Clonal variability of native willows (*Salix pylicifolia* and *Salix lanata*) in Iceland and implications for use in restoration

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ABSTRACT
There is growing interest in using native species in rehabilitation and restoration of degraded land in Iceland. Reliable information on genetic diversity of the species in question is important for selection of appropriate plant material for restoration projects. This paper reports on growth performance of 86 clones of two native willow species in Iceland, *Salix phylicifolia* L. and S. *lanata* L., in a common garden experiment over six years. The willows had considerable inter- and intraspecific variation in height, crown area and survival. The effect of species was usually larger than the clonal effect although variation among clones increased with time. Rank of growth rates for individual clones varied between years in the beginning, but stabilized with time, indicating that trials lasting longer than one or two years are needed to give a reliable assessment of clone performance. No difference in size was detected between male and female plants. Site of origin had a significant effect on plant size, which might partially be attributed to differences in height of source plants between sites. The results demonstrate a variation in willows that can be utilized in selecting plant material for various functions in restoration projects.

Keywords: common garden experiment, Iceland, native species, reclamation, woodland restoration

YFIRLIT
Breytileiki meðal klóna af innlendum víðitegundum og þýðing fyrir notkun þeirra í landgræðslu
Vaxandi áhugi er á að nota innlendar víðitegundir í landgræðslu hérlendis. Takmarkaðar upplýsingar eru til um erfðabreytileika þeirra en slíkar upplýsingar hafa meðal annars þýðingu við val á efnivið til landgræðslu. Í þessari grein er greint frá niðurstöðum mælinga á vexti 86 klóna gulvíðis og loðvíðis í tilraun á Rangárvöllum yfir sex ára tímabil. Mikill munur var á tegundum og var gulvíðirinn almennt bæði hærri og með umfangsmeiri krónu en loðvíðirinn. Klónar hvorrar tegundar voru einnig mjög breytilegir að stærð, vaxtarlagi og lifun og jókst munur á milli klóna með tímanum. Stærðarröðun klóna breyttist talsvert milli ára til að byrja með en varð síðan stöðugri, sem bendir til þess að skammtímarannsóknir í eitt til tvö ár gefi ekki nógu áreiðanlega mynd af getu einstakra klóna. Enginn stærðarmunur var á milli karl- og kvenplantna en á hinn bóginn komu fram marktæk áhrif af upprunastað klóna, sem má hugsanlega rekja til þess að plöntur sem græðlingaefni var tekið af voru afar misstórar eftir svæðum. Niðurstöðurnar benda til þess að bæði hjá gulvíði og loðvíði sé til staðar breytileiki sem nýta megi til að velja efnivið er hæfi til mismunandi nota.

INTRODUCTION

Willow species are increasingly used in environmental restoration, for erosion control, rehabilitation of degraded soils, increasing biodiversity and other mitigation functions (Kuzovkina & Quigley 2005). In Iceland, native and exotic willows are widely used in afforestation and for ornamental purposes (Pálsson 1997) and there is a growing interest in using native willows for rehabilitation and restoration of degraded areas (Svavarsdóttir 2006).

Salix phylicifolia L. and *S. lanata* L. are two of four indigenous willow species found in Iceland. Both are very common and play an important role in many ecosystems such as birch woodlands, shrub heath, dwarf shrub heath and willow shrublands, heathland and some wetlands (Steindórsson 1980). Both species can be used in a range of restoration projects (Svavarsdóttir 2006), but they are especially important in projects aimed at restoration of native birch and willow woodlands (Aradottir & Eysteinsson 2005).

The selection of genetic material is an important consideration in planning of restoration projects and it affects both their success and the long-term environmental value of the restored areas (Rogers & Montalvo 2004, Falk et al. 2006). It is therefore important for restorationists to have some information on the genetic diversity they are working with (Handel et al. 1994, Falk et al. 2006). Studies of interspecific and intraspecific genetic variability in willows have shown considerable variation within the *Salix* genus in traits such as growth and biomass production (Weih & Nordh 2002, Labrecque & Teodorescu 2005, Tharakan et al. 2005), rooting ability (Houle & Babeux 1993), herbivory resistance (Shen & Bach 1997) and biochemical characteristics (Tegelberg et al. 2003). In Iceland, clones of imported *S. alaxensis* Coville and *S. hookeriana* Barratt, primarily used for shelterbelts, showed variation in growth and survival as well as interaction between clone and experimental sites (Sigurgeirsson 2000). Most studies of willow variability have focused on fast-growing willows that are used for bioenergy production (e. g. Weih & Nordh 2002, Labrecque & Teodorescu 2005) where maximum growth and productivity are the most essential characteristics. There are fewer studies on variability of willows for restoration purposes, where effective erosion control and survival under adverse conditions are more critical (Good et al. 1985, Houle & Babeux 1993).

Common garden studies, where individuals from different sources are planted in a common environment, are the classic method for detecting intraspecific genetic variation among populations or clones (Hufford & Mazer 2003, Rogers & Montalvo 2004). In the current study we assessed variation in survival and growth of *S. phylicifolia* and *S. lanata* clones under common garden conditions. A short-term assessment (2-3 years after planting) of that plant material showed a sizeable variation in plant growth and form (Aradóttir et al. 2006). The aim of this paper is to report on the development of growth rate and growth form and their variability amongst different clones of the two native *Salix* species after six years in the common garden.

MATERIALS AND METHODS

Collection and propagation of the Salix *clones*

Cuttings from individual plants of S. *phylicifolia* and *S. lanata* were collected in lowland and low highland areas in southern Iceland (SL and SH) and northern East Iceland (NL, NH) and lowland area in eastern Iceland (EL) during the period May to June 1997 and 1998. The location, height, growth form and other characteristics of the source plants are presented in Aradóttir et al. (1999).

Forty cuttings, 15-20 cm long, were propagated from each clone. The cuttings were planted in 150 cm^3 containers and pre-grown in a greenhouse. After a few weeks the containers were stored outside in the nursery until the following spring when the cuttings were planted in a common garden experiment.

Establishment of a common garden experiment

A common garden experiment was established in an old hayfield in Gunnarsholt, South Iceland (63°51'N, 20°14'W, elevation 78 m). Five long rows, one for each replicate, were harrowed and covered with black plastic-sheet mulching. The spacing between rows was about 6 m. The plants were planted through holes in the plastic. Four plants of each clone were planted in a single row within each replicate, making in all 20 cuttings of each clone. There was a 1 m interval between plants from the same clone and 2 m between different clones. The distribution of clones within a replicate was random, with the exception that clones that were planted in different years were kept apart.

The rooting ability of the cuttings varied and there was also some mortality during their propagation and storage. Only clones with 16 or more surviving plants at the time of planting were included in the common garden, with the exception of five clones from eastern Iceland that showed poor rooting as they were collected late in the growing season. Only 12 plants of those clones were planted. In total, 68 clones from the 1997 collection and 19 clones from the 1998 collection were planted in the common garden, or 87 clones in all (Table 1). However, one of the alleged clones later turned out to be a mixture of two clones. Therefore only 86 clones were included in this study. The clones collected in 1997 were planted on 14-16 June 1998, and the collection from 1998 was planted on 10 June 1999. A few days after planting, each plant was fertilized with 2.6 g P and 2.2 g N, where a part of the N was a controlled release fertilizer (Osmocote® from Scotts & Sons. Ltd.). No irrigation was applied. Dead plants were replaced in the spring of 1999.

Measurements and observations

Survival, height and crown dimensions (maximum diameter and diameter at 90°angle to the maximum diameter) of the plants were measured in 1999, 2000, 2001 and 2004, and flowering was recorded.

The gender of the *Salix* clones was determined for plants that were flowering during the collection phase, but for other clones the gender was determined when they started flowering in the common garden experiment. In spring 2006 the gender of all clones had been identified: 38 were female and 48 were male (Table 1).

Data analyses

The average of each clone within a replicate was used for all data analyses, except that the total mean of each clone was used for correlations. The crown area of individual plants was estimated from measurements of crown diameter, assuming that the crown was elliptical in diameter. This method may overestimate the

Table 1. Number of willow clones planted in the clone garden in Gunnarsholt, by species, orgin and gender.

	Clones planted in 1998				**Clones planted in 1999**			
	Salix phylicifolia		***Salix lanata***		***Salix phylicifolia***		***Salix lanata***	
Collection area	♀[1)]	♂[1)]	♀	♂	♀	♂	♀	♂
S Iceland								
lowland (SL)	8	7	6	13				
low highland (SH)	5	2	2	4				
NE Iceland								
lowland (NL)						1	3	3
low highland (NH)	1	1	1	1	1	2	4	5
E Iceland								
lowland (EL)	3	4	4	5				
Total	31		36		4		15	

[1)] ♀ female clones, ♂ male clones.

crown area if the crown shape is irregular (Aradóttir et al. 1997). Variability in height and crown area between and within species was estimated by nested ANOVA where clones (a random variable) were nested within species. In other instances, data for *S. phylicifolia* and *S. lanata* were analysed separately and data for *S. phylicifolia* clones planted in 1999 were not analysed further because there were only four clones. ANOVA was also used to assess the effects of gender and origin on plant size, and in the latter case, means were compared with Tukeys HSD (α=0.05). Residuals were examined with regard to normal distribution and equal variances. The correlation between height of the source plants, and average size of the clones in 2001 and 2004 was tested with Pearson's correlation (r), as was correlation between height and crown area of the clones. Non-parametric correlation (Spearman's r_s) was used to assess the rank of clone size between 2001 and 2004. Statistical analyses were carried out using the statistical package SPSS version 14.0 (SPSS Inc., Chicago, Illinois).

RESULTS

There was considerable variability in the height and crown area of the *Salix* clones in 2004 (Figures 1 and 2). The effects of species and clones on height were highly significant in all instances, with the exception of species impact on one year old plants in the year 2000 (Table 2). The average height of *S. phylicifolia* clones planted in 1998 was 0.8 m in 2004 and had increased by 75% from 2001 (Figure 3) The height of the tallest clone was 1.3 m (Figure 1). The average height of *S. lanata* clones was 0.3 m in 2004 and had doubled during the same period (Figure 3), with the tallest *S. lanata* clone 0.5 m (Figure 2). The crown area of both species also increased considerably during this period (Figure 3). The average crown area of *S. phylicifolia* clones planted in 1998 more than doubled and was 1.3 m^2 in 2004, and the average crown area of *S. lanata* more than tripled, from 0.1 m^2 in 2001 to 0.35 m^2 in 2004. There was a significant positive correlation between height and crown area in 2004 for *S. phylicifolia* planted in 1998 (r=0.59, P<0.001, N=31) and *S. lanata* planted in 1999 (r=0.56, P<0.05, N=15), but not for *S. lanata* planted in

Table 2. ANOVA summary for plant height and crown diameter of *Salix phylicifolia* and *S. lantana* clones in 2000-2004, with clones as a random variable nested within species. Significance is marked with stars.

	df	F 2000	F 2001	F 2004
Height				
Planted in 1998				
Replicate	4	2.3 ns	2.0 ns	2.5 *
Species	1	71.0 ***	159.8 ***	124.9 ***
Clone (Species)	66	5.4 ***	10.3 ***	18.3 ***
Planted in 1999				
Replicate	4	4.9 ***	2,7 *	2,8 *
Species	1	0.0 ns	15.5 ***	9.2 **
Clone (Species)	17	3.5 ***	6.2 ***	15.8 ***
Crown area				
Planted in 1998				
Replicate	4	0.8 ns	4.2 **	2.0 ns
Species	1	41.5 ***	127.6 ***	138.1 ***
Clone (Species)	66	4.2 ***	5.5 ***	8.2 ***
Planted in 1999				
Replicate	4	2.2 ns	3.0 *	9.4 ***
Species	1	3.5 ns	105.1 ***	120.4 ***
Clone (Species)	17	1.8 ns	1.5 ns	6.6 ***

* P≤0.05, ** P≤0.01, *** P≤0.001, ns not significant.

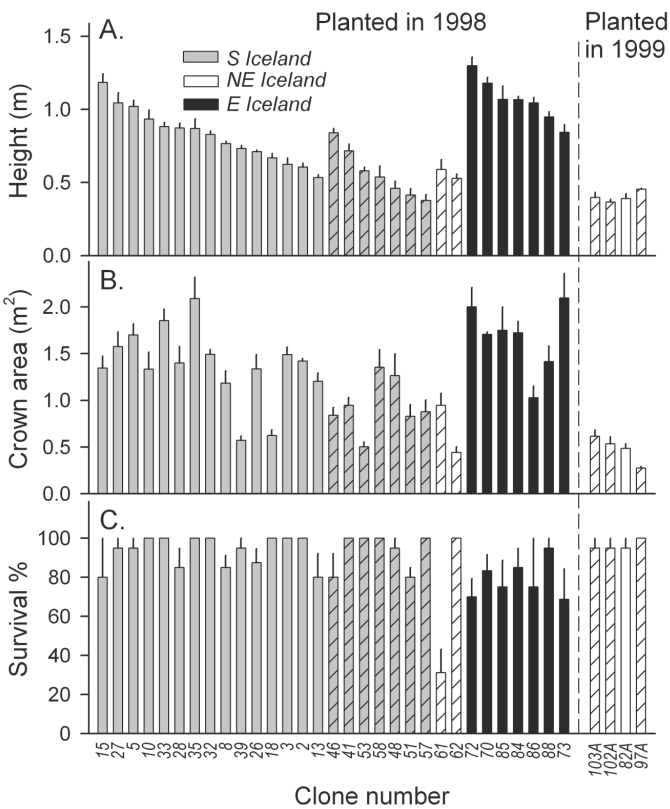

Figure 1. Height (A), crown area (B) and % survival (C) of individual *Salix phylicifolia* clones in a common garden experiment in Gunnarsholt, S Iceland, in spring 2004. Clones collected from lowland sites are shown with solid bars, clones from low highland sites are shown with hatched bars. Bars represent means and their SE for individual clones.

1998 (r=0.23, N=37). Clones planted in 1999 showed a similar growth pattern as the clones planted in 1998 (Figure 3).

There was a positive correlation between height of the source plants and the height of clones in 2001 and 2004, and this became stronger with time (Table 3). The rank of clone size in *S. phylicifolia* was similar between 2001 and 2004 for both height and crown area (Table 4). There was a little more variation in the order of *S. lanata* clones, except that the rank of height for *S. lanata* clones planted in 1999 was almost identical in 2001 and 2004 (Table 4).

Survival of the *S. phylicifolia* clones was usually high with a few exceptions (Figure 1). Survival of *S. lanata* was more variable (Figure 2). Most plant mortality occurred in the first year after planting (Figure 3).

Table 3. Relationship between the height of source plants and average height of clones in the Gunnarsholt clone-garden experiment in 2001 and 2004.

		Pearson's r	
	N	**2001**	**2004**
Salix phylicifolia			
planted in 1998	29	0.45*	0.53**
Salix lanata			
planted in 1998	34	0.36*	0.40*
planted in 1999	15	0.51	0.62*

* P≤0.05, ** P≤0.01, *** P≤0.001.

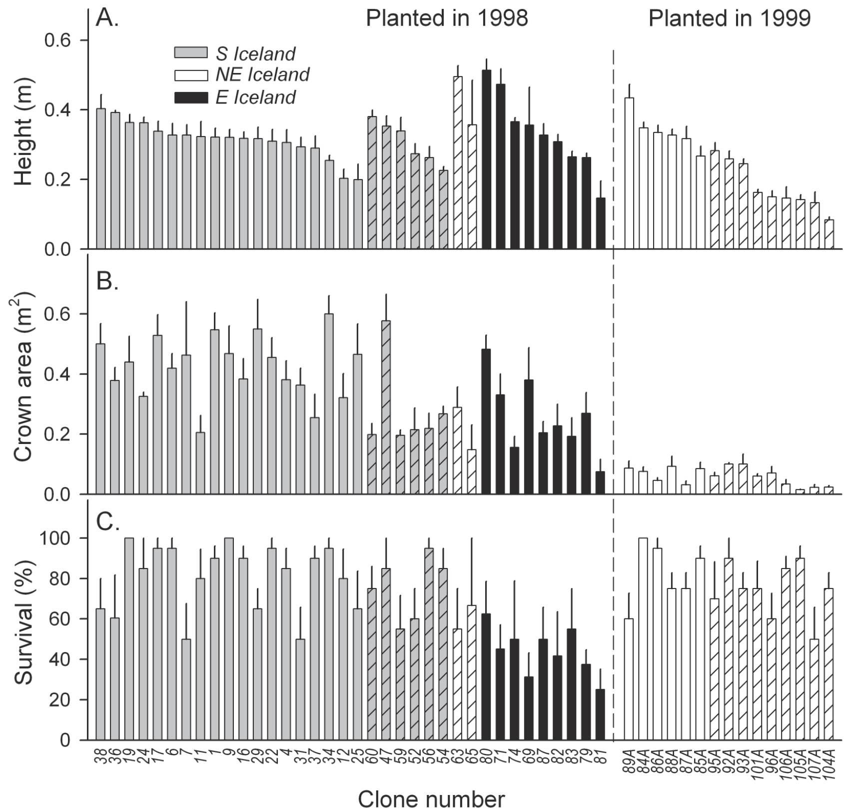

Figure 2. Height (A), crown area (B) and % survival (C) of individual *Salix lanata* clones in a common garden experiment in Gunnarsholt, Southern Iceland, spring 2004. Clones collected from lowland sites are shown with solid bars, clones from low highland sites are shown with hatched bars. Bars represent means and their SE for individual clones.

Table 4. Rank correlation (Spearman's r_s) of the size of clones in the Gunnarsholt clone-garden experiment at different observation times.

		Height			**Crown area**		
	N	**1999-2000**	**2000-2001**	**2001-2004**	**1999-2000**	**2000-2001**	**2001-2004**
Salix phylicifolia							
planted in 1998	31	0.52**	0.80***	0.91***	0.56***	0.78***	0.91***
Salix lanata							
planted in 1998	36	0.65***	0.37*	0.74***	0.68***	0.57***	0.89***
planted in 1999	15		0.69**	0.97***		0.46	0.85***

* P≤0.05, ** P≤0.01, *** P≤0.001.

Neither plant height nor crown area was significantly affected by gender in any instance (P>0.05). On the other hand, the effect of origin of the clone material was highly significant (P≤0.002; Table 5). For *S. phylicifolia* planted in 1998, clones from EL were by far the largest, both in height and crown area, followed by clones from SL (Table 5). For *S. lanata* plant-

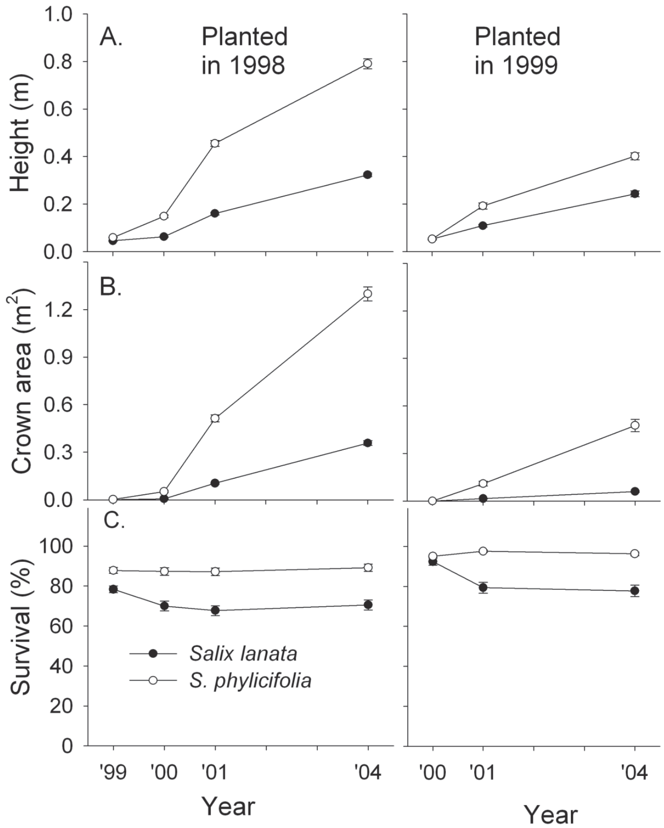

Figure 3. Height (A), crown area (B) and survival (C) of *S. phylicifolia* and *S. lanata* clones in a common garden experiment in Gunnarsholt, Southern Iceland, 1999-2004. Symbols represent means and their SE.

ed in 1998, the height of clones collected in NH was significantly greater than from other sites, but the crown area was greatest in clones from SL (Table 5). *S. lanata* clones planted in 1999 only came from NL and NH. Clones from NL were significantly taller than from NH, but the crown area was similar in clones originating from both sites (Table 5).

DISCUSSION

The high inter- and intraspecific variation in growth of *S. phylicifolia* and *S. lanata* (Figures 1-3) found in this study was consistent with the results of other studies (Good et al. 1985, Weih & Nordh 2002, Labrecque & Teodorescu 2005, Tharakan et al. 2005). *S. phylicifolia* plants were always larger than *S. lanata* due to higher growth rates (Figure 3), and the species effect was usually larger than the clone effect, although the clone

Table 5. Mean height of source plants (SP) by collection area (based on Aradóttir et al. 1999) and mean height and crown area of willow plants in the common garden experiment in 2004. Means within a column that are followed by a different letter are significantly different (Tukey's HSD, α=0.05).

	S. phylicifolia			*S. lanata*					
	planted in 1998			planted in 1998			planted in 1999		
	SP	2004		SP	2004		SP	2004	
Collection area	ht (m)	ht (m)	area (m^2)	ht (m)	ht (m)	area (m^2)	ht (m)	ht (m)	area (m^2)
S Iceland									
lowland (SL)	0.62	0.81[b]	1.37[b]	0.46	0.31[a]	0.42[b]			
low highland (SH)	0.82	0.56[a]	0.94[a]	0.67	0.30[a]	0.28[a]			
NE Iceland									
lowland (NL)							0.92	0.34[b]	0.07
low highland (NH)	0.70	0.55[a]	0.63[a]	0.90	0.42[b]	0.22[a]	0.60	0.18[a]	0.05
E Iceland									
lowland (EL)	4.34	1.06[c]	1.70[b]	1.80	0.34[a]	0.27[a]			

effect increased with time (Table 2). The rank of height and crown area of clones changed considerably between observation dates for the first two years but remained rather consistent between the assessments in 2001 and 2004, with the exception of *S. lanata* clones planted in 1998 (Table 4). These results indicate that short-term trials (one or two years) may not be sufficient to evaluate willow clones. Rank of growth rates appeared to stabilize within a few years and the 2001 assessment gave for the most part a reliable assessment of clone performance in 2004. However, as diseases, insect outbreaks or unusual weather conditions may affect growth rates of individual clones disproportionately in the future (cf. Ares 2002), we plan to re-measure the clones in the common garden within a few years in order to assess their long-term performance.

A weak, but significant, correlation between height of source plants and height of clones in the common garden was observed for the 2001 assessment and became stronger in the 2004 assessment (Table 3), indicating a genetic basis for the variation in growth rate. The observed effects of origin on clone size were most likely confounded by differences in source material (Table 5) due to much taller source plants in eastern Iceland compared to other areas. Clones from eastern Iceland were collected from source plants that were 4.3 m and 1.8 m tall for *S. phylicifolia* and *S. lanata* respectively. In comparison, source plants of *S. phylicifolia* from other parts of the country were 0.6-0.8 m tall and source plants of *S. lanata* were 0.5-0.7 m. As the clones were not randomly selected within each area, this difference in size between source plants did not in any way reflect differences in growth rates of clones in different parts of the country. *S. phylicifolia* clones from eastern Iceland were tallest and had the largest crown area in 2004, followed by clones from southern Iceland, even though the latter came from the lowest source plants (Table 5). Lowland clones from southern Iceland were larger than highland clones from the same part of the country, and had the largest crown area of all *S. lanata* clones in 2004 (Table 5). This indicates that the southern Iceland clones may have had some home-site advantage, but reciprocal transplants are needed to determine this (Hufford & Mazer 2003).

The growth form of the willow clones in the study was quite variable, as demonstrated by a rather weak correlation between height and crown area of clones (0.2 to 0.6). Some clones were tall and wide (e.g. clone number 72 and 80), others tall and rather narrow (e.g. 74 and 86), still other clones were low and wide (e.g. 34 and 58), and intermediate growth forms were also found (Figures 1 and 2). We observed some consistency between the growth form of the clones as observed in the common garden, and the description of the source plants at the time of collection, as described in Aradóttir et al. (1999). This was more common for *S. phylicifolia.* Clones numberered 62 and 86 are examples of tall and narrow clones that were described as upright or fairly upright plants, and clones 2 and 3 are examples of relatively wide and short clones where the source plants were described as prostrate (Aradóttir et al. 1999). However, there were notable exceptions to this, which is to be expected as there are numerous factors that affect plant growth in nature, such as environmental conditions, grazing history and age of the plants, which may mask the growth potential of individual clones. Other studies have shown that the height:width ratio of willow clones can vary between sites (Good et al. 1985). It would therefore be valuable to test the clones in the common garden under different conditions to assess the plasticity of their growth forms.

Gender did not affect the plant size in this study, neither in 2001 nor 2004, which agrees with studies of *S. lanata* in Iceland (Orradóttir 1993) and other willow species (Alliende & Harper 1989, Ahman 1997, Houle 1999).

Implications for restoration

Genetic diversity within a species presents a way for responding to environmental uncertainty and is one of the foundations of biodiversity (Rogers & Montalvo 2004, Falk et al.

2006). Rice and Emery (2003) have pointed out that plant material used in restoration should not only be adapted to the current environmental conditions but also should have enough genetic diversity to allow the population to cope with changes in the future, including climate change. Often the preferred option in selecting plant material for restoration projects is to use local genetic material, as this is presumably adapted to the site and compatible with the existing populations (Handel et al. 1994, Rogers & Montalvo 2004). However, it has been pointed out that in disturbed and fragmented landscapes remnant populations may well be genetically narrow and lack genotypes that are adapted to the conditions under restoration (Lesica & Allendorf 1999, Falk et al. 2006). Species that disperse genes widely and frequently tend not to be very genetically differentiated across the landscape (Falk et al. 2006) and this probably applies as well to willows as they have wind-dispersed seeds that can be dispersed over rather long distances (Gage & Cooper 2005) and are to some extent wind pollinated (Culley et al. 2002). Alternatively genetically diverse populations can be introduced, e.g. by using regional mixtures as suggested by Lesica & Allendorf (1999). If the introduced population is large there is, however, a risk of swamping the local population, which can have adverse effects if the introduced material includes a large proportion of poorly adapted genotypes (Falk et al. 2006). On the other hand, restored populations that are founded on a small effective population may be in danger of genetic drift, as may happen where only a few genotypes that are produced by cloning are used or if the founder population has a skewed sex ratio (Lesica & Allendorf 1999). Thus, it is important to select plant material for restoration projects with care and regard to the project objectives.

There has been limited commercial availability of *S. phylicifolia* and *S. lanata* for use in restoration programs in Iceland and plant material is often collected on a project base. The variability in growth rates, growth form and survival of *S. phylicifolia* and *S. lanata* clones in the current study indicates a rich genetic variation to select from amongst and within districts when collecting such plant material (Figures. 1 and 2). Our results show further that growth form and size of the source plants are expressed by the resulting clones. Thus, different growth forms can be selected for different purposes, such as prostrate clones that cover relatively large areas for erosion control and trapping of litter, and a mixture of prostrate and taller clones to increase surface roughness and thus gain increased effectiveness in reducing wind speed. Observed variability in growth form and bark colour (not shown) can also add to the visual appeal of willow plantings, which is critical where these species are used for amenity in horticulture and landscaping.

Recent studies show that direct planting of *S. phylicifolia* and *S. lanata* cuttings can give satisfactory results (Svavarsdottir et al. 2006), which makes collection and use of local plant material a straightforward process that can be accomplished within the same operation. Whether cuttings are collected for direct planting, or for pre-growing plants in a nursery before planting, an effort should be made to collect plant material from many individuals, to ensure genetic variability and sufficient population size.

Our results did not show any effect of gender on plant growth and gender can therefore be ignored when high growth rate is the target of selection. However, restoration programs are often designed in such a way that introduced populations have the role of a founder or a seed source for subsequent colonization. For that purpose it will be important to maintain an optimal gender ratio to ensure pollination and seed rain. Crawford & Balfour (1983) observed a female-biased sex ratio of 59:41 in *S. polaris* Wahlenb. in Spitzbergen and *S. herbacea* in Iceland. They argue for an optimal ratio of about 60:40, based on the assumption that the advantage gained from increased seed production by more females is progressively diminished as departure from equal an sex ratio reduces the effective population size (Crawford & Balfour 1983). A balanced ratio of female to male plants, or a ratio slightly biased towards female plants (50-60% females), seems like a reasonable target when willows are planted in restoration programs.

Further research is needed on the interaction between clones and environmental conditions. A study of the local genetic variation in *S. phylicifolia* and *S. lanata* would also give valuable information for selection of plant material for restoration projects. Our results to date indicate that reliable testing of plant material may be achieved in three years, but we plan to re-measure the common garden plants within a few years to assess the long-term performance of the clones.

ACKNOWLEDGEMENTS

Adalsteinn Sigurgeirsson helped in organizing the collection of the clone material. He also participated in the collection, as did Sigurdur H. Magnússon, Sigurdur Blöndal and Tumi Traustason. The willow plants were pre-grown at the Icelandic Forest Service nurseries at Mógilsá and Hallormsstaður. Personnel of the Soil Conservation Service assisted with setup and assessments of the common garden experiment. The Agricultural Productivity Fund, the Icelandic Research Council and the Iceland Forest Research Station at Mógilsá provided financial support for setup of the common garden experiment and its initial assessments. Anonymous referees provided constructive criticism that improved the manuscript. All persons involved deserve thanks from the authors.

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Manuscript received 23 March 2007
Accepted 27 September 2007