

**Effects of climate change on growth and seedling establishment
of young lodgepole pine (Pinaceae: *Pinus contorta*)**

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Research Experiences for Undergraduates

Rocky Mountain Biological Laboratory

2005

Abstract

Anthropogenically induced climate change is expected to effect numerous climatic alterations pertinent to ecosystems, including increased mean global temperature and altered precipitation regimes. High-elevation ecosystems are especially sensitive to climatic changes because slight fluctuations in factors like snowmelt date and soil moisture can lead to major changes in the length of growing season and other factors. Two five-year periods with contrasting climate factors in Gunnison Co. Colorado provided an opportunity to study the impacts of climate change on high-elevation ecosystems. I studied the relative influence of those two periods on six stands of young lodgepole pine and found that warming-associated climate factors enhanced growth in young trees and had little effect on seedling establishment success. These findings corroborate ecophysiological knowledge about lodgepole pine and suggest a possible shift in forest composition and distribution under climate change scenarios.

Introduction

Due to anthropogenic contributions of greenhouse gases to the atmosphere, the Earth's climate is predicted to change drastically over the coming century. Specifically, the general consensus among scientists is that the mean surface temperature globally will rise 1.4-5.8 °C by the end of the twenty-first century (Houghton et al. 2001), with even more dramatic changes to numerous local climates (Hulme et al. 2001, Sala et al. 2000).

Considering the delicacy of the relationship between ecosystems and abiotic environmental factors, climate change is predicted to affect ecosystems in numerous ways. Expected responses of ecosystems to climate change include changes in the distribution of organisms (Skov and Svenning 2004), flowering phenology (Inouye and McGuire 1991), soil biogeochemistry (Schimel et al. 1994, Shaw and Harte 2001), and damage to plants by herbivores (Malström and Raffa 2000, Roy et al. 2004).

Warming associated with climate change is expected to have especially significant effects on high elevation ecosystems (Schneider et al. 1992, Karl et al. 1993)

because ecological events in those systems are highly dependent on the timing of spring snowmelt (Peterson et al. 1991, Dunne et al. 2003). Many studies have focused on the potential impacts of warming on montane meadows (e.g., Harte and Shaw 1995, de Valpine and Harte 2001), but little emphasis has been placed on how climate change could potentially affect neighboring conifer forests. Staaterman and Harte (2004) showed that subalpine fir (Pinaceae: *Abies lasiocarpa*), one of the most prominent tree species in montane and subalpine forests, tends to respond negatively to even brief warming trends in an elevation range of 2895-3230 m, which is roughly the mid to lower end of its current natural range in Gunnison Co., Colorado. On the other hand, lodgepole pine (Pinaceae: *Pinus contorta*) is likely to respond positively to global warming scenarios near the upper end of its current natural range since it is known to grow faster at higher temperatures (Koch 1996) and increase photosynthetic production with less frequent frosts (Schwarz 1971, Fahey 1979) and earlier snowmelt (Day 1989). Currently, lodgepole pine is the dominant conifer in forests at elevations directly below spruce/fir-dominated stands. Therefore, prolonged warming as predicted by climate models could cause many changes within the forests of western North America (Peterson 1995), including the encroachment of lodgepole pine into forests traditionally dominated by subalpine fir and Engelmann spruce.

To assess the potential for lodgepole pine to invade subalpine fir forests I studied the impact that changes in climate between the years 1993-1997 and 1999-2003 (billy barr, unpublished data) had on young lodgepole pine. If young trees at the upper elevational fringe of lodgepole pine forests respond positively to warming, this result, in conjunction with that of Staaterman (2004), would suggest that lodgepole pine is apt to

encroach on subalpine fir forests under continued warming in the twenty-first century. Specifically, I focused on growth and seedling establishment of young trees because these are the factors that will determine the dispersal success of lodgepole pine into higher elevations.

Methods

Snowmelt data collected by Billy Barr at the Rocky Mountain Biological Laboratory (Gunnison Co. CO, USA) indicate significantly earlier snowmelt in 1999-2003 than in 1993-1997, consistent with other warming-related climatic observations across the western United States (J. Harte, personal communication). Annual measuring of the day on which snow completely melted at a given site since 1975 indicates that the mean snowmelt occurred on the 132nd day in 1999-2003, which was significantly earlier than the more typical 151st day snowmelt experienced in 1993-1997 (t -test: $t_8 = 2.42$, $P = 0.042$). Although the early snowmelt observed in this interval is likely attributable to natural climate fluctuations rather than anthropogenic greenhouse gas emissions, this phenomenon provided an excellent opportunity to conduct observations on the effects of climate change on montane and subalpine forests. Since I am concerned with the impact of climate change on trees that have germinated since 1993 I focused on the following aspects of young lodgepole pine: 1) growth, and 2) seedling establishment success.

Study Sites

I collected data from six study sites in the Fossil Ridge Wilderness of the Gunnison National Forest near the approximate boundary between lodgepole pine and spruce/fir forests (106°40' W, 38°45' N). With regard to environmental factors like slope, aspect, shade, and soil moisture, there was minimal variation within sites but considerable variation among sites, as shown in Table 1. The size of each site was determined primarily by the number of young trees at the site because collecting an adequate sample size was a priority over selecting sites with similar densities. I recorded the age and growth of 63, 94, 110, 120, 128, and 78 trees at sites one through six, respectively. The sites ranged in elevation from 2671 to 3191 m, providing a representative sample of lodgepole pine in the mid to upper end of its elevational range.

Growth

Traditional methods of determining age and yearly growth of trees include tree ring analysis via cutting trees down or coring them. To minimize the disturbance of my study on local populations I determined age and growth by counting nodes and measuring the distance between them, a non-intrusive technique that has been shown to be successful for many conifer species (Aplet et al. 1998), including lodgepole pine (Millar et al. 2004). To isolate the effect of warming it was necessary to age-detrend the growth data (Perfors et al. 2003) because of age-dependent growth, which accounts for differential growth rates over the course of an organism's life. To age-detrend data collected on the growth of young trees I first created a plot for each site with the amount of growth a tree experienced in a given year plotted against the age of the tree in that year. After

attempting to model the data with a variety of functions, I found that the following function most accurately described the data

$$growth = g_{inf} + \frac{b}{age} \quad (1)$$

where g_{inf} and b are parameters that are based on climatic conditions and uniquely describe the growth of trees at a certain site in a certain year. Specifically, g_{inf} is a fitted asymptotic growth value that describes the growth of trees of an age approaching infinity. This parameter was motivated by the shape of the data and accounted for the fact that it would not make sense for very old trees to experience zero or negative growth. To illustrate the data-fitting procedure, Figure 1 shows the growth experienced at site 2 in the year 2000 plotted against age, as well as the function that was used to fit those data. After fitting parameters for Eqn. 1 for all years within a site, I took the mean values $\bar{g}_{inf}$ and $\bar{b}$ for each site to form the equation,

$$E(age) = \bar{g}_{inf} + \frac{\bar{b}}{age} \quad (2)$$

which describes the growth of trees as a function of age averaged across years for each site and provides the expected growth values as shown in Eqn. 2. Finally, the observed growth $O(age)$ was divided by the expected growth for trees of the same age to obtain the age-detrended growth as shown in Eqn. 3.

$$growth_{age-detrended} = \frac{O}{E} \quad (3)$$

For each site I calculated the mean age-detrended growth for 1993-1997 and compared it to the mean age-detrended growth for 1999-2003. If the mean age-detrended growth for 1993-1997 was less than that for 1999-2003, such a result would confirm my hypothesis

that early snowmelt had a positive effect on the growth of young lodgepole pine. To determine if the two averages were significantly different I performed a *t*-test on the two age categories at each site, as well as a two-way analysis of variance with both age categories and sites as independent variables.

Seedling Establishment

Seedling establishment success is ideally determined by counting and comparing the number of successful germinants in all years of interest. However, I was not able to collect such a long-term data set and consequently had to rely on other methods to assess the effect of climate change on seedling establishment.

The only variable I was able to collect that was relevant to seedling establishment success was the number of trees that germinated in a given year at each site. Analysis of these data required the assumption that very young lodgepole pine experience high mortality and that mortality decreases as age increases. I then proceeded to determine whether there were more trees that germinated in early or late snowmelt years. If there were more trees that germinated in late snowmelt years I would know that there was a negative effect of early snowmelt on seedling establishment success. However, if there were more trees that germinated in early snowmelt years there are three possible conclusions that could be made: (a) early snowmelt increased the survivability of young trees, (b) early snowmelt had no effect on the survivability of young trees, and (c) early snowmelt decreased the survivability of young trees. In the event that warming had no effect on the survivability of young trees I would expect to find fewer trees that germinated in late snowmelt years because they would have had a longer period of

vulnerability to natural mortality. Such an equivocal result would provide a challenge in determining whether increased success of young trees is explained by climatic factors or naturally higher mortality of older trees.

To address this problem I first plotted the log-transform of the number of trees by age. Because of the assumption that mortality decreases as age increases, the aforementioned plots could be described by a linear regression of the log-transformed data. To determine whether there was an effect of snowmelt date on establishment success I performed separate linear regressions on early snowmelt and late snowmelt data. I then inferred that the regression parameters were statistically indistinguishable if there was overlap between the ranges of values for early and late snowmelt ages, described by the mean plus or minus the standard error. Otherwise, the parameters were determined to be significantly different. My null hypothesis was that the estimates for both parameters would be indistinguishable between snowmelt date treatments, indicating no effect of snowmelt date on seedling establishment success. Alternatively, differences between these estimates would imply an effect of snowmelt date on seedling establishment.

Results

Age-detrended growth

Figure 2 shows that the mean age-detrended growth of young lodgepole pine trees at all sites was greatest in the years 1999-2003, when mean snowmelt date was significantly early. Performing *t*-tests on the mean age-detrended growth between the periods 1999-

2003 and 1993-1997 revealed that greater age-detrended growth in the early snowmelt period was significant for five of six sites and marginally significant for one site. A two-way analysis of variance again showed an effect of snowmelt date on growth ($F_{2,1} = 86.7647$, $P < 0.001$) and showed that this effect was consistent across sites ($F_{2,5} = 0.3596$, $P = 0.8737$).

Seedling Establishment

Performing a t -test on the mean numbers of trees germinated in early and late snowmelt years indicated that there were more trees present at the time of observation that germinated in early snowmelt years. The total number of trees at each site that germinated in early and late snowmelt years is displayed in Figure 3. A Rank Wilcoxon test showed that the higher abundance of early snowmelt seedlings was consistent across all six sites ($P = 0.0156$). Hence, I was not able to directly conclude anything about the effect of snowmelt date on seedling establishment success based on that analysis.

Figures 4a and 4b show the slope and intercept parameter estimates, respectively, for linear regressions of age versus the log-transform of the number of trees of each age. The standard errors for the slope parameter estimates overlap for four of six sites and also for the regression of data summed across sites. This equality of slopes suggests that there was no effect of date of snowmelt on seedling establishment within treatment periods. Likewise, the standard errors of the intercept parameter estimates overlap for four of six sites and also for the regression of data summed across sites.

Although analysis of the slope and intercept parameters failed to reveal an effect of snowmelt date on seedling establishment, comparison of actual data and the predicted

values from regressions yields a different result. Figure 5 shows the number of trees for all sites plotted against age, as well as exponential fits of the numbers of early and late snowmelt germinants, respectively. I performed paired t -tests to compare the actual number of extant trees that germinated in the early snowmelt period with the number predicted to have germinated in that period and survived until the time of observation based on the exponential fit from the late snowmelt period, and *vice versa*. This analysis revealed that there were more trees that germinated in the early snowmelt period than expected from the late snowmelt exponential fit ($t_4 = 3.52$, $P = 0.024$) and fewer trees that germinated in the late snowmelt period than expected from the early snowmelt exponential fit ($t_4 = 16.4$, $P < 0.0001$). These results indicate that earlier snowmelt may increase seedling establishment success.

Discussion

The results of the growth observations strongly support the hypothesis that earlier snowmelt date correlates with increased growth in young lodgepole pine. These results also corroborate knowledge about the intrinsic responses of lodgepole pine to various climatic factors (Schwarz 1971, Fahey 1979, Day 1989, Koch 1996). Not only was there a difference in snowmelt date between the years 1993-1997 and 1999-2003, but there were also noticeable differences in other abiotic environmental factors like soil moisture, temperature extremes, and precipitation patterns at the Rocky Mountain Biological Laboratory (J. Harte, personal communication). Considering that all of those factors are

expected to accompany global climate change, this study suggests that young lodgepole pine are likely to respond positively to such changes over the coming century.

On the other hand, seedling establishment data were not as conclusive as the growth results. Parameter estimates for regressions of the demographic data were inconsistent and suggested that there was likely no effect of snowmelt date on seedling establishment success. However, comparison of the actual data in each period with the values predicted by data from the other period, as illustrated in Figure 5, indicate a strong effect of snowmelt date on seedling establishment. I only performed the latter procedure on the demographic data summed across sites because the slope parameters for individual sites were highly variable and many of those estimates were logically inconsistent with the assumption that the number of trees should decrease as age increases. This variability of parameter estimates among sites could likely be remedied by increasing the sample size at each site, a possibility corroborated by the congruency of the results summed across sites with my predictions about differential mortality among ages. Despite these mixed results, it is still possible that more dramatic climatic changes over the coming century could instigate changes in seedling establishment success. Unfortunately, such an assertion is beyond the scope of this study, but long-term studies tracking the number of germinants over a number of years would provide greater insight into the effects of climate on seedling establishment success. Manipulative experiments similar to the meadow-warming experiment at the Rocky Mountain Biological Laboratory (Harte and Shaw 1995) and FACE experiments conducted throughout the world (Nowak et al. 2004) would further clarify which mechanisms underlie the ways in which lodgepole pine and other trees respond to factors associated with anthropogenically-induced climate change.

It is important to note that the responses of young trees to changes in climate were consistent throughout six sites that displayed variation with regard to several environmental factors, most notably elevation. As a result, this study supports the hypothesis that lodgepole pine are locally adapted to climate along an elevational gradient. This result corroborates other studies that show evidence for local optimality of lodgepole pine across a wide geographic range, including sites in British Columbia and the northwestern United States (Wu and Ying 2004). However, considering that my study was limited to the southern terminus of the immense geographic range of lodgepole pine (Koch 1996), it is still possible that higher latitude forests may experience much different responses to climate change.

Another important factor expected to accompany climate change over the coming century is the increased frequency and severity of wildfires in the geographic range of lodgepole pine (Franklin et al. 1992). Because lodgepole pine have serotinous cones, which experience increased success in the presence of fire, they are likely to benefit from more frequent forest fires. Also, because lodgepole pine represent the dominant early-successional species in many forests and fir and spruce dominate climax forests in the same biogeographical region, it is reasonable to hypothesize that more frequent and severe wildfires would accelerate the return from climax to early-successional forests in many areas. This phenomenon would likely increase the range of lodgepole pine and intensify any competitive advantages conferred to young lodgepole pine by climate change.

Acknowledgements

Funding was provided by the National Science Foundation's Research Experiences for Undergraduates program. Thanks to Mel Harte, Ryan Trojan, Sue Glover, and Trixie Lee for assistance with transportation to and from my field site. Also, special thanks to Elizabeth Clark for help with data collection and to RMBL for graciously facilitating my research during the summer of 2005.

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Figures and Tables

Table 1. Environmental conditions at each site.

Site	1	2	3	4	5	6
Altitude (m)	3191	3176	3158	3047	2674	2671
Aspect	S	W	SW	SW	W	N
Slope (degrees)	30	10	30	10	5	5
Soil Moisture (% H ₂ O)	31.4	26	32.7	28.9	5	27.9
Sun (1-5, 5 = sunniest)	4	3	4	5	4	3

Figure 1. Growth experienced at site 2 in the year 2000 plotted against age and fitted with a function in the form of Eqn. 2.

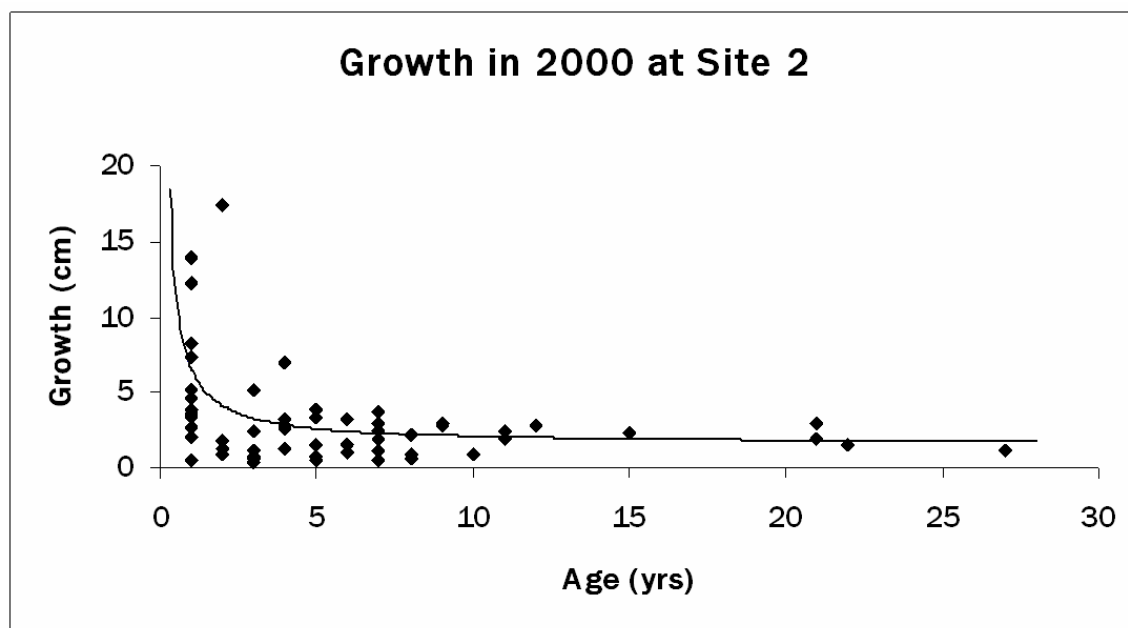


Figure 2. Differences in age-detrended growth between the periods 1993-1997 and 1999-2003 (late and early snowmelt years respectively) at each site.

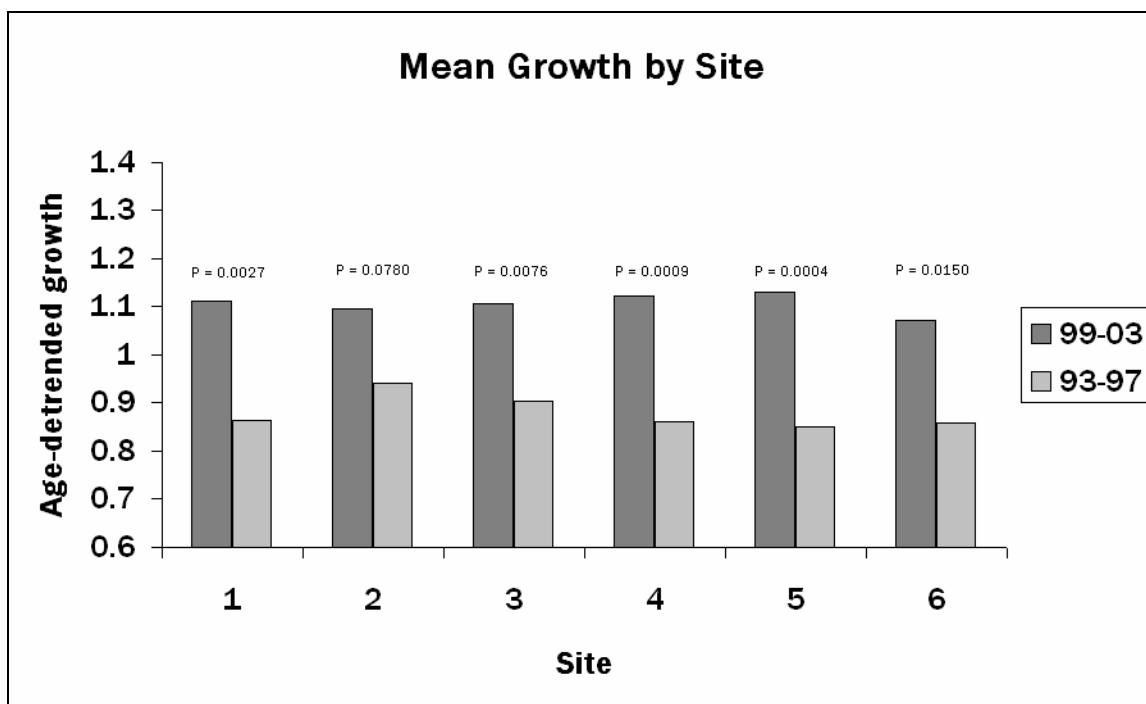


Figure 3. Number of trees at each site categorized according to the snowmelt period in which they germinated.

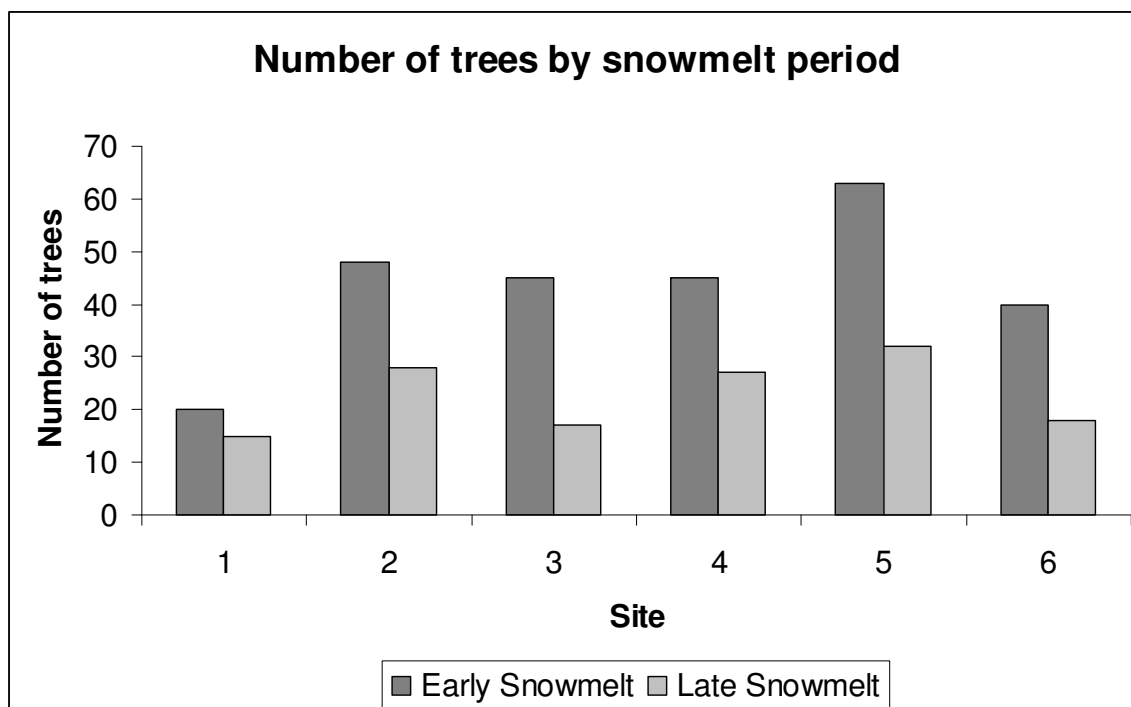


Figure 4. (a) Slope and (b) intercept parameter estimates of linear regressions performed on the log-transformed number of trees versus age at each given site and summed across sites.

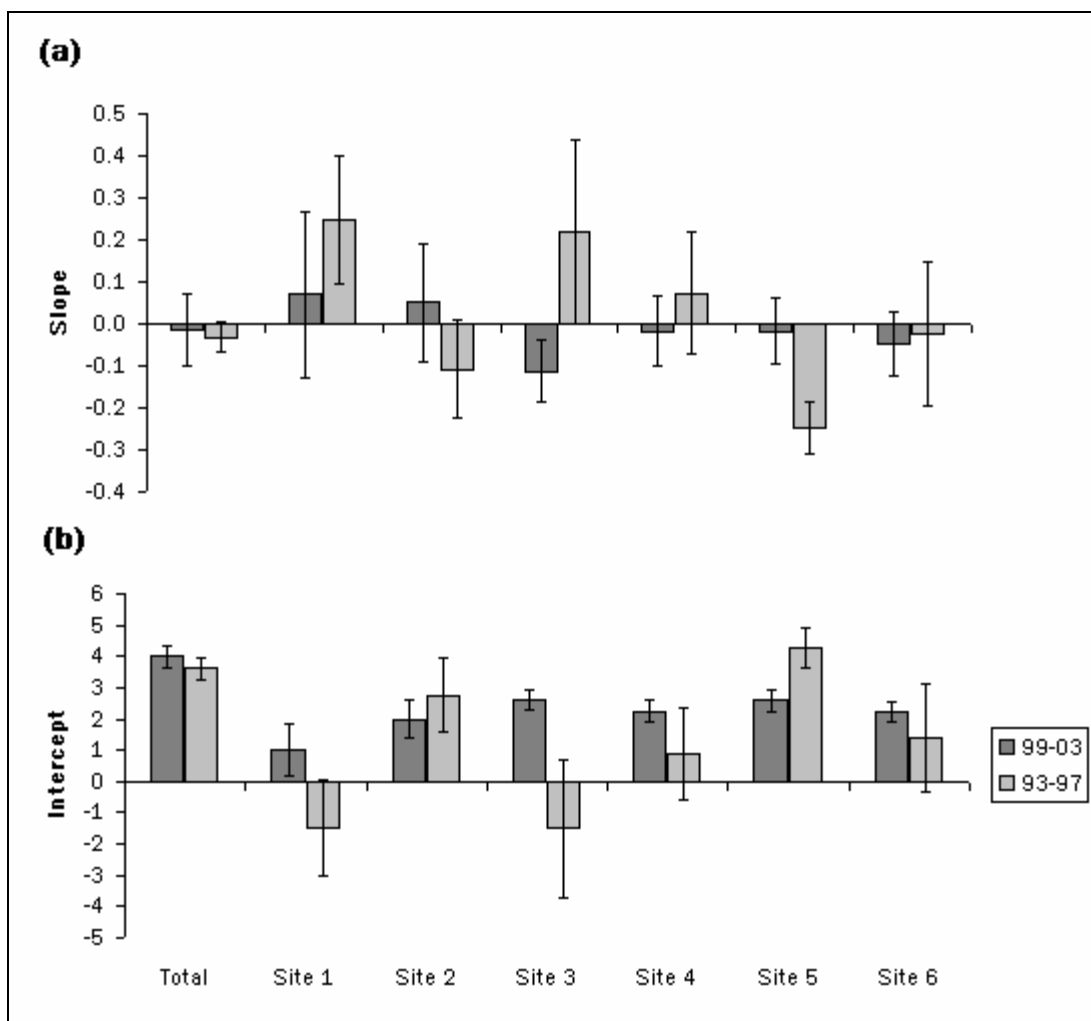


Figure 5. Number of trees at all sites plotted against age. The solid line is the exponential fit of the number of trees germinated in early snowmelt years, and the dashed line is the exponential fit of the number of trees germinated in late snowmelt years.

