Shoot growth strategy of 29 black cottonwood (*Populus trichocarpa)* clones

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ABSTRACT

Black cottonwood *(Populus trichocarpa* Torr. & Gray) is an important species for arboriculture and forestry in Iceland. Its wider use has been hampered by frequent shoot dieback, causing reduced net height increment and contorted stem form. We studied rate of shoot growth during the growing season and the dates of bud set and shoot growth cessation in 24 full-sib F_1 clones, the two parent clones and three control clones in a field trial in Southhern Iceland. Shoot growth attributes and phenology were correlated with subsequent shoot dieback by clone. The rate of shoot elongation varied by clone and time during the growing season. Shoot growth rates of clones 12, 'Pinni' and 'Salka' peaked at > 4 mm day^{-1}. The shoot extension rate of clone 'Pinni' was about 3 mm day^{-1} from mid-May to mid-June, and increased to > 5 mm day^{-1} in late June. Different clones had maximum growth rates at different times during the summer. Some clones were characterised by primarily predeterminate growth, whereas other clones were predominantly indeterminate. Shoot dieback in the winter 1997-1998 was positively correlated with the rate of shoot growth in early August and the incidence of late season (August) bud break. Shoot growth to mid-June was negatively correlated with the incidence of bud break in August. We suggest that in southern Iceland cessation of shoot growth and induction of endodormancy by August is important for both winter hardiness and predeterminate shoot growth the following spring. There may be considerable scope for selection of clones combining high early summer shoot growth rates and timely shoot growth cessation, thereby maximising net height increment with straight stem form.

Key words: predeterminate growth, indeterminate growth, bud set, frost damage, dormancy, shoot dieback

YFIRLIT

Vaxtarferill toppsprotans hjá 29 alaskaasparklónum (Populus trichocarpa)
Á Íslandi er alaskaösp (*Populus trichocarpa* Torr. & Gray) mikilvægt tré í skógrækt, skrúðgarðyrkju og skjól-beltum. Ræktun hennar takmarkast samt mjög af tíðum kalskemmdum sem valda hlykkjóttum stofni sem hækkar hægar en vænta mætti af lengd ársvaxtarins. Í klónatilraun í Hellisskógi við Selfoss var fylgst með lengdarvexti toppsprotans, hvenær sprotavexti lauk, myndun endabrums og tíðni laufgunar síðsumars hjá 1) 24 klónum sem voru alsystkin og afkvæmi klónanna 'Keisara' og 'Iðunnar', 2) foreldrum þeirra og 3) þremur óskyldum viðmiðunarklónum ('Brekkan', 'Pinni' og 'Salka'). Kannað var samband sprotavaxtar og brum-myndunar á athugunarári (1996) við kalskemmdir næstu tvö ár þar á eftir (1997-1998). Klónarnir uxu mis

hratt og luku vexti á mismunandi tíma. Klónarnir 12, 'Pinni' og 'Salka' uxu hraðast > 4 mm dag^{-1}. 'Pinni' óx um 3 mm dag^{-1} frá miðjum maí til miðs júní en > 5 mm dag^{-1} seinni hluta júní. Sumir klónar höfðu að mestu forráðinn vöxt og luku vexti í júní meðan aðrir klónar uxu langt fram eftir sumri. Fylgni reyndist milli kalskemmda veturna 1997 og 1998, sprotavaxtar fyrri hluta ágústmánaðar og tíðni ótímabærrar laufgunar endabruma í ágústmánuði. Sprotavöxtur fram til miðs júní var minni á klónum sem laufguðust að nýju í ágúst-mánuði. Sprotavöxtur í ágústmánuði og síðbúin myndun brumdvala hjá alaskaöspum á Suðurlandi virðist bæði auka líkurnar á haust- og vetrarkali og draga úr forráðnum sprotavexti vorið eftir. Það virðist mögulegt með kynbótum og úrvali að finna asparklóna sem vaxa hratt snemmsumars og ljúka vexti tímanlega og þannig fá hraðvaxnar aspir sem kala sjaldan og hafa því beinan stofn.

INTRODUCTION

Tree height and stem form are principal determinants of tree value for almost any use, tangible as well as intangible. Tree height is the result of cumulative net vertical increment. Both shoot lengths produced during the growing season and subsequent shoot dieback may affect net increment. Dieback of top shoots would reduce net height increment and cause stem defects. Hence, the length and fate of the top shoot is of principal importance for both tree stature and stem form.

The length of the leader is the result of both the duration of shoot extension and rate of elongation. Cessation of shoot elongation and bud set is a prerequisite for the development of sufficient frost tolerance for winter survival in cold climates (Junttila 1989). Late completion of shoot growth may predispose trees to frost damage in autumn and winter (Howe et al. 2000). We would, therefore, expect trade-offs between shoot lengths and shoot dieback the following winter, i.e. longer shoots might grow later into the fall and consequently be more prone to frost damage. The rate of shoot elongation during the growing season might affect that proposed relationship. Genotypes with high shoot elongation rates but early growth cessation might produce relatively long shoots of sufficient winter hardiness. Conversely, genotypes with low shoot elongation rates but late growth cessation might produce small shoots with high risk of frost damage.

Black cottonwood (*Populus trichocarpa* Torr. & Gray) is a fast growing species of inherently straight stem form that may grow to large dimensions in its native habitat in the Pacific Northwest (Fowells 1965). This species was initially introduced to Iceland in 1944 from the Kenai Peninsula, Alaska (Bragason 1995). Black cottonwood has become an important urban tree in Iceland and has been widely planted in shelterbelts and afforestation projects since the 1980s (Óskarsson et al. 1990, Sigurdsson 2001a).

In 1988, Icelandic Forest Research, Mógilsá, initiated a research programme into plantation silviculture of black cottonwood. Evaluation of growth characteristics of existing black cottonwood clones was an early priority. At sheltered inland sites, some clones of this species have straight stems and fast height growth rates (Sævarsdóttir & Óskarsson 1990). However, frequent shoot dieback that reduces net height increment and causes contorted stem form is a severe limitation for more widespread use of this species in forestry. The plains of southern Iceland are by far the biggest land area within the country with suitable growing season temperatures for afforestation. This region is also a key area for agriculture and, hence, shelterbelts. However, frequent and in some places almost annual shoot dieback restricts arboriculture and forestry in that region (Jónsson 2002). Breeding of hardy poplars for the lowlands of southern Iceland is, therefore, highly desirable. In 1989, the present authors started a breeding programme with that objective.

Very little is known about the genetic variability in rate of shoot elongation within the growing season of black cottonwood. The objectives of the present study were to: 1) determine the rate of shoot extension at different dates during the growing season, 2) estimate dates of bud set, and 3) estimate dates of growth cessation. The study covered 29 clones of black cottonwood in a clonal trial in southern Iceland. Furthermore, shoot growth

strategy by clone was correlated with subsequent shoot dieback and growth.

MATERIALS AND METHODS
Pedigree
We studied an F_1 family of full-sib progenies, including 24 clones and their parent clones, as well three unrelated control clones of black cottonwood. The pedigree's female ('Iðunn', 6310002) and male ('Keisari', 6310005: trade name, Iceland Forestry Research clone reference number) parents were both of provenance Copper River Delta, Alaska, USA, 60°20'N, 145°00'W, 20 m elevation. The control clones were 6310001 ('Brekkan', ♂, provenance: Copper River Delta, Alaska, USA, 60°20'N, 145°00'W, 20 m elevation), 6309003 ('Pinni', ♂, provenance: Cordova Flats, Alaska, USA, 60°30'N, 145°45'W, 20 m elevation) and 6314004 ('Salka', ♀, provenance: Yakutat, Alaska, USA, 59°32'N, 139°45'W, 20 m elevation). Within parentheses are clone name, sex, provenance and geographic position according to Sævarsdóttir and Óskarsson (1990). The full-sib progeny clones were of clone reference numbers 890002 to 8900025. Originally, clone 890001 of the same full-sib progeny was also intended for the experiment but sufficient plant material could not be propagated in time for the experiment. For brevity, clones 890002 to 8900025 are here referred to as clones 2 to 25. Clones 6310005 ('Keisari'), 6310002 ('Iðunn'), 6310001 ('Brekkan'), 6309003 ('Pinni') and 6314004 ('Salka') are referred to as clones 26, 27, 28, 29 and 30, respectively.

Field experiment
On 29 August 1992, a clonal trial plantation was established in an afforestation area in Hellisskógur, southern Iceland (63°57'N, 20°59'W, 32-35 m elevation) with the 29 poplar clones (numbered 2-30). The experiment consisted of a randomized block design with five blocks and 20 plants per plot of each clone (100 trees per clone). Spacing between plants in the row (plots) and between rows and blocks was 1.5 and 3m, respectively.

The site is sedge mire with a gentle slope to the east, drained by ploughing before planting. Plants were propagated in the greenhouse by greenwood cuttings (cf. Óskarsson 1990, Óskarsson et al. 1990). Cuttings were grown in the greenhouse for approximately two months in a mixture of sphagnum moss and rhyolitic pumice (cf. Óskarsson & Thorarinsson 1990) in 150 ml pots. All clones were planted on 29 August except clone 26 ('Keisari'), which was planted in the spring of 1993. In the spring of 1993 and 1994 each plant was treated with approximately 15 g of compound fertililizer (12-15-17), which corresponds to around 1.8 g N, 1.0 g P and 2.1 g K per plant on each occasion.

Measurements
In 1996, one tree per clone was randomly selected and tagged in each block, making a total of five trees per clone. Tree height, top shoot length and length of shoot dieback were measured after bud break in the spring of 1996, 1997 and 1998. Shoot dieback was measured as the distance from the terminal node to the first breaking bud on the leader shoot. During the growing season of 1996, top shoot length was measured on six consecutive dates at approximately two-week intervals: 18 June, 30 June, 14 July, 28 July, 10 August and 24 August. The presence of actively growing shoot apices, buds and bud break was also recorded. Active shoot apices were scored if leaf primordia were visible at the terminal node (not concealed by bud scales). Buds were scored if the bud scales concealed the terminal node. Bud break was scored if buds formed during the study period had swollen and leaf tips were exposed at the bud apex.

Data analysis
Cessation of shoot growth was scored if the measured shoot length was less than 5 mm of the final shoot length. Median time to shoot growth cessation and bud set was estimated by constructing a life table for each tree based on scorings of bud set and shoot growth cessation. Shoot growth cessation (and resumption) by

clone was evaluated by assigning to each tree five series of orthogonal contrasts for shoot length measurements from the six observation dates in 1996. The five contrast series (A-E) for the six observation dates 18 June, 30 June, 14 July, 28 July, 10 August and 24 August were A) -5, 1, 1, 1, 1, 1, B) 0, -4, 1, 1, 1, 1, C) 0, 0, -3, 1, 1, 1, D) 0, 0, 0, -2, 1, 1 and E) 0, 0, 0, 0, -1, 1. For each series (A-E) and tree, a sum score of the product of shoot length and orthogonal contrasts was calculated by equation 1.

$$s_i = \sum c_j l_j \qquad (1)$$

where, s_i is the sum score for tree i, c_j is the contrast value for the observation date j and l_{ij} is the measured shoot length of the tree i on that date j. The five series (A-E) were used to evaluate growth cessation by A) 18 June, B) 30 June, C) 14 July, D) 28 July and E) 10

Table 1. Shoot growth characteristics of 29 black cottonwood clones. A) Short clone identification number used presently, B) Icelandic Forest Research clone identification number, C) tree height (m) in spring 1996, D) shoot length (cm) autumn 1996, E) contribution of shoot growth by mid-June to total shoot length (%), F) maximum rate of indeterminate shoot growth (from mid-June to end of August, mm day^{-1}), G) median number of days from 16 May to bud set, H) median number of days from 16 May to shoot growth cessation, I) percent of buds breaking in August (%, five plants per clone, I=0, 20, 40, 60, 80, 100). Values for C, D and F are means ± standard deviations.

A	B	C	D	E	F	G	H	I
2	890002	39 ± 26	8.6 ± 4.9	48	1.7 ± 1.2	59	75	40
3	890003	31 ± 17	10.3 ± 3.7	53	2.3 ± 1.0	64	74	20
4	890004	44 ± 9	13.6 ± 7.3	68	2.5 ± 1.5	60	74	0
5	890005	57 ± 12	15.8 ± 1.5	64	3.1 ± 0.6	56	86	0
6	890006	49 ± 11	17.1 ± 4.9	53	3.1 ± 1.3	64	75	20
7	890007	34 ± 22	12.1 ± 3.8	78	1.5 ± 0.9	64	60	0
8	890008	47 ± 9	7.9 ± 5.5	33	1.5 ± 1.8	71	75	60
9	890009	37 ± 21	8.3 ± 3.1	68	0.8 ± 0.3	59	74	60
10	890010	57 ± 12	8.3 ± 4.7	62	1.1 ± 0.7	59	75	40
11	890011	61 ± 10	15.4 ± 7.6	43	2.9 ± 1.5	64	73	40
12	890012	53 ± 14	21.8 ± 13.8	13	5.5 ± 3.3	85	69	0
13	890013	53 ± 9	11.1 ± 11.3	37	2.0 ± 2.2	60	86	40
14	890014	50 ± 16	11.3 ± 6.8	39	1.8 ± 1.2	73	81	40
15	890015	56 ± 9	19.3 ± 15.2	23	3.5 ± 2.0	73	86	60
16	890016	51 ± 10	16.1 ± 7.2	43	3.0 ± 1.6	64	81	20
17	890017	51 ± 9	16.0 ± 7.7	57	2.9 ± 1.9	62	75	40
18	890018	33 ± 12	11.8 ± 4.9	24	2.4 ± 1.2	81	81	40
19	890019	49 ± 16	11.5 ± 3.9	71	1.5 ± 0.9	59	74	0
20	890020	45 ± 8	17.0 ± 2.6	44	3.1 ± 0.6	64	81	20
21	890021	42 ± 18	14.5 ± 13.2	29	2.7 ± 2.5	64	81	40
22	890022	50 ± 7	16.3 ± 6.1	47	2.8 ± 1.4	62	81	20
23	890023	47 ± 7	14.6 ± 13.7	44	2.2 ± 2.5	60	75	20
24	890024	43 ± 7	14.1 ± 9.4	24	2.6 ± 2.1	64	81	40
25	890025	29 ± 20	9.6 ± 6.7	58	1.3 ± 1.1	62	53	20
26[*]	6310005	28 ± 18	12.0 ± 6.5	46	2.3 ± 1.1	59	75	40
27[*]	6310002	54 ± 13	8.5 ± 2.2	43	1.3 ± 0.7	64	86	100
28[*]	6310001	58 ± 13	12.6 ± 1.7	49	2.8 ± 0.4	62	75	20
29[*]	6309003	62 ± 9	27.1 ± 6.2	35	5.2 ± 0.8	74	81	0
30[*]	6314004	62 ± 23	25.3 ± 9.2	31	4.5 ± 1.3	75	86	40

* 26: 'Keisari', 27: 'Iðunn', 28: 'Brekkan', 29: 'Pinni', 30: 'Salka'.

August. Shoot lengths produced by 18 June and subsequently to 24 August were defined as section A (primarily predeterminate growth) and B (indeterminate growth), respectively. Analysis of variance was used to compare: 1) measures of shoot lengths and shoot dieback and 2) the sum scores for each series (A-E) and lengths of shoot sections A and B, between clones. A cluster diagram for clones of similar growth characteristics was constructed by cluster analysis of the mean sum scores of the five series (A-E) used to evaluate time of shoot growth suspension. Correlation statistics and regression analyses were used to estimate relationships between factors. The data were analysed by STATISTICA software, Kernel release 5.5 A, © 1984-1999 by StatSoft, Inc.

Figure 1. Shoot growth to 18 June (Section A) and subsequent shoot growth to end of August (Section B) (mean ± standard error) by clones (see Table 1 and text for details of clones). Broken lines indicate half the range of observations by clones.

RESULTS

The growing season temperatures at the study site were low. In 1996 mean monthly temperatures for May, June, July and August were 7.3, 10.4, 11.2 and 10.5 °C at the more coastal Eyrarbakki station (63°52'N, 21°09'W, altitude 4 m) and 6.9, 9.7, 11.0 and 10.3°C at the more inland Írafoss station (64°06'N, 21°01'W, altitude 66 m), respectively (data from the Icelandic Meteorological Office).

All trees survived throughout the study period (1996-1998). In the spring of 1996, mean tree height was 47.3 ± 1.3 cm (mean ± SE, N=145, Table 1). Average top shoot length formed in 1996 was 14.0 ± 0.7 cm and varied significantly by clone ($F_{28,116}$=2.70, P<0.001, Table 1). Mean shoot lengths produced by mid-June (section A) and shoot lengths produced subsequently (section B) were 6.1 ± 0.3 and 7.9 ± 0.6 cm, respectively. The difference in length between section A and B varied by clone ($F_{28,116}$=4.55, P<0.001, Figure 1). Clones
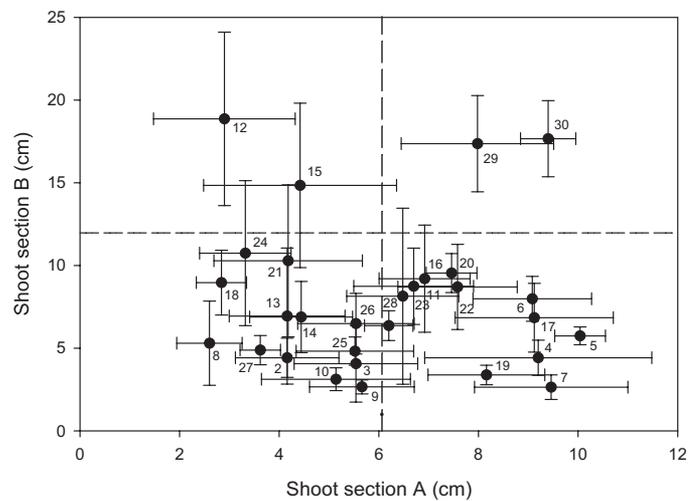
12, 15, 29 and 30 produced the longest shoot sections after mid-June (Figure 1). Shoot growth of clones 12 and 15 was, however, modest to mid-June, while clones 29 and 30 produced relatively long shoots both before and after mid-June (Figure 2). Hence, clones 29 and 30 formed the longest top shoots by the end of the growing season (Table 1).

Peak growth rate after mid-June varied significantly by clone ($F_{28,116}$=2.73, P<0.001, Table 1). The clones with the fastest shoot extension rates (> 4 mm day^{-1}) were 12, 29 and 30. Clone 'Pinni' had a shoot extension rate of about 3 mm day^{-1} from mid-May to mid-June, and increased to more than 5 mm day^{-1} during the latter half of that month (Figure 2). Clone 30 also had a high though somewhat lower growth rate during that period (Figure 2b).

Shoot growth of some clones ceased as early as mid-June (Contrast A: $F_{28,116}$=2.73, P<0.001) while clones with growing top shoots were observed at all subsequent dates (Contrast B: $F_{28,116}$=3.16, P<0.001, C: $F_{28,116}$=2.98, P<0.001, D: $F_{28,116}$=2.60, P<0.001, E: $F_{28,116}$=1.81, P=0.016, Figure 2). Clones 12, 15, 29 and 30 had the most distinct shoot growth characteristics as evaluated by cluster analysis of shoot
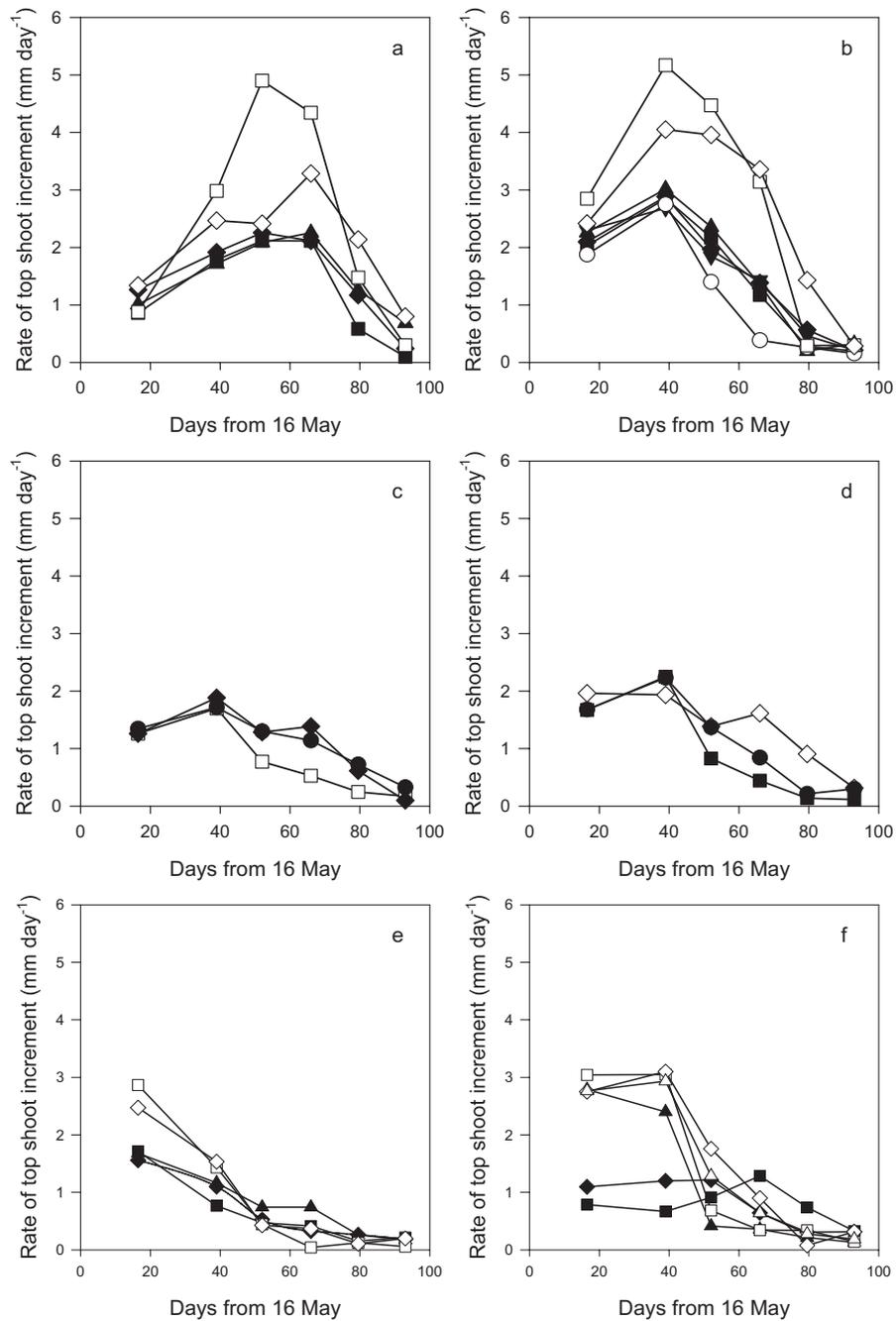
Figure 2. Rate of top shoot increment of 29 black cottonwood clones by sampling dates. (a) Clones: C12 (□), C15 (◇), C18 (■), C21 (◆), C24 (▲). (b) Clones: C11 (■), C16 (◆), C20 (▲), C22 (▲), C28 'Brekkan' (○), C29 'Pinni' (□), C30 'Salka' (◇). (c) Clones: C2 (□), C13 (◆), C14 (●). (d) Clones: C3 (■), C23 (■), C26 (●). (e) Clones: C7 (□), C19 (◇), C9 (■), C10 (◆), C25 (▲). (f) Clones: C5 (□), C6 (◇), C17 (△), C8 (■), C27 'Iðunn' (◆), C4 (▲). Clones were assigned to figure segments (a-f) by rate of shoot elongation to mid-June and similarities in subsequent growth trend.

growth and growth cessation during June to August (Figure 3). Clones 12, 15, 18 and 30 set buds in early August, whereas other clones formed terminal buds in July (Table 1). In August, breaking terminal buds were observed on the top shoots of 23 clones. The exceptions were clones 4, 5, 7, 12, 19 and 29 (Table 1). By the end of August clones 24 and 15 still had actively growing shoot apices on 80% and 60% of top shoots, respectively. Clone 24 had set bud by the end of July and clone 15 by mid-August (Table 1), but these clones had resumed shoot growth by late August.

Shoot length by mid-June (section A) varied significantly between clones that had stopped growing before the end of July and those reported growing in August ($F_{1,27}$=11.62, P=0.002). Mean shoot lengths by mid-June were 7.1 ± 0.5 cm (N = 18) and 4.6 ± 0.5 cm (N=11), respectively. For clones ceasing growth before August, shoot length by mid-June was significantly correlated with percent of terminal buds reported breaking in August (R=-0.74, N=18, P<0.001, Figure 4a). How-ever, for clones reported growing into August, no significant correlation was observed between shoot growth by mid-June and percent bud break in August (R=-0.19, N=11, P=0.568, Figure 4a).

In the spring of 1997, shoot dieback of top shoots was only observed on study trees of clones 7, 8, 12 and 15. Clones 7 and 8 had only one tree each with failing terminal bud, but 2 (40%) and 3 (60%) trees of clones 12 and 15, respectively, had necrotic shoot tips.
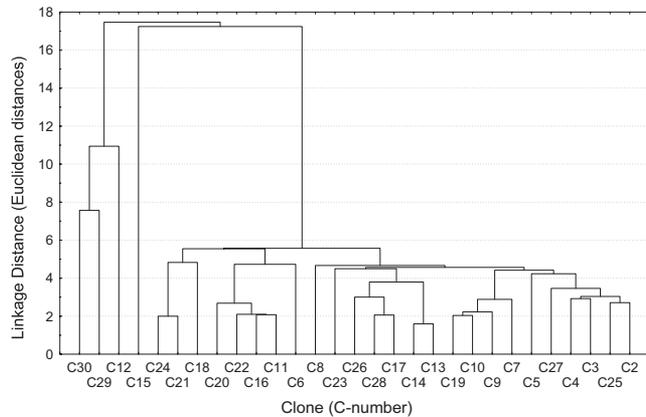
In the spring of 1998, however,

Figure 3. Tree diagram for clustering of shoot growth characteristics of 29 clones of black cottonwood (see Table 1 for details of clones C2-C30).
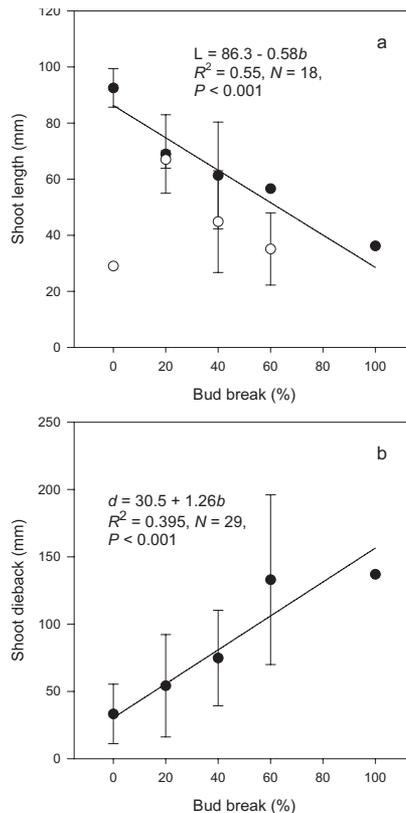

Figure 4. (a) Shoot length by mid-June (L, mean ± standard deviation) by percent of buds breaking in August, for clones ceasing growth before the end of July (●) and clones growing in August (○), with regression line for clones ceasing growth before the end of July. (b) Top shoot dieback (d, mean ± standard deviation) by percent of buds breaking in August.

shoot dieback was observed on study trees of all clones except 28, which remained undamaged. The average length of shoot dieback by clones in the spring of 1998 was positively correlated with shoot length (R=0.37, N=29, P=0.046), but not correlated with maximum growth rate in 1996 (R=-0.08, N=29, P=0.676). In the spring of 1998, the length of shoot dieback varied significantly by clone, and was related to the growth at the terminal node in August 1996, according to the following equation:

$$K =1.18+4.68I+0.10P \qquad (2)$$
$$(\text{Adj}.R^2 = 0.62, F_{2,26} = 23.66, P < 0.001)$$

where K is the length of shoot dieback in the spring of 1998 (cm), I is the rate of shoot growth in early August 1996 (mm day^{-1}), and P is the percentage (%) of buds observed breaking in August 1996 (Figure 4b). Other factors tested did not add significantly to a multiple linear model of shoot dieback in the spring of 1998.

DISCUSSION
Poplars, including black cottonwood, have an indeterminate (continuous) shoot growth strategy (Morey 1976, Howe et al. 2000, Sigurdsson 2001b). Species with an indeterminate shoot growth strategy terminate shoot elongation and form terminal buds principally in response to a shorter photoperiod. Other factors including low temperatures, soil moisture and nutrients also affect the date of bud set (Howe et al. 2000 and references therein). In poplars, the date of bud set is under moderate to strong genetic control (Howe et al. 2000). Significant differences in late summer growth characteristics and bud phenology by clones within the full-sib family and control clones were consistent with this hypothesis.

Howe et al. (2000) showed that in hybrid poplars frost damage and winter survival is under low to moderate genetic control. The high variation by clones in shoot dieback observed in the spring of 1998 suggests a significant genetic element in that dieback event.

Furthermore, the observed correlation between the length of shoot dieback by clone and the incidence of bud break in August two years earlier suggests that genetic variability in the induction of winter dormancy might be involved (Figure 4b).

Ødum (1979) suggested that incomplete maturation of shoots due to short growing seasons and low growing season temperatures is the primary cause of frequent dieback of top shoots in the cold temperate islands of the North Atlantic including Iceland. A hard frost event by mid-September 1997 has been suggested as the cause of severe shoot dieback of black cottonwood observed in Southern Iceland in that year (Aðalsteinn Sigurgeirsson, personal communication). The present results are consistent with that suggestion. However, it would be an oversimplification of a complex issue to ascribe shoot dieback in general to immature shoots. In some years black cottonwood has suffered severe dieback due to hard frosts following premature bud break (Bragason 1995). In the period 1995 to 2001 terminal bud failure of black cottonwood on Heimaey island off the south coast of Iceland was entirely explained by salt stress due to salt-laden winter storms (Jonsson 2006). In that study, bud necrosis of clone 26 'Keisari' was not observed following the frost of September 1997. However, temperatures on the island did not fall below the freezing point during the cold spell in that month (Jonsson 2006). Frost damage at that site was therefore unlikely. Shoot dieback of trees in southern Iceland is a spatially and temporally complex phenomenon. Therefore, successful breeding strategies for black cottonwood to be used in southern Iceland should consider the risks of frost damage in the autumn, winter and spring and of damage due to salt-laden storms, as well as high growth rates. Silvicultural treatments such as fertilizer applications can also affect both the rate of shoot elongation and bud phenology (Sigurdsson 2001b). Possible interactions between clones and silvicultural practices should also be considered.

Overwintering poplar buds contain stem

units in an embryonic state (Jonsson 2006). In spring, the buds flush and stem unit primordia expand to form a predetermined stem section and early leaves. Usually initiation and prompt development of new stem units that form an indeterminate shoot section and late leaves follow. Indeterminate growth continues until bud set (Morey 1976). In southern Iceland indeterminate growth of black cottonwood may commence at the beginning of June (Jonsson 2006), whereas shoot elongation to mid-June mostly occurs via the extension of existing stem units (Thorbergur Jonsson, unpublished data). Hence, some clones in the present study exhibited little indeterminate growth, e.g. clones 7, 9, 10, 19 and 25 (Figure 2e). Clones of mostly indeterminate shoot growth were also observed, e.g. clone 12 (Figure 2a).

Late bud set or interrupted bud development due to late season bud break might reduce the numbers of stem units in the bud or adversely affect maturation of these stem units and thereby suppress predetermined shoot growth the following year. Clones that extended shoots in early August or broke buds in that month had shorter shoots by mid-June (Figure 4a) and that is consistent with the above hypothesis. However, no observations were performed of stem units in the buds.

Clones of optimal traits might have: 1) a large predetermined shoot section, 2) fast early season indeterminate growth rate, 3) shoot growth cessation and bud set by the end of July, and 4) prompt induction of endodormancy (cf. Lang 1987). Sigurdsson (2001a) found that the clone 'Iðunn' (27) was highly temperature responsive with a high Q_{10} for dark respiration and growth. Even so, a number of clones in our study grew at a rate of up to 3 mm day^{-1} in June (Figure 2) and the clones 'Salka' (30) and 'Pinni' (29) extended their top shoots at mean rates of 4 to 5 mm day^{-1} in the latter half of June. This high rate of shoot extension was attained even though the mean temperature was only about 10 °C during that month.

Some clones had: 1) high average daily rates of shoot elongation during June and early-July, 2) set bud and ceased shoot growth before the end of July and 3) terminal buds that remained visually dormant to the end of the growing season. The growth strategy of clone 'Pinni' (29) was apparently nearly ideal in that respect. It is not surprising that this clone is considered fast growing and of unusually straight stem form (Sævarsdóttir & Óskarsson 1990). However, this clone was somewhat damaged in the winter of 1997-1998, indicating that it is not completely hardy at the study site. However, clone 'Brekkan'(28) was undamaged in that year. Thus, there may exist sufficient genetic variability within the Alaskan black cottonwood populations for breeding of fast growing and winter hardy clones for cultivation in southern Iceland.

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