MODELING SPATIAL VARIABILITY OF WHITE SPRUCE (*PICEA GLAUCA*) GROWTH RESPONSES TO CLIMATE CHANGE AT AND BELOW TREELINE IN ALASKA – A CASE STUDY FROM TWO NATIONAL PARKS

With 6 figures and 6 tables

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Zusammenfassung: Modellierung der räumlichen Variabilität von Weißfichte *(Picea glauca)*. Wuchstrends als Folgen von Climate Change an der alaskanischen Baumgrenze – Fallstudie aus zwei Nationalparks

Ziel dieser Untersuchung war 1) die Entwicklung eines räumlich expliziten, mittelmaßstäbigen Modells der Klimasensitivität von Weißfichte an der Baumgrenze im Denali Nationalpark (DNP) und Gates of the Arctic Nationalpark (GAAR) in Alaska und 2) mit Hilfe dieses Modells die räumlichen Veränderungen des borealen Nadelwaldes unter zukünftiger Erwärmung abzuschätzen. Dazu haben wir zuerst ein Entscheidungsmodell entwickelt, um die Beziehungen zwischen Umweltfaktoren und Baumwuchs näher zu untersuchen, und dann die Ergebnisse mit Hilfe eines GIS-Modells in den Raum extrapoliert. In DNP projiziert unser Modell mögliches Baumsterben an den Unterhängen und Baumgrenzverschiebungen und Erhöhung der Bestandsdichte an den Oberhängen. Falls sich der aktuelle Erwärmungstrend fortsetzt, kann sich die Waldfläche im Straßenkorridor um ca. 50% erhöhen, was dann zu Einschränkungen bei Wildtierbeobachtungen führen würde. In GAAR projiziert unser Modell verstärktes Baumwachstum an den Unterhängen, während sich in Mittel- und Oberhängen die Struktur des Waldes ändern könnte (größere Bestandsdichte bis zu Absterben der Bauminseln). Auf regionaler Ebene sind daher Änderungen der räumlichen Ausdehnung des borealen Waldes möglich (Verschiebung der Baumgrenze). Auf Landschaftsebene sind strukturelle Änderungen des Bestandes möglich, z.B. Verdichtung der Bestände oder begrenztes Absterben. Änderungen von Wachstumsraten einzelner Bäume aufgrund erwärmter Bedingungen können nachgewiesen werden, und weitere Erwärmung könnte diese Änderungen so intensivieren, dass Auswirkungen auf der Landschaftsebene sichtbar werden.

Summary: Aim of this study was to develop a spatially explicit, medium-scale model of the climate sensitivity of recent white spruce growth at and below treeline in Denali National Park (DNP) and Gates of the Arctic National Park (GAAR) in Alaska and then use the model to project changes in extent of boreal forest under future warming scenarios. We developed a decision-tree model to examine tree growth-environment relationships and used a GIS to extrapolate model results into space. In DNP our results indicate possible dieback of white spruce at low elevations and treeline advance and infilling at high elevations. If recent warming continues, the road corridor in DNP would experience forest increase of about 50%, mainly along the road decreasing the possibility for visitors to observe wildlife across open tundra. In GAAR our results indicate increased rate of white spruce growth at low elevation areas while other areas would experience changes in forest structure (dieback of tree-islands, infilling of existing stands). Changes in distribution of white spruce forests in Alaska are within the range of possibility on a regional scale (treeline advance, dieback). Structural changes within existing forest are possible on a medium (landscape) scale through changes in tree density, infilling and dieback. Changes in growth performance of individual trees due to climate warming are already underway, and further warming would intensify these changes with landscape-wide consequences.

1 *Introduction*

Treelines are areas where the potential of upright woody vegetation to occur ends and only the survival of prostrate vegetation is possible. Northern and alpine treeline areas are transition zones between boreal forest and alpine or arctic tundra. While sometimes conceived of as a broad transition zone, treelines in our study areas are relatively sharply defined borders between forested sites and tundra. In this paper we apply the term treeline to an imaginary line connecting the highest patches of forests on a given slope (Koerner 1998).

Historically, the survival and growth of trees at northern or altitudinal treelines was seen as limited by only one environmental factor. The lack of available warmth has generally been interpreted as the limiting factor for tree growth in cold regions. This apparent simplicity of only one controlling factor made treeline environments the focus of sustained research interest (Griggs 1934; Krebs a. Barry 1970; Elliot-Fisk 1983; Grudd et al. 2002).

Especially in the last decade treeline ecotones have been investigated as potential "early warning stations" for Climate Change (Lescop-Sinclair a. Payette 1995; Hogg a. Schwarz 1997; Kullman 1996, 2000, 2001, 2002). Warming in the high latitudes is of a greater magnitude than elsewhere (Overpeck et al. 1997; Serreze et al. 2000) and during the last century Alaska experienced one of the strongest warming trends on the globe (Chapman a. Walsh 1993).

Given the historical relationship between temperature and treeline position, the warming trend of the last decades could be expected to cause treeline advances in Alaska, which have been documented in some places (Suarez et al. 1999; Lloyd a. Fastie 2002). However, arctic treelines might be a lot more stable than expected (Szeicz a. MacDonald 1994), may not react very fast to climate warming (Lavoie a. Payette 1996), or might be relicts of warmer periods and not reflect current climatic conditions (Weisberg a. Baker 1995).

Large-scale climate-vegetation models assume linear correlation between changing climatic conditions and subsequent position of the boreal treeline (Pielke a. Vidale 1995; Elliot-Fisk 1983). Site-specific studies, on the other hand, do not document significant changes in treeline position associated with recent climate warming of the last few decades (Holtmeier 1995; Baker a. Weisberg 1997). Especially in mountainous areas, topography represents a barrier to treeline advances in response to climate warming. Models incorporating the topographic influences of mountain masses (Rupp et al. 2001) produce expansion of boreal forest onto the North slope of Alaska only after thousands of years.

Summer temperature, especially the July 10 °C isotherm (Daubenmire 1954; Holtmeier 1974) is often reported as the main factor controlling treeline position. Koerner (1998) proposed that soil temperatures of the root zone provide a far better explanation than generalized air temperatures and Goldstein et al. (1985) suggested that colder soil temperatures can limit tree growth through increased resistance of water flow in white spruce at treeline. However, within the boreal forest, well south of the treeline areas, the limiting factor for white spruce growth and establishment is moisture supply (Barber et al. 2000). In at least parts of the forest-tundra ecotone in Alaska growth limitations may have shifted from lack of warmth to lack of moisture (Jacoby a. D'Arrigo 1995; Wilmking et al. 2004). At circumpolar northern treeline sites, sensitivity of radial growth to temperature has increased since the mid 20th century (Wilmking et al. 2005).

Alaska's northern treeline consists mostly of white spruce (*Picea glauca* (Moench) Voss). In Alaska, white spruce populations at or near treeline in the Brooks Range and Alaska Range are mixed with positive, negative and no significant response to temperature (Wilmking et al. 2004). Roughly equal proportions (~30–40%) of these trees display negative and positive sensitivity to temperature. The control for growth on both positive and negative responders occurs above specific temperature thresholds. Trees responding with enhanced growth are highly positively correlated with spring temperatures, whereas trees showing a reduction in growth showed highly negative correlations with the mean monthly temperature of the previous July (Wilmking et al. 2004; D'Arrigo et al. 2004).

About 1975 Alaska's climate regime shifted to the warmest and driest in the last century (Barber et al. 2004), so that these temperature thresholds are occurring more frequently in the later part of the 20th century. Additional climate warming will have even greater effects on growth of Alaska treeline trees than has been seen in the past, because thresholds will be exceeded even more frequently.

In this paper we explore the spatial distribution of white spruce affected by these temperature thresholds in two National Parks in Alaska and attempt to build a simplified, medium scale, spatially explicit model of tree-growth climate relationships.

2 *Description of study areas*

GAAR in the Brooks Range and DNP in the Alaska Range both encompass boreal forest and arctic or alpine tundra (Tab. 1). GAAR became a National Park and Preserve in 1980. It encompasses over 34,000 km^2 in the central portion of the Brooks Range, Alaska. Boreal forest reaches from the southern foothills nearly to the continental divide, stretching along large river valleys, occupying 18% of the park area. Treeline occurs at elevations of about 800 to 900 m on south-facing slopes and 700 to 800 m on north-facing slopes and is a mixture between alpine (elevational) and latitudinal treeline. North of the continental divide, no naturally occurring white spruce is found. Our four study sites in GAAR (the site BRNC is actually 2 km outside the eastern border of GAAR) were located at or close to the northern limit of white spruce in Alaska (Fig. 1).

Table 1: Land cover types in study areas (km^2)

Oberflächengestalt der Untersuchungsgebiete (km^2)

	GAAR	DNP
Boreal forest	6,241.3	9,531.6
Shrubs	17,746.4	4,126.2
Tundra	5,358.9	3,434.6
Water bodies	335.7	438.0
Bare/burned area	2,962.8	2,605.6
Snow/ice	145.0	2,717.0
Indeterminate/clouds	1,523.5	1,750.9
Total area	34,313.6	24,603.9

Denali National Park and Preserve was originally established as Mt. McKinley National Park in 1917. Today it consists of over 24,000 km^2, 38% of which is boreal forest. Our study sites were located at treeline in three watersheds within the park (Fig. 1). Road tours into the park began in the 1920s and a comparison of historic photographs from that time period with the views of today suggests infilling of trees in scattered stands along the road (Viereck pers. com).

3 *Methods*

3.1 Tree cores

We collected tree ring samples from 793 white spruce in GAAR and DNP. Site conditions (exposure, slope angle, elevation) were recorded at each tree location and later checked against National Elevation Data (NED, 60 m resolution).

For each tree we recorded diameter at breast height (dbh), tree height with a clinometer. Dbh and tree height were used to calculate green weight (Manning et al. 1984) and tree position with a handheld GPS. Penetrating tree-cores were collected from each tree with a Hagloef increment borer. Cores were mounted, sanded (to 600 grid), counted, marked and measured using a Velmex measuring stage (0.001 mm). Annual values were then averaged from both sides of the core. Averaged values were crossdated using standard techniques (Stokes a. Smiley 1968) on the basis of prominent and well-known marker ring series. Accuracy of dating was checked using COFECHA runs for each site (ITRDB Program Library; Cook et al. 1990). Dating errors were limited to one or two years and corrected for subsequent analysis. After age determination we only included the 753 trees which were 50 years or older in the analysis. Our goal was to include two 25 year periods before and after a major climate shift in 1975 (Barber et al. 2004) and we used only trees that contributed rings continuously over that 50 year period.

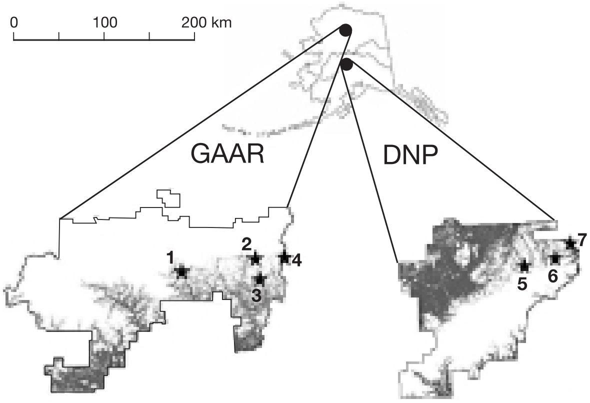

Fig. 1: Study sites in GAAR (Brooks Range) and in DNP (Alaska Range), Alaska, are at or close to treeline. Location of study sites: 1) BRHF (67.8ºN, 152.4ºW), 2) BRNF (67.9ºN, 150.5ºW), 3) BRCL (67.7ºN, 150.5ºW), 4) BRNC (67.9ºN, 149.8ºW), 5) ARCC (63.6ºN, 150.0ºW), 6) ARTL (63.4ºN, 149.2ºW), 7) ARRC (63.7ºN, 149.0ºW). Grey area is extent of boreal forest

Alle Untersuchungsgebiete in GAAR (Brooks Range) und in DNP (Alaska Range), Alaska, sind an oder in unmittelbarer Nähe der Baumgrenze. Positionen: 1) BRHF (67.8ºN, 152.4ºW), 2) BRNF (67.9ºN, 150.5ºW), 3) BRCL (67.7ºN, 150.5ºW), 4) BRNC (67.9ºN, 149.8ºW), 5) ARCC (63.6ºN, 150.0ºW), 6) ARTL (63.4ºN, 149.2ºW), 7) ARRC (63.7ºN, 149.0ºW). Graue Schattierung entspricht der Fläche des borealen Nadelwaldes

First we used the raw ring width values to establish membership in a responder class. We compared averaged raw ring width of the time periods 1950–1974 and 1975–2000 and calculated the amount of decreased or increased growth. Trees suffering a decline in growth we called "losers", trees with increased growth we called "winners".

Winners show highest correlations with a spring temperature index (March and April of the two years prior to growth) and losers with the July mean monthly temperature the year prior to growth (Wilmking et al. 2004). For the loser population of trees, we assumed a linear reduction in rate of growth once the growth reduction threshold has been crossed. Our standard for projecting the elimination of trees was when the projected empirical relationship reached zero growth. We used a responder function (modified from Wilmking et al. 2004), which models zero growth at a Fairbanks July temperature higher than about 22 °C (Fig. 2). This temperature is within range of possibility of several General Circulation Models (GCM) used in the recent Artic Climate Impact Assessment (ACIA 2004). A mean ring width index (MRWI) of 1 is the mean average growth over the life-span of each tree of the sampled population until we cored it. Piecewise linear regression was used to calculate the breakpoint of the regression lines. Mean monthly temperatures below 16.5ºC do not affect MRWI of the following year (r^2=0.05, n=55). Above 16.5 °C however, tree growth is strongly negatively correlated with warmer July temperatures (r^2=0.51, n=38) (Wilmking et al. 2004; D'Arrigo et al. 2004). Keep in mind that this is a simplified model projecting growth under scenarios currently not experienced by white spruce in Alaska or elsewhere. Therefore the linear extrapolation to model zero growth is an approximation.

3.2 Decision-tree model

We developed two models of the relationships between tree growth and environment for white spruce, one for GAAR and one for DNP. Our goal was to predict where, within our catchment areas, trees suffered a decline in growth versus areas where growth accelerated after the major climate regime shift in 1975 (BARBER et al. 2004). Input parameters for model development (predictors) included characteristics of each tree (age, dbh, tree height, green weight) and environmental variables of the site where the tree grew. Environmental variables were both categorical: aspect, competition factor, stand characteristic (closed canopy, open canopy, outlier etc.), and continuous: elevation, height above valley floor.

We used the "classification tree" module in STATISTICA for model development. "Classification trees" are used to predict membership in classes of categorical dependent variables (in our case "winner" or "loser") on the basis of measured predictor variables.

In essence the program asks a series of hierarchical questions. Each answer leads to a univariate split in the data, in our case separating mostly winners from mostly losers, i.e. all trees older than 75 years are assembled in one group of mostly winners, all younger trees in the other. After each split a new set of questions is tested against the remainder of the data-points to optimize the classification, e.g. if a tree is older than 75 years AND grows on a north-facing slope versus on a south-facing slope. The C&RT-univariate split selection method employs an exhaustive grid search of all possible combinations of univariate splits to compute the classification tree (STATISTICA, help file). Predictive power is optimized by using half of the sample (randomly selected) for model development and the other half for model testing.

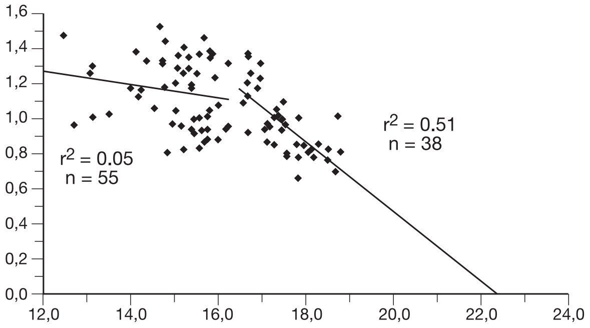

Fig. 2: Temperature threshold controlling negative growth response. Mean ring width index (MRWI) as a measure of growth of all sampled trees older than 50 years with a negative growth response versus Fairbanks mean monthly July temperatures of the year prior to ring formation

Schwellenwert der Temperatur kontrolliert verminderten Wuchs. Mittlerer Wachstumsindex (MRWI) als eine Repräsentation des Wuchses aller Bäume älter als 50 Jahre mit verminderten Wuchs, geplottet gegen mittlere Monatstemperatur des Juli in Fairbanks (nicht des Jahres des Wuchses, sondern ein Jahr davor)

The main advantage of using "classification trees" was that they produce a very adaptable algorithm. Output can be displayed as a "flowchart" with "if – then" questions and the ecological validity can be tested with expert knowledge. In addition "classification trees" are organized hierarchically and use univariate splits, which ecologically can be translated as "thresholds". In each National Park we developed the model first for all trees within that area and then tested that model against each study site within the area.

3.3 Spatial translation of decision-tree model

After model development, we used ARCVIEW to "translate" our simplified schematic model into space. We obtained landcover classification from the National Park Service (60 m resolution). In order to apply the classification results spatially, we used an elevational buffers function to calculate area around streams (our model uses elevation above stream as a base for classification) and the treeline polygon (border of forested area to shrub and/or tundra). The treeline polygon obtained by this procedure was about 50 m lower in elevation in DNP than the highest trees we cored. Therefore, we used the treeline polygon and buffered it 50 m upward to estimate area occupied by these highest communities (winners).

For GAAR we applied our model to the entire park area. In DNP, large areas classified as boreal forest are occupied by black spruce. Since our model was developed on the basis of white spruce, we used only a subsection in the northwest of the park (~25% of park area) to extrapolate our decision-tree model results into space. Boreal forests and treeline forests in the area chosen are dominated by white spruce. In addition we used a 7.2 km wide corridor in DNP with the park road in the center to examine the extent and magnitude of the projected change in the area most heavily visited. Trees in the road corridor are most exclusively white spruce as well.

Table 2: Model classification of winner (W) and loser (L) trees in GAAR, based on comparison between "decision-tree" modeling versus actual growth performance

Modellklassifizierung von Gewinnern (W) und Verlierern (L) in GAAR, basiert auf einem Vergleich zwischen Modell-Output und Realität

		TEST	correct	L misclassified as W	W misclassified as L
GAAR	n	381	260	50	71
	%	100.0	**68.2**	**13.1**	**18.6**
BRNC	n	129	88	28	13
	%	100.0	**68.2**	**21.7**	**10.1**
BRNF	n	86	52	7	27
	%	100.0	**60.5**	**8.1**	**31.4**
BRCL	n	77	59	9	9
	%	100.0	**76.6**	**11.7**	**11.7**
BRHF	n	89	61	6	22
	%	100.0	**68.5**	**6.7**	**24.7**

Table 3: Model classification of winner (W) and loser (L) trees in DNP, based on comparison between "decision-tree" modeling versus actual growth performance

Modellklassifizierung von Gewinnern (W) und Verlierern (L) in DNP, basiert auf einem Vergleich zwischen Modell-Output und Realität

		TEST	correct	L misclassified as W	W misclassified as L
DNP	n	372	269	53	50
	%	100.0	**72.3**	**14.2**	**13.4**
ARRC	n	142	97	25	20
	%	100.0	**68.3**	**17.6**	**14.1**
ARCC	n	33	29	3	1
	%	100.0	**87.9**	**9.1**	**3.0**
ARTL	n	165	125	19	21
	%	100.0	**75.8**	**11.5**	**12.7**

4 Results

4.1 Winners and Losers

Out of 753 trees tested for winner and loser status (both parks), 388 were winners and 365 were losers. In GAAR (n = 381) 57% of tested trees were winners, 43% losers. Winners in GAAR increased in radial growth 26.6% on average between the two test periods, losers decreased 17.3%. In DNP (n = 372) 46% of tested trees were winners, 54% losers. Winners in DNP increased radial growth on average by 28%, losers decreased 27%.

4.2 Decision-tree model and model test

The decision-tree model, using landscape and tree parameters as input, correctly classified between two-thirds and three-fourths winners and losers in both parks (Tab. 2 and 3). Rates of correct classifications were generally higher at DNP (Tab. 3) than at GAAR (Tab. 2). The highest rate of misclassification of winners as losers (31.4%) occurred at the BRNF site in GAAR. The highest misclassification of losers as winners (21.7%) occurred at the BRNC site in GAAR.

The model for GAAR was developed on the basis of four study sites and 378 trees (three trees lacked com-

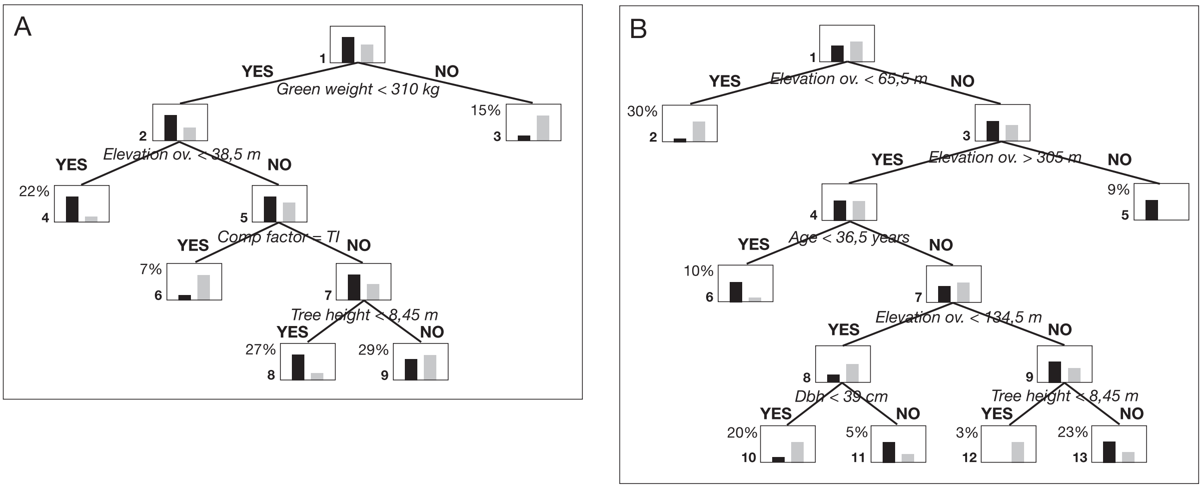

Fig. 3: Decision-tree model for GAAR (A) and DNP (B). Tree and landscape characteristics are used to compute the decision-tree models in each National Park. Black columns represent winners, grey columns loser populations. "Elevation ov." equals the relative altitude of a tree over the creek below, e.g. a low "elevation ov." corresponds to a site on the lower slopes. TI: Tree-Island, dbh: diameter at breast height

Entscheidungsmodell für GAAR (A) und DNP (B). Baum- und Landschaftseigenschaften wurden zur Berechnung des Entscheidungsmodells in jedem Nationalpark herangezogen. Schwarze Säulen kennzeichnen Bäume mit stärkeren Wachstumsraten, graue Säulen Bäume mit verminderten Wachstumsraten. "Elevation ov." bezeichnet die relative Höhe eines Baumes über der Talsohle, z.B. niedrige "elevation ov." bedeutet untere Talhänge. TI: Bauminsel, dbh: Brusthöhendurchmesser

plete site information). The model predicted 68% of class membership correctly and misclassified 13% winners and 19% losers (Tab. 2).

The model for DNP was developed on the basis of three study sites and 306 trees (66 trees lacked complete site characteristics) and was tested against the 372 trees older than 50 years. The model predicted 74% of class membership correctly and misclassified 14% winners and 13% losers (Tab. 3).

In GAAR the decision tree model proceeds in four steps to reach the final level of classification (Fig. 3A), using the following predictors: tree biomass, relative elevation, competition status and tree height. First, all trees above 310 kg (15% of sample) of green weight are categorized as losers (Node 3, for misclassification see Tab. 4). From the remaining trees, all trees growing up to an elevation of about 40 m above the floodplain are classified as winners (Node 4). If trees above the 40 m threshold grow in tree-islands, they are classified as losers (Node 6) and the remainder of trees in our sample (mostly the trees on middle to upper slopes) are classified as winners if they are smaller than 8.45 m in height (Node 8). All residual trees following the last step are classified as losers (Node 9). However, node 9 contains nearly an equal number of winners and losers and is the main contributor to the overall misclassification. In easy terms, these model parameters can be summarized as follows:

Statement 1: Big trees do not benefit from warmer and drier conditions regardless of landscape position.
Statement 2: Trees growing on lower slopes close to the creeks benefit from warming.
Statement 3: Tree-island competition is not beneficial for trees under warming conditions.
Statement 4: Small trees on middle and upper slopes benefit from warmer conditions.

The DNP decision-tree model uses five decision levels (Fig. 3B), with the following predictors: low rela-

Table 4: Misclassification of trees as winners or losers at decision nodes in the GAAR "decision-tree" model

Missklassifikation von Bäumen an jedem Entscheidungsknoten im GAAR Decision-Tree-Modell

Node	winners n	losers n	misclassification rate [%]
3	5	23	18
4	35	7	17
6	2	10	17
8	40	12	23
9	25	30	45

Table 5: Misclassification of trees as winners or losers at decision nodes in the DNP "decision-tree" model

Missklassifikation von Bäumen an jedem Entscheidungsknoten im DNP Decision-Tree-Modell

Node	winners n	losers n	misclassification rate [%]
2	5	42	10
5	13	0	0
6	13	3	19
10	6	24	20
11	5	2	28
12	0	4	0
13	23	12	34

tive elevation, high relative elevation, tree age, mid-elevation position and dbh and height. In this model, all trees growing in the lower belt around the floodplains (lower than 65 m above creek-bed) are classified as losers (Fig. 3B, Node 2; for misclassification see Tab. 5). Trees growing higher than 305 m above the creek-bed, however, are classified as winners (Node 5), and form the highest current treeline communities. The trees growing on the remaining middle slopes are classified as winners if they are younger than 64 years (Node 6). The model also classifies trees as winners if they occur lower than 135 m above the valley floor and have a dbh over 39 cm (Node 11), or are relatively tall trees (> 8.45 m) and occur higher than 135 m above the valley floor (Node 13). This seemingly more complex model can also be summarized in more intuitive terms as follows:

Statement 1: Trees growing on lower slopes do not benefit from a warmer climate.
Statement 2: The highest treeline communities are able to take advantage of warmer conditions.
Statement 3: Young trees on mid-slopes show accelerated growth after the regime shift.
Statement 4: Established, larger trees in existing stands do benefit from warming.

4.3 Ecological translation – projection into space

Since our decision-tree models incorporate both environmental parameters and tree information, such as age or green weight, which is not necessarily related to landscape position, extrapolating these models into space requires substitution of tree-specific parameters by the landscape parameters that are the best proxies for them. We tested each tree-specific predictor for it's relationship to landscape position, but did not find any reliable predictive relationship. As a result, the adaptation of the model we applied in order to identify areas predicted to support winners, losers and mixed populations consisted only of landscape parameters and is thus somewhat limited. For example, in GAAR, the model classified 15% of the trees (with a green weight over 310 kg) as losers. However, green weight as a property of each individual tree is not related to landscape position and could thus not be modeled spatially using landscape parameters. The output of the spatial models can be seen in figure 4 for GAAR and figure 5 for the subsection of DNP.

In GAAR all areas up to 40 m above the main creek or river in a catchment are classified as landscapes currently occupied by winners. These areas total 2,100–2,500 km^2 or 35–40% of the existing boreal forest within the park. We infer that these areas would experience increasing tree growth under a warming climate. The decision-tree model of GAAR also classifies 1) younger and smaller trees located higher than 40 m above a creeks or river as winners, and 2) tree-islands and older and bigger trees in the above 40 m elevation zone as losers. Since these parameters express tree to tree variability, they cannot be modeled using landscape information. Therefore, we consider the zone above the 40 m limit as "mixed", consisting of winners and losers. This mixed zone totals 60–65% or 3,500–4,000 km^2 of the existing boreal forest within the park. We infer that these areas would experience continuous forest cover in a warming climate, but composed of an increasing proportion of winners.

Boreal forest in DNP is a mixture between black and white spruce. Since our land-cover classification did not differentiate between the two forest types, we ran the spatial model only for a subset area likely occupied by white spruce, e.g. areas close to treeline, mountainous terrain (see box in Fig. 1 and 5). All areas up to about 65 m above the main creek or river in a catchment are classified as landscapes currently occupied by losers, which is the opposite response type compared with the similar landscape position in GAAR. These areas total about 383 km^2 or 49% of the existing boreal forest within the area of extrapolation in DNP. We infer that these areas would experience substantial growth decreases under a warming climate, possibly including elimination of white spruce with sufficient warming. The next node in the decision-tree model of DNP classifies all trees higher than 305 m above the creek or river as winners. We infer that these areas, which include the highest current treeline communities, would support increased tree growth, tree establishment and infilling, and possibly treeline advance into alpine tundra under future warming conditions. Infilling and treeline advance during the last few decades of unusual warmth have been reported from other high elevation

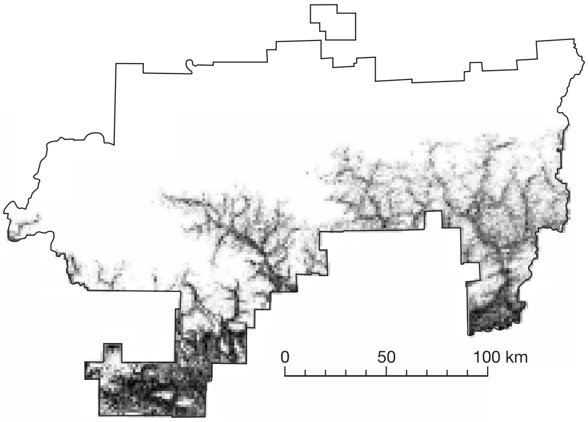

Fig. 4: Effect of further warming on GAAR. The spatial application of the decision-tree model for GAAR projects no major treeline advances. However, within the existing boreal forest (6,241.3 km^2) the model identifies areas currently occupied by winners (black shading). These areas, amounting to 35%–40% of existing forests along the creeks and rivers are projected to increase in tree growth under a warming climate. Grey shaded areas represent mixed populations of winners and losers, which cannot be modeled using only landscape information

Auswirkungen von weiterer Erwärmung auf GAAR. Keine großflächige Baumgrenzverschiebung wird durch die räumliche Anwendung des Entscheidungsmodells projiziert. Innerhalb des borealen Nadelwaldes (6.241,3 km^2) identifiziert das Modell 35%–40% der Fläche als bestanden mit Bäumen, die stärkere Wachstumsraten zeigen (dunkle Schattierung). Diesen Flächen, meistens entlang der Wasserläufe, werden weitere verstärkte Zuwachsraten unter erwärmten Klimabedingungen projiziert. Graue Schattierungen zeigen Mischflächen aus Bäumen mit verminderten und Bäumen mit stärkeren Wachstumsraten, diese können daher nicht auf Grundlage von Landschaftseigenschaften modelliert werden

treeline areas in Alaska (Lloyd a. Fastie 2003). In the decision tree model of DNP, areas between 65 m and 305 m above creeks or rivers (400 km^2) are classified as supporting mixed populations of winners and losers. In these areas very young trees (< 65 years, 10% of sample) are classified as winners similar to GAAR. Well established bigger trees are also classified as winners in the decision-tree model of DNP. However, in the middle elevation zone in DNP shorter trees and smaller diameter trees are classified as losers, suggesting that competition may be a factor in their negative response to warming. As a result we infer that in this mixed population zone warming would be associated with decreasing tree stem density.

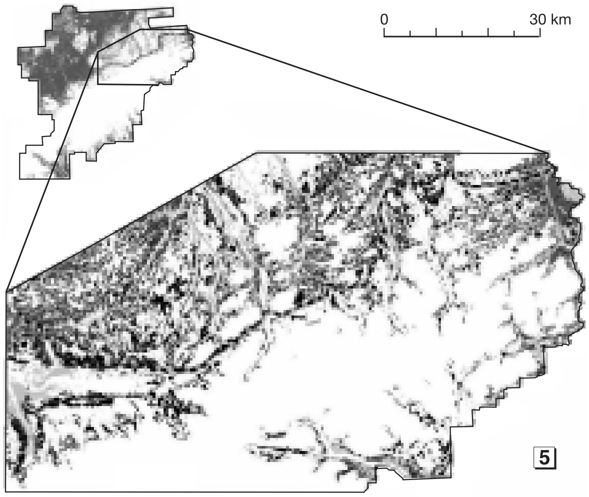

Fig. 5: Effect of further warming on DNP. Total area occupied by boreal forest in the year 2000 in the study area (box) was 784 km^2. Spatial application of the decision-tree model projects treeline advances at higher elevations (black shading) in an area of 801 km^2 (= 102% of existing forest), and less growth/dieback in areas currently occupied by losers (light grey), 384 km^2 (49% of existing forest). Taken together, the forest would expand by about 50% and occupy 1,201 km^2. Dark grey shaded areas represent mixed populations of winners and losers, which cannot be modeled using only landscape information

Auswirkungen von weiterer Erwärmung auf DNP. Gesamtfläche des borealen Nadelwaldes im Jahre 2000 im Untersuchungsgebiet (Kasten) betrug 784 km^2. Räumliche Modellierung projiziert Baumgrenzverschiebungen in den höheren Lagen (dunkle Schattierung) auf einer Fläche von 801 km^2, was 102% der Fläche des heutigen Waldes entspricht. Verminderter Wuchs und eventuelles Absterben werden für 384 km^2 modelliert (49% des existierenden Waldes, graue Schattierung). Addiert man beide Vorgänge würde sich die Waldfläche um ca. 50% vergrößern und am Ende 1.201 km^2 einnehmen. Graue Schattierungen zeigen Mischflächen aus Bäumen mit verminderten und Bäumen mit stärkeren Wachstumsraten, diese können daher nicht auf Grundlage von Landschaftseigenschaften modelliert werden

4.4 Changing environment – projection in time

A high percentage of the trees in our sample and other similar sites in the Alaska Range and Brooks Range show a statistically significant correlation between mean monthly temperatures in Fairbanks and annual radial growth, including both positive and negative correlations (Wilmking et al. 2004). Negative correlations were maximized with the mean monthly temperature of July in the year prior to ring formation.

This negative response is consistent with temperature-induced drought stress as a controlling factor for growth of white spruce in central Alaska (Barber et al. 2000) and at treeline (Jacoby a. D'Arrigo 1995; D'Arrigo et al. 2004). Negative effects of July temperature on treeline white spruce occur only above the threshold of 16°C at the Fairbanks station, which probably translates to a temperature of 11–12°C at treeline sites (Wilmking et al. 2004; D'Arrigo et al. 2004). This temperature function models tree growth equal to zero at about 22 °C at Fairbanks (Fig. 2). Sustained periods of time at or even near July temperatures that produce zero growth are likely to result in the death of white spruce negatively correlated with July temperature in our study area, e.g. through stress related factors such as insects (Hard 1985, 1987) or increase in fire frequency.

During the 20th century, mean monthly July temperatures in Fairbanks reached or exceeded the 16 °C growth reduction threshold in 52 of 93 years (record 1906–1999). Five of the GCMs used in the recent Arctic Climate Impact Assessment (ACIA 2004) project temperatures at Fairbanks above the threshold ranging from 85 out of 99 years (CSM model) to 98 out of 99 (CCC model) in the 21st century. Mean monthly July temperature of the Fairbanks grid-cell modeled by ECHAM, HAD and GFDL reach and/or exceed the 22°C zero growth threshold in the second half of the 21st century. The CCC and CSM models project highest July temperatures of around 20°C during the scenario period.

5 Discussion

5.1 Winners and Losers

Most published literature on treeline studies in the northern-hemisphere focuses on the positive growth response of treeline trees (winner trees) with warming climate (Garfinkel a. Brubaker 1980; D'Arrigo a. Jacoby 1993; Briffa et al. 1998). In our sample, however, negative growth responses of treeline trees with warming (the loser trees) are widespread (48% of trees greater than 50 years old). Temperature-induced drought stress as the major factor controlling tree growth has been reported within the boreal forest (Barber et al. 2000) and at treeline (Jacoby a. D'Arrigo 1995; Wilmking et al. 2004; D'Arrigo et al. 2004; Wilmking a. Juday 2005). Recent warming and a shift around 1975 to the warmest and driest climate regime of the last century (Barber et al. 2004) have intensified the negative growth responses of trees to warming. We report here that large areas of white spruce at or near treeline in two National Parks in Alaska are also showing reduced growth consistent with the drought stress hypothesis.

More trees responded positively to warming in the northern study areas of GAAR (57%) than in DNP (46%). While the average growth increase after 1975 is about similar in both parks, the average rate of growth decrease is higher in DNP. Both of these trends suggest that the northern treeline in GAAR (the colder environment) benefits from warming more than elevational treelines within the boreal forest (in DNP). This is the case, even though precipitation in DNP is actually higher than in GAAR (Hammond a. Yarie 1996) and probably offsets some of the drought stress there.

5.2 Error structure of the decision-tree model

In GAAR, nearly all trees misclassified as winners, which are in fact losers, grow either within south-facing forests in one study site (BRNC), or as small scattered trees on north-facing slopes. Half of the trees misclassified as losers (which are winners) grow on south-facing forest sites. A further 25% of winners misclassified as losers represent scattered trees on north-facing slopes, and large trees growing in floodplains. Since winners and losers are mostly misclassified in the same environments (south facing forests and scattered trees on north-facing slopes) misclassification is partly offset. Site variations (as in BRNC) can play a role in changing the general relationship between tree growth and environment. It is therefore important to employ an extensive sampling design, rather than concentrating on a few sampling locations, in order to control for this spatial variability.

The vast majority of trees in DNP which our model classified as losers but in fact are winners, belong to one of the following groups: 1) south-facing forests or 2) forest in floodplains. Interestingly enough, the trees classified as winners, which are misclassified as losers also belong mostly to one of these categories, leading to two conclusions: First, here again the classification errors partly compensate for each other. Second, trees in these environments can be winners or losers, but those traits are apparently not controlled by any of our predictor variables, and thus might be controlled by other variables we did not measure, or variables on a smaller scale than our investigation, i.e local moisture supply. Alternate explanations of opposite responses of trees in apparently similar environments, such as genetic differences between winners and losers, await further study.

5.3 Projection into space

The spatial application of our decision-tree models in both National Parks projects strongly reduced growth of trees at low elevations in DNP and larger trees in GAAR, possibly eliminating these trees through stress related mortality within the next 100 years. By contrast, at higher elevations in DNP all trees show a growth increase under warmer conditions. Positive growth response in these highest elevation environments is a prerequisite for future treeline advance. Actual treeline advance in the last decades in Alaska (Lloyd a. Fastie 2002, 2003) occurred during a period of climate warming, empirically validating this projection. In GAAR trees at higher elevations only show increased growth with warming if these trees are not hindered by tree to tree competition. Nearly all trees in tree islands show reduced growth after the regime shift to a warmer climate in 1975. Single trees at high elevations in GAAR are mostly winners. Tree to tree competition also seems to be a factor in the mixed mid-elevation zones in both parks where positive and negative responders can grow in close proximity to each other (sometimes < 3 m). In DNP bigger, established trees have a competitive advantage over smaller trees in the mid-elevation zones. We hypothesize that small-scale differences in soil, nutrients, and light can be overcome by trees able to integrate across these differences with larger rooting volumes and crowns. On the other hand, most trees younger than about 60 years in this elevation zone did increase their growth with warmer and drier conditions, suggesting that these trees are utilizing growth resources not recently used by established trees. In GAAR, small trees in the mid-elevation zone are mostly winners (Fig. 3A, Node 8). These inconsistent results lead us to two conclusions: Growth response in these areas is mostly controlled by 1) factors we did not measure (e.g. genetic variability, nutrient availability), or 2) by factors acting on a smaller scale than our investigation. As a result, in both national parks our models show the highest misclassification rates in these mid-elevation zones.

Trees growing close to creeks or rivers (low-elevation slopes and floodplains) show opposite growth responses to temperature in the two National Parks. In GAAR, low-elevation slopes and floodplains are the areas of increased growth with warming climate, whereas in DNP under the same warming conditions trees on such sites show decreasing growth. Floodplains and low-elevation sites in DNP today are locally the most productive sites, supporting closed canopy forest with high stem densities. Their soils are loamy and silty. In GAAR, floodplain sites in our sample areas are one of two types, either young gravelly floodplains supporting widely spaced individual trees, or older floodplains underlain by permafrost, also supporting widely spaced trees. Low elevation sites in GAAR are locally also the most productive, but stem densities are lower than in DNP. In low-elevation and floodplain areas, as in the high-elevation areas, tree to tree competition seems to be an important factor determining growth response under warming climate. Trees not hindered by other trees (as in GAAR floodplains) are able to take advantage of warmer air and soil temperatures with increased growth. The depth of the active layer in permafrost sites is increasing with warming climate and larger rooting volume and new nutrient sources probably benefit the trees. In DNP by contrast, these sites are already fully occupied by established trees and warming probably intensifies existing competition.

Surprisingly, neither tree age (Szeicz a. MacDonald 1994) nor aspect showed any significant relationship with growth response. Age was only used once as a deciding factor in our decision-tree models. Instead, tree weight and dimensions of the tree (dbh, height) seem to play an important role in the climate-tree growth relationship.

5.4 Projection in time

Opposite growth responses of treeline white spruce in Alaska have intensified in the latter part of the 20th century due to climate warming (Wilmking et al. 2004). If this warming continues (as modeled by five GCMs), we expect a further intensification of diverging growth responses of white spruce at treeline in Alaska. Winners will take advantage of warmer conditions and enhance growth, thereby increasing their carbon uptake. Losers will experience further decline in growth and drought stress-related mortality of these trees is likely due to several reasons. 1) Growth rates of zero are associated with the range of temperatures projected by the scenarios for the 21st century; 2) growth rates are averaged over a population, single trees will reach zero growth far earlier; 3) stressed trees are more likely to attract and sustain damage from factors such as insects (Hard 1985, 1987); 4) prolonged growth rates of only 30–40% of historical levels may severely diminish their ability to compete with other plants in the ecosystem for resources.

It is therefore likely that under further warming conditions landscape scale changes in white spruce distribution would take place, i.e. areas of declining growth (lower hillsides in the DNP or tree islands in GAAR) experiencing high rates of tree mortality and even possible elimination of trees, and areas experiencing enhanced growth (treeline areas in DNP and lower hillsides in GAAR) experiencing infilling and higher productivity.

6 *Example: Denali National Park Road*

We chose the road corridor in DNP as an example to illustrate the magnitude, extent and impact of possible advance of treelines and dieback of white spruce. In 2002, DNP was visited by 280,911 recreational visitors (a drop from the 350,000 visitors per year at the end of the 90s). The overwhelming majority of those visitors drove into the park with a shuttle bus. Since the park road is only open about 100 days per year, an average of 2,800 visitors traveled on the 130 km long road each day. Wildlife viewing (e.g. moose, caribou, dall sheep, grizzly bear, wolf, fox etc.) and the view of Mount

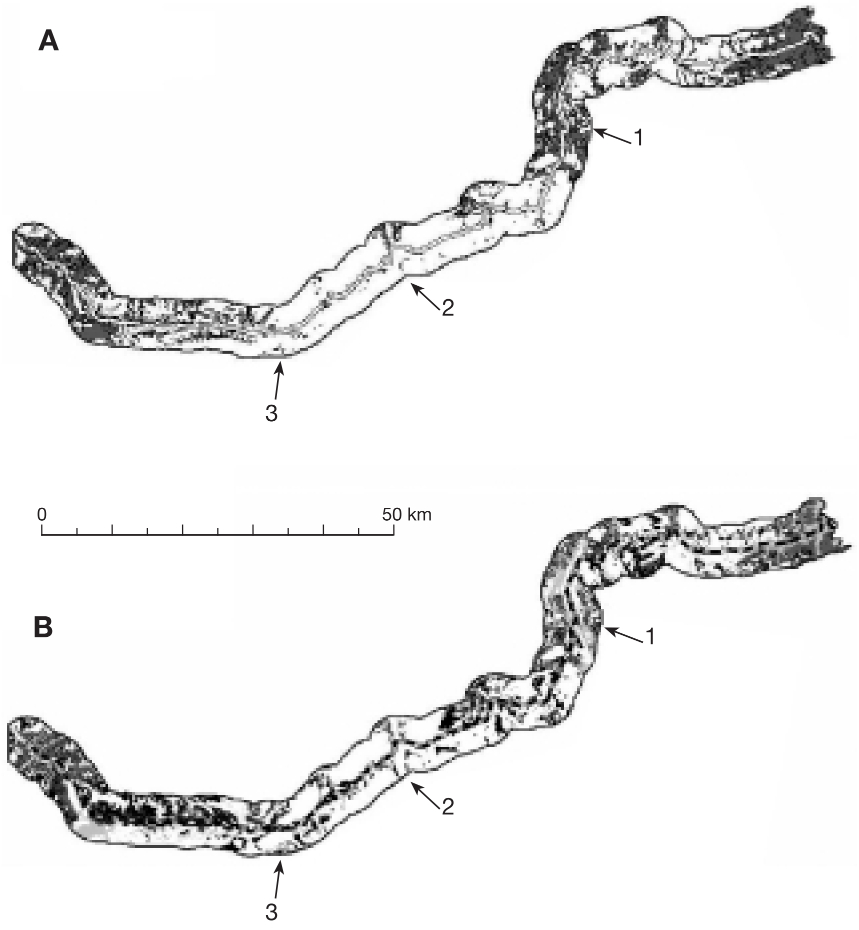

Fig. 6: Vegetation distribution in DNP road corridor today and after 21st century climate warming scenarios. In 2000, 21% of the road corridor (187.0 km^2) was classified as boreal forest (Fig. 6A). The spatial model for the road corridor (Fig. 6B) produces areas of possible forest expansion (black) and dieback (light grey). Forest area would increase to 288.6 km^2 and occupy 32.7% of the road corridor. Note that some forest areas, especially along low lying river corridors might experience forest decline (arrow 1). Some tundra areas (arrows 2 and 3) south of the park road (Fig. 6B), now prime areas of wildlife viewing, could experience increases in tree density (infilling) and treeline advance leading to reductions in scenic views along the road

Vegetationszonenverteilung im DNP-Straßenkorridor heute und am Ende des 21. Jahrhunderts (mit Temperaturerwärmung). Im Jahre 2000 wurden 21% des Straßenkorridors (187,0 km^2) als borealer Nadelwald klassifiziert (A). Das räumliche Modell für den Straßenkorridor (B) zeigt Gebiete mit Waldgrenzverschiebung (dunkle Schattierung) und Wuchsminderung/Absterben (graue Schattierung). Projiziert ist eine Vergrößerung der Waldfläche auf 288,6 km^2 (32,7% des Straßenkorridors). Einige Waldgebiete zeigen im Modell Absterben (Pfeil 1). Einige Tundragebiete (Pfeile 2 und 3) südlich der Strasse, die zurzeit hervorragende Wildtierbeobachtungen ermöglichen, könnten durch Waldgrenzverschiebung und erhöhte Baumdichte nur noch eingeschränkt als Beobachtungsstellen genutzt werden

McKinley are the major attractions of the park. Increased traffic in the last 30 years has apparently had no negative effect on the number of wildlife sightings from the road (Burson et al. 2000) and while moose behavior indicated possible traffic avoidance, this does not hold true for the distribution of grizzly and caribou (Yost a. Wright 2001).

We define the road corridor as an area extending 3.6 km out on either side of the road. In 2000, 21.1% of the road corridor (187.0 km^2) was classified as boreal forest (Fig. 6A, Tab. 6) where the distance in which wildlife can be seen (< 100m from the road) is far smaller than in terrain not forested. The application of our spatial model of tree-growth landscape relationships for the road corridor identifies areas of possible forest expansion and dieback (Fig. 6B). If climate warming occurs similar to that produced by the climate scenarios during the 21st century, based on our model, boreal forest area would increase to 288.6 km^2 and occupy 32.7% of the road corridor (Tab. 6). That is an increase of about 50% over the current forested area. Dieback of trees would occur at low-elevation areas at the park entrance and along major river valleys (about 10% of road corridor), which are now occupied by boreal forest. More important for visitors though, the tundra areas south of the western portion of the park road (see arrows) would experience increases in tree density (infilling) and treeline advance (Fig. 6B). These are the prime areas of wildlife viewing and allow on clear days stunning views of Mount McKinley. Repeating the general vision statement of the DNP goal: "The National Park Service will preserve outstanding opportunities to view wildlife and mountain scenery …" (Denali National Park and Preserve 2003), it will be interesting to see how the National Park Service will address the dichotomy of preserving natural ecosystems and all associated changes and the impact of these changes on its visitors.

Table 6: Aggregate area of spatially predicted actual tree performance under climate warming in the DNP road corridor

Projizierte Flächen für den Straßenkorridor in DNP unter Szenarien der Klimaerwärmung

Road-corridor (RC)	km^2	% of existing forest in RC	% of RC
Total area of RC	883.4		100.0
Existing forest in RC	187.4	100.0	21.2
Potential forest loss	85.3	45.5	9.7
Potential forest gain	186.5	99.5	21.1
Net forest after change	288.6	154.0	32.7

7 *Conclusions*

White spruce populations at and near treeline in Gates of the Arctic National Park and Denali National Park in Alaska include roughly equal numbers of trees that have increased (winners) or decreased (losers) in growth after a major shift in 1975 to a warmer climate. The occurrence of winners and losers was effectively modeled in GAAR and DNP using tree and site characteristics, primarily size of trees, relative elevation and age. The models were different for both National Parks, expressing regional variability.

In summary, if recent warming trends continue, changes in distribution of white spruce forests are within the range of possibility on a regional scale (treeline advance, dieback) and structural changes within existing forest are possible on a medium (landscape) scale (changes in tree density through infilling and dieback). Our results show that changes in growth performance of individual trees due to climate warming are already underway, that further warming would intensify these changes and that they would have landscape-wide consequences.

In a global context, our results indicate that large-scale models of climate-vegetation interaction will have to be coupled with medium-scale topographically based models. As an example, structural changes (dieback, infilling and treeline advance) can happen in an area smaller than 4 km^2 which might be within the extent of one grid-cell in global vegetation models. Albedo as well as carbon uptake or release-potential are directly linked to these structural changes and therefore cannot be captured using only large-scale models. Spatially explicit medium-scale models, however, can capture this variability so that a combination of large-scale and medium-scale models will greatly increase the predictive power of such approaches.

8 *Acknowledgements*

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