. and STEENACKERS,V.: Variations in photosynthetic, anatomical and enzymatic leaf traits and correlations with growth in recently selected *Populus* hybrids. Can. J. For. Res. **17**: 273–283 (1987). — CEULEMANS, R. and SAUGIER, B.: Photosynthesis. In: Physiology of Trees. Ed. A. S. Raghavendra No. **2**: 21–50. John Wiley & Sons, Inc. (1991). —

DICKMANN, D. I., GOLD, M. A. and FLORE, J. A.: The ideotype concept and the genetic improvement of tree crops. Plant Breed. Rev. **12**: 163–193 (1994). — FOOTE, K. and SCHAEDLE, M.: Seasonal field rates of photosynthesis and respiration in stems of *Populus tremuloides.* Plant Physiology Supplement 53, p. 352. (1974). — FEGE, A. S.: Evaluation of researcher's decision in short rotation forestry. For. Sci. **33**: 30–42 (1987). — GORDON, J. C. and PROMNITZ, L. C.: Photosynthetic and enzimatic criteria for the early selection of fast growing *Populus* Clone. In: Tree Physiology and Yield Improvement. Ed. M. G. R. CANNELL and F. T. LAST. Academic Press London, New York, San Francisco, p. 567 (1976). — GUZINA, V., ORLOVIĆ, S. and IVANIŠEVIĆ, P.: Black poplar clone variability of stoma numbers and sizes on the leaves of two-year-old seedlings depending on soil properties. Soil and Plant **44**, 1: 39–48 (1995). — HERPKA, I.: Wood mass production in 3 year poplar plantation. Poplar 48/49: 16-13 (Serbian with English Summary) (1965). — HINCKLEY, T. M., CEULEMANS, R., DUNLAP, J. M., FIGLIOLA, A., HEILMAN, P. E., ISEBRANDS, J. G., SCARASCIA-MUGNOZZA, G., SCHULTE, P. J., SMIT, B., STETTLER, R. F., VAN VOLKENBURGH, E. and WIARD, B. M.: Physiological, morphological and anatomical components of hybrid vigor in *Populus.* In: Structural and Functional Responses to Environmental Stresses. Ed. K. H. KREEB, H. RICHTER, T. M. HINCKLEY. SPB Academic Publishing bv, The Hague, The Netherlands. pp. 199–217 (1989). — ISEBRANDS, J. G., CEULEMANS, R. and WIARD, B.: Genetic variation in photosynthetic traits among *Populus* Clone in relation to yield. Plant Physiology and Biochemistry **26** (4): 427–437 (1988). — JONES, H. G. and OSMOND, C. B.: Photosynthesis by thin leaf slices in solution. I. Properties of leaf slices and comparison with whole leaves. Aust. J. Biol. Sci. **26**: 15–24 (1973). — KRSTINIĆ, A.: Phenotypic stability, adaptability and productivity of some clones of bush willows. Glasnik za šumske pokuse, posebno izdanje **1**: 5–24 (Croatian with English Summary) (1984). — LINDGREN, D.: Prediction and optimization of genetic gain with regard to genotype x environment interaction. Stud. For. Suec. **166**: 15–24 (1984). — ORLOVIĆ, S.: An investigation of stomata variability. M.Sc. Thessis, Forestry Faculty of Belgrade, p. 118 (Serbian with English Summary) (1993). — ORLOVIĆ, S.: Number and size of stomata and transpiration intensity of some poplar clones section *Aigeiros* (DUBY). Forestry **1–2**: 35–39 (Serbian with English Summary) (1994). — ORLOVIĆ, S.: An investigation variability some parameters of Black poplars which are important for breeding for fast growth. Dissertation, Forestry Faculty in Belgrade, p. 121 (Serbian with Englisch Summary) (1996). — ORLOVIĆ, S. and ĐOKOVIĆ, R.: Variability of stomata number and size of some poplar clones section (*Aigeiros*) DUBY. Works **23**: 45–52 (Serbian with English Summary) (1991). — ORLOVIĆ, S., MERKULOV, L. J. and GUZINA, V.: Variability of elements of poplar leaf anatomic structure. Matica srpska – Proceedings for Natural Sciences **87**: 65–72 (1994). — ORLOVIĆ, S., PAJEVIĆ, S. and KRSTIĆ, B.: Possibility of utilizing some morphological and physiological parameters in poplar breeding. IUFRO XX World Congress, Poster abstracts. pp. 70. (1995). — RONNBERG-WASTLJUNG, A. C.: Breeding in *Salix.* Genetics of quantitative characters. Dissertation, Swedish University of Agricultural Sciences, p. 35 (1996). — ŠKORIĆ, A., FILIPOVSKI, G. and ĆIRIĆ, M.: Klasifikacija zemljišta Jugoslavije, ANUBiH, Posebna izdanja, Knjiga LXXVIII, Odelenje prirodnih i matematičkih nauka ed. Tihomir Vukovič, Knjiga 13, p. 72, Sarajevo. Yugoslav Soil Classification. (Serbian) (1985). — STANKOVIĆ, Ž. S. and WALKER, D. A.: Photosynthesis by isolated pea chloroplasts. Some effects of adenylates and inorganic pyrophosphate. Plant Physiol. **59**: 428–432 (1977). — STETTLER, R. F., BRADSHAW JR., H. D. and ZSUFFA, L.: The role of genetic improvement in short rotation forestry. In: Ecophysiology of short rotation forest crops. Editors: MITCHELL, J. B., FORD-ROBERTSON, J. B., HINCKLEY, T. and SENNERBY-FORSSE, L.. Elsevier Applied Sciences, London and New York. pp. 285–304 (1992). — STETTLER, R. F., FENN, R. C., HEILMAN, P. E. and STANTON, B. J.: *Populus trichocarpa* x *Populus deltoides* hybrids for short rotation culture: Variation patterns and 4-year field performance. Can. J. For. Res. **18**: 745 (1988). — WALKER, D. A.: Automated measurement of leaf photosynthetic O_2 evaluation as function of photon flux density. Phill. Trans. R. Soc. Lond. B. **323**: 313–326 (1989). — WOLF, L.: Mikroskopicka tehnika. Praha (1950).

Defining Cryptomeria Seed Sources Useful for Taiwan by Superimposing Probabilities of Good Provenance Results over Climatic Data Maps

By J.-C. YANG[1]), CH.-CH. CHENG[2]) and F. H. KUNG[3])

(Received 12th January 1998)

Abstract

One hundred cryptomeria seedlots, originally obtained from Japan in 1972 were planted in two plantations in Taiwan. At age 23, ninety-six surviving seedlots were measured for height and diameter. Superior seed sources were identified as those with greater heights and diameters than plantation means. We also received climatic data from weather stations near the seedlots. Climatic maps for the coldness index, warmth index, mean January temperature, and mean annual temperature were overlaid on top of the map of Japan. The probability of finding superior seedlots in each climatic zone was calculated and a probability was assigned to each pixel of the climatic zones using the thematic mapping technique. The four probability maps were then overlaid one on top of the others to form an average probability map. From the final layout it shows that the southwestern seedlots grow faster than the northeastern seedlots. Seedlots from the coastal area of the Pacific Ocean grew better than those from the Japan Sea coast. In terms of administrative areas, provenances from Kyushu, Shikoku, western part of Chiugoku, and southern part of Kinki grew best in our two plantations. On the other hand, seedlots from the north-central part of Toohoku were inferior to other provenances. In terms of climatic zone, the best cryptomeria seed sources should be from areas with a coldness index higher than -5 degree-months, a warmth index between 130 and 140 degree-months, mean January temperature above 9 °C, and mean annual temperature above 18 °C.

Key words: Provenance, cryptomeria, seed collection zones, GIS, thematic mapping.

FDC: 165.52; 111.24; 111.77; 111.8; 181.65; 181.22; 232.12; 561.1/.2; 174.7 *Cryptomeria japonica;* (520); (529.1).

Introduction

Cryptomeria (*Cryptomeria japonica* D. DON) trees were first introduced from Japan to Taiwan about one hundred years ago.

[1]) Director-General, Taiwan Forestry Research Institute, Taipei, 100, Taiwan, Republic of China. The paper is contribution No. 104 of Taiwan Forestry Research Institute.

[2]) Deputy Director, Taiwan Forestry Research Institute, Taipei, 100, Taiwan, Republic of China.

[3]) Professor, Southern Illinois University, Carbondale, IL. 62901-4411, USA, and Visiting Research Scientist, Taiwan Forestry Research Institute, Taipei, 100, Taiwan, Republic of China.