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Cover and canopy development of a newly established poplar plantation in south Iceland

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SUMMARY

Secondary succession was monitored on an abandoned hayfield that was planted with black cottonwood (*Populus trichocarpa*) in 1990. This paper reports the changes in species composition, vegetation cover and leaf area index (LAI) that took place between 1991 and autumn 1996.

The number of species found at the site increased from 42 to 68 from 1991 to 1996. A rapid change was observed in cover, with cryptograms and mosses covering the bare soil, followed by an expansion of grasses and herbs, building a low canopy. By 1994, the cottonwood had formed a second canopy layer that increased to 50% cover by autumn 1996, without a decrease in understorey cover. The maximum site-LAI had already reached a relatively stable value of about 1.5 by 1993, but increased to 2.7 after fertilisation in 1996. The trees constituted only 10–40% of the site-LAI throughout this period.

Estimates of leaf area in tree stands can give valuable information about potential production and are key parameters in calculating the fluxes of carbon and water from forest ecosystems. Two non-destructive methods were used to estimate LAI: (1) the measurement of light interception of all foliage using the LAI-2000 Plant Canopy Analyzer, and (2) a regression relationship between crown volume and leaf area for the LAI of trees only.

Key words: forest plantation, Iceland, LAI, *Populus trichocarpa*, secondary succession, vegetation cover.

YFIRLIT

Breytingar á tegundasamsetningu, þekju og laufflatarmálsstuðli í ungum asparskógi

Alaskaösp var gróðursett í þökuskorið tún í Gunnarsholti sumarið 1990. Í þessari grein verður fjallað um niðurstöður mælinga á tegundasamsetningu, gróðurþekju og laufflatarmálsstuðli (LAI) sem gerðar voru á árunum 1991 til 1996.

Tegundum háplantna fjölgaði úr 42 í 68 á tímabilinu og örar breytingar urðu á gróðurþekju. Mosar og aðrar lágplöntur höfðu náð að þekja nær allan ógróinn jarðveg innan þriggja ára, en háplöntur, mest grös, fylgdu fast í kjölfarið og mynduðu jurtalag. Aspirnar fóru að mynda laufþak upp úr 1993, og 1996 þöktu þær 50% yfirborðs, án þess þó að það drægi úr þekju undirgróðurs. Hámarks laufflatarmálsstuðull svæðisins breyttist lítið milli 1993 og 1995, var nálægt 1,5, en jókst upp í 2,7 eftir áburðargjöf á svæðið, vorið 1996. Í lok tímabilsins var áætlað að aðeins 40% af heildarlaufflatarmáli svæðisins væri á trjánum.

Mælingar á laufflatarmáli er með mikilvægustu upplýsingum sem þarf til útreikninga á flæði kolefnis og vatns til og frá skógræktarsvæðum. Hér er fjallað um tvær aðferðir til óbeinna mælinga á lauf-flatarmáli: (1) notkun svokallaðs laufflatarmálsmælis (LAI-2000), sem reiknar laufflatarmál út frá mælingum á ljósorkuupptöku, og (2) með aðhvarfslíkingu milli rúmmáls laufkrónu og laufflatarmáls.

INTRODUCTION

It is important to understand how changes in land use affect the ecosystem. In Iceland, extensive deforestation has taken place (Kristinsson, 1995) and a significant effort is now put into afforestation of treeless landscapes (Bragason, 1995). The planting of a tree stand on a treeless site initiates a gradual change in environmental conditions (Chapin, 1993) and community succession. The community changes will in part be mediated by the trees as they grow and change their environment and in part by other factors such as the conditions at the site, and the existing community and migration of organisms.

The Gunnarsholt experimental site is a black cottonwood plantation that was established in 1990 on an abandoned hayfield. The main objectives in establishing the plantation were to study the changes that take place as trees grow on a flat and treeless landscape, including (1) the long-term modification of the microclimate, (2) the effects of the microclimate on tree physiology and growth, and (3) community development. Early results detailing the biometeorological site characteristics, energy balance conditions and tree growth at the Gunnarsholt site are presented by Aradóttir *et al.* (1997a). The soil physical and chemical characteristics and soil hydrology of the Gunnarsholt experimental plantation are discussed in two companion papers by Strachan *et al.* (1998ab). Community development at the site has been studied by baseline sampling of the soil and surface fauna (Sigurjónsson, 1998; Guðmundur Halldórsson and Hólmfríður Sigurðardóttir, unpublished data) and by measuring cover and species composition of the vegetation.

This paper reports changes in the plant community between 1991 and 1996, in terms of species composition, vegetation cover and leaf area index. Regular measurement of the cover of different plant groups gives information about the rapid succession at the site and makes it possible to scale up leaf-level processes to the plantation scale. Different species will contribute varying amounts to plantation-scale fluxes (e.g. carbon dioxide and water vapour) dependent upon their relative abundance at the site and the arrangement of these species within the canopy and understorey. Cover estimates provide information crucial in summing the individual contributions to the total site fluxes.

The amount and distribution of leaf area may be the single most important variable determining plant productivity (Ceulemans, 1990). Biomass production in agricultural crops has been directly related to the radiant energy intercepted by the foliage (Monteith, 1981). Such a relationship has also been shown to exist for tree stands with different productivity (Cannell *et al.,* 1988; Linder, 1985; McMurtrie *et al.,* 1994). Leaf area index (LAI = the amount of leaf area per unit ground area) is therefore a key variable needed to scale leaf processes to the canopy or site level, facilitating an understanding of how the environment may limit the productivity of the site.

METHODS

Experimental site

The experimental site is located in Gunnarsholt, S. Iceland (63°51' N and 20°13' W, elevation 78 m). It was established in co-operation between Icelandic and Canadian research teams in 1990. A 14.5 ha abandoned hayfield, from which the sod had been stripped off in 1989, was planted with propagated cuttings of a single clone of black cottonwood (*Populus trichocarpa* Torr. & Gray; clone Iðunn) and a permanent micrometeorological station was built near its centre. In 1990, the surface was essentially bare soil, however, some narrow strips of grass had been left in the process of stripping sod off the field and after a subsequent herbicide application. Mortality of the black cottonwood cuttings was 16% during the first year and in 1991 all dead plants were replaced (Eyjólfsdóttir *et al.*, 1994). After the initial mortality, tree survival at the site has been excellent (98.4% through 1995). In 1993, permanent fertilisation trials were established at the site, which were supplied with solid fertiliser each spring (60–150 kg N ha^{-1}, and other macronutrients in appropriate proportions). In May 1996, the whole site was fertilised with 80 kg ha^{-1} of solid NPK fertiliser, which lead to rapid changes in vegetation cover and leaf area. Further details about the experimental set-up can be found in Thorgeirsson *et al.* (1993), Eyjólfsdóttir *et al.* (1994) and Aradóttir *et al.* (1997a).

Plant colonisation and vegetation cover

In August, 1991, all vascular plants found at the site were recorded (Eyjólfsdóttir *et al.*, 1994). This was repeated in 1994 and 1996. Plant names are according to Kristinsson (1989).

The vegetation cover was determined by a point quadrat frame in August 1993, close to the time of the seasonal peak leaf area. Two 10×10 m permanent plots were established at random locations in each quarter of the site for a total of eight plots. A 50×50 cm frame was laid out at 10 random locations within each plot. Plant cover within the frames was measured with a regular array of 100 pins that were lowered vertically through the vegetation, recording all hits with each pin. The use of a point quadrat assumes an infinitely small point, but as the pins used do have a finite diameter the technique may give an overestimate of cover (Greig-Smith, 1983).

Vegetation cover was also estimated visually in July 1995 and 1996. Sixteen 4×50 m plots were laid out so that each quarter of the site contained four plots. Both position and direction of plots were chosen at random. Vegetation cover was estimated in a 20×50 cm frame that was placed at 50 randomly chosen points within each plot. The vegetation was divided into five categories: black cottonwood trees, grasses, other vascular plants, mosses and crust. The frame was placed on top of the vegetation and percentage cover determined as the proportion of the frame area filled by each class. In 1995, all vegetation was treated as a single layer, giving a result comparable to the cover measured by the first hit of the point quadrat method. In 1996 the vegetation cover was estimated separately in each of two layers: trees and understorey (grasses, other vascular plants, mosses and crust).

Leaf area index measurements

Total leaf area index of trees plus understorey (site-LAI) was measured with the LAI-2000 Plant Canopy Analyzer (LI-COR, Inc., Lincoln, Nebraska), which determines an apparent leaf area as all light-blocking elements are included. LAI is estimated by integrating gap fractions obtained from above- and below-canopy readings of diffuse sky radiation at five zenith angles simultaneously (Welles and Norman, 1991). The reader is referred to Welles and Norman (1991) for further information on the theory of operation of the instrument.

In 1993 and 1994, LAI measurements were done at approximately 1.5 m intervals along eight 100 m transects at an angle of 22.5° to the rows. Each time, two new transects were chosen in all four quarters of the site. In 1995 and 1996 the transects were reduced to four 100 m permanent ones (one in each quarter), with fixed measurement points. Row crops, such as a plantation forest, present an extra difficulty in sampling LAI as one must ensure that the transect readings are representative and are not biased towards or away from rows. Diagonal transects are the preferred method in this situation.

On each sample day, the operator walked the transects making above and below canopy determinations of sky brightness. Below canopy readings were made at the surface and therefore include both trees and understorey. Care was taken to ensure that the sensor head was facing the same direction (North) both above and below the canopy. As the instrument measures the attenuation of diffuse radiation, measurements were made during periods of uniform overcast (total diffuse light) to minimise the effects of changing sky brightness. A 90° view lens cap was used to restrict the view of the sensor when taking readings. This procedure reduces the chances of viewing canopy gap and full foliage in the same location when the instrument is used in a sparse canopy (Strachan and McCaughey, 1996).

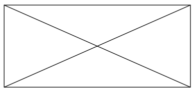
Growth- and harvest measurements

Tree growth was measured both at annual and within-season time scales. Non-destructive growth measurements were recorded routinely for 100 trees, randomly distributed over the site, and included measurements of tree height and crown diameters (maximum diameter and diameter perpendicular to the maximum; Aradóttir *et al.*, 1997a).

In September 1993 and 1994, 20 trees were chosen at random and harvested, after measuring them in the same way as the 100 monitored trees. In 1995 and 1996, the number of harvests was increased to four per growing season, harvesting 20 trees each time. Trees were also harvested from the permanent fertilisation plots at the site in 1995 and 1996. At harvest, all leaves were removed from the trees and the total leaf area was measured with a leaf area meter (LI-3000, LI-COR, Inc., Lincoln, Nebraska). In addition, measurements of crown shape were made on trees at selected harvests during 1994 through 1996. The distance from the stem base to the edge of the tree crown was measured at 5 cm height intervals in the cardinal directions (1994) and later at 10–30 cm height intervals in eight directions (1995 and 1996). These data were then used to construct relationships between dripline area, crown volume and leaf area and simple non-destructive measurements of height and canopy dimensions.

Calculations of tree cover and crown volume

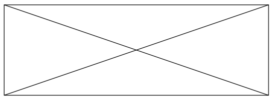
Dripline crown area, A_d, was calculated from the measurements of crown shape of the harvested trees as;



(1)

where $d_{i\max}$ is the maximum distance from the stem to the crown edge (m) measured at a given direction at any height and n is number of directions measured. Along with information about stand density (10000 trees ha^{-1}) this can easily be converted into tree surface cover by multiplying A_d by 100.

Crown volume, V_{crown}, was calculated from the measurements of crown shape of the harvested trees as;

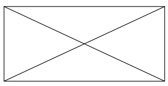


(2)

where d_i is the distance from the stem to the crown edge (m) measured at a given direction and over a given height interval, h_j (m), and n is number of directions measured. Foliage density (*FD*) was calculated by dividing the measured leaf area with V_{crown}.

Inter-seasonal cover- and LAI curves

By comparing measured A_d with non-destructive measurements of crown diameters that were obtained from the same harvest trees, it was possible to use a simple geometric formula (ellipse) to describe the dripline area (then termed A_d^*), thus;



(3)

where a is the maximum crown diameter (m), b is the maximum diameter perpendicular to a, and f is a correction factor for asymmetry equal to 0.88. The crowns were not truly elliptical in cross-sectional shape probably due to stress caused by the dominant southerly winds (Aradóttir *et al.*, 1997b). Equation (3) was used to estimate changes in tree cover by using the repeated non-destructive growth measurements from the 100 monitored trees, assuming that there were no vertical gaps in the tree crowns, that would decrease the actual cover.

Similarly, a geometric relationship was found to estimate the measured crown volume, $V_{crown}{}^{*}$, of the harvested trees. The crown shape of the cottonwood trees was best described as an elliptic cone;

(4)

where h is the tree height (m) and $A_d{}^{*}$ is the estimated dripline area according to Eq. (3). A simple linear regression was used to establish the relationship between the estimated crown volume, $V_{crown}{}^{*}$, and measured leaf area of the harvest trees, which then was applied to estimate annual and inter-seasonal changes in average tree-LAI from the 100 monitored trees.

RESULTS

Changes in species composition

Forty-two species of vascular plants were recorded in 1991 (Table 1). In 1993, 25 species were recorded in the eight 10×10 m plots established for cover measurements, three of which had not been found before (Table 2). In 1994, all except three species, *Rorippa islandica*, *Viola tricolor* and *Poa annua*, were found again and 23 new species were added. In 1996, three new species were added to the list, bringing the total number of species at the site to 68.

Vegetation cover

Three years after planting, less than 1% of the surface was bare ground, 38% was covered by mosses, 40% by grass and 9% of the surface was categorised as covered by crust, a thin organic layer formed by mosses, lichens and litter remnants. At that time, the grass *Agrostis capillaris* was by far the most abundant species with 60 hits on the average in each frame (Table 2). Other common grass species were *Poa pratensis* and *Festuca richardsonii*. The most abundant forbs were *Rumex acetosella*, *Leontodon autumnalis* and *Cerastium fontanum* (Table 2); all three are commonly found at disturbed sites. The black cottonwood saplings only covered 4% of the surface in 1993.

By 1995, the crust layer had largely disappeared and vegetation covered 98% of the surface. Moss cover increased by 9% between 1993 and 1995 and vascular plants other than black cottonwood increased only by 4%. The black cottonwood began to form the primary canopy and more than tripled its cover from 4% to 14% (Table 3). The site was fertilised in the spring of 1996 and subsequently the trees more than doubled their canopy cover to 32%. In this year, grass cover was nearly doubled and moss cover decreased by a third (Table 3).

The derived dripline area, $A_d{}^{*}$, was found to describe the measured A_d quite adequately for the 86 harvest trees ($r^2 = 0.95$, $P<0.001$; Figure 1a). Maximum tree cover calculated using $A_d{}^{*}$ was 5, 13, 16 and 50%, in 1993 to 1996, respectively (Figure 2). This method gave similar cover values as the traditional cover estimates in 1991 and 1995, but a slightly higher value in 1996 (Figure 2). This could indicate that the assumption of no gaps in the tree crown gets more critical as the trees grow larger.

Leaf area index and foliage density

The crown shape of the cottonwood was best described as an elliptic cone. Equation (4) gave a significant estimate of crown volumes for 86 harvest trees ($r^2=0.96$, $P<0.001$; Figure 1b). A significant relationship ($r^2=0.94$, $P<0.001$; Figure 1c) was found between the $V_{crown}{}^{*}$ and measured tree leaf area (*LA*);

(5)

There was no significant difference in the relationship between crown volume and leaf area for trees growing at high and low nutrient availability. This made it possible to use Eq. (5) to construct a time series of tree-LAI from non-destructive growth measurements for the whole period. For the 1993 through 1996 growing seasons, the maximum tree-

Table 1. Vascular plants recorded at the site in 1991, 1994, and 1996. (x) indicates plants presented but not recorded at the time.
1. tafla. Æðplöntur skráðar á svæðinu 1991, 1994 og 1996. (x) eru plöntur sem með vissu fundust á svæðinu en voru ekki skráðar.

Species—*Tegund*	’91	’94	’96	Species—*Tegund*	’91	’94	’96
Forbs				*Senecio vulgaris*	x	x	x
Achillea millefolium	x	x	x	*Silene acaulis*		x	x
Alchemilla alpina	x	x	x	*Spergula arvensis*	x	x	x
Alchemilla vulgaris	x	x	x	*Stellaria media*	x	x	x
Armeria maritima	x	x	x	*Taraxacum* spp.	x	x	x
Botrychium lunaria		x	x	*Thymus praecox*	x	x	x
Capsella bursa-pastoris	x	x	x	*Viola palustris*		x	x
Cardamine nymanii		x	x	*Viola tricolor*	x		
Cardaminopsis petraea	x	x	x				
Cerastium alpinum		x	x	**Woody species**			
Cerastium fontanum	x	x	x	*Betula pubescens*	x	x	x
Chamomilla suaveolens	x	x	x	*Populus trichocarpa*	x	x	x
Coeloglossum viride			x	*Salix alaxensis*	(x)	x	x
Epilobium angustifolium		x	x	*Salix borealis*	(x)	x	x
Epilobium collinum		x	x	*Salix callicarpaea*		x	x
Epilobium palustre	x	x	x	*Salix herbacea*		x	x
Equisetum arvense	x	x	x	*Salix lanata*	x	x	x
Erigeron borealis		x	x	*Salix phylicifolia*		x	x
Galium normanii	x	x	x				
Galium verum		x	x	**Grasses and rushes**			
Leontodon autumnalis	x	x	x	*Agrostis capillaris*	x	x	x
Lupinus nootkatensis		x	x	*Agrostis stolonifera*	x	x	x
Lychnis alpina		x	x	*Agrostis vinealis*	x	x	x
Matricaria maritima	x	x	x	*Alopecurus geniculatus*	x	x	x
Melandrium rubrum		x	x	*Deschampsia beringensis*		x	x
Minuartia rubella		x	x	*Deschampsia caespitosa*	x	x	x
Oxyria digyna		x	x	*Elymus repens*		x	x
Polygonum aviculare	x	x	x	*Festuca richardsonii*	x	x	x
Potentilla anserina	x	x	x	*Festuca vivipara*	x	x	x
Potentilla crantzii		x	x	*Juncus arcticus*			x
Ranunculus acris		x	x	*Leymus arenarius*		x	x
Ranunculus repens	x	x	x	*Luzula multiflora*	x	x	x
Rhinanthus minor	x	x	x	*Luzula spicata*		x	x
Rorippa islandica	x			*Phleum pratense*	x	x	x
Rumex acetosa		x	x	*Poa annua*	x		
Rumex acetosella	x	x	x	*Poa glauca*			x
Rumex longifolius	x	x	x	*Poa pratensis*	x	x	x
Sagina procumbens		x	x	*Trisetum spicatum*		x	x

LAI was 0.1, 0.3, 0.3 and 1.1, respectively. These values are only 10–40% of the maximum site-LAI measured with the LAI-2000 for the same period (1.4, 1.7, 1.4 and 2.7, respectively; Figure 3). The difference can be interpreted as the LAI of the understorey.

The cottonwoods seemed to reach a stable foliage density after forming tree crowns, ir-

Table 2. Vegetation cover measured with point quadrat method on 6–12 August 1993. Numbers for each plot show average no hits in 10 quadrats with 100 points each, x's indicate species that were found in plots but were not recorded in point quadrats.
2. tafla. Þekja metin með oddamælingum 6.–12. ágúst 1993. Tölur fyrir hvern reit eru meðaltöl 100 ramma, sem hver er með 100 odda, og x merkir að tegund fannst í reit en ekki í neinum ramma.

Species				Plots—*Reitir*					Mean
Tegundir	1	2	3	4	5	6	7	8	*Meðaltal*
Lichens			x						
Mosses	81	85	36	59	52	77	76	26	61
Achillea millefolium			x						
Agrostis capillaris	81	27	88	40	38	50	32	123	60
Agrostis vinealis	0.1		x		0.4		x	x	0.1
Alchemilla alpina				x	x				
Alchemilla vulgaris						x			
Alopercurus geniculatus							0.4		0.1
Cerastium fontanum	4	1	0.3	1	0.5	0.2		x	0.9
Chamomilla suaveolens	x	0.1	x	0.1			0.1		0.0
Epilobium sp.							x		
Equisetum arvense			x	x					
Festuca richardsonii		0.2	2		3	0.4		14	2
Festuca vivipara	0.1			0.4				x	0.1
Leontodon autumnalis	6	2	1	0.5	0.1	0.4	1	x	1
Luzula multiflora	0.1	x	0.2	0.4	0.2	0.3	x	x	0.2
Luzula spicata					x				
Matricaria maritima					x				
Poa pratensis	3	5	3	4	0.5	7	3	9	4
Polygonum aviculare	x	x							
Populus trichocarpa	13	10	7	11	3	4	13	4	8
Rumex acetosella	5	10	4	0.3	0.1	x	4		3
Salix callicarpaea							x		
Salix lanata	x	x			x		x		
Salix phylicifolia	x	x		x			x		
Spergula arvensis				0.1					0.0
Taraxacum sp.			0.1			x			0.0
Bare ground	0.3		0.1	0.8	1		0.2		0.3
Litter	16	9	51	10	18	21	11	73	26
Crust (cryptogramic)	1	6	13	29	29	2	12	0.2	11

respective of tree size and nutrient treatment (Figure 1d).

DISCUSSION

Records of plant colonisation

The vegetation at the Gunnarsholt site has gone through substantial changes since 1990. At the time of plantation establishment, the surface was essentially bare ground with narrow strips of grass, but already in 1991 cryptograms (mostly mosses) had started to rapidly colonise the bare soil, and 42 species of vascular plants were recorded (Eyjólfsdóttir *et al.*, 1994). Not all the species were new colonisers, some had survived in the narrow strips left in the process of removing the sod, others might have regenerated from roots or from active seed bank remaining in the soil. Two species, *Salix*

Table 3. Average cover (%) of different plant groups measured by point quadrat method in August 1993, and estimated visually in July 1995 and 1996.
3. tafla. Meðalþekja (%) mismundi gróðurs mæld með oddamælingum í ágúst 1993 og metin með sjónmati í júlí 1995 og 1996.

Year *Ár*	Cottonwood *Ösp*	Grasses *Grös*	Forbs *Blómplöntur*	Mosses *Mosar*	Crust and litter *Grot*
1993[a)]	4	40	4	38	14
1993[b)]	8	66	5	61	26
1995	14	37	1	47	2
1996[c)]	32	69	1	30	0

a) First hit at each point (canopy surface, 100 hits)—*Fyrsta snerting*.
b) All hits (total cover measurements, average of 177 hits)—*Allar snertingar*.
c) In 1996 the trees and understorey were measured as a separate canopy layers—*Tré og undirgróður voru mæld sem tvö aðskilin laufþök 1996*.

alaxensis and *S. borealis*, were accidentally introduced at the time of planting.

In the point quadrat measurements in 1993, only 25 species were recorded, of which three had not been found before, two willows (*Salix callicarpaea* and *S. phylicifolia*) that are found growing naturally in the local area, and a rush, *Luzula spicata* (Table 2). The relatively low number of species recorded in 1993 can be explained by the limited extent of the study, i.e. only species found in the eight permanent cover plots were recorded. The three most frequently listed grass species in 1993 *(Agrostis capillaris*, *Poa pratensis* and *Festuca richardsonii*) are common in natural grasslands and old hayfields in Iceland, and probably represented the dominant vegetation of the old hayfield.

Twenty-three new species were found in 1994, and three species were not found again, *Rorippa islandica*, a relatively uncommon flower that grows mostly in wet areas, *Viola tricolor*, which is not commonly found in the vicinity (Kristinsson, 1989), and an annual grass, *Poa annua* (Table 1). In 1996, only three new species were recorded. A rapid immigration of species seems therefore to have taken place the first years after plantation, but after 1993, when the soil was more or less covered by vegetation, the rate of immigration decreased dramatically.

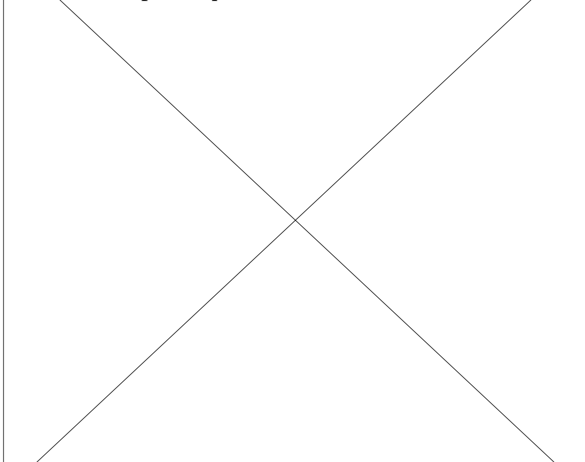


Figure 1. Relationships between (a) measured and estimated dripline area (A_d vs A_d^*), (b) measured and estimated crown volume (V_{crown} vs V_{crown}^*) of 86 young black cottonwood trees ranging in height from 0.3 to 2.5 m. Also shown are: (c) the relationship between V_{crown}^* and leaf area on fertilised and unfertilised trees and (d) foliage density in the crowns of trees growing at limiting (●) and high (□) nutrient supply.
1. mynd. Samanburður á (a) mældri og áætlaðri trjáþekju (A_d vs A_d^*), (b) mældu og áætluðu rúmmáli laufkrónu (V_{crown} vs V_{crown}^*) 86 aspartrjáa sem voru á hæðarbilinu 0,3 til 2,5 m. Einnig eru sýnd: (c) tengsl V_{crown}^* og laufflatarmáls og (d) þéttleiki laufkrónu trjáa sem uxu við takmarkað (●) og nægilegt (□) framboð næringarefna.

Vegetation cover

The bare soil was rapidly colonised by mosses in the first years (Eyjólfsdóttir *et al.*, 1994), mainly *Polytrichum* spp, which were then replaced by grasses and forbs (Tables 2 and 3). The grass, which formed a low canopy, was still increasing in cover by 1996. As the black cottonwood saplings grew larger, a second canopy layer developed, increasing light competition that eventually is expected to lead to changes in species composition and understorey cover at the site. In 1996, however, there were no signs of that the trees had begun to limit the survival of understorey species. In total, vascular plants were covering 48% of the surface in 1993, 52% in 1995, and more than 70% in 1996 (Table 3).

Although tree cover has been increasing rapidly since establishment, it had only reached 50% at the end of the 1996 growing season. Considering the current rate of increase, it is estimated that it will be at least three years before the site reaches canopy closure. It is at canopy closure that the largest changes in energy balance and the water relations of the site are expected to take place (Aradóttir *et al.*, 1997a), biological processes such as overstorey competition may begin and management practices such as thinning may be considered.

The inter-annual cover estimates are valuable in the construction of time series showing the seasonal development of tree cover, which are an essential component of many simulation models which calculate stand evapotranspiration, light interception and canopy photosynthesis (e.g., McMurtrie *et al.*, 1994; Shuttleworth and Wallace, 1985).

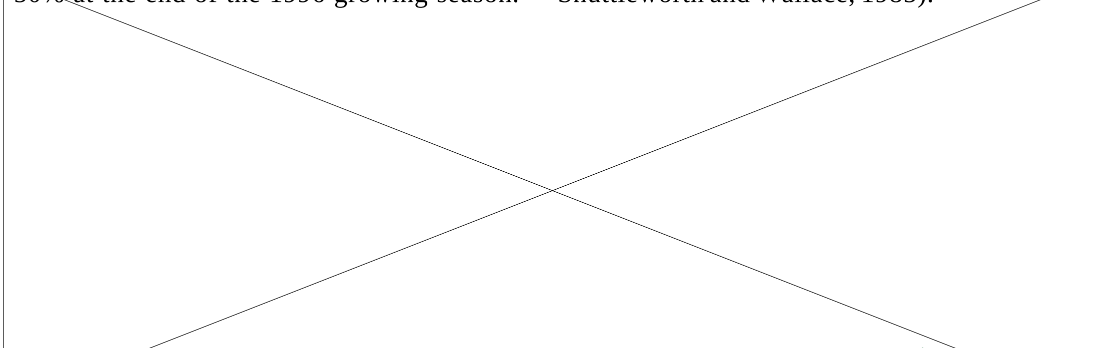


Figure 2. Time series of tree cover development for 1993–1996, estimated from changes A^*_d of 100 black cottonwood trees randomly distributed over the site (●) and direct measurements of tree-cover (□).
2. mynd. Breytingar á trjáþekju 1993–1996, reiknað út frá endurteknum vaxtarmælingum (A^*_d) *á 100 aspartrjám (●) og beint mat á trjáþekju (□).*

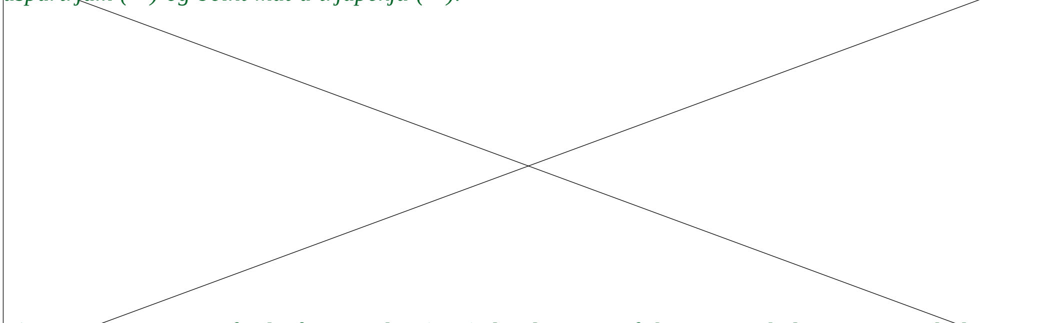


Figure 3. Time series for leaf area index (LAI) development of the Gunnarsholt experimental plantation, 1993–1996. Site-LAI represents leaf area of both trees and understorey, measured with the LAI-2000 (●), and tree-LAI was estimated from non-destructive growth measurements on 100 trees randomly distributed over the site (○). Error bars represent one standard error from the mean.
3. mynd. Breytingar á laufflatarmálsstuðli (LAI) 1993–1996. Heildarlaufflatarmál (tré og undirgróður) mælt með LAI-2000 tækinu (●), og laufflatarmál aspar metið með sambandi milli rúmmáls laufkrónu og laufflatarmáls fyrir 100 tré sem endurteknar vaxtarmælingar voru gerðar á (○).

Leaf area index

The point quadrat measurements done in August 1993 also can be used to estimate site-LAI at that point in time, since the method records all hits with a pin of a finite diameter over a point of the same size. When converted to site-LAI values, the different plots ranged from 0.53 to 1.49 with an average of 0.80 (data not shown). Corresponding LAI-2000 values, measured for much larger areas during the same period, ranged from 1.18 to 1.53, with an average of 1.35. This difference is significant (t-test, $P<0.001$) Differences can be expected between those two estimates because: (1) the site-LAI varies quite much within the site, (2) the two methods measure different areas, and (3) the number of plots measured by the point quadrat method was limited because of the labour intensive nature of these measurements.

The understorey was the dominant component of site-LAI prior to 1996. Understorey LAI was not directly measured, but could be estimated as the difference between site-LAI and tree-LAI. Some information about the understorey at the site is needed if carbon, water and nutrient cycles of the ecosystem are to be studied. Understorey species are more important in productivity and nutrient cycling than their biomass would suggest, because larger proportions of their biomass and nutrient pools turn over annually than in trees, which have greater allocation to long-lived woody tissues (Chapin, 1993).

Black cottonwood has a long and monocyclic leaf production, which makes the relationship between crown volume (V_{crown}) and tree-LAI valid for almost the entire growing season. Including a covariate of day-of-year to the regression did not lead to significant improvements of the estimate. Caution is however warranted when using these relationships to calculate LAI very early or late in the growing season. If a large portion of the canopy consists of leaves that are not fully expanded or if leaves have been lost through senescence, this relationship will overestimate the true LAI.

Leaf area index for the plantation lies well below values reported for similar plantations in the literature. Barigah *et al.* (1994) in a clonal study in France (48°50' N) with 0.8 m spacing, found that two black cottonwood clones reached the five-year Gunnarsholt LAI values after only two years. They also found that clones with the largest leaves and highest LAI's had the highest productivity. Dunlap *et al.* (1995) found that four black cottonwood clones grown at 1.2 m spacing in an extensive clonal trial in Washington, USA (47°10' N) reached leaf area indices of 3.9–9.5 two years after plantation. Ceulemans *et al.* (1990) found that northern clones had lower leaf areas and production than more southern clones. The Idunn clone originates from Copper River Delta, Alaska, which is close to the northern growth limit for black cottonwood (Ceulemans, 1990). However, the slow growth observed in Gunnarsholt can not solely be attributed to northern genetic origin, but is possibly related to the shorter growing season in Iceland or some combination of unfavourable site or environmental factors. It is clear that the actual leaf production for the Gunnarsholt site has been far lower than the growth-potential of the species allows.

In most temperate environments the major limiting factors for forest production are water and nutrients (Linder and Flower-Ellis, 1992). Both water- and nutrient status greatly influence the amount of leaf area produced, directly affecting the amount of radiation intercepted and hence production. At the Gunnarsholt site, a lack of water is not likely to be a limiting factor in the site's productivity (Strachan *et al.*, 1998b). Nutrients, on the other hand, seem to have strongly limited productivity of the site during the first five years after establishment. The fertilisation caused the large increase in the site-LAI in 1996. In early September 1996, LAI-2000 measurements were taken on both fertilised and unfertilised parts of the southwest quarter of the site. The fertilised part showed a significantly greater site-LAI (t-test, $P<0.001$) of almost three times (data not shown) after the spring fertilisation. A typical response to reduced availability of nitrogen is increased allocation of photosynthates to roots, with consequently slower leaf production (Ericsson, 1995). The slow cover- and leaf area development of the black cottonwood, compared to results obtained elsewhere can at least partly be explained by poor nutrient status of the local volcanic soils. Further studies will reveal if additional factors limit tree growth at the Gunnarsholt site.

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