Clonal Variation in Nutrient Content in Woody Biomass of Hybrid Aspen (*Populus tremula* L. × *P. tremuloides* Michx.)

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Differences in the nutrient concentrations and nutrient amounts of stems and branches amongst clones of hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) were investigated. Seven clones with superior and seven with medium growth rates were selected from a test of 119 clones in southern Sweden. Four trees per clone were randomly identified and harvested in dormant conditions. Sample discs from the stems and branches were collected and analysed for N, K, P, Ca, Mg, and S concentrations, as well as wood density. The analyses revealed significant genetic differences in wood density, K, P, and Mg concentrations in the stems. There were weak (non-significant) and negative genetic correlations between stem volume and concentrations of all the nutrients, except potassium, suggesting that nutrient-efficient clones could be selected without significantly sacrificing genetic gain for growth. In the branches K, Ca, and Mg concentrations differed significantly among clones. After selecting more nutrient efficient clones, the potential savings of nutrients compared with current hybrid aspen material was estimated to be around 5%, which seems fairly low, at least in a short-term perspective. However, the use of clones with different nutrient storage strategies may be regarded as a possible way in the long run to save nutrients in hybrid aspen ecosystems, or of removing them when sludge is applied.

Keywords branches, genetic correlations, growth, heritability, nutrient concentration, nutrient removal, stems
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1 Introduction

Plantation forestry offers a possible way to increase the access of renewable energy. In Sweden, so far, developments of this kind have mainly focused on energy forests, i.e. cultivation of willow (*Salix* sp.) clones in rotation periods of up to five years (e.g. Sirén et al. 1987, Christersson et al. 1993, Ledin 1996). However, in the last decade interest in other tree species for biofuel production has intensified (Johansson 1992, 1999, Sonesson et al. 1994, Telenius 1999, Rytter 2002). The attraction of using systems with ordinary forestry species is that the production of merchantable wood and biofuel wood, in the form of tops and branches, can be combined, resulting in a more flexible and less market-sensitive mode of cultivation.

For this purpose, in Swedish conditions, hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) has been found to be highly competitive because of its high productivity and ability to regenerate through root suckers. Hybrid aspen, a cross between the European aspen (*P. tremula* L.) and its North American counterpart, trembling aspen (*P. tremuloides* Michx.), has shown mean annual increments of more than 15 m^3 ha^{-1} yr^{-1} during approximately 25-year rotation periods in the Nordic countries (Jakobsen 1976, Elfving 1986). These growth rates are anticipated to increase in the near future, since the Swedish breeding programme (Karlsson and Danell 1992, Stener 2002) has generated more productive plant material (Rytter et al. 2000, 2002, Rytter 2002, Stener 2002), that is expected to exceed 20 m^3 ha^{-1} yr^{-1} in mean increment over 20–25 year rotation periods.

However, high productivity implies that large quantities of wood and biomass, and thus substantial amounts of nutrients, will be removed at harvest. Estimates derived by Rytter (2002) indicate that whole-tree utilization systems (i.e. harvest of all above-ground tree parts) will cause net losses of N. Similarly, K, P, Ca and Mg is also lost, and must be replaced, via reapplications of ash or weathering, to sustain the productivity of the site. One way to reduce nutrient removal in hardwood plantations is to harvest during the wintertime, thereby avoiding removal of nutrient-rich leaves. Another alternative would be to use nutrient-efficient clones, provided clonal differences occur in nutrient efficiency in the harvested tree parts.

Recent genetic studies of hybrid aspen have revealed significant clonal differences in several tree characteristics such as growth, phenology, wood density and other wood properties (Ilstedt and Gullberg 1993, Stener 1998, Yu et al. 2001a, 2001b). Therefore, clones are likely to display differences in nutrient concentrations in their stems and branches, especially since such differences have been reported for other *Populus* species (e.g. Heilman and Stettler 1986, Singh 1998).

The objectives of this study were to investigate the extent of clonal differences in nutrient concentrations and amounts in stems and branches of hybrid aspen in dormant conditions, and their practical implications with respect to nutrient removal at harvest. Our hypothesis was that genetically based nutritional differences exist between clones and are worth considering when selecting plant material for future cultivation.

2 Material and Methods

2.1 The Stand

The study was performed in a 14-year-old field trial of 119 hybrid aspen clones (Svalöv, Sweden; lat. 55º57'N; long. 13º06'E; alt. 80 m.a.s.l.). One-year-old container plants were established at a density of 1600 plants ha^{-1} (2.5 m × 2.5 m) as single tree plots in a randomised block design with a total of 15 ramets per clone. No thinning was carried out before the study. The site was on fertile former agricultural land with clayish moraine, and the stand consisted of 1360 stems ha^{-1}. The average height of all clones was 12.8 m and the average breast height diameter of the stem of mean basal area was 12.5 cm. Growth in the four years preceding the study averaged 21.6 m^3 stemwood ha^{-1} yr^{-1}.

Table 1. Origin of the parent trees for the hybrid aspen clones included in the study.

Clone no	Origin (Mother × Father)
1	Våle 3, Y-county, Swe × Wolverine 75, Wisconsin, USA
3	Mykinge F27, F-county, Swe × Woodstock 39, New H., USA
8	Misterhult 97, H-county, Swe × Cass Lake 2, Minnes., USA
12	Bisset Creek 2, Ontario, Can × Misterhult, H-county, Swe
14	Ånhammar 116, D-county, Swe × Bracebridge, Ontario, Can
18	Bisset Creek 2, Ontario, Can × Ehle 4X (tetraploid *P. tremula*), Swe
35	Hamar 10/60, Nor × Grand Rapids 38, Minnesota, USA
51	Bisset Creek 4, Ontario, Can × Damhult 44, E-county, Swe
59	Gränna F16, F-county, Swe × Petawawa, Ontario, Can
76	Häggeby, C-county, Swe × Matapedia, Qubec, Can
79	Våle 3, Y-county, Swe × Wolverine 75, Wisconsin, USA
82	–
106	–
119	Blizyn 4, Pol × Moran, Michigan, USA

2.2 Sampling

All 119 clones in the trial had been selected as plus-trees in trials and commercial stands from the 1950's and 1960's. Based on assessments from the autumn of 1999, all the clones were divided into three categories: 1) superior, 2) medium and 3) poor, depending on their volume growth. For this study, 14 clones (Table 1) were randomly selected from amongst the first two of these groups, i.e. seven clones of superior growth and seven of medium growth. For each clone four individuals, free from visible external stem damage, were randomly selected and harvested in January 2001.

Breast height diameter, green crown height, and total tree height were recorded for each selected stem. Stem discs of 3–5 cm thickness were cut at every third metre along the stem, starting at stump height and continuing to the top. Depending on tree height, five or six discs were collected from each tree.

Immediately after cutting, the discs were transported to the nearby Skogforsk laboratory at Ekebo research station. The diameter of each disc was recorded by cross measurement and the disc volume over bark was estimated by the water displacement method, thereby allowing individual density estimates to be made. All discs were dried at 85ºC to constant weight (~ one week) before dry weight determinations.

From each sample tree, three representative living branches were collected from the lower, middle, and upper thirds of the green crown. The fresh weights of these branches were determined. Three subsamples of exactly 2 cm length were collected from each sampled branch. The subsamples were cut at a distance of 10 cm from the stem, exactly in the middle of the branch, and 10 cm from the tip. Fresh and dry weights (85ºC) were recorded for each subsample. The total fresh weight was recorded for the rest of the living branches of each tree.

Dead branches were also collected from each tree. However, they were few in number and their weight was low in comparison to that of the living branches (data not shown), so they were not included in further investigations.

2.3 Nutrient Analyses

In order to produce a representative sample for nutrient analysis from each stem disc, a cross section of even thickness was removed by a circular saw blade, when sawing each disc into two horizontal halves. The sawdust thus produced was carefully collected and mixed and a sample of it was used to analyse concentrations of nitrogen, phosphorus, potassium, calcium, magnesium, and sulphur. The branch subsamples from each tree were combined, ground and thoroughly mixed. A sample was taken to analyse the same nutrients as for the stem discs. The sampling procedure described above was assumed to give representative estimates of weight-based averages of the nutrient concentrations.

Nitrogen was analysed by gas chromatography in an elemental analyser (CarloErba NA 1500, Rodano, Italy; Kirsten and Hesselius 1983). The other macronutrients (K, P, Ca, Mg, and S) were analysed with an inductively coupled plasma with

optical emission spectrometry (ICP-OES, Perkin Elmer, Shelton, CT, USA). Milled samples were prepared by digestion in a solution of concentrated HNO_3 and $HClO_4$, 2 M HNO_3 was added to the digest and the solution was finally diluted with distilled water (cf. von Fircks et al. 2001).

2.4 Volume and Weight Calculations

Stem volume over bark was estimated for each tree by summing the volumes of the 3 m stem sections and the top, using the formulas for the frustum of a cone ($V = (\pi H/3)(R^2 + Rr + r^2)$), and a circular cone ($V = (\pi R^2 H)/3$), respectively, where V = volume, H = height of the stem section, R = lower radius and r = upper radius. The tapering of trees, including European aspen according to Opdahl (1989), normally follows a sigmoidal pattern. This deviation from an ideal cone shape might introduce some error into the stem volume estimations based on 3 m sections, but the potential effects were regarded as marginal and were not therefore further considered. Fresh stem volume estimates were converted to stem dry weights using the recorded disc density of each sample tree. An average stem density value was estimated for each stem section by taking the mean of the densities from the two discs at the section ends. For the top of the stem the density of the uppermost disc was used.

The dry weight of living branches was estimated for each sample tree by using the average ratio between the dry weight and fresh weight of the subsamples, and multiplying the resulting figure by the total fresh weight of all living branches.

2.5 Nutrient Calculations

When calculating the amounts of the different elements in each 3 m stem section, average figures for the nutrient concentrations in the discs at the bottom and top of the section were used. For the rest of the top, the nutrient concentrations of the uppermost sampled disc were used. The nutrient amounts in the whole stem were obtained by summing the amounts found in all the stem sections, including the top.

The nutrient amounts in living branches per sample tree were calculated by multiplying the concentration of each nutrient obtained from the combined subsamples with the estimated total dry weight of branches of each tree.

2.6 Statistical Analyses

The statistical analysis was based on individual tree observations according to the model:

$$y_{iik} = \mu + b_i + c_j + e_{ijk} \quad (1)$$

where y_{ijk} = observation k, in block i for clone j, μ = trial mean, b_i = fixed effect of block i, c_j = random effect of clone j, NID(0,σ_c^2), and e_{ijk} = random error term for observation ijk, NID(0,σ_e^2). The variances σ_c^2 and σ_e^2 were estimated for different traits according to Henderson's method 3 (Henderson 1953) as performed in LSMLMW software (Harvey 1990). Values of BLUP (Best Linear Unbiased Predictors) for each clone were obtained using Proc Mixed (SAS 1997). Genetic parameters were interpreted as $\sigma_G^2 = \sigma_c^2$ and $\sigma_E^2 = \sigma_e^2$, where σ_G^2 = the genotypic variance among clones and σ_E^2 = environmental variance. The individual broad sense heritability (H^2) was calculated as:

$$H^2 = \sigma_G^2/(\sigma_G^2 + \sigma_E^2) \quad (2)$$

The genotypic coefficient of variation (CV_G) was calculated as:

$$CV_G = \sigma_G \cdot 100/\mu \quad (3)$$

The genotypic correlations (r_G) between traits were estimated by LSMLMW software (Harvey 1990) from:

$$(r_G) = \sigma_{G1G2} / (\sigma_{G1} \cdot \sigma_{G2}) \quad (4)$$

where σ_{G1G2} is the genotypic covariance between traits 1 and 2, while σ_{G1} and σ_{G2} are the genotypic standard deviations for traits 1 and 2, respectively.

Most traits displayed normal distributions. However, stem and branch concentrations of K and Ca and the total amounts of N, K, P, Ca

and Mg were only approximately normally distributed. Since both normal-score (Gianola and Norton 1981) and arcsin transformation prior to statistical analysis changed the results only marginally, all traits were left untransformed.

The significance level used for testing the null hypothesis of no difference was equal to or less than 5% ($p \leq 0.05$)

3 Results

Tree growth, stem wood density, and dry weight of stem and branches all showed significant and high broad sense heritabilities (H^2), indicating that there were significant differences among clones (Table 2, Fig. 1). The genetic coefficients of variation (CV_G) were high for volume and dry weight of stems.

The genetic correlations among growth traits (H, Dbh, V_S, W_S) were all significant (Table 3).

Table 2. Mean values with standard deviation and range based on individual observations (n = 56), heritabilities (H^2) with standard error (S.e. H^2), and genetic coefficients of variance (CV_G) for different traits of 14 hybrid aspen clones. Bold figures for H^2 and CV_G are significantly different from zero ($p \leq 0.05$).

Trait	Unit	Mean	S. Dev. of mean	Range, Min–Max	H^2	S.e. H^2	CV_G, %
Height	dm	156	14.3	124–180	**0.59**	0.13	**6.4**
Diameter, breast height	mm	154	22.9	114–198	**0.63**	0.12	**11.4**
Green crown height	dm	35.9	11.6	6.5–63.5	0.24	0.15	15.7
STEMS							
Stem volume	dm^3	133	45.8	61.9–240	**0.68**	0.11	**27.3**
Stem wood density	kg/m^3	348	28.6	292–408	**0.90**	0.04	**8.0**
Stem dry weight	kg	47.0	15.6	22.6–81.0	**0.65**	0.12	**25.3**
N conc.	mg g^{-1}	2.15	0.358	1.45–2.95	0.13	0.14	6.0
K conc.	mg g^{-1}	1.56	0.263	1.11–2.32	**0.38**	0.15	**10.4**
P conc.	mg g^{-1}	0.281	0.0469	0.159–0.369	**0.48**	0.15	**11.7**
Ca conc.	mg g^{-1}	2.28	0.374	1.67–3.26	0.30	0.16	8.9
Mg conc.	mg g^{-1}	0.234	0.0422	0.150–0.333	**0.76**	0.09	**15.6**
S conc.	mg g^{-1}	0.179	0.0269	0.113–0.236	0.24	0.15	7.4
N amount	g	99.3	32.7	49.7–188.7	**0.52**	0.14	**23.3**
K amount	g	73.2	73.2	30.73–131.18	**0.72**	0.10	**30.6**
P amount	g	12.9	4.05	5.49–22.9	**0.57**	0.13	**23.9**
Ca amount	g	105.4	33.2	46.3–171	**0.60**	0.13	**24.3**
Mg amount	g	10.8	3.46	4.17–20.1	**0.69**	0.11	**27.0**
S amount	g	8.20	2.60	4.04–14.1	**0.58**	0.13	**22.7**
BRANCHES							
Branch dry weight	kg	14.4	7.00	3.55–31.1	**0.57**	0.13	**37.1**
N conc.	mg g^{-1}	6.02	1.06	4.00–8.50	0.22	0.15	8.4
K conc.	mg g^{-1}	3.01	0.417	2.34–4.14	**0.41**	0.15	**8.5**
P conc.	mg g^{-1}	0.814	0.125	0.590–1.07	0.10	0.14	4.7
Ca conc.	mg g^{-1}	6.73	1.14	4.66–9.64	**0.38**	0.15	**10.0**
Mg conc.	mg g^{-1}	0.681	0.124	0.425–1.03	**0.38**	0.15	**10.5**
S conc.	mg g^{-1}	0.476	0.0695	0.327–0.633	0.30	0.16	8.1
N amount	g	84.7	31.0	23.1–206	**0.36**	0.16	**29.4**
K amount	g	43.3	22.3	11.9–102	**0.58**	0.13	**40.3**
P amount	g	11.6	5.84	3.12–29.8	**0.40**	0.15	**32.2**
Ca amount	g	95.3	47.6	28.6–211	**0.54**	0.14	**38.1**
Mg amount	g	9.60	4.63	2.03–23. 6	**0.48**	0.15	**34.6**
S amount	g	6.70	3.15	1.82–15.9	**0.44**	0.15	**31.3**

Table 3. Genetic correlations (r_G) between growth, wood density, and nutrient concentration traits in the hybrid aspen stems ($_S$) and branches ($_B$). Bold figures indicate significant correlations ($p \leq 0.05$). Abbreviations: H = tree height; Dbh = diameter of breast height; V = stem volume; Dens = wood density; W = dry weight.

Traits	H	Dbh	V_S	$Dens_S$	W_S	W_B	N_S%	K_S%	P_S%	Ca_S%	Mg_S%	S_S%
H		**0.81**	**0.87**	–0.18	**0.89**	0.43	–0.45	0.35	–0.24	–0.06	–0.22	–0.34
Dbh			**0.99**	–0.47	**0.91**	**0.82**	–0.73	**0.66**	–0.24	–0.03	–0.12	–0.26
V_S				–0.41	**0.94**	**0.71**	–0.67	**0.64**	–0.22	–0.06	–0.12	–0.23
$Dens_S$					–0.09	–0.18	–0.18	**–0.85**	–0.39	–0.24	–0.24	–0.68
W_S						**0.71**	–0.75	0.39	–0.37	–0.21	–0.23	–0.46
N_B%	–0.45	–0.45	–0.45	0.24	–0.45	–0.78	0.37					
K_B%	0.55	**0.78**	**0.76**	**–0.72**	0.52	0.31		**0.94**				
P_B%	0.37	0.32	0.36	–0.43	0.22	–0.57			–0.51			
Ca_B%	**0.72**	0.47	0.48	–0.53	0.34	–0.17				0.29		
Mg_B%	0.10	0.01	0.03	–0.21	–0.06	–0.25					**0.57**	
S_B%	–0.20	–0.18	–0.19	–0.21	–0.31	–0.65						0.64

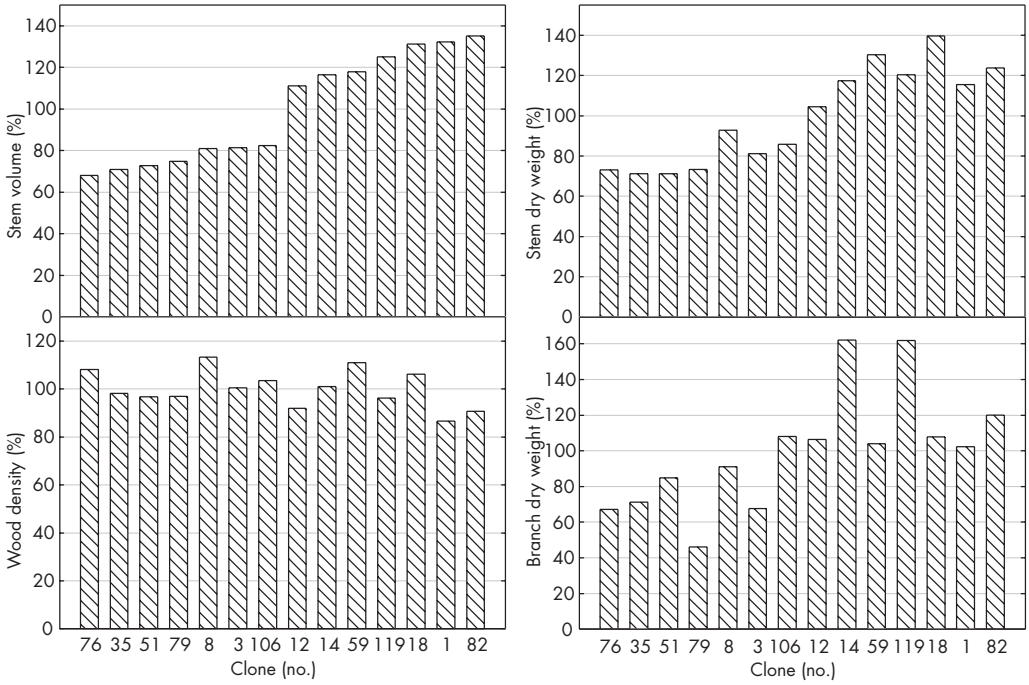

Fig. 1. Genetic values (BLUP) for stem volume, stem wood density, stem dry weight, and branch dry weight, expressed as relative values for each of the 14 clones included in the study. The mean relative value for all clones is equal to 100. The clones are presented in ascending order of stem volume, where the seven clones to the left belong to the medium and the seven to the right to the superior growth category. Average standard errors of BLUP values for volume, density, stem weight, and branch weight, were 12, 3, 11, and 18%, respectively.

Table 4. Concentration and amount of nutrients with significant stem differences among clones (K, P and Mg) in stems, branches and entire trees. The clone selection was based on a process in which clones with the lowest and highest relative stem concentrations (BLUP-values) of all three nutrients combined were selected. The clones were selected from within category 1, i.e. from clones with superior growth.

	K		P		Mg	
	Lowest BLUP	Highest BLUP	Lowest BLUP	Highest BLUP	Lowest BLUP	Highest BLUP
Clones (no.)	14, 59	12, 119	14, 59	12, 119	14, 59	12, 119
Conc. in stems (g kg^{-1})	1.44	1.70	0.250	0.313	0.184	0.275
Amount in stems (g m^{-3})	539	571	93.6	105.5	68.9	92.6
Conc. in branches (g kg^{-1})	2.91	3.11	0.816	0.810	0.680	0.677
Amount in trees (g kg^{-1})	1.81	2.08	0.391	0.446	0.307	0.383

Wood density showed a weak and negative genetic correlation ($r_G = -0.41$) to stem volume. Thus, the r_G correlation between volume and dry weight of the stems was strong (0.94). Branch weight was positively correlated with stem volume and stem weight (Table 3), although individual deviations from this pattern were seen (Fig. 1).

Significant H^2 values for nutrient concentration traits in stems were found for K, P and Mg, while for branches H^2 was significant for K, Ca and Mg (Table 2). Thus, H^2 was not significant for N and S concentrations, which is why they were not included in further analysis. The CV_G was high for total amounts of nutrients in stems and branches, while for nutrient concentration traits, in both stems and branches, it was more modest but still around the same magnitude as for diameter and height. Apart from P there was a positive genetic correlation for the concentration of each element between stems and branches, although the correlations were only significant for K and Mg (Table 3).

To assess the significance of clonal differences in nutrient concentrations on the whole tree level an additional analysis was carried out, in which the nutrients in stem and branches were summed (data not presented in tables). This resulted in approximately the same genetic parameters as in the previous analysis, where stems and branches were evaluated separately (Table 2), with two exceptions. If compared to the H^2 of the stem nutrient concentration the H^2 of Ca increased to 0.36 (significant) and H^2 of P decreased to 0.32 (not significant). These results were expected since the genetic correlations between stem and branches were positive for Ca and negative for P (Table 3).

Significant genetic correlations between stem volume and stem/branch nutrient concentrations were only found for K. Thus, stem and branch concentrations of P and Mg were independent of stem size. This relationship is also indicated in Figs. 2 and 3, where clone values of K, P, and Mg are presented in order of increasing stem volume.

The range of clone differences in nutrient concentrations can be illustrated by selecting clones with the lowest and highest overall BLUP-values for several nutrients in stems. This was done for the superior clones by summing the relative BLUP-values per clone for the elements showing significant between-clone differences in stem concentrations (K, P and Mg). The pairs of clones with the lowest (clones 14 and 59) and highest (clones 12 and 119) levels of nutrients were selected (Fig. 2, Table 4) in order to stabilize the values and avoid individual variations affecting the overall nutritional patterns (Table 3). The differences in stem concentrations between these two groups of clones were 18%, 25% and 49%, for K, P, and Mg, respectively, corresponding to amounts of 32, 12 and 24 g m^{-3} of stem wood (Table 4). If the stem and branch nutrients on a weight basis were combined, a total tree concentration of 1.81 g K kg^{-1} was found for the low-nutrient group of clones. The corresponding value for the high-nutrient clone group was 2.08 g K kg^{-1} (Table 4). Thus, the difference was 0.27 g kg^{-1}, equivalent to a 15% difference in K levels between the K-rich and low-K clones. The corresponding differences for P and Mg were 14% (not significant) and 25%, respectively.

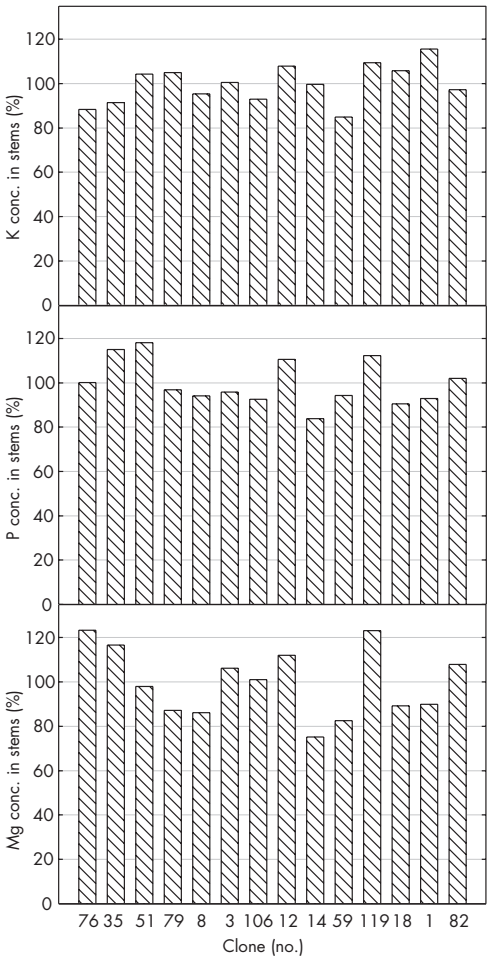

Fig. 2. Relative genetic values (BLUP) for concentrations of K, P, and Mg in the stems with bark included. The clones are presented in ascending order of stem volume (see Fig. 1). Standard errors of BLUP values for K, P, and Mg concentrations, were 6, 6, and 6%, respectively. For more details, see Fig. 1.

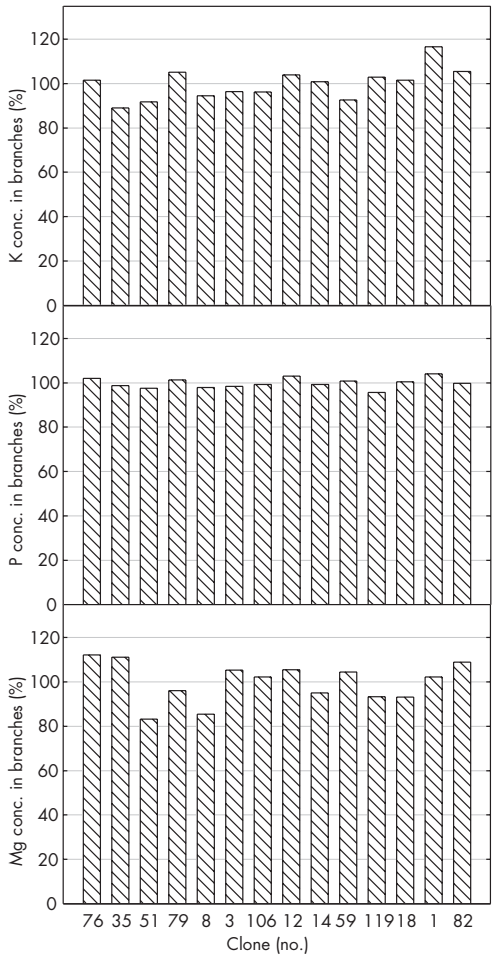

Fig. 3. Relative genetic values (BLUP) for concentrations of K, P, and Mg in the branches, with bark included. The clones are presented in ascending order of stem volume (see Fig. 1). Standard errors for the BLUP values of K, P, and Mg concentrations, were 19, 19, and 18%, respectively. More details are given in Fig. 1.

4 Discussion

Intensive cultivation with the removal of high amounts of biomass during harvest operations increases the need to replace nutrients at a site (cf. Ericsson et al. 1992, Jug et al. 1999, Rytter 2002). The need to replace nutrients can be reduced by harvesting during the winter, since no leaves are removed from the stand. Another possibility could be to use plant material for which the nutrient concentration in aboveground woody biomass is low during dormancy, and in this sense could be regarded as nutrient efficient. This study showed that clonal differences exist in stem and branch nutrient concentrations. Knowledge of genotypic coefficients of variation (CV_G) and heritability (H^2) values are essential for evaluating how traits will respond to selection. In the present

study the CV_G and H^2 values for K, P and Mg concentrations of the stem were of roughly the same magnitude as for diameter and height (Table 2), which are usually the primary selection traits in tree breeding. It should be pointed out that the stratified sampling procedure, i.e. division of all the material into three growth categories for which the best two thirds were used in the study, probably influenced the results. In addition, some of the clones were related, i.e. clone 1 and 79 were selected within the same full sib family and clones 12 and 18 within the same half sib family (Table 1). It is likely that the overall genetic variation for at least the growth and dry weight traits was reduced by this selection process, resulting in underestimations of H^2 and CV_G, and a poorer precision for r_G. On the other hand H^2 was relatively high and CV_G was similar to previous estimates (Karlsson and Danell 1992, Stener unpublished data).

In practical hybrid aspen forestry only clones belonging to the superior and possibly the medium growth groups will be of commercial interest. Thus, the sampling strategy was consistent with likely future commercial clone selection. We also chose to consider the nutrient concentrations and amounts of stems and branches separately, because the future use and assortments of stems and branches are difficult to predict. For example, it has long been expected that tops and branches will continue to be the main tree parts used for biofuel purposes. Recently, however, new economic estimates have shown that stems may be the most valuable energy component of the trees (Alriksson 2002a, 2002b).

The results from the present study should be interpreted with caution since it is based on a single trial with 14 clones (Figs. 1, 2, 3). The results may reflect the specific conditions at the study site in the restricted period examined. To our knowledge there are no reports about genotype – environment interactions on nutrient contents in trees, and further investigations are needed to confirm the results obtained in this study. The existence of nutritional differences is, however, consistent with clonal differences found for other characteristics in aspen and hybrid aspen (Stener 1998, Yu et al. 2001a, 2001b, Fernandez et al. 2002). The tested material also contained similar concentrations of nutrients in stems and branches (Table 2), as reported for fast-growing hardwood trees (Alkan 1985, Heilman and Stettler 1986, Ericsson et al. 1992, Jug et al. 1999). Thus, the nutrient concentrations of the selected hybrid aspen clones seem to have been within the normal ranges expected for the species at such a site.

The differences in stem and branch nutrient concentrations among clones may reflect differences in various physiological processes in the trees. It is possible that the nutrient use efficiency varies among the clones, i.e. that there is a difference in the amounts of nutrients they require to produce a certain amount of biomass. Such differences in nutrient use efficiency have been reported for short rotation forest species (e.g. Heilman and Stettler 1986, Simon 1992, Heilman and Xie 1993). Another possibility is that the amount of nutrients withdrawn from the leaves before leaf fall varies between clones. The amounts of nutrients removed from the leaves can be substantial in fast-growing hardwood species (e.g. Bernier, 1984, Alkan 1985, Pregitzer et al. 1990, von Fircks et al. 2001). Delays in dormancy may result in less nutrients being transported back to the woody tissues (Ericsson et al. 1992). Differences in phenology, i.e. the timing of leaf-colour change and leaf fall, have been reported among hybrid aspen clones (Yu et al. 2001b). A third possibility is that the nutrient storage allocation pattern may differ between clones. Pregitzer et al. (1990) showed that large diameter structural roots constituted a major site of N storage in young hybrid poplars, and that differences existed among the clones they studied. In our study we only observed the overall effect of the processes mentioned above. This may be enough to draw conclusions about practical implications for hybrid aspen forestry, but in order to improve nutritional efficiency in future breeding programmes it would be desirable to have more precise knowledge about nutrient use and circulation.

The study detected significant clonal differences in stem concentrations of K, P, and Mg (Table 2). Except for K, the genetic correlations between nutrient concentrations and stem volume were negative but not significant (Table 3). This suggests that selection for nutrient efficient clones would generally be possible without any signifi-

cant reduction in genetic gain for growth. Moreover, the correlations between stem and branch nutrient concentrations were positive, except for P (Table 3). This indicates that when selecting clones with high or low nutrient concentrations in stems, the corresponding nutrients in the branches will be changed in the same direction.

The practical implications of the identified clonal differences for the amounts of nutrients removed during harvest operations were evaluated after making some assumptions. The first was that the hybrid aspen would grow with a mean annual increment of 20 m^3 over bark volume ha^{-1} yr^{-1} during a 25-year rotation period (Rytter 2002, Rytter et al. 2002). Therefore, only the superior clones were used. The second assumption was that clones with the lowest stem concentrations of the elements would be used instead of those with the highest stem concentrations (Table 4). The annual differences per hectare due to this clonal selection would be 0.64 kg K, 0.24 kg P, and 0.47 kg Mg for stemwood, and 1.02 kg K, and 0.44 kg Mg if branches were included. Phosphorus was not included in the whole-tree estimates due to a lack of significant differences at the whole-tree level (see Results). It also seems reasonable to assume that nutrient concentrations in existing Swedish hybrid aspen material are on average close to the mean of the 14 clones included in the present study. Consequently, a third assumption was that half of the difference between the "extreme" clones (Table 4) could be expected when our nutrient-efficient clones are compared with the average existing hybrid material in Sweden. This indicates, according to the results presented here, that it would be possible to save the removal of about 0.3 kg of K, 0.1 kg of P, and 0.2 kg of Mg ha^{-1} yr^{-1} from stem harvests using nutrient-efficient clones. For a whole-tree system the figures would be 0.5 kg of K, and 0.2 kg of Mg ha^{-1} yr^{-1}, which correspond to 12.5 kg of K and 5 kg of Mg during a 25 year rotation period. According to estimates from Rytter (2002) for a whole-tree hybrid aspen system, around 18, 4, and 4 kg ha^{-1} yr^{-1} of K, P, and Mg, respectively, is likely to be removed by harvest. The potential gain indicated here that could be obtained using high-productivity clones with low nutrient concentrations in woody biomass during the dormancy period would be in the order of 5% for a whole-tree system. This gain seems fairly low in a short-term perspective, but in the long run cultivation of nutrient-efficient trees may be regarded as a small but possible way of saving nutrients and decreasing the reliance on reapplication of ash and weathering.

Low concentrations of nutrients in stems and branches are generally desirable in plantation forests. However, if the objective is to remove nutrients from the ecosystem, as in sludge application systems, clones with high concentrations (i.e. those showing a high capacity to store nutrients in woody tissues) should be preferred. The results of this study could therefore also be exploited for the opposite purpose, i.e. to identify potentially valuable clones that store high amounts of nutrients in woody tissues during dormancy.

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References

Alkan, D.H. 1985. Seasonal changes in nutrient concentration and content of aspen suckers in Minnesota. Forest Science 31: 785–794.

Alriksson, B.-Å. 2002a. Energived ger mer betalt än grot – men massaindustrin motvillig. Skogseko 3/2002, Bilagan: 10–11. (In Swedish)

— 2002b. Han skapar nytt lönande trädbränsle. Skogseko 3/2002, Bilagan: 12–13. (In Swedish)

Bernier, B. 1984. Nutrient cycling in Populus: A literature review with implications in intensively-managed plantations. IEA/ENFOR, Rep. 6. Canadian Forestry Service, Ottawa, 46 p.

Christersson, L., Sennerby-Forsse, L. & Zsuffa, L. 1993. The role and significance of woody biomass plantations in Swedish agriculture. The Forestry Chronicle 69: 687–693.

Elfving, B. 1986. Odlingsvärdet av björk, asp och al på nedlagd jordbruksmark i Sydsverige. Sveriges Skogsvårdsförbunds Tidskrift 5/86: 30–41. (In Swedish, English summary)

Ericsson, T., Rytter, L. & Linder S. 1992. Nutritional dynamics and requirements of short rotation forests. In: Mitchell, C.P., Ford-Robertson, J.B., Hinckley, T. & Sennerby-Forsse, L. (eds.). Ecophysiology of Short Rotation Forest Crops. Elsevier Appl. Sci., London. p. 35–65

Fernandez, M.P., Breuil, C. & Watson, P.A. 2002. Natural clonal variation of wood extractives in Populus tremuloides. Canadian Journal of Forest Research 32: 1192–1199.

Gianola, D. & Norton, H.W. 1981. Scaling threshold characters. Genetics 99: 357–364.

Harvey, W.R. 1990. User's guide for LSMLMW and MIXMDL, PC-2 Version. Ohio State University. 92 p.

Heilman, P.E. & Stettler, R.F. 1986. Nutritional concerns in selection of black cottonwood and hybrid clones for short rotation. Canadian Journal of Forest Research 16: 860–863.

— & Xie, F.-G. 1993. Influence of nitrogen on growth and productivity of short-rotation Populus trichocarpa × Populus deltoides hybrids. Canadian Journal of Forest Research 23: 1863–1869.

Henderson, C.R. 1953. Estimation of variance and covariance components. Biometrics 9: 226–252.

Ilstedt, B. & Gullberg, U. 1993. Genetic variation in a 26-year-old hybrid aspen trial in southern Sweden. Scandinavian Journal of Forest Research 8: 185–192.

Jakobsen, B. 1976. Hybrid aspen (Populus tremula L. x Populus tremuloides Michx.) Det Forstlige Forsøgsvæsen i Danmark 34: 317–338. (In Danish, English summary)

Johansson, T. 1992. Production of forest fuelwood in hardwood stands growing on former farmland. In: T. Johansson (ed.). Forest energy production from conventional forestry systems on a small scale. Swedish Univ. of Agricultural Sciences, Dept. of Forest Yield Res., Report 33, Garpenberg. p. 27–35.

— 1999. Dry matter amounts and increment in 21- to 91-year-old common alder and grey alder and some practical implications. Canadian Journal of Forest Research 29: 1679–1690.

Jug, A., Hofmann-Schielle, C., Makeschin, F. & Rehfuess, K.E. 1999. Short-rotation plantations of balsam poplars, aspen and willows on former arable land in the Federal Republic of Germany. II. Nutritional status and bioelement export by harvested shoot axes. Forest Ecology and Management 121: 67–83.

Karlsson, B. & Danell, Ö. 1992. Genotypic variation and possible selection gain in two clonal tests with hybrid aspen (Populus tremula × P. Tremuloides). The Institute for Forest Improvement, Report 26, Uppsala. 15 p. (In Swedish, English summary)

Kirsten, W.J. & Hesselius, G.U. 1983. Rapid, automatic, high capacity Dumas determination of nitrogen. Microchemical Journal 28: 529–547.

Ledin, S. 1996. Willow wood properties, production and economy. Biomass & Bioenergy 11: 75–83.

Opdahl, H. 1989. Tapering and volume of aspen (Populus tremula L.) in South Norway. Communications of the Norwegian Forest Research Institute 43(2). 42 p. (In Norwegian)

Pregitzer, K.S., Dickmann, D.I., Hendrick, R. & Nguyen, P.V. 1990. Whole-tree carbon and nitrogen partitioning in young hybrid poplars. Tree Physiology 7: 79–93.

Rytter, L. 2002. Nutrient content in stems of hybrid aspen as affected by tree age and tree size, and nutrient removal with harvest. Biomass & Bioenergy 23: 13–25.

— , Werner, M. & Stener, L.-G. 2000. Utnyttjande av hybridasp för att kombinera produktion av biomassa med högkvalitativt gagnvirke. SkogForsk, Arbetsrapport 460, Uppsala. 30 p. (In Swedish)

— , Stener, L.-G. & Werner, M. 2002. Hybrid aspen: a cost-effective alternative for new forestry. SkogForsk, Resultat 10/2002, Uppsala. 4 p. (In Swedish, English summary)

SAS, 1997. SAS/STAT software: Changes and enhancements through release 6.12, SAS Institute Inc., Cary, USA, 1162 p.

Simon, M. 1992. Variation in nitrogen status and efficiency in some North American willows. Swedish Univ. of Agricultural Sciences, Dept. Ecology and Environmental Sciences, Section of Short Rotation Forestry, Report 48, Uppsala. p. 54–62.

Singh, B. 1998. Biomass production and nutrient dynamics in three clones of Populus deltoides planted on Indogangetic plains. Plant and Soil 203: 15–26.

Sirén, G., Sennerby-Forsse, L. & Ledin, S. 1987. Energy plantations – short rotation forestry in Sweden. In: Hall, D.O. & Overend, R.P. (eds.).

Biomass. John Wiley & Sons. p. 119–143.
Sonesson, J., Albrektson, A. & Karlsson, A. 1994. Björkens produktion på nedlagd jordbruksmark i Götaland och Svealand. Swedish Univ. of Agricultural Sciences, Dept. of Silviculture, Arbetsrapport 88, Umeå. 31 p. (In Swedish)
Stener, L.-G. 1998. Analys av fiberegenskaper för kloner av hybridasp. SkogForsk, Arbetsrapport 387. 11 p. (In Swedish)
— 2002. Hybrid aspen improvement in Sweden during the period 1939–2000. In: Pulkkinen, P., Tigerstedt, P.M.A. & Viirros, R. (eds.). Aspen in papermaking. University of Helsinki, Dept. Applied Biology, Publications 5. p. 9–13.
Telenius, B.F. 1999. Stand growth of deciduous pioneer tree species on fertile agricultural land in southern Sweden. Biomass & Bioenergy 16: 13–23.
von Fircks, Y., Ericsson, T. & Sennerby-Forsse, L. 2001. Seasonal variation of macronutrients in leaves, stems and roots of Salix dasyclados Wimm. grown at two nutrient levels. Biomass & Bioenergy 21: 321–334.
Yu, Q., Pulkkinen, P., Rautio, M., Haapanen, M., Alén, R., Stener, L.-G., Beuker, E. & Tigerstedt, P.M.A. 2001a. Genetic control of wood physicochemical properties, growth, and phenology in hybrid aspen. Canadian Journal of Forest Research 31: 1348–1356.
— , Tigerstedt, P.M.A. & Haapanen, M. 2001b. Growth and phenology of hybrid aspen clones (Populus tremula L. × Populus tremuloides Michx.). Silva Fennica 35(1): 15–25.

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