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Maritime tree limit of black cottonwood (*Populus trichocarpa*) exposed to salt-laden winter storms

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ABSTRACT

Maritime tree limits are rarely defined or addressed in the scientific literature. It has been proposed that maritime tree limits are ultimately set by airborne salt inducing top shoot dieback. The maritime tree limit would then be at the point of zero average net height increment. In order to evaluate this hypothesis, survival, top shoot lengths, shoot dieback and net height increment were monitored during a six year period in an experimental belt of black cottonwood (*Populus trichocarpa*) clones extending 693 m inland from an exposed 29 m high sea cliff on Heimaey Island off the south coast of Iceland (63° 26' N, 20°18' W, 37-50 m a.s.l.). Survival and net height increment increased with distance from the coast line. Zero net height increment during six consecutive years of study was at 510 m from the coastline. Annual net increment at 600 and 693 m from the coast was 1.6 and 3.3 cm year^{-1}, respectively. Survival rate of all clones combined was significantly explained by a logit model of the inverse of the distance to the coast. According to that model estimated limits of 1%, 50% and 75% survival were at 109, 280 and 448 m from the cliff, respectively.

Keywords: aerosol, dieback, height, Iceland, tree line, oceanic moor lands

YFIRLIT

Trjámörk alaskaaspar nærri hafi

Trjámörk við sjó eru sjaldséð umræðuefni í vísindaritum. Á það hefur verið bent að nærri opnu hafi setji kalskemmdir á toppsprotum vegna sjávarseltu trjágróðri hæðarmörk. Trjámörk við sjó verða þar sem kalskemmdir eru jafnar eða meiri en hæðarvöxtur trjánna þannig að trén hækka ekkert. Til að meta þessa tilgátu var fylgst með lifun, lengdarvexti toppsprotans, lengd sprotakals og hækkun trjánna á sex ára tímabili í klónatilraunabelti af alaskaösp (*Populus trichocarpa*) sem náði 693 m frá skjóllausum 29 m háum sjávarhömrum á Heimaey (63° 26' N, 20°18' W, 37-50 m y.s.). Trén hækkuðu hraðar og lifun var betri með aukinni fjarlægð frá hafi. Nær ströndinni en 510 m hækkuðu trén ekkert á þessu sex ára tímabili. Árleg hækkun trjánna var 1,6 cm ár^{-1} við 600 m en 3,3 cm ár^{-1} 693 m frá ströndinni. Lifun allra asparklóna mátti skýra með logit-falli af andhverfu fjarlægðar að hafi. Samkvæmt þessu falli voru mörk 1%, 50% og 75% lifunar við 109, 280 og 448 m fjarlægð frá bjargbrúninni.

INTRODUCTION

Trees and woodlands are important for amenity, recreation and shelter, especially in windswept coastal communities. However, successful arboriculture or forestry is difficult to achieve in stormy coastal areas such as those of the cold temperate North Atlantic (e.g. Ødum 1979, Sharp & Jacyna 1993, Jónsson 2002).

Heimaey Island off the south coast of Iceland is an important fishing community. The island has been considered naturally treeless (Kjartansson 1966), but trees of various conifer and broadleaved species have been planted in private gardens at least since the early 20th century (Johnsen 1946). In 1931 a forestry society was established on the island with the objective of creating woodlands for amenity and recreation (Guðmundsson 1942). However, arboriculture and forestry beyond the shrub stage have been proven extremely difficult to maintain due to low survival and for most species severe annual shoot dieback. The small exposed island has an extremely stormy climate (Eythorsson & Sigtryggsson 1971) and is exposed to high marine aerosol loads. Salt-laden storms have long been suggested as the primary limiting factor for tree growth on Heimaey Island (Johnsen 1946, Kjartansson 1966), but that hypothesis has only recently been confirmed (Jonsson 2006).

The top shoot is the part of a tree generally most exposed to wind (Lee 1978) and marine aerosols (Boyce 1954, Zhu et al. 2002.). Dormant shoots of deciduous trees absorb surface-deposited salt that preferentially accumulates at the shoot apex causing shoot dieback at high concentrations (Buschbom 1968, Lumis et al. 1976, Sucoff & Hong 1976, Barrick et al. 1980). The foliage partially shields shoots of dormant evergreen conifers from deposition of aerosol particles. However, conifer needles absorb surface-deposited salt (Barrick et al. 1980,) causing needle burn, shoot dieback and deformed tree crowns (Sucoff 1975).

Stature is the principal defining characteristic of a tree and tree height and stem form largely define the value of trees for most purposes. Tree height is the sum of the net increment of the vertical axis. The length of the top shoot sets the limit for gross height increment, but the fate of the top shoot and the terminal node in particular is most important for the development of a tree. Failure of the terminal node reduces net height increment and produces a kink in the stem as auxiliary buds or subordinate branches take the lead. Frequent top shoot failure obviously reduces both net height growth and results in contorted stem form (Figure 1).

Net height increment would become zero or even negative if shoot dieback equals or exceeds the length of the current annual top shoot. The replacement shoots emerge at an

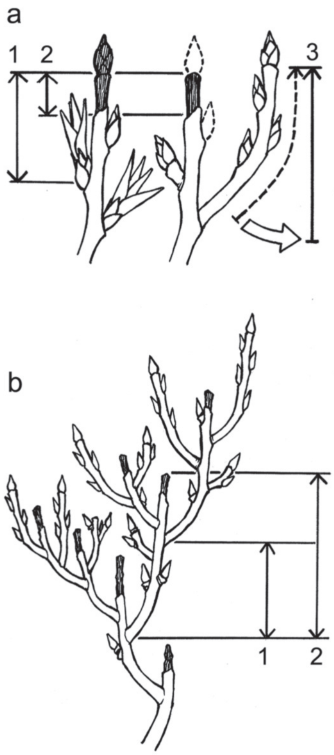

Figure 1. (a) Shoot length and shoot dieback: 1) distance to the topmost breaking bud, 2) length of necrotic shoot section and 3) length of shoot emerging from an auxiliary bud. (b) Elongation of the vertical axis of a tree: 1) net height increment and 2) vertical length of the top shoot (without the terminal bud).

angle to the top shoot from buds at or below the limit of shoot dieback or from lower branches (Figure 1). Therefore, zero height increment would occur at a shoot dieback length less than the total top shoot length. Conditions causing a zero average net height increment for extended periods of time would set the limit for tree existence. Trees would inevitably perish if average net height increments were consistently less than zero. At zero net height increment plants of a tree species might survive but would not attain tree size. However, given a continuously positive average net height increment trees might grow to almost any size given sufficient time.

Black cottonwood (*Populus trichocarpa* Torr. & Gray; syn. *Populus balsamifera* subsp. trichocarpa (Torr. & Gray) Brayshaw) is a fast growing tree species that was first introduced to Iceland in 1944 from Alaska, USA (Bragason 1995). In Iceland, black cottonwood is an important urban tree that has also been widely planted for shelter and timber. On sheltered inland sites, black cottonwood has attained a height of 24 m in 40 years (Blöndal 2006). It has a potentially straight stem that extends from a terminal bud on the top shoot. Therefore, net height increment should approximately be equal to the sum of all annual top shoot lengths. However, on Heimaey Island and other exposed coastal sites black cottonwood has a contorted stem form and a low net height increment (authors' observations).

Identification of a potential maritime tree limit is important for planning purposes in coastal communities. During onshore storms marine aerosol concentrations as well as particle size declines strongly with distance from the shoreline (Boyce 1954, Gustafsson & Franzen 1996). The level of salt-induced shoot dieback should, therefore, decrease with distance from the coastline. The objective of the present study was to evaluate if: 1) top shoot dieback increased and plant survival decreased along a transect toward an exposed sea cliff; 2) evaluate the position of zero net height increment along that transect; and 3) assess if survival decreased beyond that point during a six year study period. An experimental belt of black cottonwood and various willow species extending 693 m inland from an exposed sea cliff on Heimaey Island was used for the evaluation.

MATERIALS AND METHODS

Pedigree

We studied four clones ('Iðunn', 'Haukur', 'Salka', 'Brekkan') and four F1 families of full-sib progenies of black cottonwood ('Jóra' x 'Haukur', 'Húsa' x 'Fursti', 'Linda' x 'Keisari', 'Oddný' x 'Keisari'). The studied clones and full-sib progenies' parents were of three provenances from Alaska, USA: 'Oddný' (6309001, ♀), 'Linda' (6309005, ♀), 'Húsa' (6309018, ♀) of provenance Cordova Flats (60° 30' N, 145°45' W, 20 m a.s.l.), clones 'Brekkan' (6310001,♂), 'Iðunn' (6310002, ♀), 'Keisari' (6310005, ♂), and 'Haukur' (6310006, ♂) of provenance Copper River Delta (60° 20' N, 145°00' W, 20 m a.s.l.), and clones 'Fursti' (6314001,♂), 'Salka' (6314004, ♀) and 'Jóra' (6314010, ♀) of provenance Yakutat, 59° 32' N, 139°45' W, 20 m elevation (Icelandic Forest Research clone reference number and sex within brackets) (Sævarsdóttir & Óskarsson 1990). For brevity clones 'Iðunn', 'Haukur', 'Salka', 'Brekkan' are referred to as genotypes A1, A2, A3 and A4, respectively. Families 'Jóra' x 'Haukur', 'Húsa' x 'Fursti', 'Linda' x 'Keisari', 'Oddný' x 'Keisari' are referred to as genotypes B1, B2, B3 and B4, respectively. Clones were chosen on the basis of their adaptability to climatic conditions on the mainland of southern Iceland.

The plantation

The study plantation is a single line of poplar plants on both sides of a road (Hraunhamar) running perpendicular (E-W direction) to the coastline on the west side of Heimaey Island off the south coast of Iceland (63° 26' N, 20°18' W, 37-50 m a.s.l., Figure 2). The coastline is a 29 m high cliff. The experiment commenced at a point 189 m from the cliff edge and extended to 360 and 693 m distance

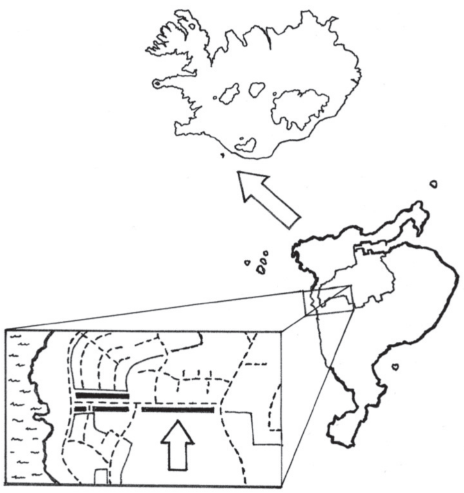

Figure 2. Location of experimental belt of black cottonwood on Heimaey Island off the south coast of Iceland. Experimental belts indicated by black bars on detail map of the west coast of Heimaey Island.

inland on the north and south sides of the road, respectively.

A belt approximately 5 m wide was tilled repeatedly three times. Three perpendicular lines with 2 m spacing were covered with 2 m wide black polythene mulch secured by an approximately 5 cm layer of pebbles. A low timber fence 1 m high was erected around the experimental belt at a 1 m distance from the centre line of the outer polythene beds. A net of 30 mm mesh was secured on the fence for protection. In June 1995 plug plants (150 cm^3 pots) of different clones were planted in the experimental belts. The plants were raised in the greenhouse from rooted cuttings or seed in a mixture of pumice and sphagnum moss. The experiment was planted in the centre polythene bed with various willow clones planted in the bed on either side. The poplar experiment was of simple random design with plots (lines with plants of a clone or family) randomly assigned to locations along the length of the belt. Clone 'Iðunn' and family 'Húsa' x 'Fursti' were replicated in three plots and clone 'Salka' was replicated in two plots. Plots of other clones or families were not replicated.

Measurements and data analysis

The position of all plants along a transect line to the edge of the cliff defining the coastline was measured with a 50 m surveyor's measuring tape. GPS points were also measured along the transect lines. A fourth order polynomial equation was fitted to the GPS measured elevation points along the transect line and used to estimate elevation for each tree.

In late May or early June 1999-2005 tree height, length of top shoot and distance from the terminal node to uppermost breaking bud was measured. In 2000, 2003-2005 the length of necrotic terminal section of top shoots was also included. Shoot necrosis was defined as the distance from the terminal node to the boundary between apparently living bark and blackened and usually scorched bark. If there was a doubt a small cut was made in the shoot at the junction. Necrotic shoot sections had dark brown or black cambial tissue in contrast to living shoot sections which had a green and apparently turgid cambium layer.

Plants were scored dead if no buds broke and cambial necrosis was observed at the root crown. The fate of the plant was confirmed the following year if no shoot growth was observed from the roots. A logit model (cf. Lindén et al. 1996) was fitted to scores of survival and mortality by the end of the experiment. Probability limits of 1%, 50% and 75% were derived from the coefficients of that model by equation (1):

$$L_p = \frac{\ln\left(\frac{p}{1-p}\right) - \alpha}{\beta} \qquad (1)$$

where L_p is the distance from the cliff edge (m) at the probability for survival p and α and β are coefficients of the logit model.

Repeated measures analysis of variance of the inverse of distance from the coast as a covariate was used to compare tree height, shoot lengths, shoot dieback and net vertical increment between genotypes and years. The dataset is only orthogonal in respect of genotype and location within the experimental belt for clone 'Iðunn' and family 'Húsa' x 'Fursti'. Comparison between clones was thus restricted to clones 'Iðunn' and family 'Húsa' x 'Fursti' with distance from the cliff edge as covariate. Results shown for the genotypes not replicated by plots along the experimental belt should only be viewed as approximate. Correlation statistics were used to estimate relationships bet-ween factors and the Kruskal-Wallis test used to compare survival by clones. The data were analysed by the STATISTICA software, Kernel release 5.5 A, © 1984 -1999 by StatSoft, Inc.

RESULTS

Survival

Overall, 63% of trees survived to year 10 (37% mortality; data not shown). About 6% mortality was observed during the study period (1999-2005) and mostly in the year 1999-2000 (5%). Survival by year 10 varied significantly by clones (Kruskal-Wallis test: H (7, N = 448) = 35.8, P < 0.001). Clones were at a different mean distance from the coast and mean survival by clones decreased linearly with the inverse of that distance (Figure 3a). Hence, survival was primarily a function of distance from the coast. Accordingly, survival rate did not vary significantly between clone 'Iðunn' and family 'Húsa' x 'Fursti' that were replicated in three plots along the coastal inland line. The survival rate of all clones combined was significantly explained by a logit model of the inverse of distance to the coast (Logit model: α = 2.93, β = -819, χ^2 = 69.16, DF = 1, N = 448, P < 0.001). According to that model the estimated limits of 1%, 50% and 75% survival were at 109, 280 and 448 m from the cliff, respectively (Figure 3a).

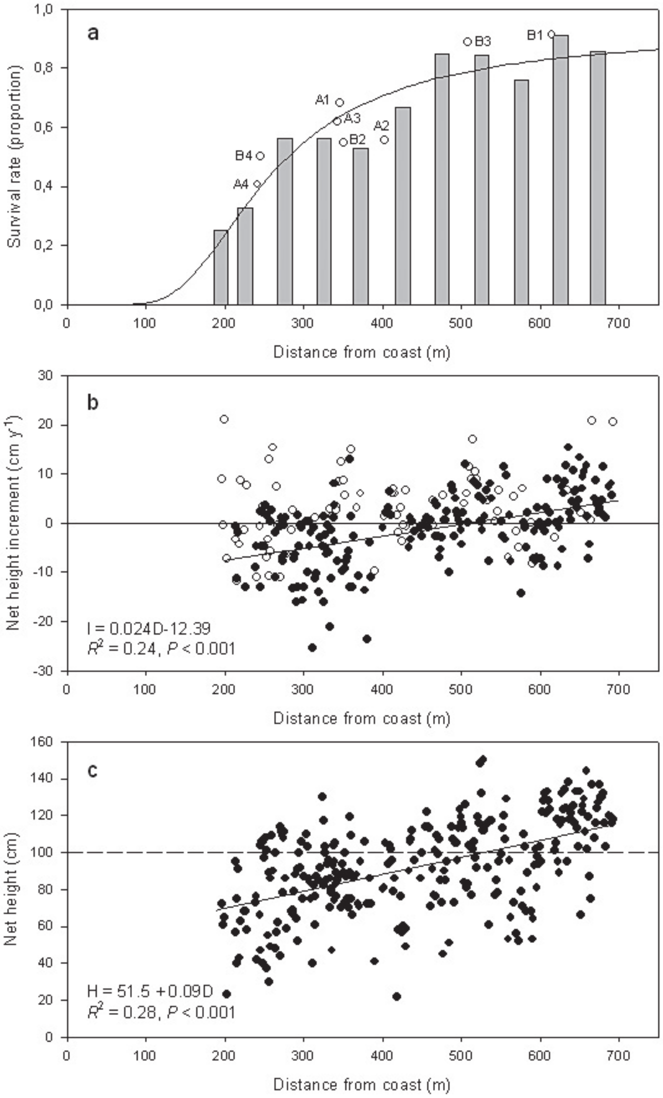

Figure 3. (a) Tree survival rate by distance from the coastline. Shaded bars show average survival by plots, open circles average survival by clones (A1, A2, A3 and A4) and families (B1, B2, B3 and B4). See main text for details of poplar clones and families. (b) Net height increment during the period 2001 to 2005 by distance from the coastline of trees with top shoots starting in year 2001 from buds (filled circles) above 80 cm and (open circles) below 80 cm above ground level. (c) Net tree height by distance from the coastline.

Shoot length

Top shoot lengths of clone 'Iðunn' and family 'Húsa' x 'Fursti' decreased significantly with distance from the coast (covariate: $R = 0.31$, $F_{1,112} = 12.24$, $P = 0.001$). Adjusted for distance from the coast, shoot growth varied by years ($F_{6,678} = 101.23$, $P < 0.001$), but not between the two genotype groups. Including all genotype groups in the analysis, shoot lengths decreased significantly with distance from the coast (covariate: $R = 0.24$, $F_{1,259} = 15.36$, $P < 0.001$), varied by genotype group ($F_{7,259} = 5.63$, $P < 0.001$) and years ($F_{6,1560} = 154.81$, $P < 0.001$). Shoot lengths decreased significantly with year of observation (Linear trend: $F_{1,260} = 156.67$, $P < 0.001$).

Shoot dieback

In all years except 2001 and 2003 less than 2% of terminal buds on top shoots broke. In spring 2001 and 2003 17% and 8% of terminal buds on leader shoots flushed leaves, respectively. Length of terminal shoot section with non-breaking buds decreased significantly with distance from the coast (covariate: $R = 0.41$, $F_{1,112} = 23.12$, $P < 0.001$). Adjusted for proximity to the coast, shoot dieback varied highly by years ($F_{6,678} = 74.61$, $P < 0.001$), but not between the two genotype groups. The years of highest and lowest degree of shoot dieback were 1999 (year 4) and 2001 (year 6), respectively. Analysed for all genotype groups shoot dieback decreased by distance from the coast (covariate: $R = 0.31$, $F_{1,259} = 27.52$, $P < 0.001$) and varied significantly by genotype group ($F_{7,259} = 3.24$, $P = 0.003$) and highly so by year ($F_{6,1560} = 128.23$, $P < 0.001$). The years of longest and shortest terminal sections with non-breaking buds were 1999 and 2001 and the difference was highly significant (contrast: $F_{1,260} = 684.81$, $P < 0.001$).

The lengths of the necrotic terminal shoot sections were recorded in years 6, 8, 9 and 10, only. Length of necrotic shoot tips decreased significantly with distance from the sea (covariate: $R = 0.37$, $F_{1,270} = 43.86$, $P < 0.001$). Adjusted for distance from the coastline, necrotic shoot tips varied significantly by genotype groups ($F_{7,270} = 4.23$, $P < 0.001$) and years ($F_{3,813} = 87.44$, $P < 0.001$).

Net increment

Net height increment increased with distance from the coastline (covariate: $R = 0.22$, $F_{1,259} = 12.80$, $P < 0.001$). Adjusted for proximity to the coastal cliff net height increment varied significantly by genotype group ($F_{1,259} = 6.35$, $P < 0.001$, Figure 4) and year ($F_{5,1300} = 205.80$, $P < 0.001$, Figure 5). The net height increment stagnated by year 7 (2002) when the mean net height exceeded about 80 cm (Figure 4). The net annual height increment (years 7-10) of trees ≥ 80 cm by year 7 was linearly related to distance from the sea (coefficients ± SE: $\alpha = -9.28 \pm 1.09$, $\beta = 0.0182 \pm 0.002$, Adj. $R^2 = 0.24$, $F_{1,199} = 64.07$, $P < 0.001$). Mean distance of zero net increment was 510 m from the

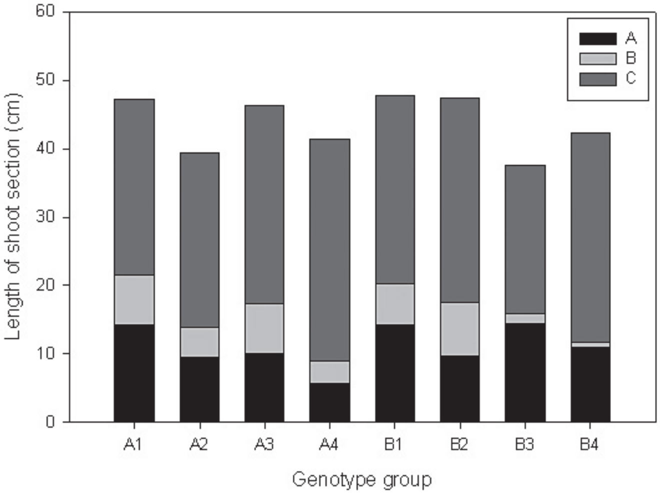

Figure 4. Mean length of shoot section contributing to net height increment (A), length of shoot section with breaking buds but not contributing to net height increment (B), length of terminal shoot section with non-breaking buds (C), and total shoot length (A+B+C) adjusted for distance from the coastline for clones A1, A2, A3 and A4 and families B1, B2, B3 and B4. See text for details of poplar clones and families.

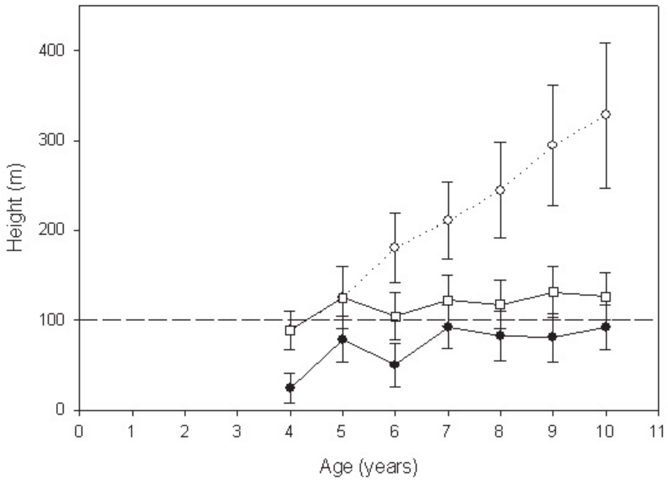

Figure 5. Net height (filled circles), total height including shoot dieback (open squares) and potential height (open circles) by age with standard deviation.

coastline (Figure 3b). The annual net increment according to that equation at 600 m and the far end of the experimental belt (693 m) was 1.6 and 3.3 cm year^{-1}. The mean height of trees ≥ 600 m from the coastline was 117.5 ± 15.9 (Figure 3c). At age 50 expected mean tree height 600-700 m from the coast, assuming a mean net annual increment of 1.6 to 3.3 cm, would only be 1.8 to 2.5 m. The estimated survival rate (logit model) at 510 m distance was 79%.

DISCUSSION

On exposed coastal sites, oceanic moorlands (cf. Hustich 1979) are frequently found between the shoreline and the forested areas (e.g. Moore 1983, Bohn et al. 2000/2003, Griffiths & Orians 2003a, 2003b). Fierce winds with salt spray as well as locally poor soil conditions are believed to determine the natural distribution of oceanic moorlands by preventing successful seedling establishment and growth to tree size (Ellenberg 1966, Griffiths & Orians 2003b). Hence, exposure to marine aerosols might ultimately set the *maritime tree line* (cf. Hustich 1979) of natural forest ecosystems and for tree planting.

Shoot dieback decreases the number of buds breaking, the size of early leaves (Jónsson, unpublished data) and thus total plant leaf area. A detrimental effect of reduced leaf area on the total plant carbon balance might explain the high and increasing mortality presently observed beyond the estimated limit of zero net height increment.

The cultivation methods used in the present study should be considered when interpreting the results. These included total cultivation of the soil, annual fertilization of every tree and polythene mulch to control competition. Furthermore, a low fence with a net of dense mesh, as well as willow rows on both sides gave shelter and probably reduced salt deposition on the study plants. Thus, the conditions for seedling survival and early growth were probably considerably more favourable than would be expected in conventional forest plantations or for naturally established tree seedlings. The presently estimated coastal limit of zero net height increment might, thus, indicate a maritime limit to high input arboriculture with black cottonwood. A maritime tree limit for low input forestry and natural forest ecosystems would probably be further inland.

Black cottonwood has relatively robust top shoots with diameters about 4 – 7 mm at the narrow end. The quantity of aerosol particles deposited per surface area of shoot increases with aerosol particle concentration in the air, wind speed and deposition efficiency (Green & Lane 1964). Deposition efficiency of aerosols on cylindrical objects, such as leafless shoots or conifer needles, increases with wind speed and aerosol particle size and decreases with the inverse of object diameter (Green & Lane 1964). The surface area to volume ratios of cylindrical objects also vary with the inverse of shoot diameter. Therefore, shoot chloride concentrations in black cottonwood shoots exposed to salt-laden air should decrease with the inverse of the squared shoot diameter. Observations on Heimaey Island support this hypothesis (Jónsson, unpublished data). Hence, deciduous species of narrow top shoots may be at a disadvantage at sites exposed to salt-laden air during winter storms. The birch native to Iceland (*Betula pubescens* Ehrh. var. *pumila* (L.) Govaerts) (Govaerts & Frodin 1998) has narrow top shoots of less than 2 mm diameter (authors' unpublished data). Assuming identical shoot permeability to salt, birch might tolerate an order of magnitude higher shoot salt concentrations than does poplar. Genetic variability in tissue level salt tolerance of tree shoots at bud break is apparently low (Jonsson & Magnusdottir 2007). Hence, tree species with narrow shoots would be expected to be disfavoured at exposed coastal sites unless the species had bark that was more impermeable to surface salt. Birch would therefore be expected to be more susceptible than black cottonwood to salt-laden air. Accordingly, in the town of Heimaey native birch only survives in the lee of buildings.

In the northern hemisphere latitudinal tree lines are retracted toward the south in oceanic areas, both in the Pacific and Atlantic regions (Hämet-Ahti 1963, Hustich 1979). Prior to human settlement the coastal areas on the exposed islands of the cold temperate North Atlantic were probably characterised by oceanic moor lands while forests were found in sheltered valleys. The Faeroe Islands were then mostly treeless with mountain birch (*Betula pubescens*) woodlands in some sheltered valleys whereas extensive willow scrub of low stature covered most of the lowland areas (Johansen 1989). The situation in the Shetland Islands was apparently similar with some woodland cover but extensive oceanic moor lands (Johansen 1989). In Iceland some exposed coastal areas including parts of the Reykjanes Peninsula have been suggested as having been oceanic moor lands beyond the maritime tree line (Kristinsson 1995). Also, the island of Heimaey has been considered to have been naturally treeless (Kjartansson 1966).

No trees or shrub species are considered a part of the present indigenous flora of Heimaey Island (Johnsen 1948). Even so, macrofossils of willow formed during the Saefell eruption in 6220±180 years BP demonstrate that willow scrub existed on the island before human setlement in the 9th century AD (Kjartansson 1966, Mattsson et al. 2005). At least three willow species have established naturally in sheltered locations on Surtsey Island, which was formed in a volcanic eruption in 1963 to 1967. The species are: *Salix herbacea* L. (1995), *S. lanata* L. (1999) and *S. phylicifolia* L. (2003). In addition, a specimen suggested as *S. myrsinifolia* Salisb. (1998) has been recorded from Surtsey Island (year of observation within brackets, Borgþór Magnússon, Icelandic Institute of Natural History, personal communication). The present lack of woody species in the flora of Heimaey Island is probably human induced, the result of intensive livestock grazing for more than a millennium. Prostrate birch scrub in exposed areas on the southern Reykjanes Peninsula and the poor success of planted birch on the island of Heimaey suggests the inability of this species to attain tree size in areas highly exposed to salt-laden air. Heimaey Island might therefore be naturally treeless. However, some introduced tree species including Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and some willows are able to grow on the island with no or only intermittent damage.

In the present six-year study top shoot dieback increased and plant survival decreased toward the coastline. Survival decreased abruptly beyond the indicated position of zero net height increment at about 500 m distance from the sea. The present results are consistent with the proposed hypothesis that maritime tree limits occur at the points of persistently zero net height increment. However, that point is probably species specific and might be extended seaward by appropriate treatment and selection of genotypes with robust top shoots and low cuticule and bark permeabilities to salt.

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