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Variability, contingency and rapid change in recent subarctic alpine tree line dynamics

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Summary

1 Boundaries between forest and tundra ecosystems, tree lines, are expected to advance in altitude and latitude in response to climate warming. However, varied responses to 20th century warming suggest that in addition to temperature, tree line dynamics are mediated by species-specific traits and environmental conditions at landscape and local scales.

2 We examined recent tree line dynamics at six topographically different, but climatically similar, sites in south-west Yukon, Canada. Dendroecological techniques were used to reconstruct changes in density of the dominant tree species, white spruce (*Picea glauca*), and to construct static age distributions of willow (*Salix* spp.), one of two dominant shrub genera. Data were analysed to identify periods and rates of establishment and mortality and to relate these to past climate.

3 Tree line elevation and stand density increased significantly during the early to mid 20th century. However, this change was not uniform across sites. Spruce advanced rapidly on south-facing slopes and tree line rose 65–85 m in elevation. Tree line did not advance on north-facing slopes, but stand density increased 40–65%. Differences observed between aspects were due primarily to the differential presence of permafrost. Additional variability among sites was related to slope and vegetation type. Results were less conclusive for willow, but evidence for an advance was found at two sites.

4 Increases in stand density were strongly correlated with summer temperatures. The period of rapid change coincided with a 30-year period of above average temperatures, beginning in 1920. The highest correlations were obtained using a forward average of 30–50 years, supporting the hypothesis that tree line dynamics are controlled more by conditions influencing recruitment than by establishment alone.

5 The changes observed at several sites are suggestive of a threshold response and challenge the notion that tree lines respond gradually to climate warming. Overall, the results provide further evidence to support the idea that the pattern and timing of change is contingent on local, landscape, and regional-scale factors, as well as species' biology.

Key-words: climate change, dendroecology, ecotones, forest-tundra, non-linearity, *Picea glauca*, *Salix glauca*, stand dynamics, timberline, Yukon

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Introduction

Recent evidence supports the prediction that climate warming and subsequent effects will be greatest in Arctic and subarctic regions (ACIA 2004; Hinzman *et al.* 2005). Impacts in mountainous areas are also expected to be marked, although perhaps more complex because of the climatic diversity resulting from topographic variation (Beniston 2003; Huber *et al.* 2005). The potential ecological effects of climate change in these biomes have been the subject of many studies. One of the more consistent predictions is that the boundary between forest and tundra zones, hereafter referred to as 'tree line', will undergo a significant change in structure and position (Grace *et al.* 2002). The rationale for this prediction extends from the relationship between thermal regime and the position of tree line (Jobbágy &

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Jackson 2000; Körner & Paulsen 2004) and the critical role that temperature plays in controlling the reproduction, establishment and growth of trees in this environment (see Tranquillini 1979; Körner 1998). Thus, tree lines are expected to advance as temperature continues to warm, and there is abundant evidence of tree lines at higher altitudes and latitudes during warmer periods of the mid-Holocene to support this (e.g. MacDonald *et al*. 2000; Payette *et al*. 2002).

Numerous studies have investigated tree line responses to climate change over the past 150 years. In some regions, trees have invaded tundra, extending the altitudinal or latitudinal limit of tree species (e.g. Suarez *et al*. 1999; Kullman 2002; Lloyd & Fastie 2003). In other areas, a shift from stunted, low-growing individuals (i.e. krummholz) to upright growth forms (i.e. trees) has been observed (e.g. Lescop-Sinclair & Payette 1995). Other studies have observed an increase in stand density across the forest-tundra ecotone but have not observed any consequential extension of the upper limit (e.g. Szeicz & MacDonald 1995a; MacDonald *et al*. 1998; Klasner & Fagre 2002). There have been no significant changes in some areas (e.g. Butler *et al*. 1994; Cullen *et al*. 2001; Cuevas 2002) and in other areas tree line occupies a position thought to be a relic of past climatic conditions (e.g. Hansen-Bristow & Ives 1984). This variability is mediated by species-specific traits and environmental conditions at multiple scales (Holtmeier & Broll 2005). Additional studies, particularly those attempting to identify these mediating factors, are therefore required to improve our understanding of climate-tree line relationships and are critical for accurate forecasts of landscape change.

Tree lines in subarctic mountains exhibit characteristics typical of both alpine and arctic tree lines. Low solar angles combine with topographic variability to create a diverse array of ecotonal environments within relatively short horizontal distances. South-west Yukon is particularly useful for examining tree line dynamics in this environment. The region has experienced a significant warming trend since records began (Zhang *et al*. 2000) and some of the highest deviations from normal temperature of any region in Canada during the past decade (MSC 2005). Models of future climate change predict that these trends will continue (Laprise *et al*. 2003). Studies of past tree line dynamics in this region should be useful in forecasting tree line response to the present and anticipated future, warming trend.

The objectives of this investigation were to: (i) identify periods and rates of establishment and mortality of woody vegetation across the forest-tundra ecotone at several topographically different sites in south-west Yukon; (ii) interpret these data in terms of structural and elevational change of the ecotone at each site; (iii) explore relationships between these changes and climate; and (iv) examine and identify the causes of variability between sites. We used dendrochronological techniques to obtain data relevant to the dominant tree species, white spruce (*Picea glauca* (Moench) Voss), but also examined trends in willow (*Salix* spp.), which, along with birch (*Betula* spp.), is one of two dominant shrub genera. Tall shrubs often form a key structural component of forest-tundra ecotones, play critical roles in nutrient cycling in these systems and exert significant influence on community composition (Anthelme *et al*. 2003). Recent shrub expansion has been documented in some arctic and alpine areas and continued expansion is expected to have significant effects on ecosystem function (Sturm *et al*. 2001). Despite this, few studies have examined shrub dynamics in a forest-tundra environment.

Materials and methods

STUDY AREA

We conducted this study in the northern section of the Kluane Ranges of the St Elias Mountains (Fig. 1). This area was chosen because the forest-tundra ecotone occurs on a wide range of grades and aspects, allowing for an examination of the influence of terrain characteristics on tree line dynamics without the confounding effect of different climatic regimes. In addition, large natural disturbances such as fire, insect infestations, slope failure and avalanches are relatively infrequent at tree line in this area. Population changes observed in stand reconstructions are therefore more likely to be a response to climatic change than to other causes.

The ecotone generally extends from 1200 to 1400 m elevation. Spruce forests thin with increasing altitude, and an open canopy prevails at the lower end of the ecotone (the 'open-forest' zone). By 1300 m, the canopy is discontinuous and the crowns of individual trees generally do not overlap (the 'woodland' zone) (Fig. 2). Only occasional spruce are found above 1400 m and these are typically short, krummholz-type growth forms. Aspect plays an important role in ecotone structure and composition, with tree line typically 50–150 m higher on drier south-facing slopes than on the more mesic north-facing slopes. Deciduous shrubs span the entire length of the ecotone. Dwarf birch (*Betula glandulosa* Michx.) and grey-leaf willow (*Salix glauca* L.) are the two dominant species, frequently forming a dense layer over 1 m high (Birks 1977).

FIELD METHODS

Spruce and willows were sampled from six sites during July 2001 and 2002 (Fig. 1). We stratified sampling with the primary objective of incorporating the differences related to aspect. Sites were divided between north- and south-facing slopes. These were further subdivided into gentle, moderate and steep grades to facilitate capture of any variation related to inclination. All locations were identified *a priori* using a digital elevation model. We established three sampling points along an altitudinal transect at each site. The lowermost

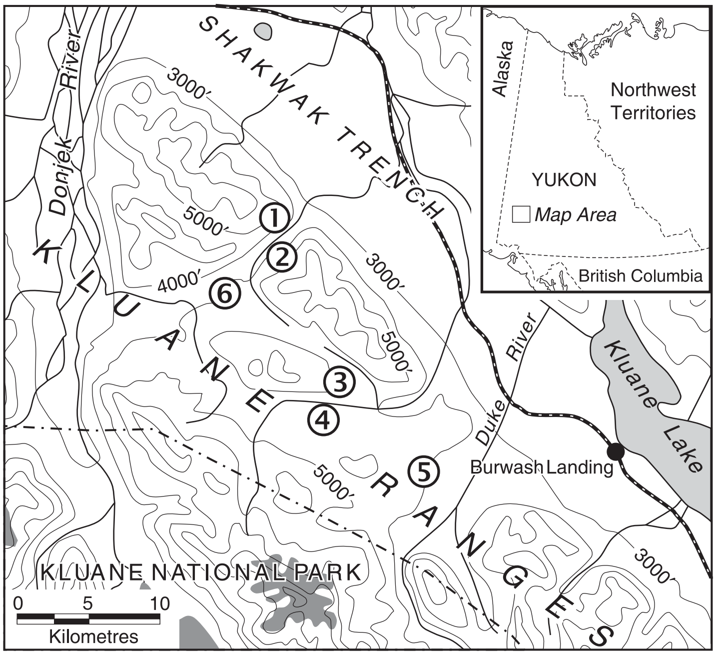

Fig. 1 Location of the south-west Yukon study area (inset) and the six sampling sites in the northern section of the Kluane Ranges, Saint Elias Mountains. Site numbers correspond to the sampling transects described in the text. Contour interval 1000 feet (305 m).

Fig. 2 The forest-tundra ecotone on a steep, south-facing slope. Labels represent the shrubland (a), woodland (b), and open-forest (c) zones. The line dividing forest from woodland is referred to as the timberline and the line dividing woodland and shrubland is referred to as the tree line. Scattered spruce are present in the shrubland zone but are generally stunted and in a krummholz-type growth form.

point (C) was located near the upper edge of open-forest. The middle point (B) was located near the upper edge of the woodland. The uppermost point (A) was located in the shrubland. The difference in elevation between transect points was approximately equal to the difference between tree line and timberline elevation at each site (see Fig. 2). Circular sampling plots were established at each point using the nearest individual method (Kent & Coker 1992). Plot areas differed with the objective of including the 50 individuals nearest the sampling point.

Spruce was sampled at points B and C on each transect. Low densities in the shrubland zone precluded sampling at point A. The height and diameter of each individual was measured. Vegetative clones and standing dead trees were also sampled. Individuals were considered clones if a vegetative connection existed with another stem (Szeicz & MacDonald 1995a). Stems were either sectioned (*n* = 645) or cored (*n* = 123) as close to the root crown as possible. Intact samples could not be obtained from two dead individuals due to severe rot. Only individuals taller than 0.5 m were included in sampling. Shorter individuals were classified as seedlings and were counted but not sectioned.

Willows were measured and sampled at all three points on each transect. As for spruce, willow plots included the 50 genets closest to the sampling point. The distinction between individual genets was sometimes unclear in areas of high stem density and partial excavation of roots was used to help differentiate individuals in these instances. The largest ramet from each genet was sectioned, based on the assumption that it was among the oldest of all living ramets and its age would provide a minimum year of establishment. Sections were obtained at ground level if the plant was growing directly in soil, or below adventitious roots when growing in moss. Presence or absence of dead stems on each genet was noted. Individuals less than 25 cm tall were not sampled. This size class was extremely abundant and its inclusion would have come at the exclusion of older age classes, yielding virtually no information related to the establishment history of willow in a given zone. All shrub-forming species were included in sampling, though more than 90% were *Salix glauca*.

LABORATORY METHODS

Spruce samples were air-dried and sanded to a high polish. Annual rings were counted and measured using one of two techniques. Samples with ring boundaries easily distinguishable to the naked eye ($n = 283$) were dated using a WinDendro digital image measurement system (Regent Instruments Inc., Quebec, QC, Canada). Remaining samples were dated using a stereomicroscope and Velmex sliding stage micrometer with digital encoder (Velmex Inc., Bloomfield, New York). Samples were cross-dated with the aid of CDendro (Cybis Elektronik & Data, Saltsjöbaden, Sweden) and COFECHA (Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona, USA) software programs.

Twenty-three spruce could not be completely aged due to rotten piths. These came from large, older trees and elimination of these samples from analysis would have skewed data towards younger age structures. We therefore estimated the establishment date of these individuals using age-diameter regressions constructed from other individuals sampled at the same site. Estimated ages ranged from 10 to 131 years ($\bar{x} = 49$) greater than the total number of intact rings in the samples. None of the estimates yielded establishment dates earlier than the oldest intact sample from each plot.

Two adjustments were applied to inner ring dates after cross-dating. First, in instances where coring missed the pith, the number of rings to the pith was estimated geometrically in WinDendro. Secondly, the number of years for trees to reach coring height was estimated and subtracted from inner ring dates of core samples. Values of 2.5 cm year^{-1} and 2.0 cm year^{-1} for individuals on south and north-facing slopes, respectively, were used (Danby & Hik 2007). The error introduced by these two adjustments is minimal as only 24 cores had missing ring estimates greater than 10, and 90% of all cores were obtained within 30 cm of ground surface.

Outer ring dates of dead spruce were adjusted to account for loss due to weathering. Cross-dating indicated that all individuals with mortality after 1950 had at least some trace of bark. For all other individuals ($n = 41$), we used an adjustment based on an estimated weathering rate of one ring per decade (Szeicz & MacDonald 1995a). While there is no definitive way of assessing the accuracy of this adjustment, it had little effect on the overall distribution of mortality events because of the 10-year age classes used in the analysis (see below).

Willow sections were air-dried and sanded, but annual rings proved difficult to discern under the stereomicroscope. As such, stems were sectioned to 25 µm using a sledge microtome. Sections were suspended in water and examined under the stereomicroscope using a transmitted light source. Annual rings were counted but not measured. Visual cross-dating was carried out using iteratively identified pointer years. No age adjustments were necessary as all willows were sectioned at soil surface.

DATA ANALYSIS

Spruce and willow characteristics measured at the plot and individual level were analysed using nested mixed-model ANOVAS to compare differences between aspect and zone. Stem data for willow and spruce required log transformation to achieve normality and homoscedasticity. All statistical analyses were carried out using SPSS 12.0.2 (SPSS Inc., Chicago, Illinois, USA).

Two general approaches were used to examine spruce age data. First, age-structures of living trees were constructed by grouping data into decadal age-class frequency distributions. Comparison of open-forest and woodland age distributions was used to evaluate whether tree line advanced or remained stable. Three statistical tests were used: (i) age distributions were compared using a Kolmogorov-Smirnov test; (ii) median age was compared using a Mann–Whitney *U*-test; and (iii) mean age of the five oldest living individuals was compared using a Mann–Whitney *U*-test.

The second approach was based on reconstruction of stand density over time, a more dynamic approach that incorporates data from dead individuals. A slow but steady rate of increase would be expected as individuals die and decompose. Significant deviation from a steady increase would be indicative of a sudden change in recruitment (Lloyd & Fastie 2003). In contrast to the static age distributions, density reconstructions excluded the sapling size class (i.e. 0.5–1.3 m) to avoid the potentially more rapid decomposition of dead individuals in this size class. We determined the decade in which a population density of 50 trees ha^{-1}, the approximate density of adult spruce at tree line, was attained and a Wilcoxon signed ranks test was used to compare the open-forest and woodland zones.

Pearson correlation analysis was used to examine relationships between regional and synoptic climate and spruce density at tree line. Changes in the density of genets during each decade were quantified and correlated with: (i) average June–July temperature for north-western Canada (Szeicz & MacDonald 1995b); (ii) summer-weighted Arctic temperature anomalies (Overpeck *et al.* 1997); (iii) June–August Palmer drought severity index (PDSI) for south-west Yukon (Cook *et al.* 2004); and (iv) annual Pacific Decadal Oscillation (PDO) (D'Arrigo *et al.* 2001). Successful recruitment may be related to climate beyond a forward window of 10 years, so changes in density were also compared with averages over 20, 30, 40 and 50-year periods (Szeicz & MacDonald 1995a).

Age structures of the 18 willow plots were derived by grouping data into 5-year age-class frequency distributions. We compared age structures with distributions predicted by a negative exponential function and a power function (see Balogh & Grigal 1988). Deviations are probably indicative of a change in the pattern of recruitment and/or survival during a given time period (Hett & Loucks 1976). Regression coefficients obtained when fitting the models to the data were used

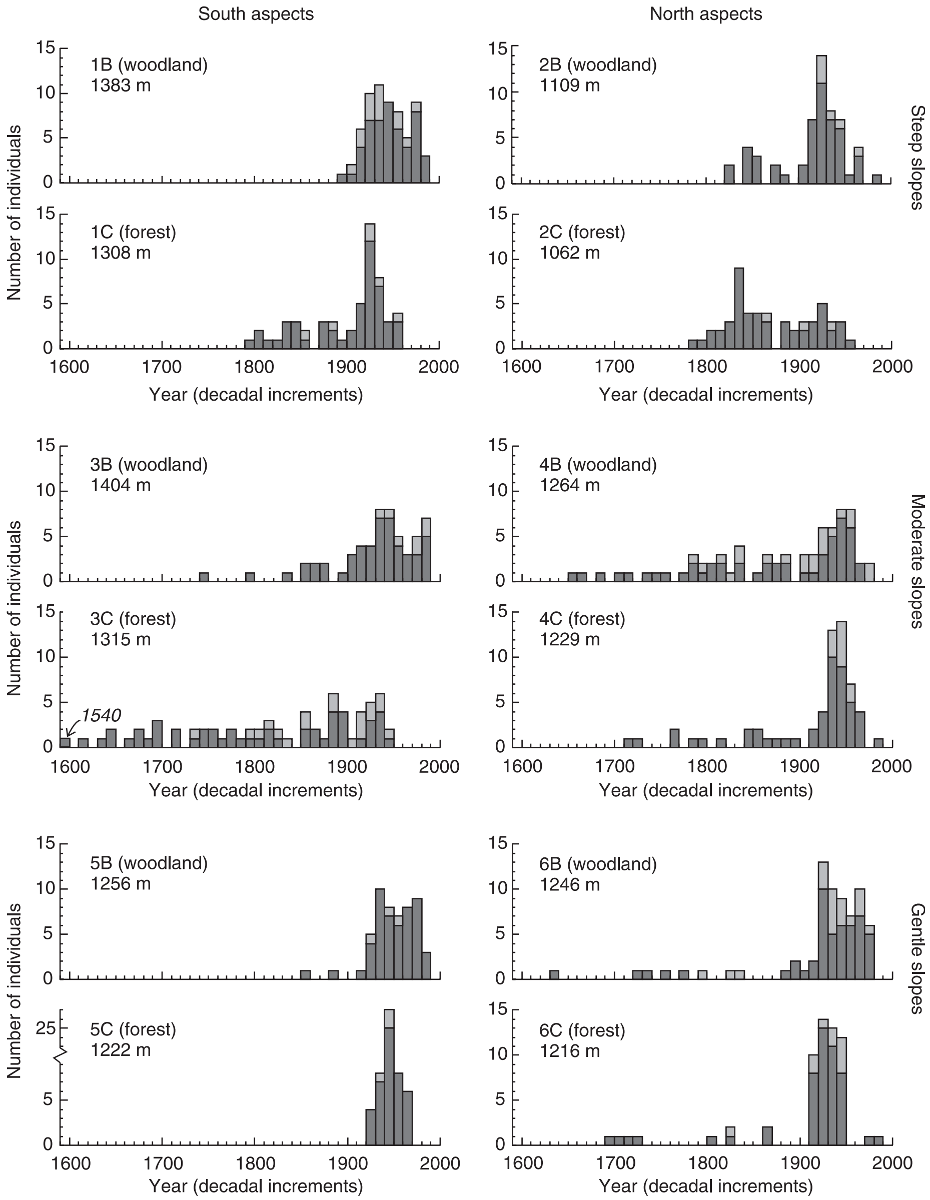

Fig. 3 Age distribution of living individuals in spruce plots, divided into 10-year classes. Darker bars are for individuals of suspected seed origin, lighter bars are for confirmed vegetative origin. Note *y*-axis scale break for 5c.

to identify such deviations, and regression residuals indicated when they occurred. Standardized Z-scores were calculated to facilitate comparison of residuals between plots (see Bégin & Payette 1991). As sampling did not include individual stems shorter than 25 cm, the 1990–95 and 1995–2000 age classes are probably under-represented in the data and only individuals dated earlier than 1990 were included in the analysis.

Results

SPRUCE CHARACTERISTICS AND AGE STRUCTURES

Spruce diameter and height were significantly greater on south aspects ($F_{1,6.3} = 37.25$, $P = 0.001$; $F_{1,6.0} = 33.11$, $P = 0.001$, respectively), and in the open forest ($F_{1,6.3} = 23.67$, $P = 0.002$; $F_{1,6.0} = 20.21$, $P = 0.004$, respectively). Stem density was more than twice as great on north aspects and in the open forest (see Table S1 in Supplementary Material). North-facing slopes had significantly higher densities of seedlings ($F_{1,8} = 12.2$, $P = 0.008$) and standing dead individuals ($F_{1,8} = 10.2$, $P = 0.013$), but there were no significant differences between woodland and open-forest. There was a tendency for higher vegetative regeneration in the open-forest ($F_{1,8} = 5.0$, $P = 0.055$) and on north-facing slopes ($F_{1,8} = 7.6$, $P = 0.025$).

Stands on north-facing slopes were generally older than those on south-facing slopes and trees in woodland plots were generally younger than those in open-forest plots (Fig. 3). The age of the oldest individuals in each plot was significantly greater on north-facing slopes (*t*-test: $t_{58} = -3.2$, $P = 0.002$). A significantly

Table 1 Results of age distribution statistical comparisons. Values represent *P*-values generated by each test in comparing woodland (b-plots) with open-forest (c-plots) age characteristics. Bold text indicates comparisons where the null hypothesis was not rejected (i.e. not statistically different)

Comparison	Age class distribution (K-S test)	Median age (M-W test)	Establishment date (M-W test)
1b × 1c	$Z = 2.40$; $P < 0.001$	$Z = -5.63$; $P < 0.001$	$Z = -2.65$; $P = 0.008$
2b × 2c	$Z = 2.30$; $P < 0.001$	$Z = -4.31$; $P < 0.001$	$Z = -2.66$; $P = 0.008$
3b × 3c	$Z = 3.10$; $P < 0.001$	$Z = -6.52$; $P < 0.001$	$Z = -2.62$; $P = 0.009$
4b × 4c	**$Z = 1.20$; $P = 0.112$**	$Z = -2.06$; $P = 0.040$	$Z = -2.20$; $P = 0.028$
5b × 5c	$Z = 1.60$; $P = 0.012$	**$Z = -1.52$; $P = 0.129$**	$Z = -2.00$; $P = 0.045$
6b × 6c	$Z = 1.70$; $P = 0.006$	$Z = -2.62$; $P = 0.009$	**$Z = -0.63$; $P = 0.530$**

greater proportion of individuals dated to recent decades (i.e. 1960–90) in the woodland than in the open-forest at each site (paired *t*-test: $t_5 = -3.7$, $P = 0.014$). The more recent and contracted timing of recruitment differentiates woodland from open-forest at sites 1, 2 and 3. Differences at sites 4, 5 and 6 were related more to stand structure (i.e. density or tree size) (Table 1).

Many plots exhibited a considerable recruitment pulse during the second quarter of the 20th century. This is most evident in the open-forest and woodland at sites 1, 5 and 6, but is also evident in the woodland at sites 2 and 3 and the open-forest at site 4 (Fig. 3). For instance, at site 1, 46% of all woodland and 45% of all open-forest spruce established during the period from 1920 to 1950. Distinct periods of mortality are also evident, though synchrony between sites was not pronounced (Fig. 4).

The threshold of 50 stems ha^{-1} was reached significantly earlier in open-forest than in woodland plots (Wilcoxon signed ranks test, $Z = -2.03$, $P = 0.042$) (Fig. 5). Tree density in open-forest at sites 1, 4 and 6 nearly doubled as a result of the 1920–50 cohort. Density in the north-facing woodland plots 2B and 6B also doubled and density in the south-facing woodland plots 1B and 3B nearly tripled. Site 5 warrants special attention, as the changes observed in both the open-forest and woodland plots are exceptional. Apart from two individuals, all trees sampled at this site established after 1910.

SPRUCE RECRUITMENT-CLIMATE RELATIONSHIPS

Significant positive correlations between changes in stand density and June–July temperature reconstructions and summer temperature anomalies were found at all sites except site 2 (Table 2). On south aspects these correlations were generally present only in the woodland zone. On north aspects there were no consistent patterns with respect to elevation. No one single window of temperature averaging consistently performed best, though 50-year and 30-year forward means commonly yielded the highest correlations. There were few significant correlations with reconstructions of PDO or PDSI, and these did not exhibit trends with respect to site, aspect or elevation.

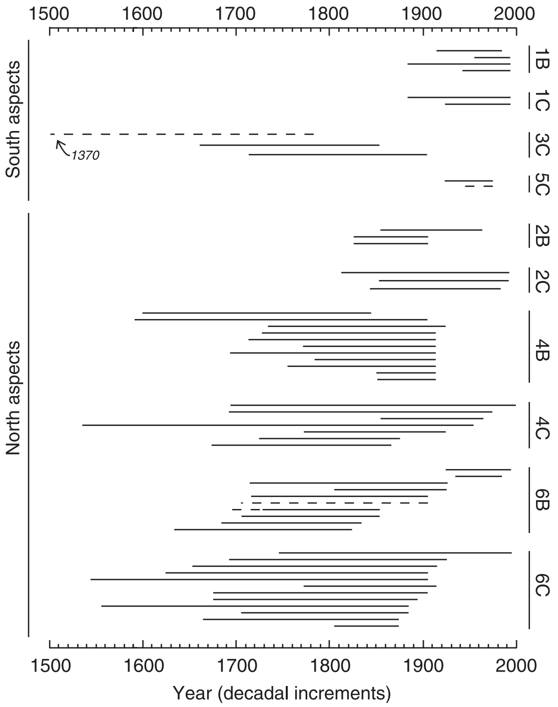

Fig. 4 Ages of dead stems in each sampling plot. Solid horizontal lines represent life spans of individual trees. Dashed horizontal lines are indicative of uncertainty in dating due to rotten piths, short ring-width series, or non-overlapping ring-width series. No dead individuals were located in plots 3b or 5b.

WILLOW CHARACTERISTICS AND AGE STRUCTURES

Density of willow genets increased with elevation ($F_{1,12} = 6.5$, $P = 0.012$). There were no differences in density related to aspect, though field observations indicate that genets on south-facing slopes had a higher number of stems per individual. Willows were taller on south-facing slopes ($F_{1,12} = 6.43$, $P = 0.026$) but there was no significant difference with elevation ($F_{1,12} = 0.314$, $P = 0.737$). Average diameter did not vary significantly with zone or aspect. However, maximum values decreased with elevation, and were greater on south-facing slopes (Table S2). Shrubland plots were typically the youngest in terms of maximum

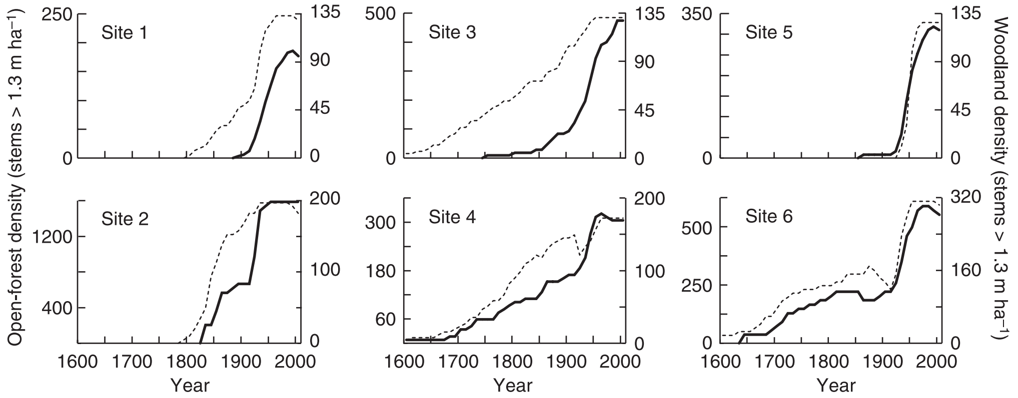

Fig. 5 Spruce density reconstructions for individuals ≥ 1.30 m, year 1600 to 2000. Data points represent density in the first year of a given decade based on changes in recruitment and mortality during the preceding decade. Solid lines correspond to woodland density at each site, and are plotted against the right *y*-axis. Dotted lines correspond to open-forest density and are plotted against the left *y*-axis. Top row corresponds to south aspects, bottom row to north aspects.

Table 2 Correlations between changes in stand density and reconstructed climate from 1800 to 1980. Cell values are Pearson correlation coefficients with proportional change in density. Values are followed by the length of forward average (in years) yielding the best correlation for each variable. Column variables: (A) temperature (Szeicz & MacDonald 1995b); (B) temperature (Overpeck *et al.* 1997); (C) PDO (D'Arrigo *et al.* 2001); (D) drought (Cook *et al.* 2004). Only values associated with $P \leq 0.10$ are shown; $P \leq 0.05$ for bold values, $P \leq 0.01$ for asterisked values. Sample size (*n*) varies with the age of the stand at each site. W = woodland, F = open forest

			Temperature		PDO	PDSI	
Aspect	Site	Zone	A	B	C	D	*n*
South	1	W	**0.777* (50 year)**	**0.872* (30 years)**	–	–	10
		F	–	0.440 (50 years)	**0.592* (20 years)**	–	18
	3	W	**0.762* (50 year)**	**0.860* (40 years)**	**0.493 (10 years)**	–	18
		F	–	–	–	0.435 (50 years)	18
	5	W	**0.901* (50 years)**	**0.867* (10 years)**	–	–0.581 (50 years)	13
		F	–	**0.843 (30 years)**	–	**–0.976* (20 years)**	6
North	2	W	–	0.433 (40 years)	**0.557 (20 years)**	–	16
		F	**–0.612* (10 years)**	**–0.514 (20 years)**	0.431 (30 years)	**0.524 (50 years)**	18
	4	W	0.425 (40 years)	**0.599* (30 years)**	–	–	18
		F	**0.568 (50 years)**	**0.693* (30 years)**	0.429 (10 years)	–	18
	6	W	**0.798* (50 years)**	**0.866* (30 years)**	–	–0.426 (50 years)	18
		F	–	**0.610* (40 years)**	**0.539 (30 years)**	–	18

ages (Fig. 6). No similar trends were evident with respect to mean age.

The negative exponential function modelled willow age distributions significantly better than the power function (paired *t*-test: $t_{17} = 6.77$, $P < 0.001$). Model agreement was generally high, with r^2 values averaging 0.71 (Fig. 6). Shrubland, woodland and open-forest populations were served equally well by the model. Populations on south-facing slopes exhibited better fit than those on north-facing slopes, although this was influenced heavily by low r^2 values at site 2 where irregular or random age distributions were exhibited.

Standardized regression residuals were pooled in several ways to identify common and/or divergent patterns in population dynamics. Pooling of residuals from all 18 plots yielded no definite trends. When examined on a site-by-site basis, there was little agreement between plots on any of the three south-facing slopes. Plots on north-facing slopes were in greater agreement, with residual curves from site 6 overlapping remarkably well. Examination of residuals on an elevation basis yielded no regionally common signal when all six transects were considered together. However, a common positive deviation from model predictions followed by a strongly negative deviation was evident at all three elevations on north-facing slopes during the 1980s.

Discussion

SPRUCE POPULATION DYNAMICS

The results indicate that the forest-tundra ecotone advanced rapidly or underwent a significant increase in density during the 20th century. However, change was neither ubiquitous nor uniform. Each south-facing slope experienced a rapid advance in white spruce

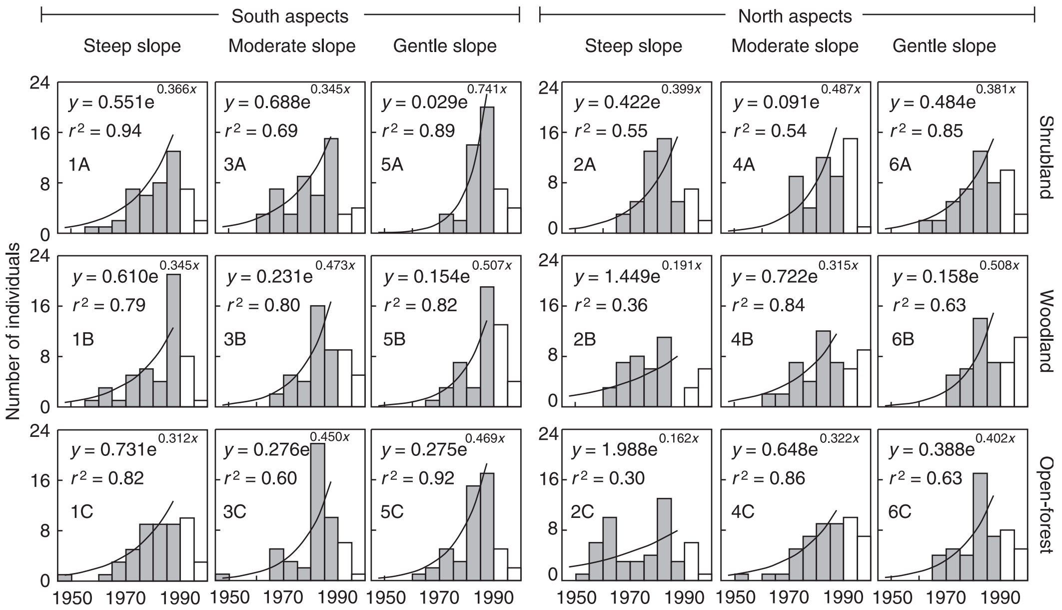

Fig. 6 Age distribution of willow ramets sampled within each plot, grouped into 5-year age classes (all vertical bars). Negative exponential models were fitted to each distribution (equations and curves). Individuals established after 1990 (open bars) were not used in model fitting (see methods section). Regression coefficients provide a measure of fit between model and data.

distribution during the early to mid 20th century. A minimum 80% of all spruce in woodland plots established after 1900. Dynamics in the open-forest differed between the three sites. Data from site 3 indicate a rather stable, self-replacing open-forest stand. Site 1 experienced a slow colonization of spruce during the 19th century followed by a rapid increase in density in the early to mid 20th century. Evidence from site 5 suggests that few spruce were present prior to 1920.

North-facing slopes experienced very different and more variable change. Instead of an advance in tree-forming spruce, plots from these sites exhibited increased population density. Spruce older than 350 years were found in both zones at sites 4 and 6, demonstrating a long history of establishment. Data from site 6 indicate an infilling in both the woodland and open-forest during the early to mid 20th century. At site 4 a less extensive infilling is evident in the open-forest, but not woodland. Site 2 did not have as long an establishment history. Both the open-forest and woodland date to approximately 1800. But while spruce dynamics in the open-forest have been stable since the mid 19th century, the woodland zone experienced the rapid infilling observed at the other sites.

Trends in establishment and mortality related to slope inclination were far less evident. The one noteworthy trend was related to gentle slopes (sites 5 and 6) where both the woodland and open-forest plots had very similar age structures. Additionally, the rates of change in stem density in the woodland and open-forest at the two sites were nearly identical over the past four centuries.

Differences observed between aspects are related to the differential occurrence of permafrost. Random shallow test pits (< 60 cm) confirmed the presence of permafrost across the tree line ecotone on north aspects but not on south aspects. Suarez *et al*. (1999) also found differences related to permafrost in northwestern Alaska where tree line advance was observed on all sites except those with a shallow active layer. Lescop-Sinclair & Payette (1995) demonstrated an advance of the black spruce (*Picea mariana*) tree line in the extensive discontinuous permafrost of northern Quebec not by establishment of new individuals but by changing growth form of pre-established individuals. Individuals in the woodland zone of our study area were present at low densities on north aspects prior to 1900, and it is possible that they underwent a similar change. However, without stem analysis of these older individuals it is impossible to evaluate this possibility.

The changes observed at each site result from the nearly ubiquitous recruitment pulse between 1920 and 1950. Recruitment continued at some of the sites, specifically south-facing woodland areas and the gently sloping north-facing woodland plot, where a significantly greater proportion of individuals date to recent decades (i.e. 1960–90). This is indicative of more recent infilling of these stands. Recruitment rates subsided at other sites after 1950, despite continuation of recruitment at sites with lower densities, suggesting that these stands attained at least a temporary equilibrium or upper density threshold (but see Discussion below).

Vegetative regeneration typically increases with altitude as seed production declines and damage that triggers vegetative regeneration increases (Holtmeier 2003). We did not observe such a difference, and attribute this to the fact that many of the vegetative stems in the open-forest date to when these trees occupied a higher position in the ecotone. The rapid expansion of trees and subsequent woodland recruitment indicates that sexual reproduction has not been problematic in this zone and that the population has not had to rely on vegetative regeneration. The greater propensity for vegetative regeneration on north-facing slopes is explained by the widespread presence of a thick moss layer on these slopes and the greater capacity for the development of adventitious roots in this environment.

WILLOW POPULATION DYNAMICS

The fit of the negative exponential model with willow population data supports the view that *Salix*, at least in tall shrub form, has a constant probability of death throughout its life span and that its abundance is controlled by regeneration, not mortality (Balogh & Grigal 1988). Age structures at site 2, particularly in the open-forest, are a notable exception and may be related to the lower elevation or higher density of spruce.

Previous studies of boreal shrub dynamics have illustrated renewal synchrony among populations in response to events such as herbivore dynamics (Ericson *et al*. 1992) and periodic disturbance (Bégin & Payette 1991). The general agreement in model residuals between populations on north-facing slopes is suggestive of such synchrony, but the mechanism is unknown. The lack of residual agreement between populations on south aspects suggests that the mechanism is either absent or unimportant on these slopes.

Interpretation of shrub advance is limited by the relatively short life span of willow stems when compared with the possible, but largely undeterminable, age of the parent genet. Nevertheless, a recent upslope expansion of shrubs should be indicated by the absence of older individuals in plots from the shrubland zone, a disproportionately large number of individuals in the oldest age class (due to a rapid change), or a combination thereof. The results do not offer evidence of a widespread expansion but suggest it may have occurred at two of the six sites. Data from site 4 best fit these indicators, with the oldest age class (1970–75) comprising nearly 20% of all individuals. All plots at site 5 also warrant discussion. As with spruce stands, there was an absence of older individuals and a relatively high proportion of younger stems in all three plots at this site. This could be indicative of more recent establishment, or a higher rate of turnover. The fact that the negative exponential model fits the data well is suggestive of higher turnover. However, there were no individual ramets greater than 40 years old while older individuals were present elsewhere. Given the rapid transformation of this area evident from the spruce data, we cannot rule out an advance, or at least significant population increase, of willow in this area.

The relatively short age-span of willow stems also limits an examination between shrub and spruce population dynamics. An interaction between these two ecotone components is undoubtedly important, but its specific nature and extent is unknown. It is likely that this relationship changes with elevation, and it is conceivable that spruce limits the growth and establishment of willows in the open-forest. In turn, willow may influence spruce establishment and seedling growth in the shrubland zone. There is evidence to suggest that these competitive relationships are density dependent and vary significantly with aspect (Green & Hawkins 2005). Identifying the magnitude of these interactions and their influence on tree line dynamics is an important avenue for further work.

TREE LINE ECOTONE DYNAMICS AND CLIMATE CHANGE

The strongly positive correlations between recruitment and temperature reconstructions at most sites are indicative of the influence of temperature on spruce population dynamics in the forest-tundra ecotone. With one exception, increase in stand density on north aspects and advance of tree line on south aspects were significantly positively correlated to periods of above-average temperatures. The negative correlations in the forest zone at site 2 are inconsistent with all other sites. Combined with the low elevation of this site and the timing and pattern of stand establishment, the data suggest a rebound from an unknown disturbance or cessation of a constraint that had previously depressed tree line at this location.

The fact that multidecade windows of forward temperature averaging performed best reinforces the idea that temperature influences recruitment as much as establishment. Low temperatures reduce seedling and sapling growth rates at tree line, extending the time between germination and maturation and increasing the risk of seedling mortality (Danby & Hik 2007). Thus, favourable temperature regimes throughout these early life stages, not just at the time of establishment, are critical for successful recruitment (see also Wang *et al*. 2006).

The relationship between increases in the abundance and elevation of spruce and periods of warmer temperatures is not unexpected. Yet, while summer temperatures increased gradually since the 1850s, the increase in spruce density lagged and was abrupt at many sites. This is suggestive of a threshold response (Groffman *et al*. 2006) and implies that a critical temperature was surpassed, above which seedlings could more readily grow and survive to maturity. The reduction in recruitment following the 1950s could be related to a temperature decline from 1950 to 1980 and a drop in average long-term conditions below this threshold level. Individuals established during the recent warming period (i.e. 1980 to present) would not necessarily have been detected given that sampling excluded individuals < 0.50 m. Alternatively, it is possible that recruitment slowed as a result of temperature-induced moisture stress. This appears to be responsible for recent reduction of secondary growth in some tree line white spruce (Wilmking & Juday 2005) as well as seedling survival (Black & Bliss 1980), and would partly explain the

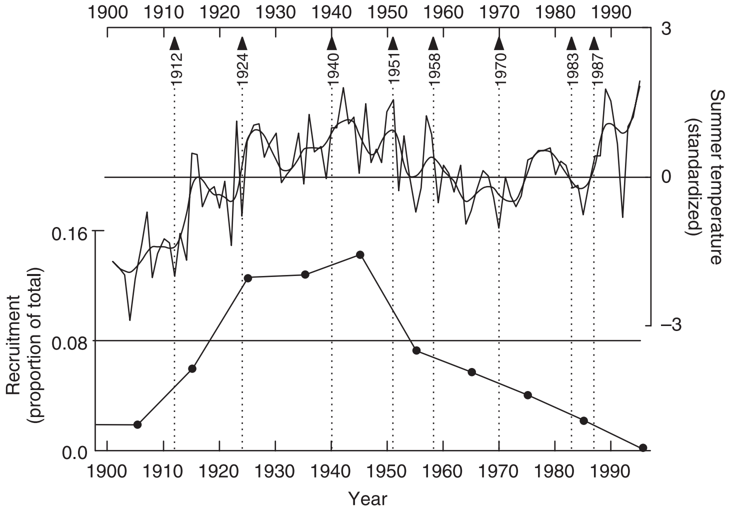

Fig. 7 Relationship between forest-tundra dynamics, spruce masting and climatic change during the 20th century. Bottom: Proportion of the total number of stems sampled in this study that established themselves in the noted decade. Top: Average May–September temperatures for the area bounded by 141° W, 61° N and 138° W, 62° N, from New *et al.* (2000). The thin line is the raw data standardized over the 95-year period. The thick line is the same data fitted with a compound smoothing filter. Vertical lines indicate white spruce mast years in Alaska from Juday *et al.* (2003). Masts after 1957 are based on observational data. Masts prior to 1957 are inferred from a combination of climate and ring-width data. Low recruitment since 1980 is partly related to sampling, which excluded individuals less than 50 cm in height. In combination the three data sets illustrate that the recruitment pulse during the second quarter of the 20th century fell within a period of sustained above-average temperatures coinciding with two mast events.

inconsistent correlations between density changes and PDO and PDSI, as moisture availability, not just total precipitation, is responsible.

P. glauca seeds lose viability in the seedbank within 1–2 years (Nienstadt & Zasada 1990). Above tree line, seeds have low germination rates and germinants have low survival (Hobbie & Chapin 1998). Large or regular seed crops are therefore necessary for an advance of tree line (Holtmeier 2003). White spruce periodically undergoes synchronous production of large seed crops (masts) at regional scales, which are critical in establishment and regeneration dynamics (Peters *et al.* 2005). One or more of these events could have facilitated the episodic establishment in south-west Yukon. Juday *et al.* (2003) found a relationship between warm, dry summers and the occurrence of masts in Alaska the following year, conditions which are also conducive for forest fires. Alaska and Yukon experienced their most extensive fire year on record during 2004, followed by a large cone mast in 2005. The previous mast years on record in south-west Yukon were 1993 and 1998 (McAdam & Boutin 2003). Alaska's previous mast year was also 1998 (Fig. 7), suggesting periodic synchrony between the two regions. Additionally, there is a significantly positive correlation between summer temperatures in interior Alaska (Fairbanks Airport, 64.8° N, 147.9° W) and south-west Yukon (Burwash Airport, 61.4° N, 139.1 °W) ($r = 0.624$, $P < 0.001$).

Our field observations indicate that the 2005 mast extended into the forest-tundra in south-west Yukon (Fig. S1), confirming that tree line spruce are capable of synchronous masting. Still, a year of high seed production will not necessarily result in subsequent episodic recruitment in the forest-tundra ecotone. Sustained warmer temperatures and climatic stability are also necessary for successful germination and, more importantly, seedling growth (Hobbie & Chapin 1998; Danby & Hik 2007). As illustrated in Fig. 7, at least two mast years (1924 and 1940) fall within a sustained multiyear period of above average temperatures, indicating that such conditions existed during the second quarter of the 20th century. Although subsequent mast events occurred, annual summer temperatures were not elevated for a sustained period afterwards and therefore not conducive to seedling growth or survival.

Conclusion

Periods of heightened recruitment as well as significant and rapid advance have been observed at subarctic tree lines elsewhere during the 20th century (Payette & Filion 1985; Gervais & MacDonald 2000; Kullman 2002). The changes we observed in south-west Yukon contribute to the growing body of evidence of these phenomena. The pattern and rate of change observed at some of the Yukon sites are particularly noteworthy because they are suggestive of a threshold response. The notion of inertia or slow gradual change followed by rapid change has gained increased attention in the literature, particularly with respect to ecosystem responses to global climate change (Chapin *et al.* 2004; Burkett *et al.* 2005). This type of lagged, non-linear response to climate change has been hypothesized for tree line ecotones (Kupfer & Cairns 1996; Malanson 2001; Lloyd 2005) but few studies have provided empirical evidence for it. Thus, the response of tree line to future warming may not necessarily be gradual (cf. Slatyer & Noble 1992).

The study of tree line characteristics (e.g. vegetation pattern, species composition, etc.) in relation to local and landscape-scale variables is a longstanding theme (reviewed by Holtmeier 2003). That these differences are accentuated at higher latitudes because of lower solar angles is not new either (Dingman & Koutz 1974). However, studies of the variation in ecological processes have been far less common. As shown for other mountainous subarctic regions (Kullman 1979; Dalen & Hofgaard 2005), our results demonstrate that population-level responses can vary significantly at regional, landscape and even local scales and are partially contingent on terrain variability, landscape setting and existing vegetation.

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Supplementary material

The following material is available for this article:

Table S1 *Picea glauca* characteristics in each sampling plot.

Table S2 Characteristics of *Salix* spp. in each sampling plot.

Figure S1 White spruce above tree line with abundant ovulate and pollen cones during the 2005 mast event.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2745.2007.01200.x