Long-term monitoring of climatic and nutritional affects on tree growth in interior Alaska[1]

J. Yarie and K. Van Cleve

Abstract: The comparative analysis of a large set of long-term fertilization and thinning studies in the major forest types of interior Alaska is summarized. Results indicate that nutrient limitations may only occur during the early spring growth period, after which moisture availability is the primary control of tree growth on warm sites. The temperature dynamics of both air and soil set seasonal bounds on the nutrient and moisture dynamics for all forest types. Air and soil temperature limitations are the primary control of intraseasonal growth in the colder topographic locations in interior Alaska. These locations are usually dominated by black spruce *(Picea mariana* (Mill.) Britton, Stems, Poggenb.) vegetation types. The seasonal progression of factors controlling growth is strongly tied to the state factor structure of the landscape.

Résumé : Nous avons synthétisé l'analyse comparative d'un grand nombre d'études à long terme sur la fertilisation et l'éclaircie des principaux types forestiers de l'intérieur de l'Alaska. Les résultats indiquent que des carences nutritives peuvent survenir seulement au début de la période de croissance printanière, après quoi la disponibilité en eau devient le principal facteur qui limite la croissance des arbres sur les stations chaudes. La dynamique de la température de l'air et du sol fixe les limites de la dynamique des nutriments et de l'eau pour tous les types forestiers. Pendant la saison de végétation, la croissance des arbres est surtout affectée par la température de l'air et du sol sur les sites topographiques les plus froids de l'intérieur de l'Alaska. Des types forestiers dominés par l'épinette noire (*Picea mariana* (Mill.) Britton, Sterns, Poggenb.) recouvrent généralement ces endroits. La progression saisonnière des facteurs qui régissent la croissance est intimement liée à la structure des facteurs d'état du paysage.

[Traduit par la Rédaction]

Introduction

Long-term studies dealing with the growth of individual trees and forest stands are not common. A number of studies have reported natural changes in forest stand structure over various time periods in the life of a forest (Whitney 1984; Peterken and Jones 1987; Yolk and Fahey 1994). Other studies have related tree growth to climate (Jozsa et al. 1984; D'Arrigo and Jacoby 1993; Brooks et al. 1998; Courchesne et al. 2001), single fertilizer applications with growth measured over longer time periods (Bradley et al, 2000), repeated fertilizer applications over 5 to 30 year time periods (Andersson et al, 2001; Kishchuk et al. 2002), optimum nutrition experiments (Weetman et al. 1997), and elevated CO_2 environments (Hattenschwiler et al. 1997). A greater understanding of the mechanisms by which environmental factors influence tree and forest productivity is still needed to improve our understanding of forest development and to develop sound management recommendations for both natural and human manipulated ecosystems (Andersson et al 2000),

The state factor model proposes that vegetation and its functional characteristics are controlled by a set of five relatively independent factors: climate, parent material, topography, biota, and time (Major 1951). State factors provide a theoretical and operational basis for understanding specific patterns and potential changes in forest productivity tied to environmental constraints. Vegetation production is directly controlled by specific components of the soil, climate, topography, and parent material over various time periods. State factors also have many indirect effects on productivity, and their control of productivity may co-vary in a complex fashion across the landscape and at individual sites.

The environmental controls of ecosystem function are tied directly to state factors. The state factor approach then allows for the development of a basic view of a cause-effect relationship for ecosystem function. Within interior Alaska, the general nature of state factor control of ecosystem function has been summarized into five basic components: (1) occurs in a cold-dominated environment (2) topographic position is an important factor, (3) soils are highly uniform within landscape (upland or floodplain) position, (4) early successional species distribution is relatively constant, and (5) fire cycles control the successional time frame (Van Cleve et al, 1996). Forest growth studies conducted in interior Alaska have been designed using these proposed state factors to organize site selection and treatment placement in an environmental structure that would minimize the environmental variability.

Here, we synthesize data from a number of long-term forest growth studies conducted in interior Alaska, where continuous observations of annual tree growth and stand

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litterfall were measured for up to 40 years (J. Yarie, K. Van Cleve, J. Downing, R. Erickson, and B. Schlentner, unpublished data). The 40-year time period is approximately one-fifth to one-third of the life-span of the major hardwood and coniferous forest types, respectively, in the Alaskan portion of the boreal forest. Studies were conducted in upland secondary successional forests that established following fire and were dominated by the midsuccessional hardwoods trembling aspen (*Populus tremuloides* Michx.) and Alaska paper birch (*Betula neoalaskana* Sarg.) or by the late successional white spruce (*Picea glauca* (Moench) Voss). Studies included combinations of fertilizer applications and forest stand density manipulations and were designed to examine the direct and interactive roles of soil fertility, temperature, and moisture supply on forest productivity. Indices of productivity measured included tree basal area growth and stand litterfall estimates, but only growth data are summarized here. Early, middle-aged, and older stands were included in the study design for the hardwood forest types, thus expanding the information base to a successional context. White spruce and paper birch stands were thinned to evaluate density-dependent control of growth and changes in soil temperature and moisture that might influence tree growth. These data sets were collected during a time period (1967 to present) when drought tied to climate warming had become a significant environmental factor limiting tree growth (Barber et al. 2000). Environmental variables were monitored in control sites at each location throughout the experimental period and included atmospheric temperature and precipitation, soil temperature (at the soil surface; at the organic-mineral soil interface; and at depths of 15, 30, 60, and 90 cm), and moisture content (at depths of 10, 41, 71, 102, 132, and 163 cm from the top of the organic layer).

Additional research sites in upland forests (aspen, birch, and white spruce) and in primary successional forests on the floodplain of the Tanana River were established by the Bonanza Creek Long-Term Ecological Research Program (BNZ LTER) in 1987 to study responses of tree growth to changes in soil nutrient availability. The primary successional floodplain stands added to the study were alder - young balsam poplar (*Alnus tenuifolia* Nutt. - *Populus balsamifera* L.), mature balsam poplar, and white spruce.

Successional structure of study sites

Selection of upland sites included a range of ages in forest types typical of the Fairbanks region of interior Alaska. For hardwood types in the 40-year study (aspen and birch), young (6 and 25 years old), intermediate (25-50 years old), and mature (120 years old) age classes were selected. For the conifer types (white and black spruce), intermediate to mature age class stands (60, 150-250 years old) were selected. In some of the hardwood stands, white spruce occupied a subordinate crown class to more mature early successional species (balsam poplar, birch, or aspen). In one case, a mature white spruce forest was replaced by white spruce as the first successional species on the site following fire.

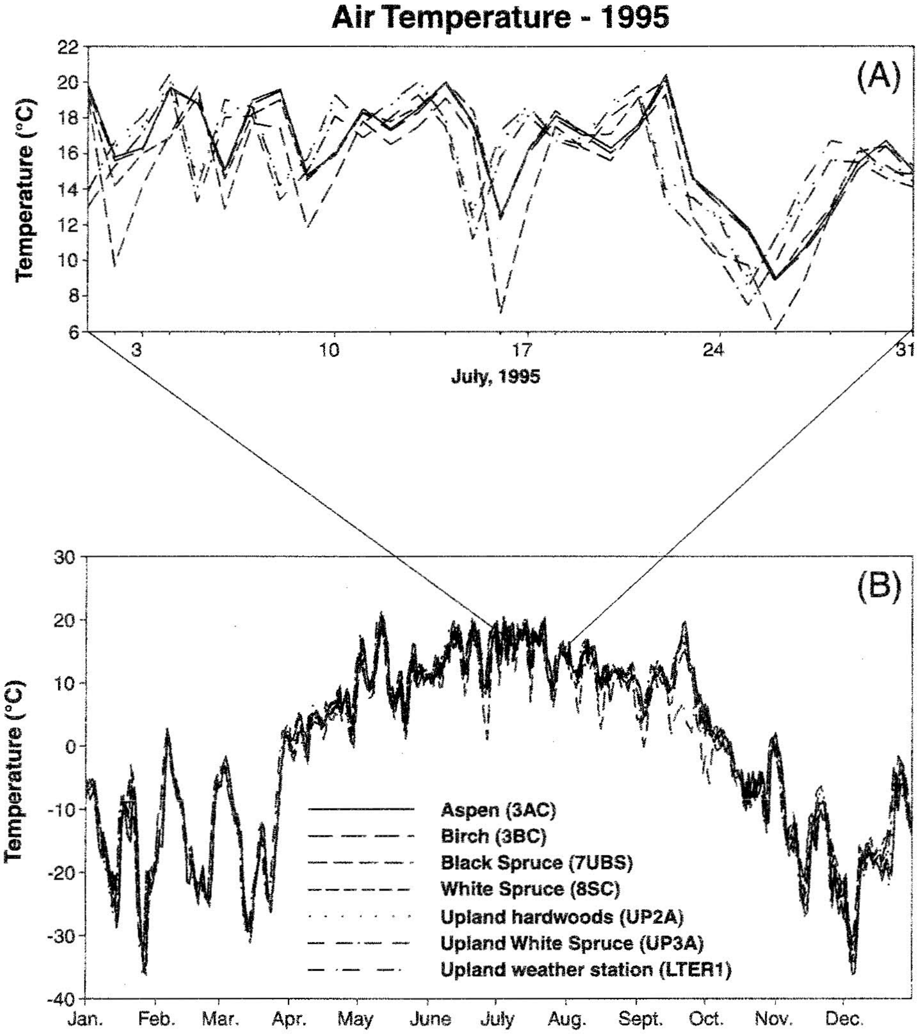
The white spruce stands included in the long-term growth study were dense post fire stands that represent a variation of the typical upland successional trajectory (Van Cleve et a1. 1996) by not having earlier stages dominated by hardwoods, Fire occurred during an optimum period for seed productivity, allowing rapid and direct recruitment of white spruce, although scattered aspen and birch are present. This stand represents a variation of succession by not having earlier stages dominated by hardwoods. The treatments applied to this stand represent two similar studies. The first study ineludes a control (stem density of 7200 stems·ha-^{1}), fertilization (112 kg·ha^{-1} N as NH_4NO_3, 56 kg·ha^{-1} P as triple superphosphate, and 112 kg·ha^{-1} K as KCI), thinning to a stem density of 1600 stems·ha^{-1}, and thinning plus fertilization treatment. In the second study, a greater number of fertilizer types were applied (J. Yarie, K. Van Cleve, B. Schlentner, R Erickson, and J. Downing, unpublished data) and the thinning treatments included a 1600 and 800 stems-ha^{-1} intensity.

Black spruce sites were represented by intermediate (60 years old) and mature (130 years old) postfire stands. The 60-year-old stands illustrate development of nonvascular plant ground cover and a thick forest floor, which typifies the cold-soil, permafrost conditions of this forest type (Viereck et al. 1983). The old age class stand demonstrates the development of feathermoss ground cover on a cold but permafrost-free site (Viereck et al. 1983). Because of the very low growth rates of trees in these stands, no thinning or fertilization treatments were applied and only air and soil climate variables were measured.

In the BNZ LTER study, sites selected represent important turning points in forest development from young to mature forests (Van Cleve et al. 1991). Turning points can be defined as dramatic changes in forest structure and function that occur over relatively short time periods that have long-term consequences for further ecosystem function and development (Van Cleve et al. 1996). They represent key time periods that maintain a resilient successional pathway typical in interior Alaska. One example is the transition from a floodplain alder stand with an understory of balsam poplar to a midsuccessional hardwood stand dominated by balsam poplar. Given the influence of alder on ecosystem nitrogen (N) dynamics (Van Cleve et al. 1971; Uliassi and Ruess 2002), the complete removal of balsam poplar by beavers during this transition could prolong N-fixation inputs by alder and potentially influence the successional trajectory. The collection of sites and time periods for both studies was designed to establish long-term trends in tree growth and changes in ecosystem structure and function. The time dynamics of major short-term structural changes in factors controlling tree growth and ecosystem function were an additional thrust of the BNZ LTER study.

The sites within the BNZ LTER program encompassed the successional sequences typical of the Tanana River floodplain and adjacent uplands in interior Alaska. The floodplain sites represented transitions between an alder-dominated system to a balsam poplar-dominated system, between balsam poplar and white spruce, and finally from an even-aged white spruce forest to either an uneven-aged white spruce system or black spruce (Van Cleve and Viereck 1981; Powers and Van Cleve 1991; Van Cleve et al. 1993, 1996). Similar stages were also established in the uplands where the first transition is from a shrub-dominated system to a hardwood sapling ecosystem, the second is from hardwoods to conifer domination, and the third is from the

Fig. 1. Air temperature dynamics of several forested sites and an open-area climate station (LTER1) for the year 1995 for the month of July (A) and at the annual scale (B).



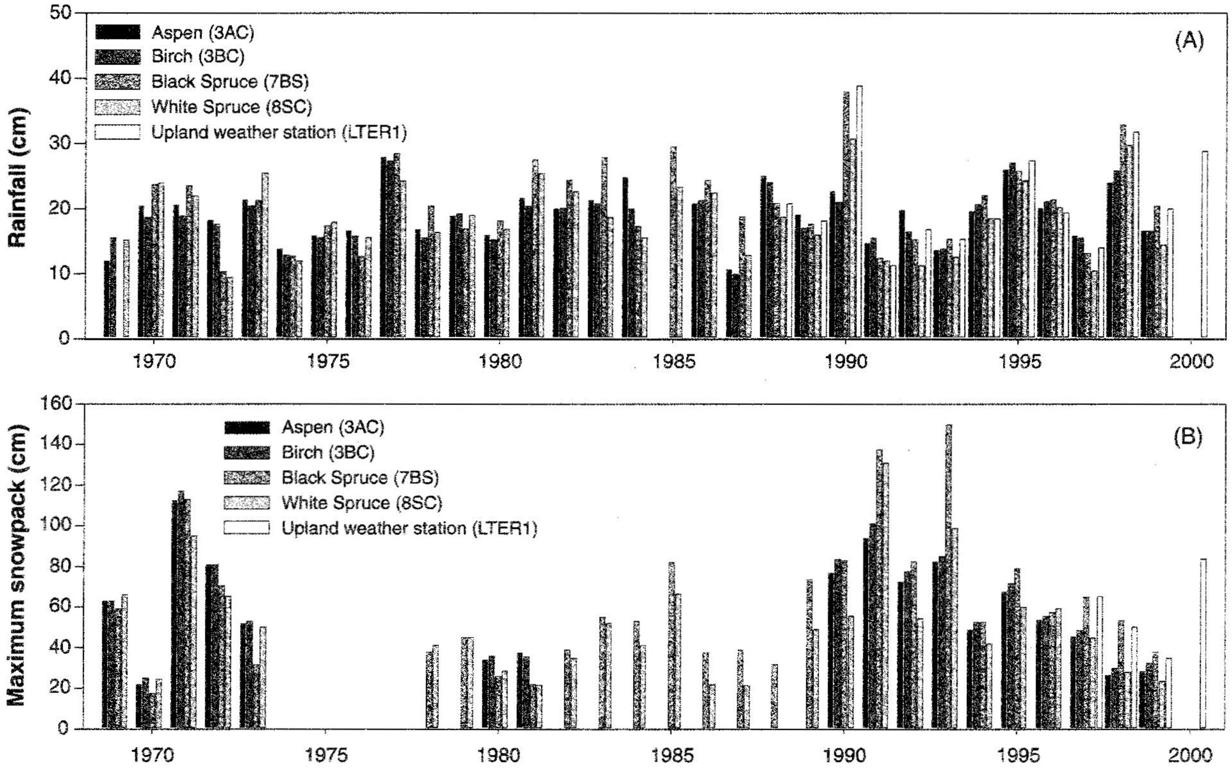
old-growth white spruce to an uneven-aged white spruce system or a black spruce dominated forest. Five treatments were applied across the successional turning points (J. Yarie, K. Van Cleve, J. Downing, R. Erickson, and B. Schlentner, unpublished data): annual N fertilization at a rate that approximately doubled soil N mineralization; carbon (C) additions in the form of sawdust and sugar to increase the *C/N* ratio of the forest floor to the level typically found in black spruce stands (*C/N* = 50); and summer rainfall exclusion using seasonal covers in the hardwood-conifer transition sites in both the uplands and floodplain (Yarie 2008).

In contrast to the sites selected for the long-term growth studies mentioned above, the BNZ LTER experimental study sites represent a different phase in the successional development of the ecosystems studied. Instead of representing a relatively stable state of community development they represent a major turning point in both the structure and functioning of the system. The time period related to the turning point is often substantially shorter than development of the successional stages on either side of the turning point. In general, the anticipated turning points represent expected successional development of the ecosystem that is consistent with the anticipated adaptive cycle (Hollingsworth et al. 2010).

Comparative results across all sites

Seasonal dynamics of air temperatures at all sites were very similar (Fig. 1) with small differences in the inter-day fluctuations (Fig. 1A). For example, the black spruce site showed consistently lower air temperatures on many occasions throughout the year (Figs. 1A and 1B). In addition, during late September and early October, the cleared upland weather station (LTER1) site showed much lower lows than any of the forested sites (Fig. 1A). These types of dynamics are typical of other studies in the Fairbanks area in which air temperature was monitored across a number of locations (Kittredge 1948; Slaughter and Viereck 1986; Viereck et al. 1993). Although no significant differences were found among sites for either annual rainfall or maximum seasonal snowpack when averaged over the 40-year measurement pe-

Fig. 2. Annual rainfall and maximum snowpack for four stand types and an open-air weather station (LTER1) from 1968 through 2000. There were no significant differences between quantities among years when averaged across the sites measured.



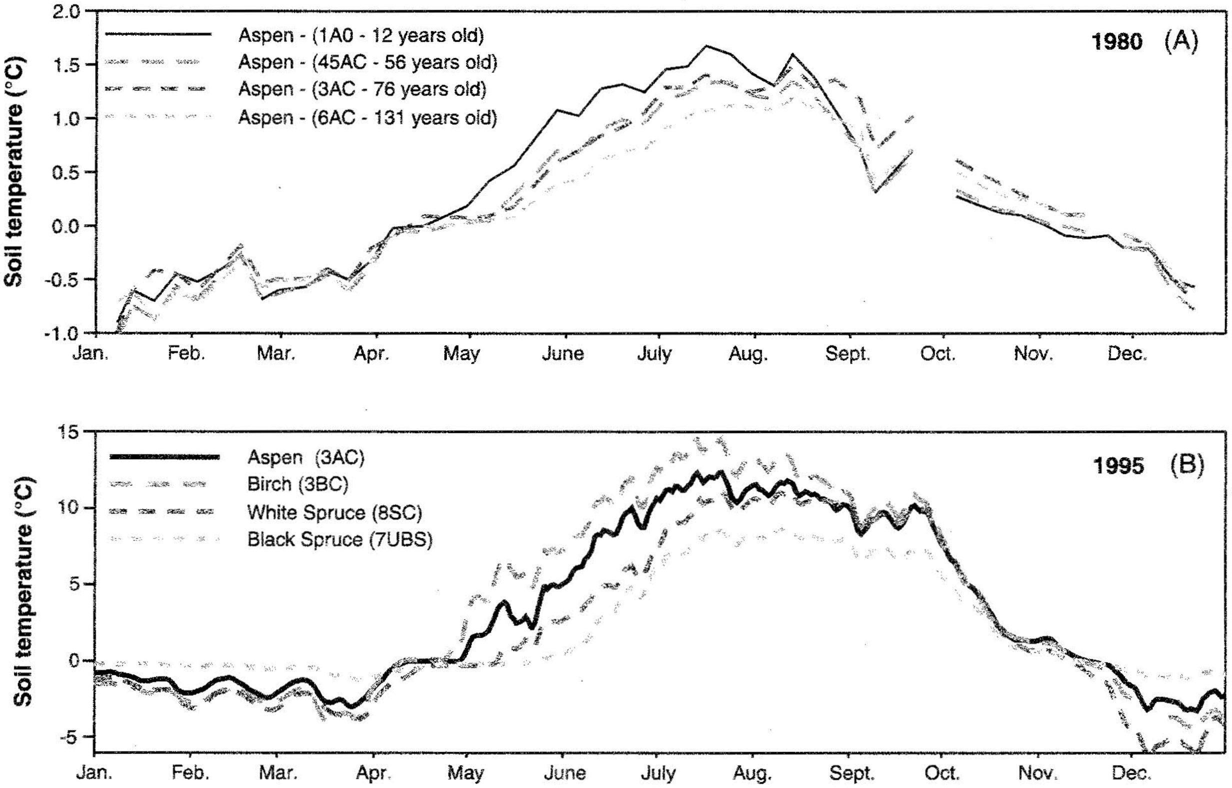
riod, there was a large amount of variability among years for both climate parameters (Fig. 2). An overall cooling of soil temperature was observed across age classes within a stand type (Fig. 3A) and across the successional chronosequence (Fig. 3B). Development of a thick surface organic layer tied to forest floor moss growth in the conifer stands and the north-facing location of black spruce stands are responsible for this pattern of late-successional cooling of soil temperature (Flanagan and Van Cleve 1983; Van Cleve et al. 1983). In general, seasonal fluctuations in soil temperature are greater in hardwood ecosystems than black spruce ecosystems, and average annual soil temperature in black spruce is lower than in hardwood stands. These factors are especially important for the greater observed rates of forest floor organic matter decomposition and element supply observed in hardwood stands than in conifer stands in interior Alaska (Piene and Van Cleve 1978; Gordon and Van Cleve 1983; Van Cleve et al. 1993).

State factor relationships from individual sites to the interior Alaska landscape - a view of environmental complexity

The state factor concept of Jenny (1941, 1980) provides a conceptual framework for the development of ideas that define relationships between environmental controls and ecosystem processes, such as tree growth and element cycling. The factors included in the model can be used to develop a structured framework for the hierarchical controls over stand production in interior Alaska (Chapin et al. 1996, 2002). This hierarchical structure is tied to landscape dimensions. At the regional scale, macroclimate, topography, soil order and parent material, and biotic structure influence the distribution and growth of vegetation communities. Smaller-scale surrogates of these controls become important when analyzing smaller landscape units, for example, a change from macroclimatic controls to microclimatic controls. Finally, time represents a confounding factor due to its influence on the other state factors. A vegetation type chronosequence is assumed to present age dynamics that would be seen if an individual stand were studied over a long time period. A primary assumption in chronosequence studies is that major changes in state factors would be occurring at a sufficiently slow rate so that results gained from studies across age classes of ecosystems would be applicable to several generations of the vegetation's successional development (Yarie et al. 1988).

The structure of the limiting factors that control forest growth are complex. Air and soil temperatures define the length of the growing season in boreal ecosystems. Once a threshold temperature is reached in the spring additional environmental factors control vegetation production and form a complex hierarchical structure related to other ecosystem properties. The key hypothesis of fertilization studies is that soil fertility is the primary limitation to forest growth during the growing season. In this simple view of state factor control, tree growth is limited by a single environmental variable, soil fertility (specifically the availability of a single nutrient), at the lowest level of a potential hierarchical structure of limiting factors.

Fig. 3. Soil temperature dynamics (at 15 cm depth from forest floor-mineral soil interface) within an age sequence of aspen stands (A) and through a potential successional chronosequence, aspen to black spruce (B), in interior Alaska.



Data from the long-term growth studies indicate that aspen stands were limited by soil fertility (nutrient availability) only during the first half of stand life history (Yarie *2009a;* J. Yarie, K. Van Cleve, B. Schlentner, R. Erickson, and J. Downing, unpublished data). Middle-aged stands showed a positive response to fertilization in the first half of the measurement period, and a negative response in the later half, while growth of trees in the oldest aspen stand was decreased by fertilization. These results, based on the annual growth data, are similar to the results presented for the total study time period (40 years) (Fig. 4A). Even though soil moisture did not differ among the three stand age classes (J. Yarie, K. Van Cleve, B. Schlentner, R. Erickson, and J. Downing, unpublished data), fertilization in the younger age classes of aspen reduced the negative correlations between current years growth and evaporation in the preceding year (Yarie 2009a; J. Yarie, K. Van Cleve, B. Schlentner, R. Erickson, and J. Downing, unpublished data). One explanation for this result is that during high-evaporation summers, carbohydrate (CHO) production and subsequent winter storage in the root systems may be decreased because of lower total photosynthesis caused by a soil moisture limitation during the growing season. As a result, spring growth during the following year may be reduced. With fertilization, CHO production in the current year is increased, root CHO storage may be increased, and the following year's growth may not be as strongly affected by moisture limitation (Raitio et al. 1994; Gaul et al. 2008). Ewers et al. (2005) showed that aspen displayed the lowest transpiration rates compared with other boreal species in Manitoba. Another possible explanation is that the N fertilization will increase the amount of available N and potentially reduce the spatial variability of the quantities of available N across the research plot. A more uniform distribution of N could increase the spatial distribution of the root biomass (Haynes and Gower 1995). These dynamics could increase the soil volume used by the tree, which could increase the quantity of available moisture and diminish potential moisture stress even though soil moisture dynamics for the control and fertilized plots were equivalent (J. Yarie, K. Van Cleve, B. Schlentner, R. Erickson, and J. Downing, unpublished data). The tree's capacity to deal with the moisture supply may have improved as a result of improved soil fertility and potential utilization of a larger volume of soil.

Natural stand dynamics due to mortality in the control plot on the oldest (starting age of 120) aspen fertilizer treatment was probably the factor that resulted in the observed significant decrease in growth for the 17-year measurement period. The control plot actually showed a 48% mortality rate compared with *13%* mortality in the fertilized plot. As a result, the greater stand density in the fertilized plot resulted in higher competition for the available soil moisture and the potential for significant lower tree growth in the fertilized plot compared with the control. Only one significant decrease in the fertilized area was observed in the yearly data set (J. Yarie, K. Van Cleve, B. Schlentner, R. Erickson, and J. Downing, unpublished data) but the fertilized plot did show nonsignificant smaller tree growth throughout the 17-year study period.

Fig. 4. Comparison of the average annual basal area growth (BAG) per tree between control and fertilization treatments averaged across the entire study period in an age sequence of aspen (A) and birch (B) stands in interior Alaska. The total number of years measured is indicated at the bottom of the figure. The starting age of the aspen stands was 15, 45, 60, and 120 years for the 1A, 45A, 3A, and 6A stands, respectively. The starting age of the birch stands was 25, 65, and 120 years for the 5B, 3B, and 6B stands, respectively. C represents the control plot and F represents the fertilized plot. Fertilized plots received 112 kg·ha^{-1}·year^{-1} N as NH_4NO_3, 56 kg·ha^{-1}·year^{-1} P as triple super phosphate, and 112 kg·ha^{-1}·year^{-1} K as potassium chloride during the first 5 years of the experiment. Paired control and fertilized plots within classes for each species sharing different letters have growth rates that differ at the $P < 0.05$ level.

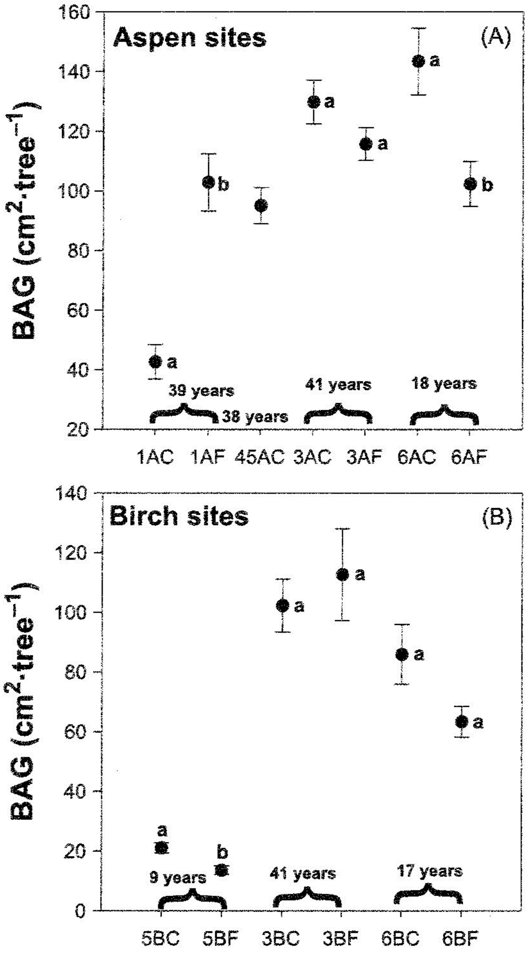
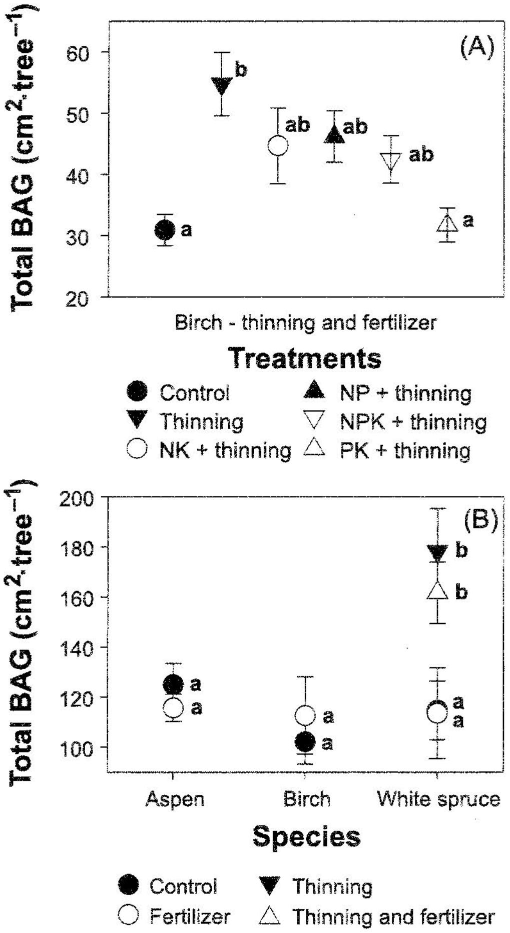


Fig. 5. Comparison of the 15-year total basal area growth (BAG) per tree in the middle-aged birch stand (starting age of 65) in control, thinned, and thinned plus fertilization treatments (A) and across three vegetation types with a starting age of approximately 65 years and a total measurement period of 40 years (B). Thinning and the thinning plus fertilization treatments were only applied to the white spruce stands presented in B. Fertilizer was applied at the rates of 112 kg·ha^{-1}·year^{-1} N as NH_4NO_3, 56 kg·ha^{-1}·year^{-1} P as triple super phosphate, and 112 kg·ha^{-1}·year^{-1} as potassium chloride during the first 5 years of the experiment in the combinations listed in the legend of panel A and as an NPK treatment in the treatments displayed in panel B. Paired control and fertilized plots within classes for each species sharing different letters have growth rates that differ at the $P < 0.05$ level.



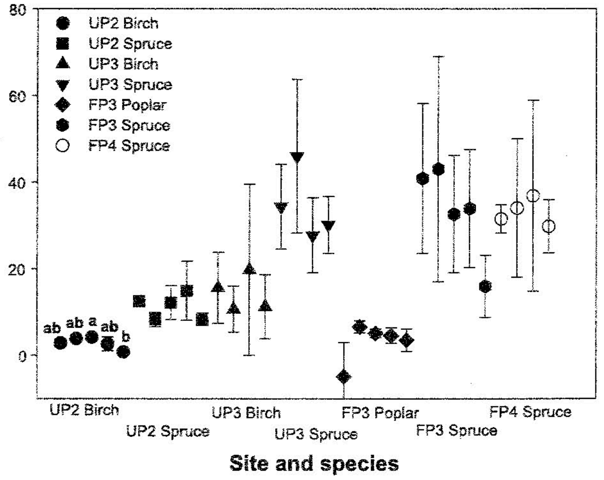
August rainfall (positive correlation) and August evaporation (negative correlation) were the two climatic factors that were significantly correlated with the growth of birch. Thinning treatments resulted in an increase in individual tree growth (Fig. 5A), suggesting that as with white spruce (Fig. 5B), stand density and thus water availability may be a major control on the growth dynamics of birch. Across the fertilization study, the results were mixed, with a decrease in growth in the youngest site and no significant changes in the two older sites (Fig. 4B). In the young age class of the unthinned fertilized treatment. fertilization could have resulted in an increase in foliar biomass. which would increase moisture demands and, as a result decrease individual tree growth (Fig. 4B).

The differences between the aspen and birch response to fertilization could possibly be tied to the species' ability to handle moisture stress on these particular study sites. Aspen is generally found on the driest sites in interior Alaska and displays a tendency to handle moisture stress better than birch. The thinning treatment in the birch stand most likely eased moisture stress and resulted in an increase in growth of the remaining trees. Once thinned, there was a tendency for fertilization to reduce tree growth, perhaps because of an increase in the moisture stress resulting from higher photosynthetic rates brought on by increased nutrient availability. The result was a tendency for a lower growth rate than that seen on the thinning-only treatment but a tendency for higher growth than that seen on the control treatment.

Similar to birch, the growth of upland white spruce was increased by stand thinning but was insensitive to fertilization (Fig. 5B) (Yarie *2009a;* J. Yarie, K. Van Cleve, B. Schlentner, R Erickson, and J. Downing, unpublished data). Moreover, the growth of white spruce in thinned plus fertilized stands tended to be less than in thinned stands alone by the end of the experimental period (Fig. *5B),* similar to responses seen in birch (Fig. *5A).* However, during years 4 and *5* of the experiment, thinning plus fertilization increased white spruce growth relative to thinning alone (data not shown), but the duration of increase was limited to the time frame in which the fertilizer was actually applied (J. Yarie, K. Van Cleve. B. Schlentner, R Erickson. and J. Downing, unpublished data). Thus, while significant increases in growth as a result of thinning lasted for over 20 years after the initial one-time treatment. responses to fertilization were short-lived. These results are consistent with the drought studies reported by Yarie (2008). White spruce growth in upland midsuccessional sites displayed no significant reduction in growth following exclusion of summer rainfall, suggesting that tree growth is strongly controlled by spring soil moisture recharge from late fall rains and spring snowmelt. Tree growth primarily occurs in the first half of the frost-free season, so the depth of the preseason soil moisture recharge is likely an important factor controlling tree growth. Thus, long-term growth increases in both birch and white spruce in response to thinning treatment are most likely due to reductions in competition for soil moisture.

Tree growth on the long-term BNZ LTER experimental plots was insensitive to C and N treatments, concurring that an environmental factor other than site nutrient status is the primary limiting factor of tree growth on these sites (Fig. 6). The one time sugar and sawdust additions, designed to raise the forest floor *C/N* ratio to 50 showed virtually no effect on tree growth in either floodplain or upland landscapes. Moreover. annual fertilizer addition designed to double the estimated N mineralization rate also resulted in no change in tree growth. However, results from these long-term experiments suggest that the structure of growth-limiting factors appears different between upland and floodplain landscapes in the midsuccessional stands. White spruce basal area growth and average tree diameters measured in the deciduous-to-coniferous turning point were double on the floodplain (FP3) compared with upland sites (UP2), with tree ages at 44 and 49 years, respectively (Fig. 6). Trees in upland sites do not have access to groundwater supplies, and soil N availability could be lower because of a lower density of alder in early successional upland stands prior to the presence of the hardwood - white spruce turning point. However, estimates of N availability indicated that quantities of mineralized N are higher in the uplands (Gordon and Van Cleve 1983; Van Cleve et al. 1986, 1993; Pare and Van Cleve 1993). A second factor is tied to the groundwater dynamics on the floodplain. It has been shown that hyporheic water flow through floodplain terraces can result in a substantial movement of N through the subsoil layers (Clilverd et al. 2008; Lisuzzo et al. 2008).

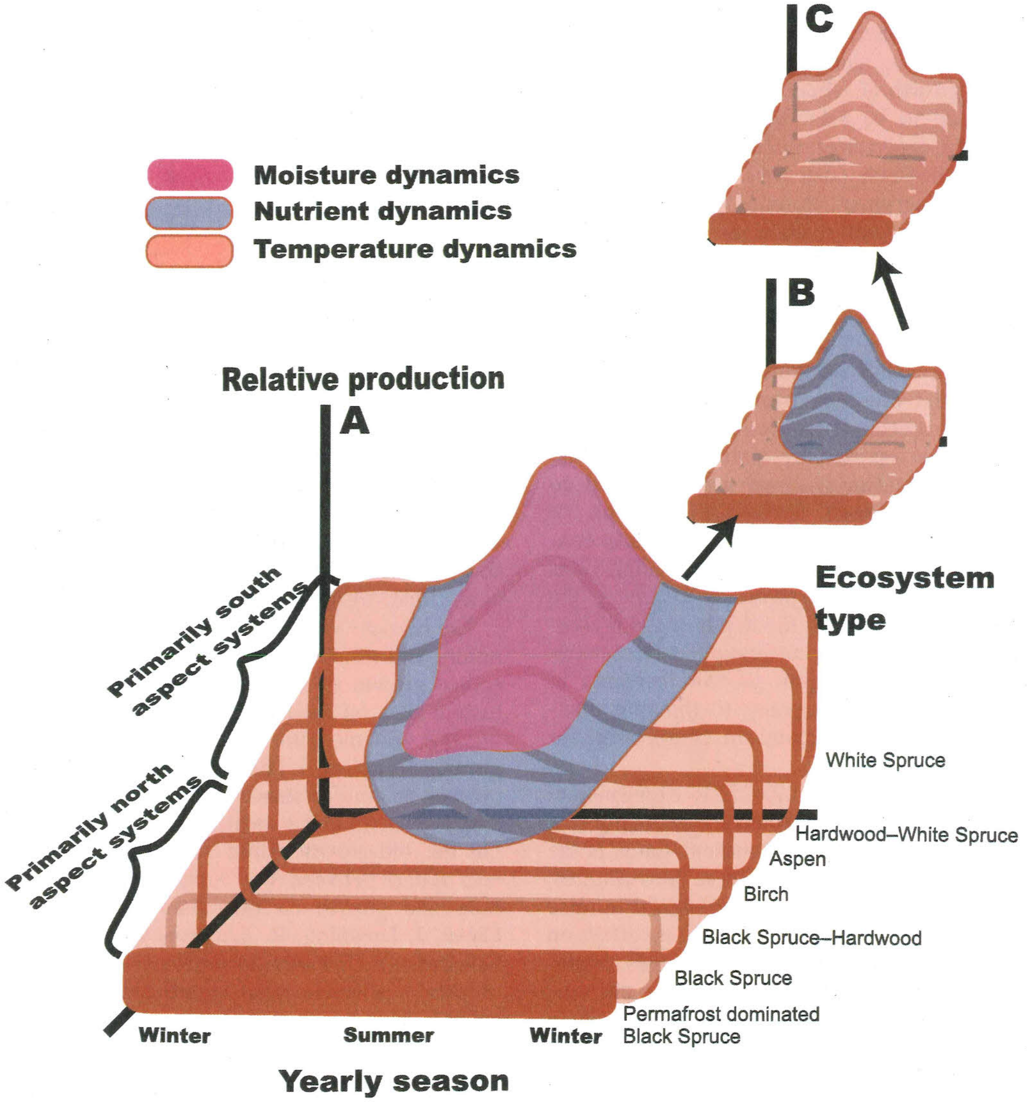
Fig. 6. Total basal area growth (BAG) in two successional stages for a 20-year period in the upland (UP) and floodplain (FP) landscape positions for birch, white spruce, and balsam poplar. Treatments for each site and species are in the order of sugar, control, sawdust, fertilizer, and drought (left to right). Drought treatments were applied only on the UP2 and FP3 sites. Only one significant difference was found for birch — on the UP2 site between the sawdust and drought treatments.



The climate variables of evaporation/rainfall ratio, evaporation, and rainfall were significantly correlated with white spruce growth on control sites in the FP3 and FP4 experimental sites on the floodplain of the Tanana River, suggesting that soil moisture was an important factor limiting tree growth. In upland LTER sites during the transition from deciduous to conifer stands (UP2 sites). the primary control of tree growth is tied to soil moisture dynamics (Yarie 2008). On the old-growth white spruce site (UP3), a correlation was found between the current year's evaporation/rainfall ratio and growth on the control plots (J. Yarie, K. Van Cleve, J. Downing, R. Erickson, and B. Schlentner, unpublished data). However, in fertilized plots, a larger number of climatic variables were significantly correlated with tree growth. This suggests that the major control of tree growth on deciduous and old-growth white spruce upland sites is tied to climatic variables that have a strong influence on soil moisture dynamics.

Spring soil water content was close to field capacity, and the drought treatment resulted in a significant decrease in available soil water during the growing season at shallow measurement depths (Yarie 2008). These results suggest that in contrast to responses seen in upland stands, summer rainfall plays a major role in supplying water for tree growth in these floodplain forests, where tree growth was reduced 34% in drought plots relative to controls (Yarie 2008). Given that the majority of fine-root production is concentrated in surface soil layers (0-30 cm, Ruess et al. 2006), floodplain trees may have limited access to groundwater as a major source of moisture during the growing season. In contrast, root growth in upland stands extends deeper into soils (Viereck et al. 1986), and soil moisture measurements

Fig. 7. Seasonal progression of productivity limiting factors for the forested vegetation types in interior Alaska (A). The primary limiting factors are for middle- to late-aged stands of the vegetation types presented in the figure. The yearly dynamics are not drawn to scale. If the stands had lower stocking levels or if thinning had occurred in the stand, then the limiting-factor scenario could approach that shown in B. In the event of stand thinning and a significant increase in nutrient input then the limiting-factor dynamics could approach that shown in C. In this case, the productivity would be controlled by species phenology related to regional climate dynamics. The three figures represent a hierarchical structure of potential growth-limiting factors, starting with the least significant factor (C) and moving to the most significant factor (A).



show higher moisture contents at deeper levels in the soil profile (Yarie 2008). A similar summer reduction of moisture in the deeper soil layers did not occur in floodplain midsuccessional stands, indicating a shallower functioning root system and capillary rise of moisture from the water table of the floodplain soil profiles. The availability of this capillary water will be directly tied to the river level dynamics (Clilverd et al. 2008) and may not actually influence the rooting zone water content. Fine-root biomass did not change as a result of throughfall displacement in a mixed hardwood forest (Joslin et al. 2000); however, the root distribution did marginally shift to deeper depths (Joslin and Wolfe 2003). A downward shift in fine-root growth was also found for a loblolly pine stand and was due to moisture deficits (Torreano and Morris 1998). Similarly, Runck (2008) found that total coarse-root biomass (>2 mm diameter) was not significantly affected but that there was an increase in coarse roots at deeper depths in the BNZ LTER summer rainfall exclusion treatments for both upland and floodplain sites.

Hierarchical structure of state factor controls

The complexity of ecosystem dynamics across the landscape is related to the differential structure and interaction of the process-limiting factors at different locations. From the temporal perspective, tree growth may be limited by nutrient availability early in the growing season when leaf-out imposes high plant N demands, after soil temperature limitations have been reduced by increasing air and soil temperature. Later in the growing season, the growth-limiting factor may change when precipitation and temperature dynamics result in a significant reduction of available soil moisture. Productivity may be less than that seen in the early season and may reflect seasonal characteristics of plant phenology and the temporal progression of plant growth throughout the growing season.

The limiting factor differences could also be related to the spatial environment created after ecosystem disturbances such as fire, topographic features such as slope and aspect, and landscape position such as uplands versus river floodplains and lowlands. For example, it is a common result of fire to produce a patchy landscape caused by variability in fire intensity at a relatively small spatial scale ($< m^2$ patches). These patches would have different nutrient composition and availability in addition to contrasting soil moisture dynamics. This variability would then have significant effects on site regeneration and growth of colonizing vegetation.

One potential structure of growth-limiting factors for the interior Alaska taiga forest is presented in Fig. 7. Assuming all other environmental factors were optimum, tree productivity would be controlled by seasonal temperature dynamics (Fig. 7C). During optimal temperature conditions, a second level of growth constraints - nutrient availability - will dominate. This is supported by the thinning and fertilization studies conducted in both white spruce and birch ecosystems **(J. Yarie, K. Van Cleve, B.** Schlentner, **R.** Erickson, **and** J. Downing. unpublished data). This condition could be related to the potential nutrient productivity of the vegetation (Agren 1983, 1985). In this context, the only limiting factor is the availability of the single limiting nutrient on the site. However, productivity has been shown to be limited by environmental factors other than nutrients (Yarie *2009a. 2009b;* J. Yarie, K. Van Cleve, B. Schlentner, R. Erickson, and J. Downing, unpublished data). So the addition of a limiting variable that is structurally at a higher level (nutrients) could result in a system that has even stronger control by the primary limiting factor (moisture availability). This is supported by an increase in the number of negative correlations between growth and water availability variables (evaporation, evaporation/rainfall ratio) in fertilized stands. After a short period of utilization of soil water during the spring flush of growth, water becomes the primary limiting variable. A direct change in that controlling factor, such as irrigation in a dry environment. should increase growth up to the limit set by the next environmental factor. say N. However a change in the amplitude of a limiting factor, caused by thinning a forest stand to improve soil water supply (an indirect change related to the limiting factor water availability), may not change the control of growth with comparable effectiveness that would be observed as a result of irrigation (a direct change in the limiting factor availability),

A number of growth-limiting factors can be alleviated as a result of thinning a forest stand (Devine and Harrington 2009). For example, in a dense stand, an increase in light availability would be expected to enhance growth if another environmental factor were not limiting. Nutrient availability would be expected to increase as a result of reduced competition and greater site utilization by the remaining trees (Claveau et al. 2006). Thinning may also increase nutrient turnover in the soil as a result of higher soil temperature. The lack of an increased response of the thinning plus fertilization treatment over the thinning treatment suggests that thinning did improve growing conditions but there was still an overall moisture limitation on the sites tied to the precipitation timing and quantities typical of interior Alaska. Changes in these environmental factors tied to increased root coverage may require several years to produce an increase in growth in contrast to light or moisture availability (Waterworth et al. 2007). Such time lags in addition to age-related changes in growth partitioning (Litton and Giardina 2008) make characterization of changes in growth-limiting factors extremely complex. As indicated in Fig. 7A, nutrient limitation of tree growth may not be the primary limiting factor in all locations or across the entire yearly time frame.

The limiting-factor diagram (Fig. 7) provides a refined, generalized view of the relationship between ecosystem function and vegetation production. However, long-term data on aboveground and belowground tree growth coupled with detailed monitoring of soil moisture, temperature, and nutrient availability are required to translate this model into a mechanistic framework that allows us to predict potential changes in vegetation distribution and productivity in response to changing climate. Where the climate change dynamics would place us in the water-temperature space would give us an indication of the resilience of our current ecosystem structure to the future climate.

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