

SENSITIVITY OF BOREAL FOREST CARBON DYNAMICS TO LONG-TERM
(1989-2005) THROUGHFALL EXCLUSION IN INTERIOR ALASKA

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Abstract

The objective of this study was to assess the effect of throughfall exclusion (1989-2005) on forest vegetation and soil in upland and floodplain landscape positions. In uplands, imposed drought reduced soil moisture at 5, 10, and 20 cm depths and increased soil C storage by slowing decomposer activity at the surface. In the drought plots, aboveground tree growth was reduced and root biomass in mineral soil was increased. In floodplains, imposed drought did not reduce soil moisture as strongly as it did in uplands, though near-surface soil C storage was still increased as a result of reduced decomposer activity. Floodplain vegetation response to imposed drought differed from that of uplands; imposed drought did not reduce aboveground tree growth but instead reduced root biomass in mineral soil. At both landscape positions, imposed drought accelerated the loss of understory vegetation. Overall, the results of the throughfall exclusion indicated that chronic soil drying is likely to increase forest C storage only in floodplains. In uplands, where soil moisture is more limited, forest C storage is not as likely to change because an increase in soil C may be offset by reduced tree growth.

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Chapter 1 General Introduction

1.1 Introduction

General circulation models predict that the greatest temperature increases will occur at high latitudes, where the boreal forest houses a large fraction (20-60 %) of the world's terrestrial carbon (C) in its soil and vegetation (Post *et al.* 1982). In interior Alaska, increased atmospheric CO₂ concentration has resulted in a longer growing season and increased mean annual temperature with no concurrent change in annual precipitation, causing drought stress in many parts of the state (Barber *et al.* 2000). It is well established that soil moisture affects soil C storage both directly and indirectly. Directly, it influences decomposer activity and leaching; indirectly, it influences plant growth and thus the amount and composition of plant litter that is eventually deposited in or on the soil (Porporato *et al.* 2003). Therefore, changes in soil moisture are likely to alter the amount, quality, and depth at which C is stored in the soil profile, particularly in arid and semi-arid regions, such as interior Alaska. Depending on the degree to which climate conditions influence the balance between C inputs (photosynthesis) and C outputs (heterotrophic respiration), Alaska's boreal forests may serve as a significant source or sink of global C.

In 1989, a throughfall exclusion experiment was established in the Bonanza Creek Experimental Forest (BCEF) with the objective of assessing how growing-season drought influences boreal forest productivity across the landscape of interior Alaska (Yarie 2008). The nature of this experiment, both long-term (1989-2005) and ecosystem-scale, has provided a unique opportunity to examine how boreal forest vegetation and soil respond to chronic soil moisture reductions. To date, researchers have investigated the sensitivity of soil respiration (Billings *et al.* 1998, Gulledge and Schimel 2000), methane fluxes (Billings *et al.* 2000, Gulledge and Schimel 2000), and growth of individual trees (Yarie 2008) to imposed drought in this forest. The objective of this present study was to build upon these earlier studies and examine how imposed

drought affects above- and belowground biomass and soil C storage in the upper ~1/3 meter of the soil profile.

1.2 *Vegetation hypotheses*

I tested three hypotheses regarding the response of vegetation to imposed drought:

Hypothesis 1: Imposed drought reduces stand-level tree growth in uplands but not in floodplains, where soil moisture may be augmented by groundwater.

Hypothesis 2: Reduced moisture near the surface results in increased root biomass deep in the profile because resource limitations near the soil surface often stimulate root growth deeper in the soil profile where resources are more available.

Hypothesis 3: Imposed drought accelerates the loss of understory vegetation (*e.g.*, shrubs, herbs, and bryophytes) based on observations that limited root extension (excluding bryophytes) and C reserves of most understory species make them highly susceptible to drought stress (Donovan and Ehleringer 1991, Hanson and Weltzin 2000).

1.3 *Soil hypotheses*

I tested three additional hypotheses addressing the effect of imposed drought on soil C storage:

Hypothesis 1: Imposed drought impedes decomposer activity but not aboveground foliar litterfall, causing a buildup of C at the surface.

Hypothesis 2: Imposed drought reduces decomposer activity near the surface but not in underlying soil because surface soils are more prone to drying from evaporative moisture losses.

Hypothesis 3: The effect of imposed drought on soil C storage depends on landscape position and will therefore vary across the landscape. For example, floodplain forests have the potential to receive moisture from rainfall, snowmelt, and groundwater capillarity and are therefore less exposed to drought stress than upland forests, which solely rely on precipitation (*i.e.*, rainfall, snowmelt) as a source of soil water.

The effects of imposed drought on forest vegetation and soil are described in Chapters 2 and 3 (respectively). In Chapter 4, I provide a general summary of our results and discuss the implications for future boreal forest C storage.

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Chapter 2 Landscape Position Influences the Response of Boreal Forest Vegetation to Long-term Experimental Drought in Interior Alaska¹

2.1 Abstract

The objective of this study was to examine the response of mid-successional boreal forest vegetation to long-term (1989-2005) experimental throughfall exclusion (“imposed drought”) in interior Alaska. We examined the stand-level response of aboveground tree biomass, root biomass (O horizon and underlying 30 cm mineral soil), and understory vegetation to imposed drought at two landscape positions (upland and floodplain). In uplands, imposed drought lowered soil moisture at 5, 10, and 20 cm between July and September, reduced aboveground tree growth by 17 %, and increased root biomass in mineral soil by 25 % compared to controls. In floodplains, imposed drought had less effect on soil moisture, only reducing moisture at 5 and 10 cm between July and September. Imposed drought reduced floodplain root biomass at the 15-30 cm depth by 66 % compared to controls, which was not accompanied by a change in aboveground tree growth. At both landscape positions, understory vegetation disappeared more rapidly in the drought plots. This study’s results indicated that upland forests are overall more sensitive to throughfall exclusion and respond to prolonged soil drying by reducing aboveground biomass and increasing belowground biomass. In contrast to uplands, imposed drought in floodplain forests did not elicit a reduction in tree growth, though it reduced the presence of understory vegetation and root biomass.

¹S. Runck, D. Valentine, and J. Yarie. Landscape Position Influences the Response of Boreal Forest Vegetation to Long-term Experimental Drought in Interior Alaska. Prepared for submission in the Canadian Journal of Forest Research.

2.2 Introduction

The large quantity of organic carbon (C) stored in boreal forest soils is controlled, in part, by plant growth, which fixes atmospheric CO₂ and transfers it to the soil through litterfall, root turnover, and death of individual plants (Kirschbaum 2000). Therefore, vegetation's capacity for continued growth under environmental stress is key to the future of forest soil C storage. To date, several studies have reported that changes in precipitation patterns, increased frequency and duration of drought, and warmer temperatures limit soil moisture and exacerbate growing season drought stress. For example, Barber *et al.* (2000) found that growth of white spruce, the principal commercial tree species in interior Alaska, decreased throughout Alaska during the 20th century in response to warming-induced drought stress. In Canada, drought stress has also proven detrimental to tree growth. Investigations conducted by Girardin and Tardiff (2005) showed that deciduous and coniferous tree growth in Manitoba was sensitive to summer drought. Hogg and Ross (2005) came to a similar conclusion for aspen and white spruce in the interior of western Canada. The response of floodplain forests to drought stress has received less attention due to the widely-held assumption that floodplain forests are less exposed to moisture stress than their upland counterparts. This assumption requires further testing, however, because some of the most productive forests in interior Alaska occur on floodplains (Van Cleve *et al.* 1983).

The interior Alaskan region is expected to continue experiencing increasing temperatures and total annual precipitation during the remainder of the 21st century, though it remains uncertain if precipitation increases will offset increased soil moisture loss driven by increased temperatures (Stafford *et al.* 2000). To improve our understanding of the response of vegetation to potential future drought stress, this study examined how forest vegetation responds to long-term (16 years) experimentally reduced soil moisture (hereafter referred to as “imposed drought” or “drought treatment”) at two landscape positions (uplands and floodplains) in an interior Alaskan boreal forest. We hypothesized (H₁) that imposed drought reduces stand-level tree growth in uplands but not in floodplains, where soil moisture may be augmented by

groundwater. Our second hypothesis (H₂) was that reduced moisture near the surface results in increased root biomass deep in the profile because resource limitations near the soil surface often stimulate root growth deeper in the soil profile where resources are more available. Our final hypothesis (H₃) was that imposed drought accelerates the loss of understory vegetation (*e.g.*, shrubs, herbs, and bryophytes) based on observations that limited root extension (excluding bryophytes) and C reserves of most understory species make them highly susceptible to drought stress (Donovan and Ehleringer 1991, Hanson and Weltzin 2000).

2.3 *Methods and materials*

2.3.1 Study overview

This study is part of a larger ongoing throughfall exclusion experiment established in 1989 to assess how growing season drought influences boreal forest productivity in interior Alaska (Yarie 2008) and includes data collected by Bonanza Creek Experimental Forest (BCEF) personnel (identified by reference to the Bonanza Creek data bank, www.lter.uaf.edu). Study sites are located within the BCEF (Fig. 2.1), a major focus of the Bonanza Creek Long-term Ecological Research program. Sites differ in topography (upland, floodplain), parent material (bedrock of Precambrian schist overlain with loess in uplands and alluvium in floodplains), and disturbance regime (forest fire in uplands, erosion and deposition from river flooding in floodplains), but they are similar with respect to vegetation (transitioning from dominance by deciduous trees to white spruce), regional climate (subarctic), and age.

2.3.2 Site description

Upland sites are located on a well-drained ridge 308 m above mean sea level facing east-southeast on a 20 degree slope, where soil moisture is derived from snowmelt and rainfall. Moisture flow is unsaturated and depends on soil hydraulic conductivity. Soils in these sites are rock- and permafrost-free well-drained loessal Alfic Cryochrepts; the soil texture is a silt loam (Viereck *et al.* 1986). Silt loam has an

approximate wilting point of 14 % volumetric water content (VWC). A forest fire occurring in about 1920 was the last major disturbance, and charcoal is present to a depth of 30 cm in the soil profile. Upland forests have a closed canopy and are transitioning from dominance by deciduous species (birch, aspen, and balsam poplar) to white spruce (Table 2.1).

Floodplain sites are located along the Tanana River, which receives approximately 85 % of its water from glacial melt in the Alaska Range (Yarie *et al.* 1998). River terraces are approximately 139 m above mean sea level. Floodplain sites receive moisture from precipitation (rainfall, snowmelt) and groundwater capillarity and flooding, though high terrace heights generally prevent the latter except under extreme conditions (Yarie *et al.* 1998, Magoun and Dean 2000). Soils in floodplain sites are well-drained, rock- and permafrost-free Typic Cryofluvents. The soil texture is progressively coarser with depth; silt loam near the surface and sandy loam further down (Viereck *et al.* 1986). Sandy loam has an approximate wilting point of 9 % VWC. The flood of 1967 was the last major disturbance in these sites and multiple buried O horizons are present to a depth of 40 cm in the soil profile. Floodplain forests have an open canopy and are transitioning from dominance by deciduous species (balsam poplar) to white spruce (Table 2.1).

2.3.3 Regional climate

Interior Alaska's climate is continental, characterized by low humidity and low annual precipitation (280 mm at Fairbanks International Airport, averaged over 1929-2006), of which approximately 35 % occurs as snow (Slaughter and Viereck 1986). Convective storms produce most of the summer precipitation, though major frontal systems can occasionally generate substantial precipitation (Streten 1967). In the summer, a soil moisture deficit is created by relatively high evapotranspiration that can consume up to 100 % of the mean annual precipitation (Slaughter and Viereck 1986). Snow cover is generally present from mid-October through mid-April. Growing season (May-September) length is approximately 120 days. Mean annual air temperature is

low (-3.7°C); winter temperatures can drop to as low as -50°C and summer temperatures can reach as high as 35°C (Viereck *et al.* 1993).

2.3.4 Drought treatment

In 1989, three paired control and drought treatments were established in upland and floodplain forests at the BCEF near Fairbanks, Alaska. In uplands replicates were positioned over a 2 km distance and in floodplains a 4.5 km distance (Fig. 2.1). Greenhouse panels were secured on top of a slanted wooden frame ≥ 1.75 m tall (Fig. 2.2) from early May through mid-September, creating a “roof” underneath the forest canopy to prevent throughfall from reaching the soil surface. The height of the frame allowed unconstrained air movement beneath the roof. In each location where a tree was taller than the roof, a hole slightly exceeding the diameter of the tree stem was cut and a wooden “dam” was positioned up-slope from the hole to prevent water from entering into the treatment area. Until 2003, the roof panels were constructed of translucent greenhouse panels; in 2003 they were replaced with transparent greenhouse panels. In mid-September of every year, the roof was removed to prevent snowfall disruption and litter collected on the roof was returned to the treatment area to minimize litter losses. A plastic barrier buried to a depth of 75 cm around the stand perimeter prevented water movement from the surrounding area into the exclusion area.

In 1994, time domain reflectometry (TDR) probes were installed at 5, 10, 20, and 50 cm below the O horizon-mineral soil interface to monitor soil moisture. Throughfall was measured with standard rain gauges, and in floodplains, depth to groundwater was measured with groundwater wells constructed from 10.2 cm diameter perforated plastic pipe. Soil moisture, throughfall, and groundwater depth measurements were accessed from the Bonanza Creek data bank.

2.3.5 Aboveground biomass change

To determine how imposed drought influences aboveground forest biomass, we examined forest vegetation change between 1989, when the throughfall exclusion was initiated, and 2003, when the most recent tree inventory occurred. All changes were examined at the plot-level (150 m² treatment area). Growth, ingrowth, mortality, and the resulting net change of forest biomass, indicating whether a stand has undergone a net biomass loss (negative values) or gain (positive values) for a given period, were all based on tree diameter measurements accessed from the Bonanza Creek data bank. Radial tree growth measurements were made on all trees > 2.54 cm diameter at breast height (DBH). Understory vegetation, which represents a small fraction of the aboveground biomass in these forests, was excluded from this analysis. Species-specific allometric equations developed by Yarie *et al.* (2007) were used to convert tree diameter into tree biomass (foliage, branches, stemwood, and bark), expressed as kilograms of biomass. To express tree biomass at the plot-level, the total tree biomass was divided by the 150 m² treatment area.

Net change of aboveground forest biomass was calculated with the following equation:

$$\Delta \text{ Aboveground biomass} = \text{Aboveground biomass}_{2003} - \text{Aboveground biomass}_{1989}$$

where

$\Delta \text{ Aboveground biomass}$ is the net change of aboveground biomass of all trees between the 1989 and 2003 interval, which takes into account biomass gained from tree growth and ingrowth and biomass loss from tree mortality

$\text{Aboveground biomass}_{1989}$ is the total amount of aboveground biomass of all trees \geq 2.54 cm DBH in 1989

*Aboveground biomass*₂₀₀₃ is the total amount of aboveground biomass of all trees \geq 2.54 cm DBH in 2003, when the most recent tree inventory occurred.

2.3.6 Understory vegetation

Cover estimates were used to determine how understory vegetation responded to imposed drought. Change in the presence of understory vegetation was assessed by comparing absolute understory cover (percent) in 1988 or 1989 with that in 2005 or 2006. Initial cover of low shrubs, herbs, forbs, and bryophytes was recorded for 20 1-m² plots in the BNZ-LTER long-term control plots (data accessed from the Bonanza Creek data bank). In 2005 and 2006, we measured vegetation cover in the actual treatment plots along two diagonal transects, amounting to approximately 28 sample points per treatment replicate.

2.3.7 Belowground biomass

We quantified belowground biomass (root biomass) with measurements of live root biomass (2-25 mm diameter). Although fine (< 2 mm diameter) roots are important to nutrient and water uptake, their biomass is extremely variable within even a single growing season (Ruess *et al.* 1996); measuring fine root biomass was beyond the scope of this study. Instead, we relied upon the distribution patterns of coarse (\geq 2 mm diameter) roots, which provide structural support and serve as a C and nutrient sink (Nadelhoffer and Raich 1992), as an indicator of fine root distribution. Root biomass measurements were determined on soil cores taken in August 2005. Cores were taken \geq 1 m from the base of trees > 1.5 m tall (*i.e.*, trees that extended through the throughfall roof) to avoid any influence of stemflow. Samples included O horizons (11 cm diameter cores) and underlying 30 cm of mineral soil (5.5 cm diameter cores), the depths where most root biomass and biological activity occur (Jackson *et al.* 1996). In the field, we separated soil cores into four segments (O horizon, 0-5, 5-15, 15-30 cm). In the laboratory, live roots (\geq 2 mm diameter) were sieved and hand-picked from the soil cores, rinsed free of debris and fungal hyphae, and oven dried (65 ° C). The

remaining soil was set aside for soil C and nitrogen (N) analyses (Chapter 3). Root biomass was calculated as the mass of roots per mass of dry soil and converted to an area basis based on bulk density determination for each depth increment. All laboratory work was conducted in the University of Alaska Fairbanks Forest Soils Laboratory.

2.3.8 Statistical analysis

The experimental unit in this study was the 150 m² treatment area, which we subsampled to obtain the best estimate of the mean. The experimental design was paired, meaning that the difference between paired control and drought plots was the measurement of interest. Replicate stands within a landscape were separated spatially (Fig. 2.2); variability due to spatial differences was addressed by treatment pairing. Statistical analyses consisted of paired student's *t*-tests of means. *T*-tests were one-tailed when we expected imposed drought to cause a directional change and two-tailed when the direction of change was not specified *a-priori*. *T*-tests were performed using GraphPad Prism (V. 5.00). Data were presented as the mean ($n = 3$) and standard error of the mean, the latter provided to give the reader a sense of the amount of variability among replicates within a given treatment. With a paired *t*-test, the consistency of change or difference between treatments is more important than the amount of variability within a treatment. Therefore, the degree to which error bars overlap between treatments is not indicative of whether a given variable differed between treatments.

Post-hoc power analyses were performed using R (V. 2.6.2). Due to the large-scale and long-term nature of this study, practicality necessitated a limited number of replications (three paired replicates at two landscape positions) at the expense of statistical test power and the increased probability of a Type II error. Given the relatively small sample size of this study and the trade-off between significance level and power, we set alpha at 0.1 rather than the traditional alpha of 0.05.

2.4 Results

2.4.1 Long-term soil moisture (1994-2005)

Soil moisture was generally greatest at the beginning of the growing season, due to moisture recharge from snowmelt. After snowmelt, soil moisture began a progressive decline that was periodically interrupted by rainfall events. In uplands, soil moisture increased with depth; in July, August, and September, imposed drought lowered soil moisture at all three depths (Fig. 2.3). At 20 cm, upland soil moisture was consistently lower in the drought treatment over the entire growing season.

In floodplains, imposed drought reduced soil moisture between July and September, though only at the 5 and 10 cm depths (Fig. 2.4). Despite this reduction, soil moisture remained above the wilting point at 10 cm. At 20 cm, soil moisture was relatively constant and similar between treatments over the entire growing season. Depth to groundwater, which ranged between 1.5 to 1.8 m, was influenced by the river water level (Yarie 2008), which, in turn, was influenced by rainfall. Thus, months when precipitation was high (*e.g.*, August) were also months when groundwater was relatively shallow.

2.4.2 Upland vegetation

In the upland tree growth analysis, ingrowth was combined with growth because ingrowth comprised a small fraction of the biomass gained from growth (approximately 4 %) and was not affected by imposed drought ($p = 0.85$, $n = 3$, two-tailed t -test, $\alpha = 0.1$). Net aboveground biomass change was consistently lower in the drought replicates (Fig. 2.5), as was aboveground tree growth (17 % lower compared to controls) (Fig. 2.6a). Biomass loss, which was not increased by imposed drought (Fig. 2.6b), was largely due to mortality of deciduous species that was independent of initial (1989) deciduous biomass (Fig. 2.7a). In 2003, when the most recent stand inventory occurred, control and drought treatments still contained similar amounts of aboveground standing biomass, controls averaging 18.52 kg m^{-2} and the drought treatment averaging 18.13 kg m^{-2} ($p = 0.86$, $n = 3$, two-tailed t -test, $\alpha = 0.1$).

Understory vegetation disappeared from both upland treatments. However, imposed drought accelerated the loss of understory shrubs and herbs almost two times faster compared to controls (Fig. 2.8). Cover of bryophytes was low at the start of the experiment and was not significantly reduced by imposed drought. Although imposed drought did not significantly increase root biomass for the entire depth examined (O horizon-30 cm mineral soil) ($p = 0.28$, $n = 3$, one-tailed t -test, $\alpha = 0.1$) or in the O horizon, it increased root biomass in 0-15 cm mineral soil by 15 % and 15-30 cm mineral soil by 34 % (Fig. 2.9).

2.4.3 Floodplain vegetation

In floodplains, imposed drought did not affect stand-level net biomass change, biomass gain from growth, or biomass loss from tree mortality (Fig. 2.5, 2.10a, and 2.10b). As in uplands, ingrowth was combined with growth because it comprised a small fraction of the biomass gained from growth (< 1 %) and was not affected by imposed drought ($p = 0.72$, $n = 3$, two-tailed t -test, $\alpha = 0.1$). Stand composition (*i.e.*, number of deciduous versus coniferous trees) at the start of the experiment was important in determining the direction of aboveground net biomass change. In all cases, loss of deciduous biomass strongly corresponded to initial (1989) deciduous biomass (Fig. 2.7b). In 2003, aboveground biomass remained similar between treatments, controls averaging 13.89 kg m^{-2} and the drought treatment 16.15 kg m^{-2} ($p = 0.62$, $n = 3$, two-tailed t -test, $\alpha = 0.1$).

Imposed drought sharply reduced the presence of understory vegetation in floodplains, accelerating shrub and herb cover loss seven times faster and bryophyte cover loss four times faster compared to controls (Fig. 2.8). Similar to what was observed in uplands, imposed drought did not affect near-surface root biomass. In subsurface soils, however, imposed drought reduced 15-30 cm root biomass by 66 % (Fig. 2.11), corresponding to an overall 56 % reduction of root biomass for the entire depth examined (O horizon-30 cm mineral soil) ($p = 0.08$, $n = 3$, one-tailed t -test, $\alpha = 0.1$).

2.5 Discussion

2.5.1 Imposed drought decreased biomass gain from tree growth and net change in biomass in uplands but not in floodplains

The forests at both landscape positions were at a turning point in which white spruce replaced deciduous species, thus explaining why aboveground biomass losses tended to be high and net biomass change tended to be low (Fig. 2.6b, 2.10b, and 2.5). Although we did not observe increased biomass loss from mortality in the drought plots at either landscape position, the generally high deciduous tree mortality in this forest indicated that at this stage of forest development, a relatively large quantity of C (compared to the amount contained in living trees) is deposited on the forest floor in the form of felled trees, where it will eventually be broken down and converted into soil organic matter.

In uplands, tree growth was reduced by imposed drought, providing support for our first hypothesis (H_1), although drought had no such effect on either deciduous or coniferous species measured separately. This observation is consistent with Yarie's (2008) investigation of individual tree growth in this forest. Similar to our present study, Yarie found that imposed drought did not significantly reduce growth of any tree species in upland forests. The fact that we were able to detect reduced growth at the stand-level but not at the taxonomic-level is likely due to variability in community composition among the three replicates. Two of the replicates (UP2A and UP2B) were dense mixed stands of white spruce, paper birch, balsam poplar, and aspen whereas the third replicate (UP2C) was a dense mixed stand of aspen and white spruce. As such, inter- and intraspecific competition probably differed between UP2C and the other two replicates.

In floodplains, we did not observe a drought effect for aboveground tree growth (additional support for H_1), net aboveground biomass change, or tree mortality (Fig. 2.10a, 2.5, and 2.10b), possibly explained by differences in initial stand stocking, though it should be noted that although throughfall was excluded, soil moisture in the drought plots was generally still available to vegetation at most depths for most of the

growing season. Like uplands, floodplain replicates were transitioning from dominance by deciduous species to white spruce. Forests in floodplains differed from uplands, however, in their initial (1989) proportion of deciduous and coniferous biomass, which varied considerably within and among replicates. By 2003, 40 % or more of the deciduous trees initially present were lost to mortality, and plots initially stocked with a greater amount of deciduous species biomass tended to have greater biomass loss over the study period (Fig. 2.7b and 2.10b).

Yarie's (2008) analysis of individual tree growth in floodplains found that imposed drought consistently reduced growth of individual white spruce. Based on this information, we took our analysis of white spruce growth one step further and compared average individual white spruce growth between treatments and found that mean individual white spruce growth was consistently lower in each drought replicate (68 % lower). However, the limited number of replicates and relatively large variation in the degree of growth reduction prevented this difference from being statistically significant ($p = 0.13$, $n = 3$, one-tailed t -test, $\alpha = 0.1$). To have detected a reduction in mean individual white spruce growth with 90 % power, seven additional paired replicates would have been necessary ($p = 0.13$, $n = 3$, one-tailed t -test, $\alpha = 0.1$). Thus, our and Yarie's results suggest that although individual trees (white spruce) may exhibit sensitivity to drought stress, individual tree response does not necessarily result in a reduction of stand-level tree growth.

2.5.2 Drought-induced soil moisture reductions corresponded to root biomass differences between treatments

In uplands, soil moisture was significantly lower in the drought plots late in the growing season (July-September), even as far down as 20 cm (Fig. 2.3). Soil moisture values below the wilting point indicated that moisture was not available for plant uptake. Considering that moisture availability increased with depth (down to 20 cm), it is not surprising that root biomass also increased with depth, which supports our second hypothesis (H₂).

In contrast to uplands, the timing and extent of moisture reductions in floodplains soil were less severe (Fig. 2.4). Soil moisture remained above the wilting point in the controls, and in the drought plots, soil moisture only dropped below the wilting point at the 5 cm depth. Both treatments displayed relatively constant soil moisture at 20 cm, possibly due to the steady supply of groundwater through capillary rise or hydraulic lift, the process by which roots passively redistribute water from deeper soils to shallower soils at night. The influence of groundwater capillarity on floodplain soil moisture has been reported by Brenner *et al.* (2006), who observed that the height of the Tanana River influences the amount of groundwater entering the unsaturated zone through capillary flow.

In addition to remaining nearly constant over the entire growing season, floodplain soil moisture at 20 cm was not lowered in the drought treatment (Fig. 2.4). Combining this observation with the reduced presence of roots in 15-30 cm soil (Fig. 2.11) suggests that imposed drought reduced, rather than increased, water uptake by vegetation, though it is also possible that soil moisture at 20 cm was simply more influenced by groundwater than by rainfall. Even if rainfall was not an important influence on soil moisture at 20 cm, why vegetation would reduce root biomass at 15-30 cm, especially considering the moisture reduction closer to the surface at 5 cm, is unknown. One possible explanation is that coarse root biomass in floodplains may not be a good approximation of fine root biomass, which is responsible for water and nutrient uptake. A reduction of roots in response to drought is not unusual, however. In the Solling roof project, for example, Blanck *et al.* (1995) observed that drought imposed on a Norway spruce plantation reduced fine root growth near the soil surface that was not compensated for by fine root growth in the subsoil. Cattânio *et al.* (2002) similarly observed that drought imposed on an old growth forest in eastern Amazonia reduced root growth, though this was not related to a decrease of root biomass (fine and coarse roots) because turnover also decreased.

2.5.3 Imposed drought accelerated the loss of understory vegetation, regardless of landscape position

At both landscape positions, disappearance of shrubs and herbs was accelerated by imposed drought (Fig. 2.8), providing support for our third hypothesis (H₃). Soil moisture reductions generally occurred near the surface, where we would expect most roots of understory species to be located. As such, the near-surface moisture reductions likely drove the increased disappearance of understory vegetation, which was probably out-competed by larger, longer-lived trees having more extensive root systems and carbon reserves (Donovan and Ehleringer 1991; Hanson and Weltzin 2000).

2.5.4 The effects of imposed drought on forest biomass varied by landscape position

Combining the observed reductions of net aboveground biomass change, tree growth, and understory vegetation with the increase in root biomass in mineral soil in upland forests leads us to conclude that upland forests have responded to imposed drought by increasing belowground biomass and decreasing aboveground biomass. The floodplain forest response to imposed drought is less clear, possibly because variable stand composition prevented the detection of a consistent aboveground response to drought or soil moisture was still generally available to vegetation in the drought plots, despite the exclusion of throughfall, and as such, did not reduce tree growth.

Common to both landscape positions was the observation that forests exposed to imposed drought continued to maintain large quantities of root biomass near the surface, even though this was where soil moisture reductions were most evident. This observation implies that water availability of surface soils, although reduced by imposed drought late in the growing season, still benefited vegetation sufficiently that vegetation continued to grow and maintain a large number of roots in surface soils.

2.6 *Summary*

In uplands, where imposed drought reduced soil moisture at all depths examined, the observed reduction of aboveground tree growth and understory vegetation and increase in root biomass in mineral soil indicates that upland forests have responded to imposed drought by increasing belowground biomass and decreasing aboveground biomass. In floodplains, where soil moisture generally remained above the wilting point in the drought plots, imposed drought did not consistently reduce aboveground tree growth even though it reduced understory vegetation and root biomass in mineral soil.

2.7 *Acknowledgements*

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Table 2.1. Upland and floodplain forest communities. Control and drought treatments were replicated three times ($n = 3$) at both landscape positions.

Landscape position	Forest description
Upland	Closed stands of white spruce (<i>Picea glauca</i>) ranging in age between 46 to 60 years-old and deciduous trees (paper birch (<i>Betula papyrifera</i>), balsam poplar (<i>Populus balsamifera</i>), and aspen (<i>Populus tremuloides</i>) roughly ranging in age between 45 and 82 years-old. White spruce beginning to replace deciduous species.
Floodplain	Open stands of balsam poplar (<i>Populus balsamifera</i>) ranging in age between 60 and 96 years-old and white spruce (<i>Picea glauca</i>) ranging in age between 41 and 80 years-old. White spruce beginning to replace deciduous species.

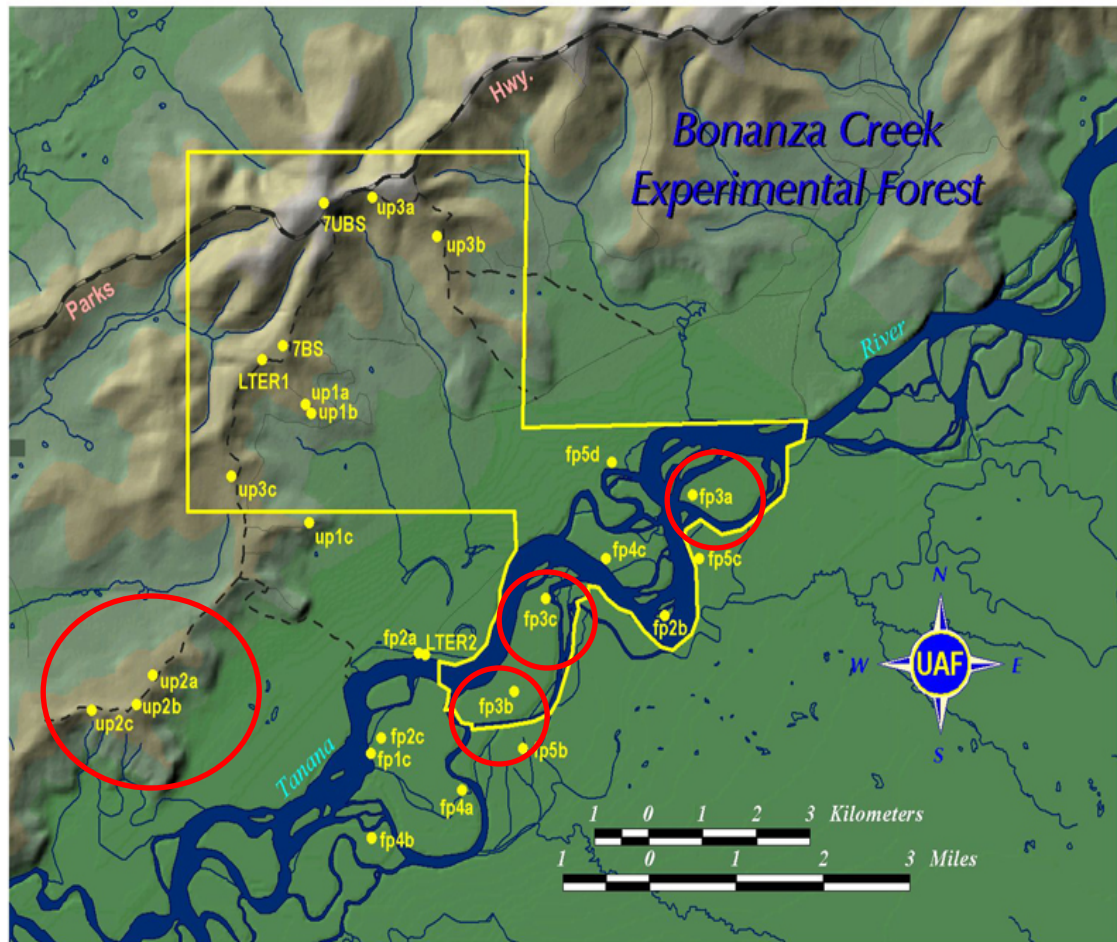


Figure 2.1. Bonanza Creek Experimental Forest. Sites (circled in red) are located south of Fairbanks, Alaska (www.lter.uaf.edu/bnz_map_bcef_static.cfm). Upland sites (UP2-A, B, C) are located northwest of the Tanana River and floodplain sites (FP3-A, B, C) are located along the Tanana River.



Figure 2.2. Example of the throughfall exclusion treatment. Site depicted in photo is UP2C, an aspen-dominated forest located on 30 degree slope in the uplands. Photo was taken perpendicular to the slope in late August 2007.

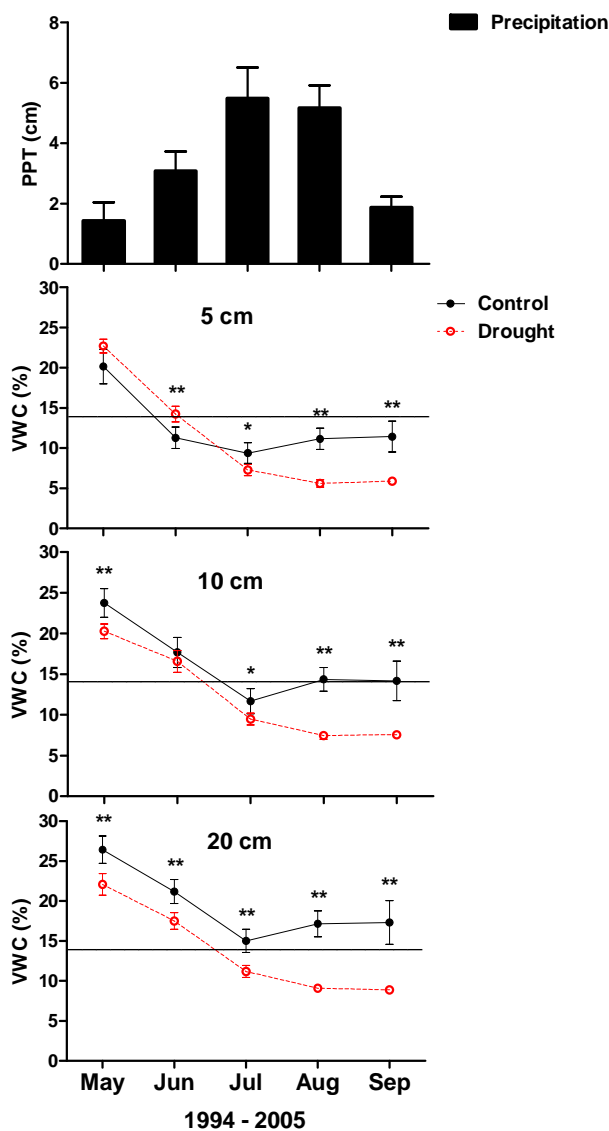


Figure 2.3. Throughfall and volumetric water content (VWC) averages in uplands. VWC was measured at 5, 10, and 20 cm beneath the O horizon - mineral interface from 1994 to 2005. The wilting point (approximately 14 % VWC) is indicated by a horizontal line for each depth. Symbols indicate mean values and error bars indicate the standard error of the mean ($n = 12$, $\alpha = 0.1$). *Denotes a difference between drought and control plots significant at 5 -10 % level of probability. **Denotes a difference between drought and control plots significant at < 5 % level of probability.

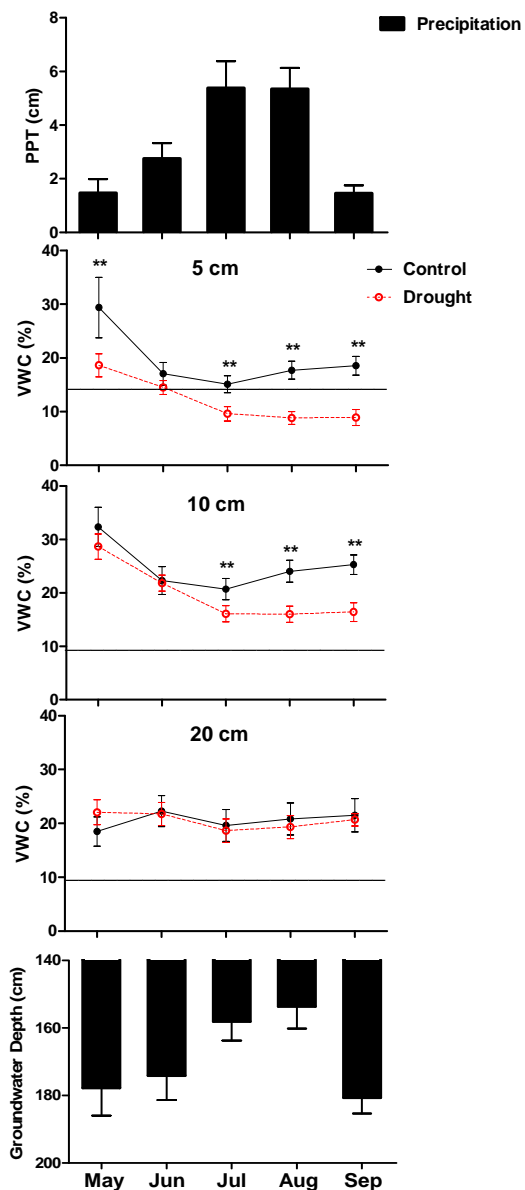


Figure 2.4. Throughfall, volumetric water content (VWC), and depth to groundwater in floodplains. VWC was measured at 5, 10, and 20 cm beneath the O horizon-mineral soil interface from 1994 to 2005. Soil texture is progressively coarser with depth; the approximate wilting point of each depth is indicated by a horizontal line. Symbols indicate mean values and error bars indicate the standard error of the mean ($n = 12$, $\alpha = 0.1$). *Denotes a difference between drought and control plots significant at 5 -10 % level of probability. **Denotes a difference between drought and control plots significant at < 5 % level of probability.

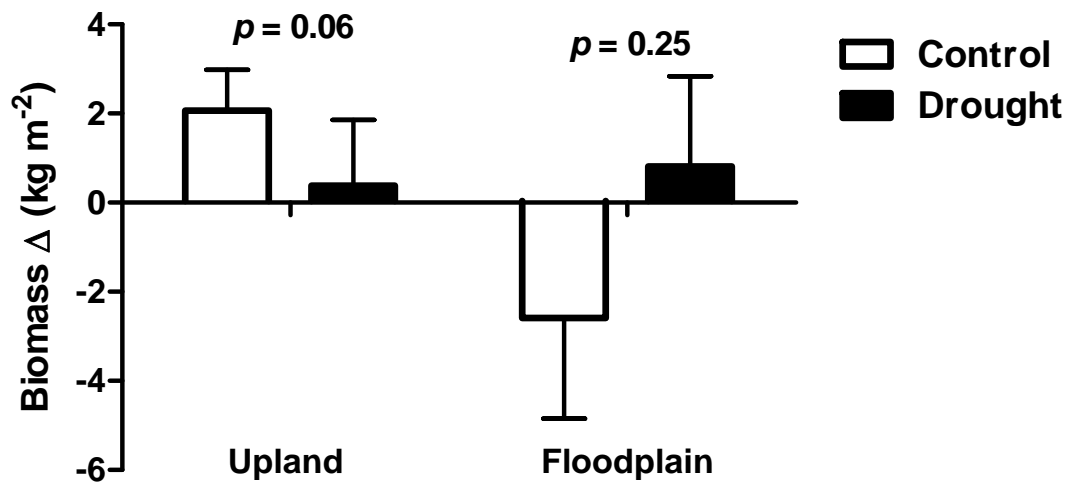


Figure 2.5. Net change of aboveground tree biomass (1989-2003). Error bars indicate the standard error of the mean ($n = 3$). P -values indicate the significance level of treatment differences determined from a paired t -test (one-tailed, $\alpha = 0.1$).

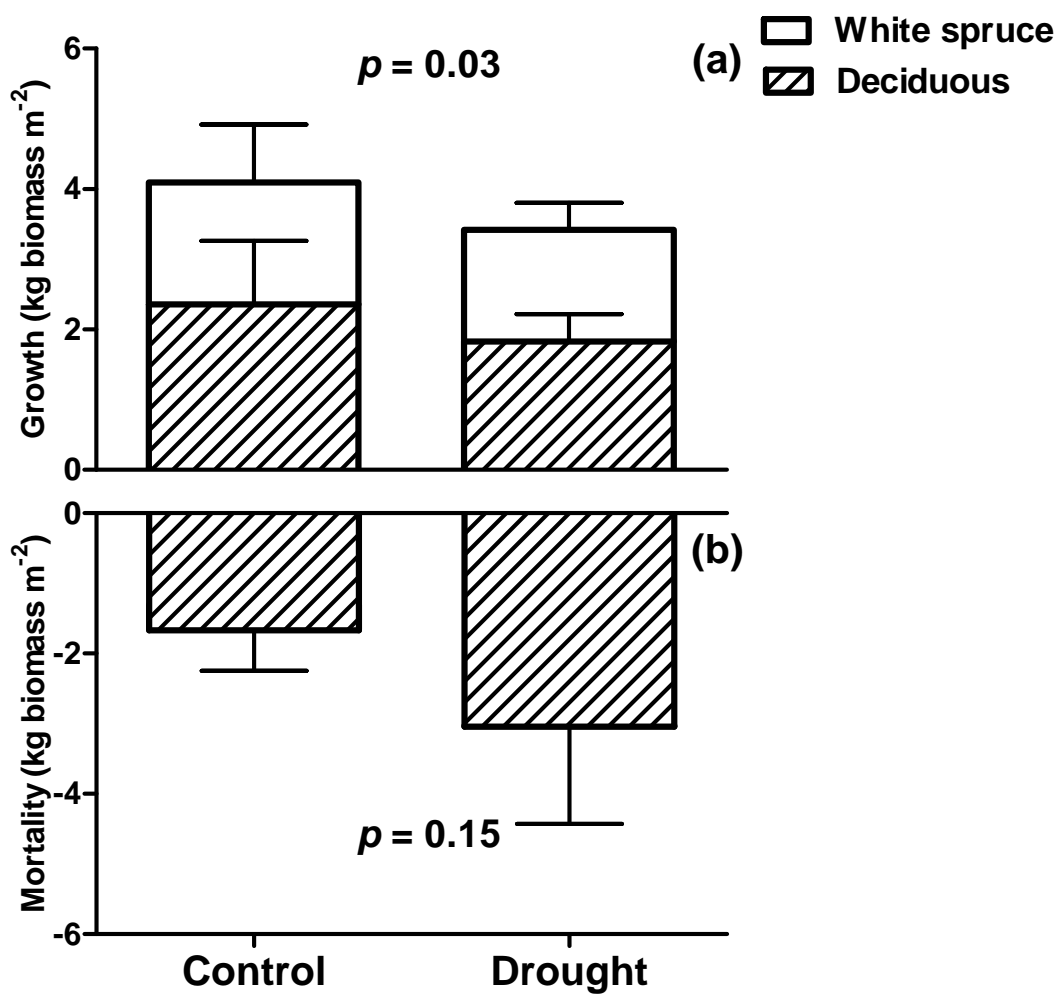


Figure 2.6. Aboveground biomass change (1989-2003) in upland forests. (a) represents biomass gains from tree growth and ingrowth; p -values indicate significance level of treatment differences in biomass gains (deciduous trees + white spruce). (b) represents biomass loss from mortality (white spruce mortality in both treatments was ~ 0 kg m⁻²) and p -values indicates significance level of biomass loss (deciduous trees and white spruce combined) between treatments. Error bars in both panels indicate the standard error of the mean ($n = 3$, $\alpha = 0.1$).

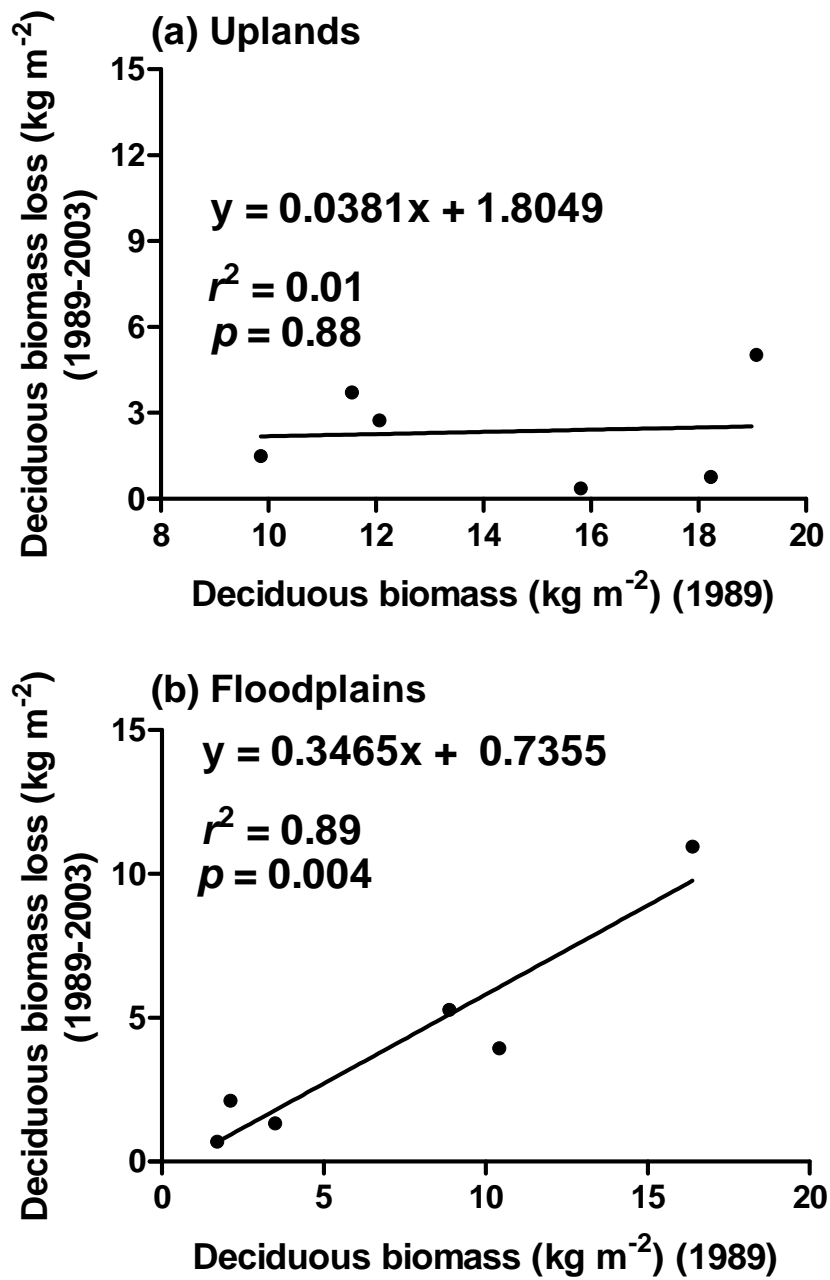


Figure 2.7. Relationship between initial (1989) deciduous species biomass and loss of deciduous species biomass during the 1989-2003 interval. (a) indicates uplands and (b) indicates floodplains ($\alpha = 0.1$).

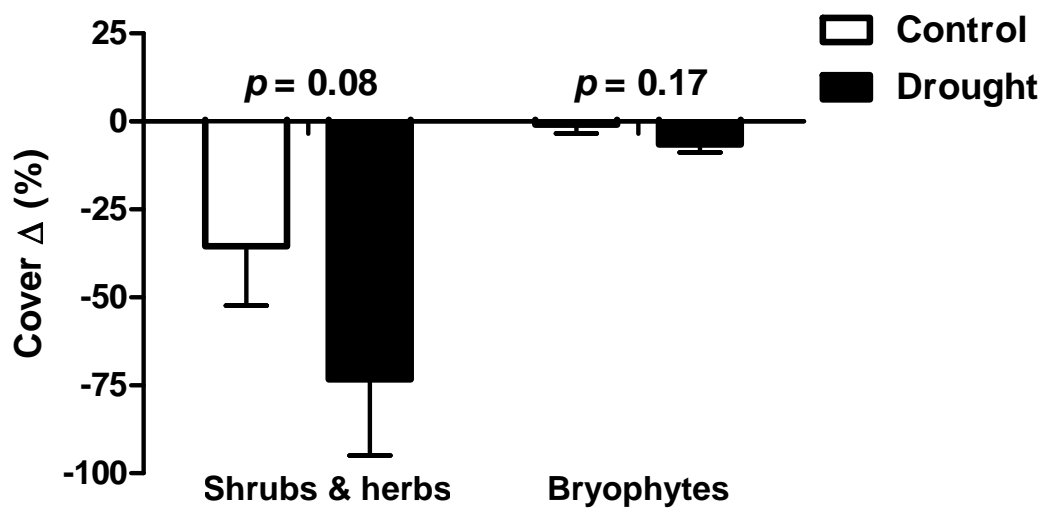


Figure 2.8. Understory vegetation cover change (1988-2005) in upland forests.

Negative values indicate a net loss of cover. Error bars indicate the standard error of the mean ($n = 3$). P -values indicate the significance level of treatment differences, based on a paired t -test (one-tailed, $\alpha = 0.1$).

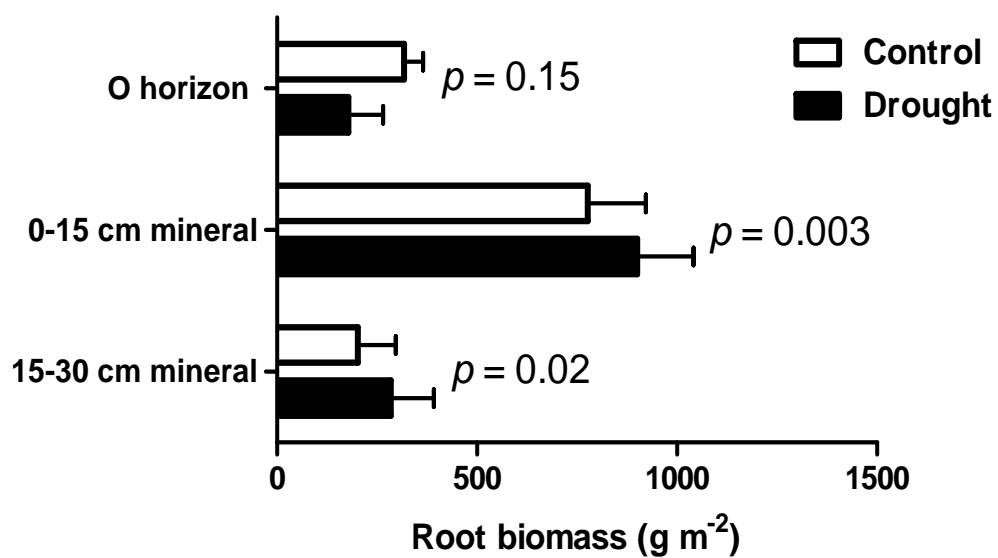


Figure 2.9. Upland live root biomass (2-25 mm diameter) in August 2005. Three consecutive depth increments are presented: O horizon, 0-15, and 15-30 cm. Error bars indicate the standard error of the mean value ($n = 3$). P -values indicate the significance level of treatment differences for each depth increment, based on a paired t -test (one-tailed, $\alpha = 0.1$).

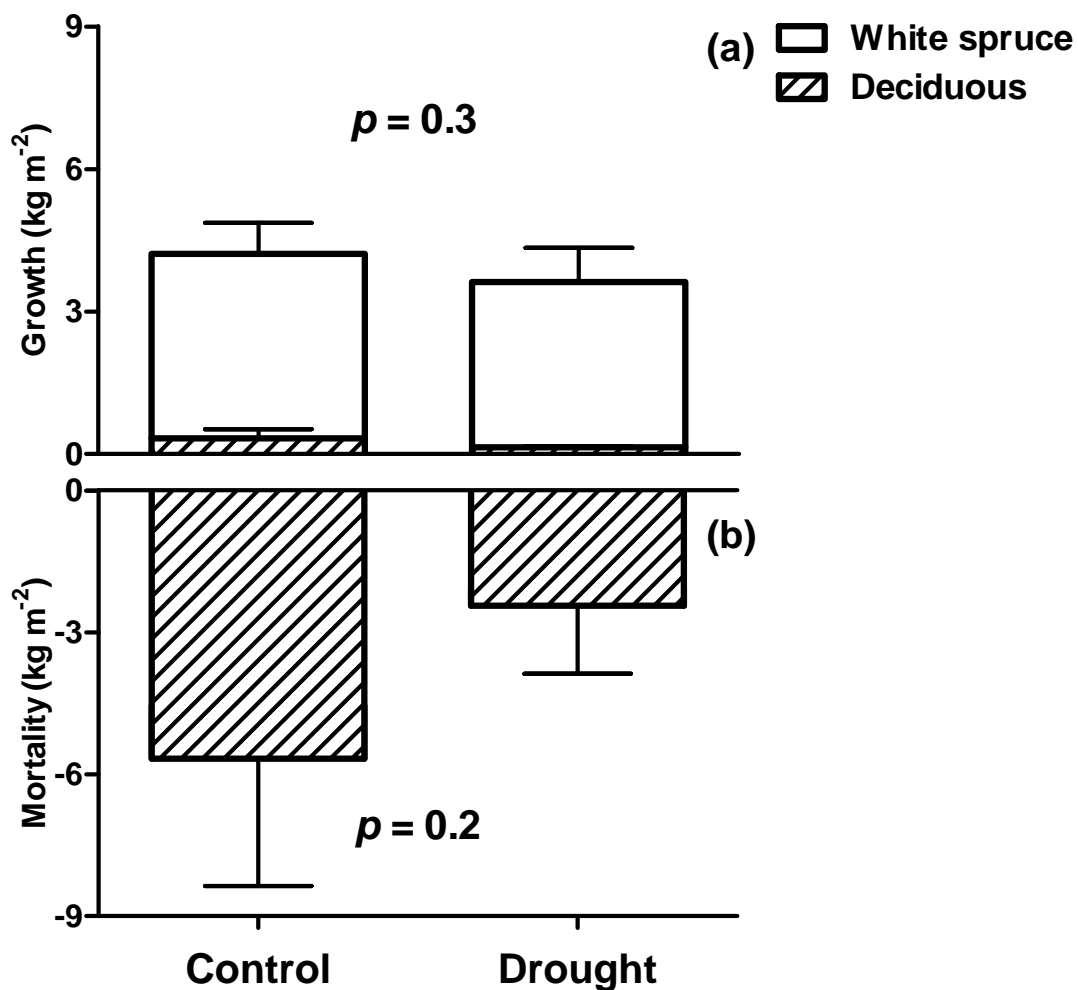


Figure 2.10. Aboveground biomass change (1989-2003) in floodplain forests. (a) represents biomass gain from tree growth and ingrowth; p -values indicate significance level of treatment differences in biomass gain (deciduous trees + white spruce). (b) represents biomass loss from mortality (white spruce mortality in both treatments was ~ 0 kg m⁻²); p -values indicate significance level of treatment difference in biomass loss (deciduous trees + white spruce). Error bars in both panels indicate the standard error of the mean ($n = 3$, $\alpha = 0.1$).

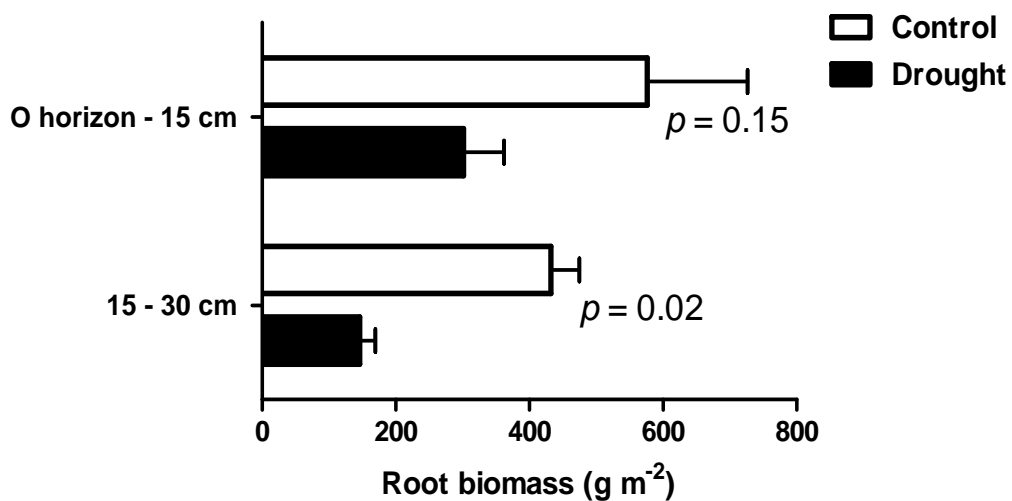


Figure 2.11. Floodplain live root biomass (2-25 mm diameter) in August 2005. Two consecutive depth increments are presented: O horizon-15 cm and 15-30 cm. Error bars indicate the standard error of the mean ($n = 3$). P -values indicate the significance level of the mean treatment difference, determined from a paired t -test (one-tailed, $\alpha = 0.1$).

Chapter 3 Long-term (1989-2005) Experimental Drought Increases Surface Soil Carbon Storage in an Interior Alaskan Boreal Forest²

3.1 Abstract

The objective of this study was to examine the response of mid-successional boreal forest soil C storage to long-term (1989-2005) experimental throughfall exclusion (“imposed drought”) in interior Alaska. We expected imposed drought to slow decomposer activity near the surface and accelerate the accumulation of C in surface soil. To test this, we decomposed birch tongue depressors (index of decomposer activity) at two depths in the soil profile and examined soil C changes and litterfall quantities between 1989 and 2005. Our results showed that imposed drought decreased surface decomposer activity (72 % in uplands and 87 % in floodplains) without increasing detrital inputs, thus accelerating the accumulation of C near the surface (30 % in the O horizon of uplands and 14 % in the O horizon-15 cm mineral soil of floodplains). Because the C distribution in the soil profile varied between uplands and floodplains as a result of different disturbance regimes (fire in uplands, fluvial processes in floodplains), the extent to which surface soil moisture reductions affected the overall C storage in these forest soils depended on landscape position, in which uplands were more sensitive to moisture reductions.

²S. Runck, D. Valentine, and J. Yarie. Long-term (1989-2005) Experimental Drought Increases Surface Soil Carbon Storage in an Interior Alaskan Boreal Forest. Prepared for submission in the Canadian Journal of Forest Research.

3.2 Introduction

During the second half of the 20th century, rising atmospheric CO₂ concentrations led to warmer mean annual temperatures without concurrent changes in annual precipitation, causing drought stress in many parts of Alaska (Barber *et al.* 2000). Depending on the degree to which climate-induced moisture limitation influences the balance between carbon (C) inputs (plant growth) and outputs (organic matter decomposition), the amount of C housed in Alaska's boreal forest and its role in the global C cycle may quickly change. Experimental and observational studies suggest that future temperature increases have the potential to compromise the overall C sequestration potential of this ecosystem, yet it remains uncertain if this will be primarily due to changes in vegetation or soil or a combination of both.

Historically, the boreal forest has served as a C sink, though changes in climate and disturbance can alter its role in the global C cycle. Among the many factors that set the boreal forest apart from other biomes is its unique distribution of C in the soil profile (Valentine *et al.* 2006), in which a large proportion of labile organic matter is located near the surface. Surface soil C stores are extremely vulnerable to temperature and moisture changes that can alter decomposer activity.

It is well established that climate exerts dominant control over biological activity in interior Alaska. Temperature is frequently cited as the leading factor limiting biological activity in this region; however, in areas where moisture is limiting, such as well-drained south facing slopes, the importance of moisture can exceed that of temperature. For example, in poorly drained, permanently frozen soils, a small increase in temperature can accelerate the rate at which soil organic matter decomposes, but in well-drained soils, increased temperature can result in drought stress and decrease the rate at which soil organic matter decomposes. Schlentner and Van Cleve (1985), who investigated the effects of temperature and soil moisture on soil respiration in interior Alaskan forests, concluded that temperature increases have a negligible effect on soil respiration (*i.e.*, heterotrophic and autotrophic respiration) when soil moisture content drops below 75 %. Similarly, Billings *et al.* (1998), examining the relationship between

reduced soil moisture and soil respiration, observed that throughfall exclusion reduced surface soil respiration in boreal forests throughout the growing season by as much as 40 % in uplands and 85 % in floodplains. Investigations conducted by Wagener and Schimel (1998) and Schimel *et al.* (1999) have also emphasized the importance of moisture extremes in decomposition, noting that extended drought suppressed microbial activity in the forest floor and episodic wetting and drying events promoted large surges of microbial activity and biomass.

The objective of this study was to understand how long-term (~16 years) soil moisture reduction affects soil C storage in mid-successional boreal forests across the landscape. We tested three hypotheses. Our first hypothesis (H_1) was that chronic throughfall exclusion (hereafter referred to as “imposed drought” or “drought treatment”) impedes decomposer activity but not aboveground foliar litterfall, causing a buildup of C at the surface. Our second hypothesis (H_2) was that imposed drought reduces decomposer activity near the surface but not in underlying soil because surface soils are more prone to drying from evaporative moisture losses. Our third hypothesis (H_3) was that the effect of imposed drought on soil C storage depends on landscape position and will therefore vary across the landscape. For example, floodplain forests have the potential to receive moisture from rainfall, snowmelt, and groundwater capillarity and are therefore less exposed to drought stress than upland forests, which solely rely on precipitation (*i.e.*, rainfall, snowmelt) as a source of soil moisture recharge. We tested these hypotheses by examining annual foliar litterfall quantity, soil C stocks (upper third meter of the soil profile), and decomposer activity (indexed with birch tongue depressor decay) at two landscape positions (upland and floodplain).

3.3 *Methods and materials*

3.3.1 Study overview

This study is part of a larger ongoing throughfall exclusion experiment designed to assess how growing-season drought influences boreal forest productivity in interior Alaska (Yarie 2008). Much of the data reported here were collected by Bonanza Creek personnel; we identify these data throughout this paper by indicating their acquisition from the Bonanza Creek data bank (www.lter.uaf.edu). Study sites are located within the Bonanza Creek Experimental Forest (BCEF), a major focus of the Bonanza Creek Long-term Ecological Research program (BNZ-LTER). Sites differ in topography (upland, floodplain) and parent material (loess, alluvium) but are similar with respect to vegetation (transitioning from dominance by deciduous to coniferous trees), regional climate (subarctic), and age. Below is a brief description of the study sites, climate, and throughfall exclusion design; a more detailed account is provided in Chapter 2.

3.3.2 Study area and regional climate

Upland sites are located on a well-drained ridge 308 m above mean sea level facing east-southeast on a 20 degree slope, where soil moisture is derived from snowmelt and rainfall. Upland soils are rock- and permafrost-free loessal Alfic Cryochrepts (Viereck *et al.* 1986). A forest fire occurring in about 1920 was the last major disturbance, and charcoal is present to a depth of 30 cm in the soil profile. Floodplain sites are located along the Tanana River on terraces approximately 139 m above mean sea level. Floodplain sites receive moisture from precipitation (rainfall, snowmelt) and groundwater capillarity and flooding, though high terrace heights generally prevent the latter except under extreme conditions (Yarie *et al.* 1998, Magoun and Dean 2000). Floodplain soils are rock- and permafrost-free Typic Cryofluvents (Viereck *et al.* 1986). The flood of 1967 was the last major disturbance in these sites and multiple buried O horizons are present to a depth of 40 cm in the soil profile.

The local climate is continental, characterized by low humidity and low annual precipitation (280 mm at Fairbanks International Airport, averaged over 1929-2006), of

which 35 % occurs as snow (Slaughter and Viereck 1986). Mean annual air temperature is low (-3.7°C); winter temperatures can drop to as low as -50°C and growing season (May-September) temperatures can reach as high as 35°C (Viereck *et al.* 1993). In the summer, a soil moisture deficit is created by relatively high evapotranspiration that can consume up to 100 % of the mean annual precipitation (Slaughter and Viereck 1986).

3.3.3 Drought treatment

In 1989, three paired control and drought treatments were established in upland and floodplain forests. From early May to mid-September, greenhouse panels were secured on top of a slanted wooden frame, creating a “roof” underneath the forest canopy to prevent throughfall from reaching the soil surface. The panels were removed each mid-September to prevent snowfall disruption and litter collected on the panels was returned to the treatment area. In 1994, time domain reflectometry (TDR) probes were installed at 5, 10, 20, and 50 cm below the O horizon-mineral soil interface to monitor soil moisture. Throughfall was measured with standard rain gauges. Soil moisture and throughfall measurements were accessed from the Bonanza Creek data bank.

3.3.4 Standard substrate decomposition experiment

We conducted a standard substrate decomposition experiment to provide an interpretable measure of relative decomposer activity as a function of environmental factors while avoiding confounding factors such as differences in substrate quality. We used birch tongue depressors (BTDs) (Puritan Medical Products) because they were uniform in shape, easily inserted in the soil with minimal soil disturbance, and did not require mesh bag enclosure, thereby avoiding problems associated with confining substrates in mesh bags (*e.g.*, macroinvertebrate exclusion, microclimate alteration).

In July 2005, we deployed 15 cm long BTDs into the control and drought treatments. Individual replicates were separated into four quadrants in which two

groups of six BTDs were inserted at two depths: the surface O horizon (“surface BTDs”) and the upper 15 cm mineral soil (“subsurface BTDs”), which in floodplains, often contained buried O horizons (Fig. 3.1). Surface BTDs were inserted so that they spanned the entire depth of the O horizon (*e.g.*, BTDs were inserted at an angle where the O horizon < 15 cm deep). Subsurface BTDs were inserted vertically. BTDs were placed > 1 m away from the base of trees taller than the throughfall roof (generally trees ≥ 1.5 m tall) in order to avoid soils receiving stemflow. In controls, we kept a similar distance from trees ≥ 1.5 m tall. Half of the BTDs were collected after one year (July 2006) and the remaining half after two years (July 2007). After retrieval, BTDs were stored in plastic bags at -18°C until processing. Before oven-drying and weighing, we rinsed the BTDs with water to remove organic matter and mineral soil attached to the BTDs.

We compared surface BTD mass loss in the controls with foliar litter mass loss to determine if BTD decay rates accurately approximated litter decay rates. Litter decay data were accessed from the Bonanza Creek data bank. The litter decay study took place from 1989 to 1991 in forests adjacent to the study sites (BNZ-LTER control plots), where foliar litter was enclosed in mesh bags and placed on the forest floor. Litterbag contents were reported on an organic matter basis (correcting for mineral soil contamination) after ashing in a muffle furnace at 400°C for 10 hours and analyzed for total C content on a LECO analyzer.

3.3.5 Soil sampling

In August 2005, we took 16 soil cores from each replicate, sampling > 1 m away from the base of trees taller than the shelter roof (generally trees ≥ 1.5 m tall) in order to avoid soils receiving stemflow. In controls, we kept a similar distance from trees ≥ 1.5 m tall. Samples of the O horizon, which included leaf litter, white spruce cones, hare and moose droppings; the non-photosynthetic portion of moss, and coarse woody debris (≤ 5.5 cm diameter), were cut with a serrated knife and 11 cm diameter soil corer. The upper 30 cm mineral soil was sampled with a 5.5 cm diameter slide-hammer soil

corer. O horizon and mineral soil samples were stored in plastic bags at -18°C until processing. During processing, live roots ≥ 2 mm diameter were removed by hand from the O horizons and set aside for root biomass calculations (Chapter 2) and the remaining soil was oven-dried (65°C) and ground to obtain a representative subsample. Mineral soil was gently sieved to facilitate removal of live roots ≥ 2 mm diameter, which were also set aside for root biomass calculations (Chapter 2), and the soil was oven dried (105°C), sieved a second time to remove ≥ 2 mm fraction, and ball-milled to increase homogeneity and reduce sample variability. Total C and nitrogen (N) content was determined on a LECO analyzer.

Change in soil C and N content (1989-2005) was determined by subtracting 1989 soil C and N contents from 2005 soil C and N contents. Nitrogen and C contents at the start of the drought treatment (1989) were determined on soils sampled from pits dug in the BNZ-LTER control plots (data accessed from the Bonanza Creek data bank). Because landscape position influenced the distribution of organic matter within the soil profile, we presented C and N data for uplands in terms of the O horizon, 0-15 cm, and 15-30 cm mineral soil and for floodplains in terms of the O horizon-15 cm and 15-30 cm mineral soil. All laboratory work and chemical analyses were conducted in the University of Alaska Fairbanks Forest Soils Laboratory.

3.3.6 Litterfall measurements

Litterfall measurements were obtained from the Bonanza Creek data bank. Between 1990 and 2004, litterfall collected in three 0.5 m x 0.5 m litter trays was oven-dried (65°C) and weighed; litterfall collections generally occurred in spring, shortly after snowmelt. In the litterfall analysis, we excluded samples weighing > 125 g because these samples were likely to have contained coarse woody debris that was not included in the O horizon samples.

3.3.7 Mass balance

Fine roots are known to contribute a substantial amount of C in this and other boreal forests (Ruess *et al.* 1996), often exceeding the of C input from litterfall by more than two times. Therefore, we approximated the contribution of C associated with fine root (*e.g.*, turnover, exudates, *etc.*) through mass balance, based on the concept that a change in soil C storage must equal C inputs minus C outputs over a defined period (Fig. 3.2). Stated another way, C inputs from foliar and root detritus must either be lost through decomposition and leaching or result in a change in storage:

$$\Delta_{\text{Storage}} = F_{\text{Foliar litterfall}} + F_{\text{Root detritus}} - F_{\text{Decomposition}} - F_{\text{Leaching}}$$

where

Δ_{Storage} is the difference between 2005 and 1989 soil C contents, determined from 2005 and 1989 soil samples

$F_{\text{Foliar litterfall}}$ is the influx of C from litterfall, determined from foliar litterfall quantities measured between 1989 and 2005

$F_{\text{Root detritus}}$ is the influx of C from fine roots from 1989 to 2005 and the primary unknown in this equation

$F_{\text{Decomposition}}$ is the efflux of C from decomposition between 1989 and 2005, determined from LTD and foliar litterbag decay rates

F_{Leaching} is the efflux of C from downward leaching within the soil profile between 1989 and 2005, estimated from the literature.

We used Simile (V. 4.9) to simulate the annual input and output of C to and from the soil. The simulation model was run for 16 years (representing the duration of the throughfall exclusion) while constrained with known values for initial and final soil C content, C input from foliar litterfall, and C output from decomposition, thereby allowing us to obtain a reasonable estimate of the C contribution of roots.

3.3.8 Statistical analysis

The experimental unit in this study was the 150 m² treatment area, which we subsampled to obtain the best estimate of the mean. The experimental design was paired, meaning that the difference between paired control and drought plots was the measurement of interest. Replicate stands within a landscape were separated spatially; variability due to spatial differences was addressed by treatment pairing. Statistical analyses consisted of paired student's *t*-tests of means. *T*-tests were one-tailed when we expected imposed drought to cause a directional change and two-tailed when the direction of change was not specified *a-priori*. *T*-tests were performed using GraphPad Prism (V. 5.00). Data were presented as the mean ($n = 3$) and standard error of the mean, the latter provided to give the reader a sense of the amount of variability among replicate stands within a treatment. With a paired *t*-test, the consistency of change or difference between treatments is more important than the amount of variability within a treatment. Therefore, the degree to which error bars overlap between treatments is not indicative of whether a given variable differed between treatments.

Post-hoc power analyses were performed using R (V. 2.6.2). Due to the large-scale and long-term nature of this study, practicality necessitated a limited number of replications ($n = 3$ at two landscape positions) at the expense of statistical test power and increased probability of a Type II error. Given the relatively small sample size of this study and the trade-off between significance level and power, we set alpha at 0.1 rather than the traditional alpha of 0.05.

3.4 *Results*

3.4.1 Soil moisture (2005-2007)

In all cases, bi-weekly soil moisture was greatest at the start of the growing season (May), following snowmelt. The most obvious and important difference between the two treatments was the absence of rainfall-induced moisture fluctuations in the drought plots. Shortly after snowmelt, soil moisture started a gradual decline until the end of the growing season that, in controls, was interrupted by rainfall events (Fig. 3.3 and 3.4). O horizon soil moisture values determined on soil cores sampled in August 2005 revealed that imposed drought also lowered moisture in the O horizon at both landscape positions (Fig. 3.3 and 3.4).

3.4.2 Decomposer activity

At both landscape positions, imposed drought only reduced decomposer activity in the surface soil (Fig. 3.5 and 3.6a). In uplands, surface soil supported more than twice the decomposer activity observed in subsurface soil; imposed drought reduced surface BTD decay by 72 % over the study period but had no such effect in subsurface soil (Fig. 3.5). In floodplains, surface and subsurface soils supported similar amounts of decomposer activity (Fig. 3.6a), presumably due to the presence of multiple buried O horizons. Therefore, we presented BTD mass loss pooled across the two depths (surface combined with subsurface) as well as separately (surface versus subsurface). Floodplain decomposer activity responded to imposed drought in a manner similar to that in uplands; imposed drought reduced decomposer activity in surface soil by nearly 87 % but had no such effect in subsurface soil (Fig. 3.6a). When combined (surface + subsurface), imposed drought reduced floodplain decomposer activity by 58 % (Fig. 3.6b).

Two-year BTD decomposition rates in the control plots were similar to the two-year decomposition rates of foliar litter confined in mesh litterbags. In uplands, foliar litter and BTDs both underwent approximately 40 % mass loss (Fig. 3.7a), and in

floodplains, foliar litter and BTDs underwent 31 % and 39 % mass loss, respectively (Fig. 3.7b).

3.4.3 Litterfall

Annual litterfall summed over all years (1989-2004) did not differ between treatments at either landscape position (Fig. 3.8). However, uplands generally received greater amounts of litterfall than floodplains.

3.4.4 Soil C and N content

At both landscape positions, C was concentrated near the soil surface and progressively decreased down to 30 cm (Table 3.1 and 3.2). Near-surface change in soil C content (1989-2005) was generally positive. Imposed drought accelerated C accumulation at the soil surface; in uplands, this was a 30 % additional increase (Fig. 3.9) and in floodplains, a 14 % additional increase (Fig. 3.10). Neither increase was related to an increase in bulk density (data not presented). Imposed drought did not significantly change C content in subsurface soil at either landscape position (*i.e.*, 0-30 cm in uplands and 15-30 cm in floodplains) (Fig. 3.9 and 3.10). In uplands, however, soil C change at the 15-30 cm depth was consistently (not significantly) smaller in all drought replicates compared to controls. A *post-hoc* power analysis revealed that five additional paired replicate stands would have been necessary to have detected the mean treatment difference (121 g C m^{-2}) with 90 % power. Imposed drought did not change soil nitrogen (N) content for any depth (Table 3.1 and 3.2), though a wider C/N was observed in the O horizon of uplands (Table 3.1) ($p = 0.009$, $n = 3$, one-tailed *t*-test, $\alpha = 0.1$).

3.5 Discussion

3.5.1 Imposed drought impeded decomposition more than aboveground foliar litterfall, accelerating the accumulation of C near the soil surface

Several lines of evidence suggest that surface decomposer activity slowed in response to reduced moisture and accelerated the accumulation of soil C at the surface, thus supporting our first hypothesis (H_1). Imposed drought slowed BTD decay at the surface, where an increase in C content was observed, but had no such effect in subsurface soil (0-15 cm), where C content was unchanged (Fig. 3.5, 3.6, 3.9. and 3.10). BTD and foliar litter underwent a similar amount of decay in a two-year period (Fig. 3.7a and 3.7b), indicating that BTD decomposition rates were reasonable approximations of actual litter decomposition rates. The amount of aboveground litterfall was not significantly altered by imposed drought (Fig. 3.8), ruling out the possibility that the soil C increase resulted from increased foliar litterfall. Nor were belowground litter inputs (fine root-derived C), determined by mass balance, responsible for the surface soil C increase (data not presented).

Other studies have observed a similar relationship between soil moisture reductions and decomposition. For example, Joslin *et al.* (2000) showed that a 30 % reduction of annual throughfall increased foliar litter accumulation at the soil surface of a Tennessee oak forest. O'Neill *et al.* (2003) similarly demonstrated that precipitation exclusions caused a short-term reduction of litter decomposition in a mixed mesic hardwood forest.

3.5.2 Imposed drought slowed decomposer activity near the soil surface but not further down in the profile

August 2005 soil moisture measurements in the O horizon and 5 cm mineral soil revealed that between treatment moisture differences were greater in the O horizon than in the 5 cm soil (Fig. 3.3 and 3.4). The reduction of surface soil moisture corresponded to the reduction of surface BTD decay rates, providing support for our second hypothesis (H_2) that chronic throughfall exclusion impedes decomposer activity near the

surface but not further down in the profile. Similar results have been observed elsewhere. For example, Borken *et al.* (2006), studying the effect of experimental drought in a mixed deciduous stand in the Harvard Forest, showed that drought decreased heterotrophic respiration in the O horizon but not in the A horizon. Likewise, Fierer *et al.* (2003) found that moderate drought conditions in California grasslands decreased heterotrophic respiration more strongly in surface than in subsurface soils.

Figures 3.11 and 3.12 depict the change in soil C content in upland and floodplain soils during the study period. In 1989 (year 0), both treatments contained similar amounts of soil C. In uplands, a higher proportion of initial C and annually deposited C were retained near the surface of the drought plot as a result of slowed decomposer activity (Fig. 3.11a). Slowed surface decomposition apparently restricted the downward movement of C from the O horizon because the underlying mineral soil underwent a small net loss of C, even though decomposer activity at this depth was not affected by imposed drought (Fig. 3.11b). In floodplains, imposed drought also reduced decomposer activity and caused the C content of the surface O horizon-15 cm mineral soil to increase more rapidly compared to controls (Fig. 3.12).

3.5.3 The extent to which drought-reduced decomposer activity influenced soil C storage depended on the depth at which C was stored in the soil profile

In addition to revealing that surface decomposer activity slows in response to imposed drought, the BTD decomposition experiment also indicated that the degree to which imposed drought influenced soil C storage depended on the distribution of C within the soil profile, which in turn varied as a result of landscape-specific disturbance regimes (*i.e.*, fire in uplands versus fluvial processes in floodplains). In uplands, rapid decomposition rates and high C concentrations were only observed in surface soil (*i.e.*, O horizon). In floodplains, both surface (O horizon) and subsurface (underlying 15 cm) soils exhibited rapid decomposition rates and high soil C content due to the presence of buried O horizons. Thus, surface moisture reductions were less consequential to the overall decomposer activity in floodplain forest soils, where buried O horizons were

exposed to relatively constant moisture (Van Cleve and Yarie 1986). As the buried O horizons decompose, they may serve as source of mineralized nutrients that may be particularly important to plants if mineralization of nutrients in the surface O horizon is limited by the reduction of decomposer activity.

3.6 *Summary*

Decomposer activity in surface soils was sensitive to the gradual drying effect of imposed drought in both upland and floodplain landscape positions, though no such response was observed in the subsurface soil. Our findings indicate that the reduction of decomposer activity at the surface caused the observed increase in surface soil C. Because the C distribution in the soil profile varied between uplands and floodplains as a result of differing disturbance regimes (fire in uplands, fluvial processes in floodplains), the extent to which surface soil moisture reductions affected the overall C storage in these forest soils depended on landscape position, in which uplands were more sensitive to moisture reductions.

3.7 *Acknowledgements*

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Table 3.1. Carbon, nitrogen, and C/N values for upland soils in 1989 and 2005. Values represent the mean of three replicates; numbers in parentheses are the standard errors of the mean.

		Carbon*	Nitrogen*	C/N
O horizon	1989	1240 (44.70)	44.37 (3.664)	28.25 (2.218)
	Control (2005)	2681 (276.5)	93.43 (3.877)	28.72 (1.445)
	Drought (2005)	3307 (111.8)	103.4 (7.814)	32.26 (1.822)
0-15 cm	1989	2104 (131.2)	126.5 (6.210)	16.62 (0.359)
	Control (2005)	2243 (212.9)	147.9 (12.09)	15.14 (0.4424)
	Drought (2005)	2165 (146.9)	144.7 (8.906)	14.96 (0.3744)
15-30 cm	1989	1150 (39.82)	78.86 (3.793)	14.65 (0.8779)
	Control (2005)	1157 (120.7)	175.3 (5.044)	6.623 (0.7491)
	Drought (2005)	1035 (92.04)	164.2 (7.481)	6.364 (0.7603)
O horizon - 30 cm	1989	4494 (123.3)	249.7 (3.613)	**
	Control (2005)	6081 (459.5)	416.6 (10.17)	**
	Drought (2005)	6506 (227.9)	412.2 (18.49)	**

* g m⁻²

** Values not available

Table 3.2. Carbon, nitrogen, and C/N values for floodplain soils in 1989 and 2005. Values represent the mean of three replicates; numbers in parentheses are the standard errors of the mean.

		Carbon*	Nitrogen*	C/N
O horizon-15 cm	1989	4686 (635.8)	229.1 (22.11)	20.29 (1.029)
	Control (2005)	6276 (706.1)	275.7 (27.87)	22.84 (1.575)
	Drought (2005)	6530 (810.9)	293.5 (24.36)	22.25 (2.042)
15-30 cm	1989	1235 (141.2)	57.7 (11.16)	22.2 (2.080)
	Control (2005)	1729 (780.7)	111.8 (46.46)	15.09 (1.39)
	Drought (2005)	1822 (610.6)	144.3 (27.02)	11.99 (2.97)
O horizon - 30 cm	1989	5922 (620.2)	286.8 (24.83)	**
	Control (2005)	8005 (1445)	387.6 (64.47)	**
	Drought (2005)	8352 (1411)	437.8 (44.32)	**

* g m⁻²

** Values not available

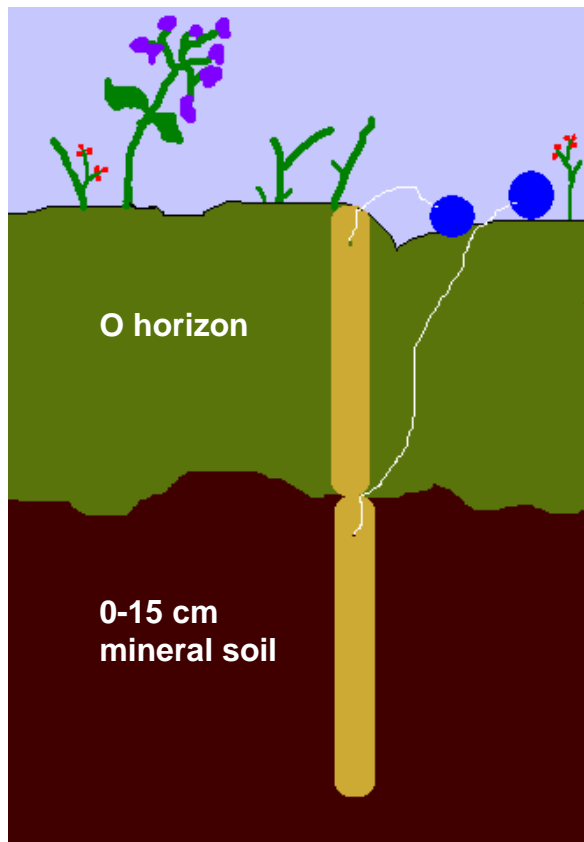


Figure 3.1. Placement of birch tongue depressors (BTDs) in the soil profile. BTDs (15 cm long) were placed in the O horizon and underlying 15 cm of mineral soil in upland and floodplain forests.

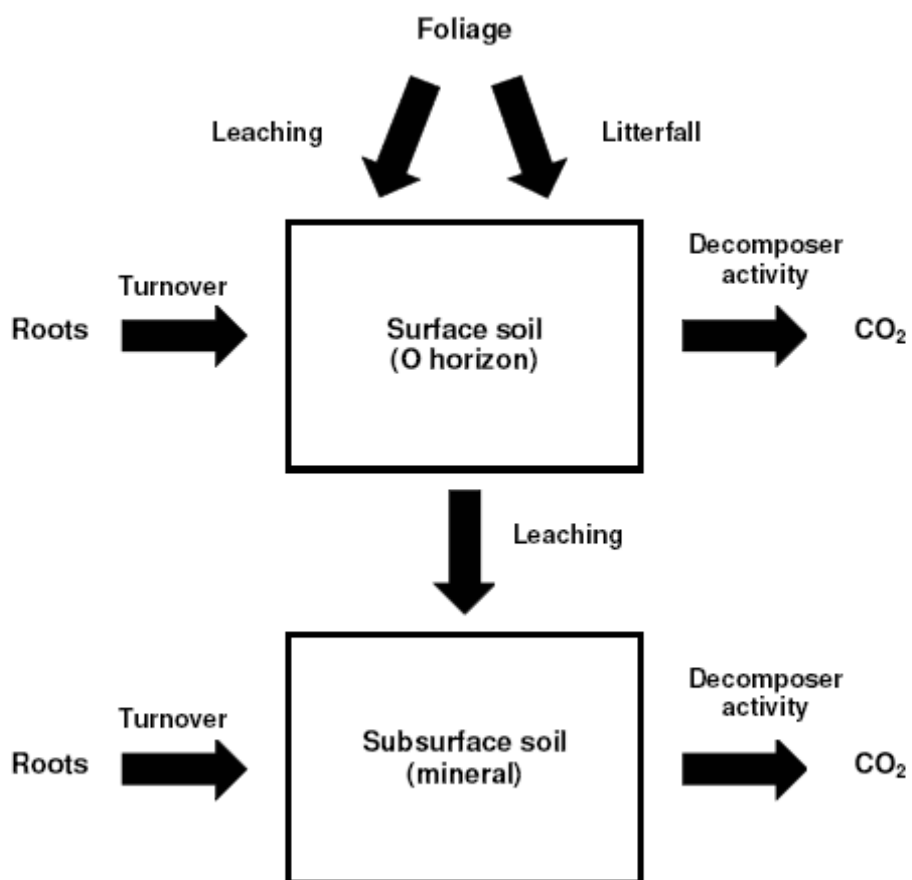


Figure 3.2. Major pools and fluxes of C in the soil system.

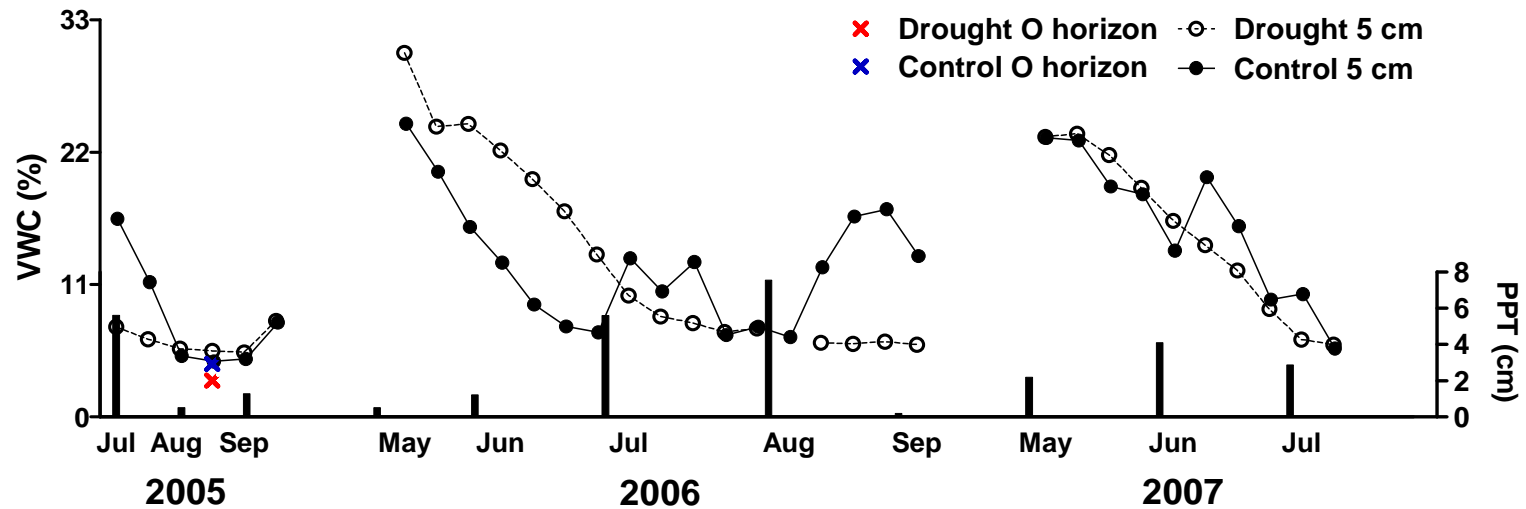


Figure 3.3. Upland soil moisture and throughfall during the birch tongue depressor decomposition experiment. Volumetric water content (VWC) (—○— ●—) at 5 cm below the O horizon-mineral interface and throughfall (PPT) (black spikes) were measured between 2005 and 2007. VWC data are also presented for O horizon, determined on soil cores sampled in August 2005 (× ×). PPT and VWC values represent the mean value of two replicates ($n = 2$).

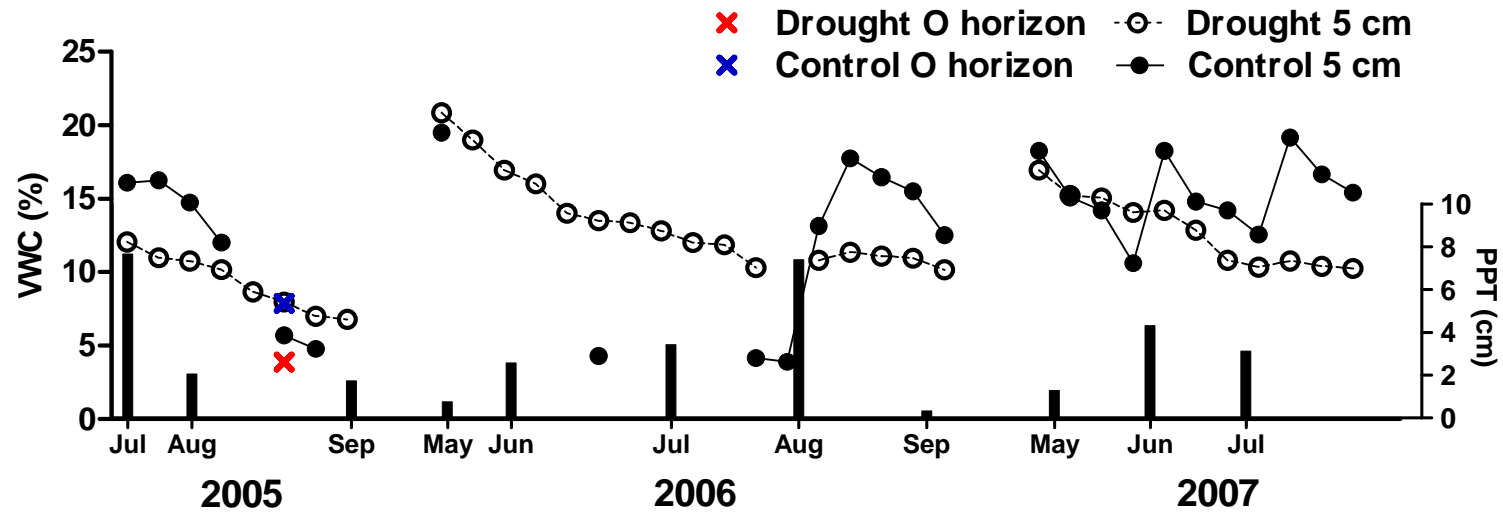


Figure 3.4. Floodplain soil moisture and throughfall during the birch tongue depressor decomposition experiment. Volumetric water content (VWC) (\circ \bullet) at 5 cm below the O horizon-mineral interface and throughfall (PPT) (black spikes) were measured between 2005 and 2007. VWC data are also presented for O horizon, determined on soil cores sampled in August 2005 (\times \times). PPT and VWC values represent the mean value of two replicates ($n = 2$).

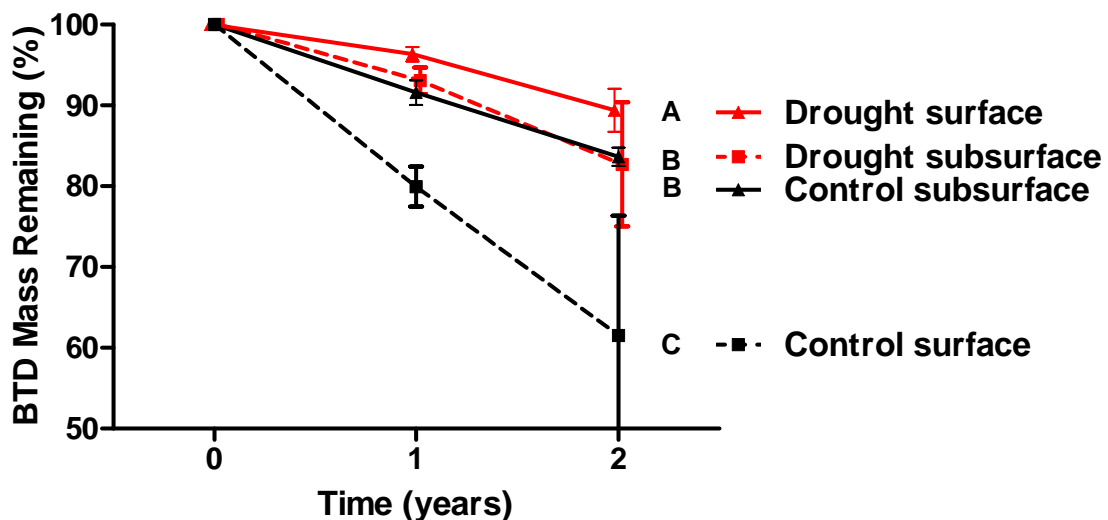


Figure 3.5. Fraction of original birch tongue depressor (BTB) mass remaining after two years decomposition in upland forests. Error bars indicate standard error of the mean value of three replicates. Mass remaining after two years in the field was analyzed with a paired t -test (one-tailed); treatments followed with different letters were statistically different ($\alpha = 0.1$).

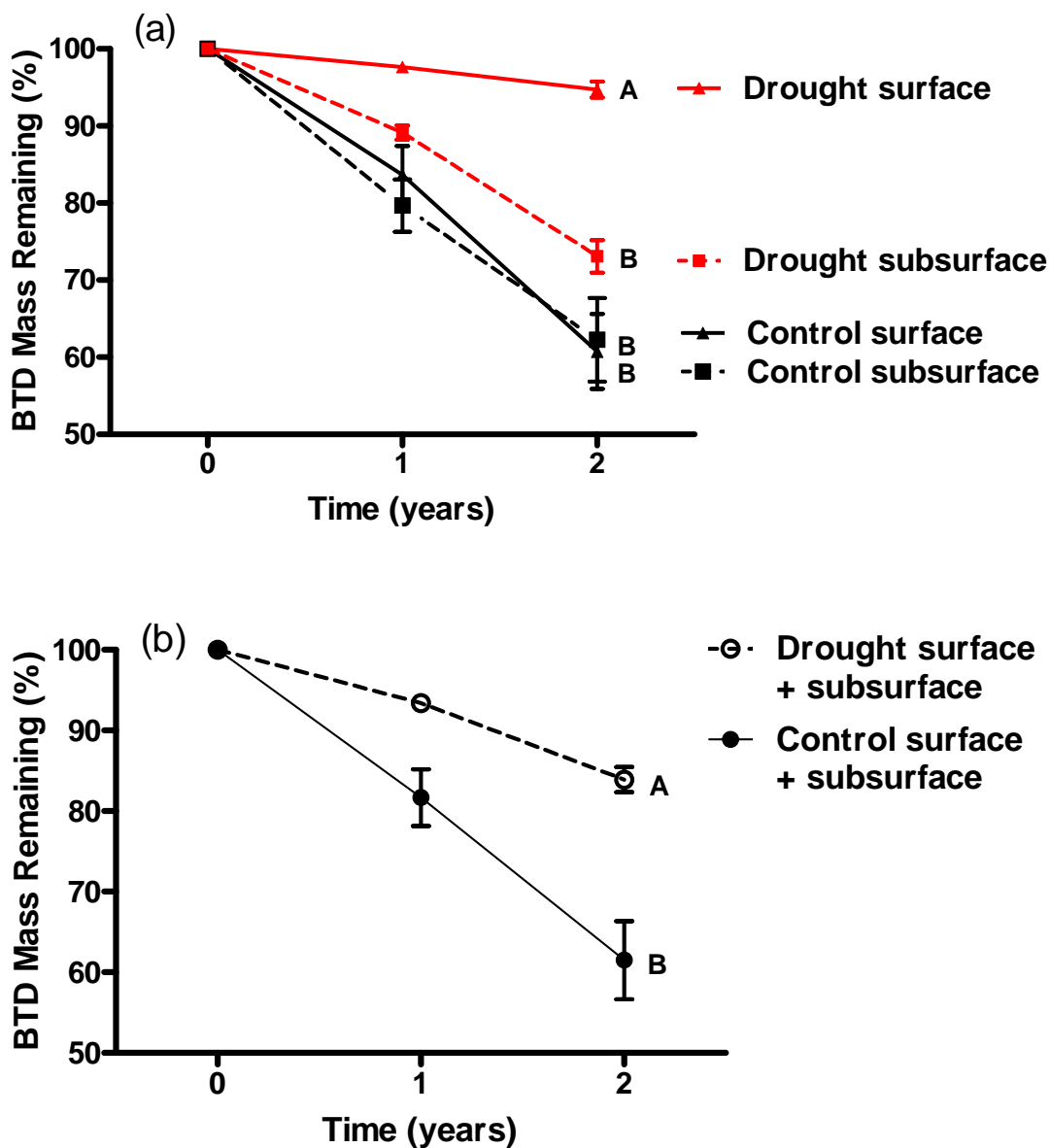


Figure 3.6. Fraction of original birch tongue depressor (BTD) mass remaining after two years decomposition in floodplain forests. BTD decay rates are presented for separate (a) and pooled depths (b). Error bars indicate the standard error of mean values of three replicates. Mass remaining after two years in the field was analyzed with a paired *t*-test (one-tailed); treatments followed with different letters were statistically different ($\alpha = 0.1$).

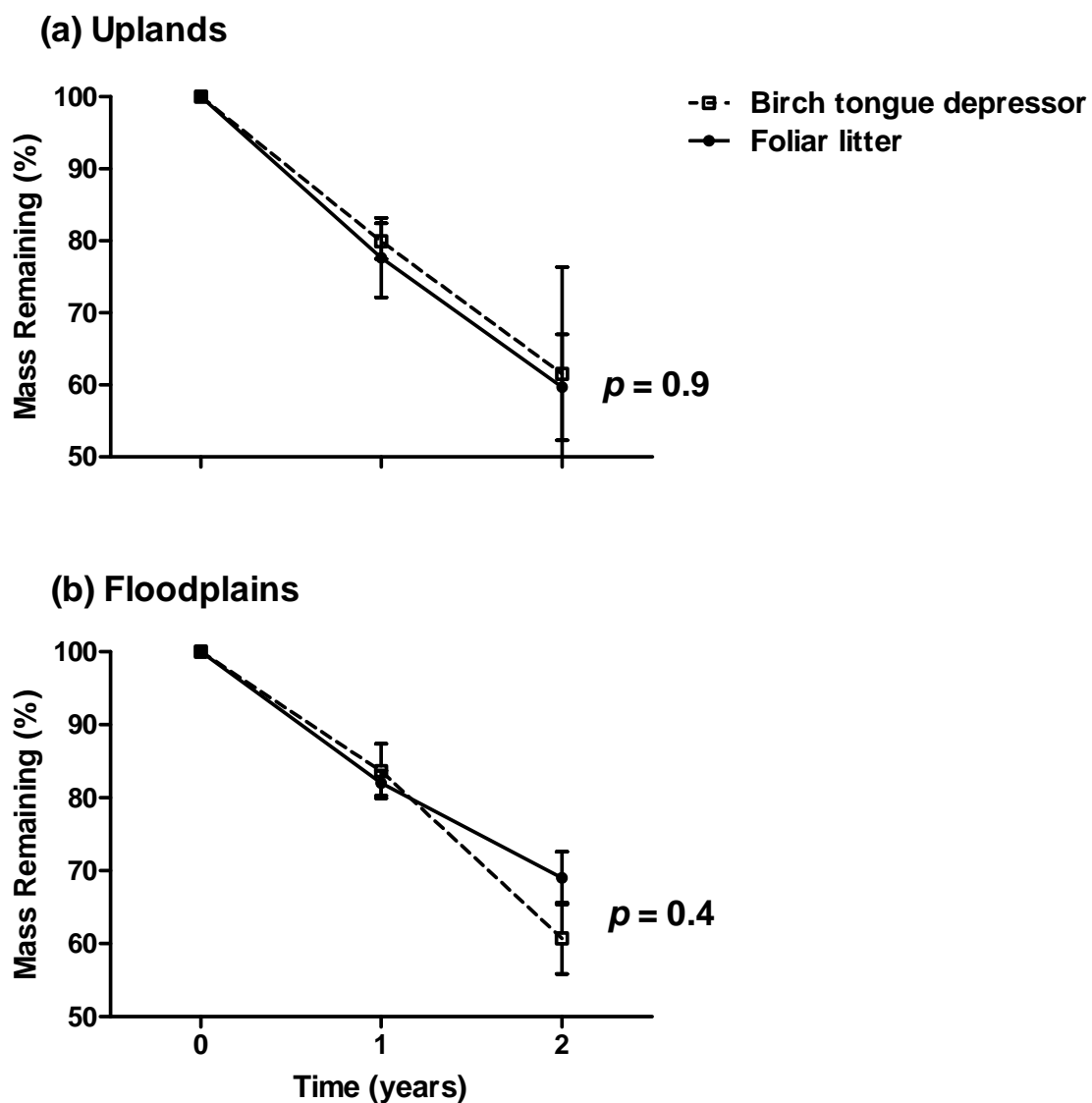


Figure 3.7. Original mass remaining for foliar litter and birch tongue depressors in upland (a) and floodplain (b) forests. Litterbags were deployed on the O horizon from 1989 to 1991; BTDs were deployed in the O horizon from 2005 to 2007. Error bars indicate the standard error of mean values of three replicates. P -values indicate significance level of the difference between foliar litter and BTD decay (two year decay), based on a paired t -test (two-tailed, $\alpha = 0.1$).

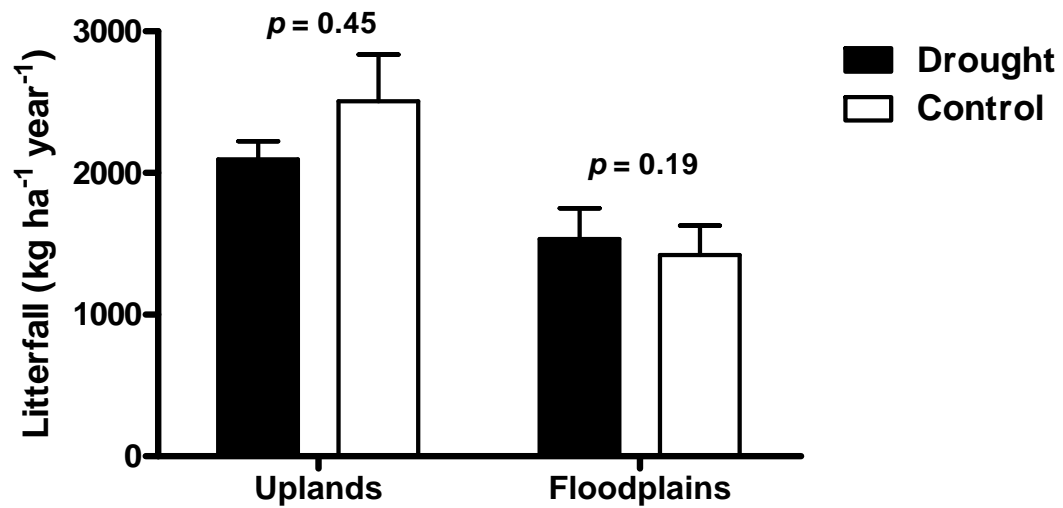


Figure 3.8. Mean (1990-2004) annual litterfall in upland and floodplain forests. Error bars indicate standard errors of mean values of three replicates. *P*-values indicate significance level of the mean difference between treatments based on a paired *t*-test (two-tailed, $\alpha = 0.1$).

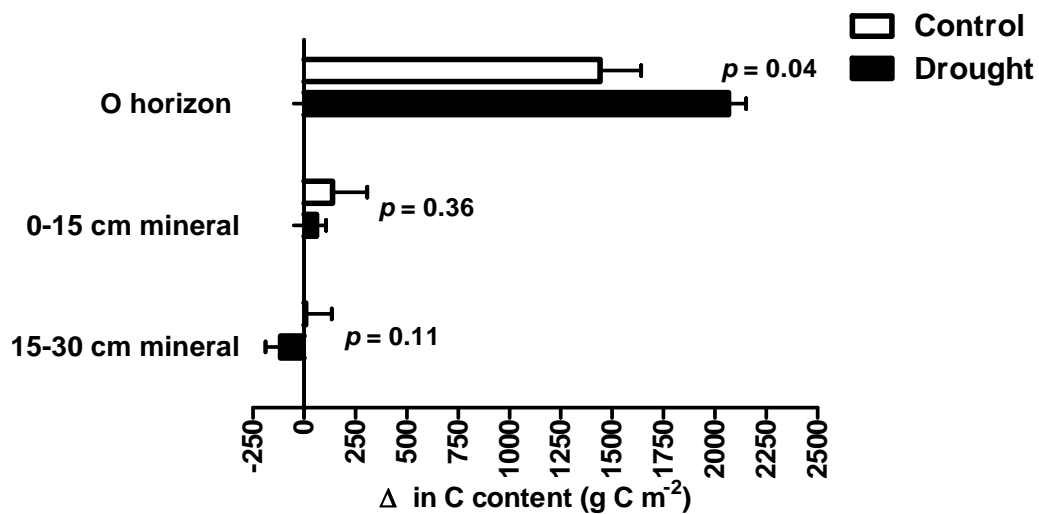


Figure 3.9. Soil C content change (1989-2005) in the O horizon, 0-15 cm, and 15-30 cm mineral soil in uplands. Error bars indicate standard errors of mean values of three replicates. P -values indicate significance level of the mean difference between treatments for a given depth, based on a paired t -test (one-tailed, $\alpha = 0.1$).

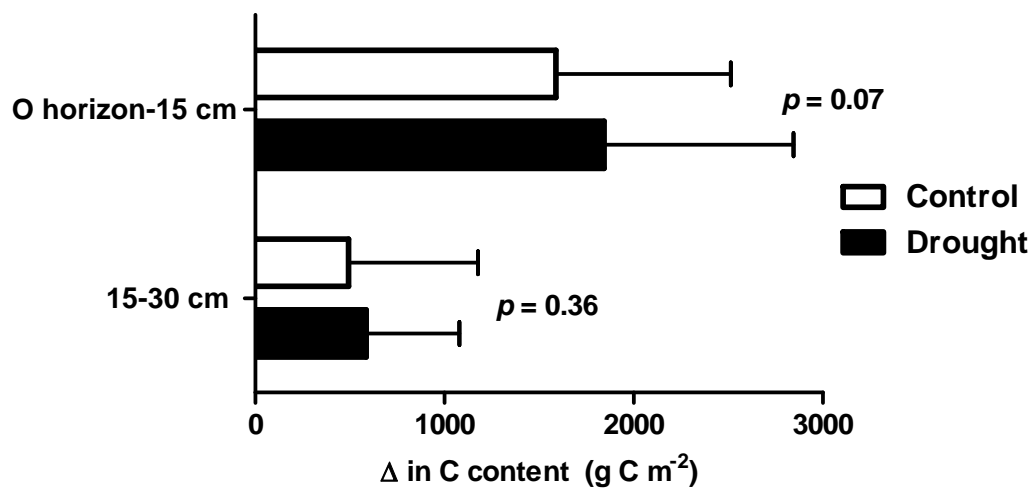


Figure 3.10. Soil C content change (1989-2005) in the O horizon-15 cm and 15-30 cm mineral soil of floodplains. Error bars indicate standard errors of mean values of three replicates. *P*-values indicate significance level of the mean difference between treatments, based on a paired *t*-test (one-tailed, $\alpha = 0.1$).

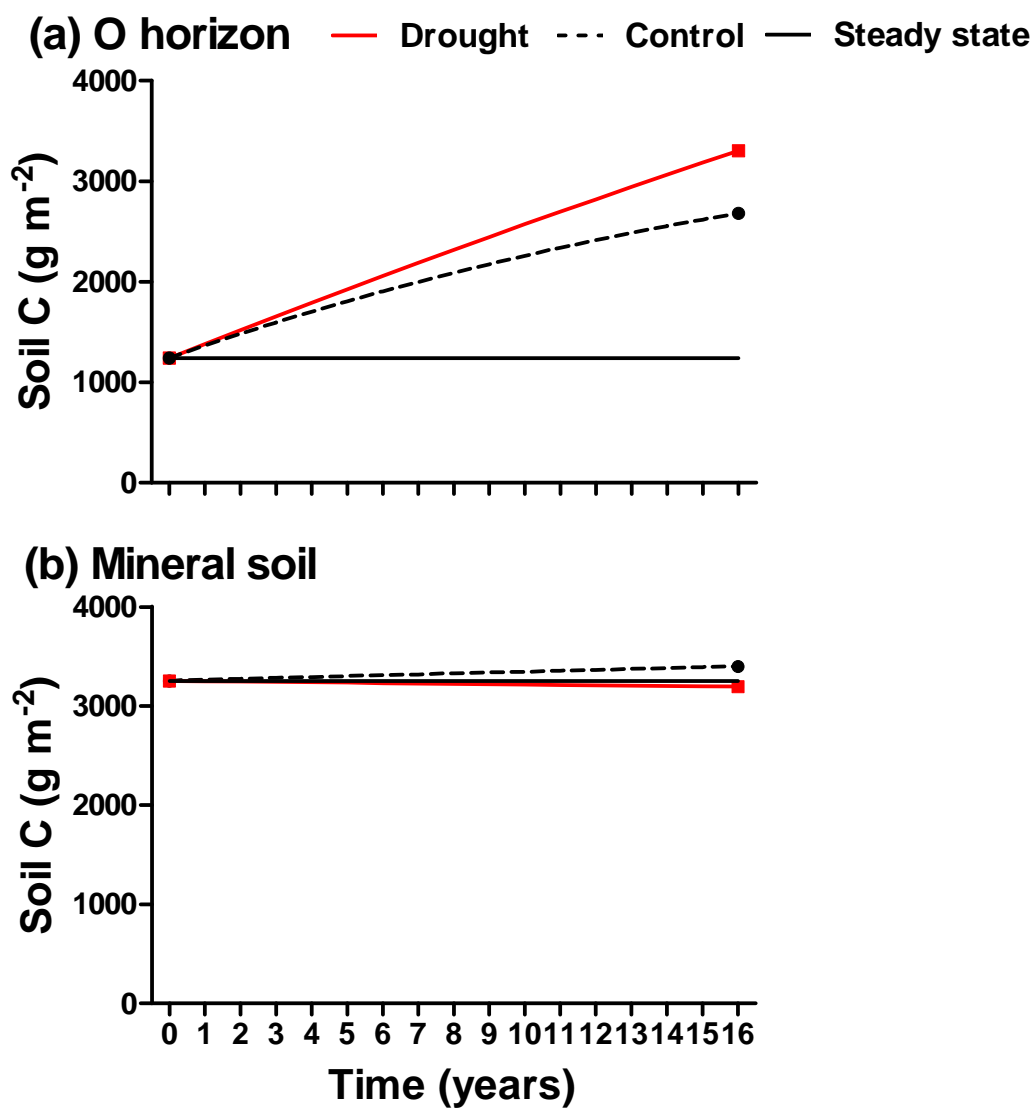


Figure 3.11. Soil C dynamics (1989-2005) in upland forests. The change in soil C content resulting from C inputs (foliar and root detritus) and losses (decomposition and, to a lesser extent, downward leaching) is presented for both the O horizon (a) and underlying 30 cm mineral soil (b). Symbols (■ •) indicate data points based on field measurements.

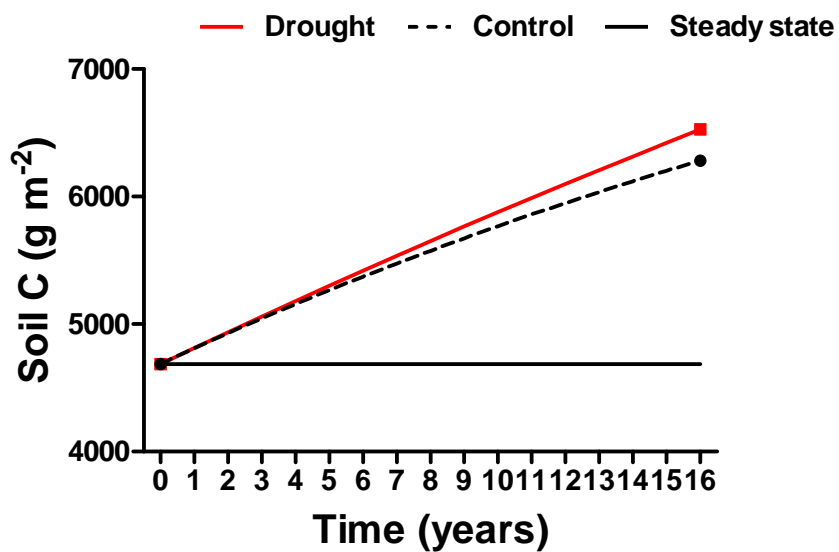


Figure 3.12. Soil C dynamics (1989-2005) in floodplain forests. Change in soil C content resulting from C inputs (foliar and root detritus) and losses (decomposition and, to a lesser extent, downward leaching) is presented for the O horizon-15 cm mineral soil. Symbols (■ •) indicate data points based on field measurements.

Chapter 4 General Conclusion

4.1 *Forest soil and vegetation response to imposed drought*

The results of this study indicated that reduced soil moisture slows decomposer activity near the surface, thereby accelerating the accumulation of foliar litter in surface horizons. In the context of climate change, which may increase soil temperatures that subsequently reduce soil moisture, I conclude that increased soil temperature in well-drained sites will ultimately hinder surface decomposition and enhance surface carbon (C) storage. In sites characterized by poor soil drainage (*e.g.*, north-facing slopes, lowlands), temperature increases are more likely to stimulate decomposition.

Organic matter quality tends to decrease with depth in the soil profile whereas the activation energy and temperature dependence of enzymatic reactions increase with decreasing substrate quality (Davidson and Janssens 2006). Therefore, in subsurface mineral soil, where imposed drought did not slow decomposer activity, soil warming may stimulate soil organic matter decomposition. If so, reduced decay at the surface and increased decay beneath the surface may lead to forest soils that are increasingly “top-heavy”, storing a greater proportion of C at the surface where it may be lost to disturbance (*e.g.*, fire, erosion) or, if environmental conditions allow, biologically degraded.

Vegetation in northern forests tends to be shallow-rooted, reflecting where resources are most concentrated in the soil profile (Gale and Grigal 1987). If climate change reduces growing season soil moisture that subsequently slows decomposition and nutrient cycling in near-surface soils, then vegetation may be forced to grow more roots in a region of the profile where these resources are more available. In floodplains, the obvious strategy for vegetation would be to increase root growth at a depth where buried organic horizons and groundwater are located, especially considering that warmer temperatures are expected to increase glacial melt and river discharge that can elevate floodplain water tables (Serreze *et al.* 2000). Thus, it stands to reason that the

moisture reductions imposed on floodplain forests in this present study would, in reality, be at least partly offset by elevated groundwater.

In uplands, where rainfall was observed as an important source of soil moisture, especially late in the growing season, vegetation strongly responded to imposed drought by reducing aboveground growth and understory vegetation presence and increasing root biomass in mineral soil. When taken together, these results suggest that upland forests are sensitive to soil moisture reductions and respond to drought stress by slowing growth aboveground, possibly to compensate for increased growth belowground.

4.2 *Whole-forest C balance*

In uplands, the reduction of C captured by tree growth (1989-2003) was offset by the increased quantity of C stored in the O horizon, indicating that the net effect of imposed drought on upland forest C balance was minimal (Fig. 4.1). In contrast to uplands, imposed drought in floodplains increased soil C content in the O horizon-15 cm mineral soil without reducing aboveground tree growth (Fig. 4.2). Thus, the results of this throughfall exclusion indicate that chronic soil drying is likely to increase forest C storage only in floodplains. In uplands, where soil moisture was generally more limited, our results indicate that overall forest C storage is less likely to change.

4.3 *Recommendations for future research*

Although ecosystem-level throughfall manipulations are an important research tool for studying the whole forest response to prolonged drought, they are relatively scarce because they are expensive and logistically challenging to conduct. This being said, the results of this study will undoubtedly contribute to our understanding of the response of boreal forest ecological processes to future climate scenarios. To build on the results of this current study, I recommend that future investigations consider the following questions:

1. Has imposed drought altered litter chemistry?
2. To what extent does groundwater influence floodplain soil moisture, especially during the later stages of succession, when floodplain terraces are well-developed?
3. How would imposed drought affect the forest C balance at different stages of forest development (*e.g.*, early versus late succession)?
4. Has imposed drought led to a depletion of nutrients (*e.g.*, potassium) due to the removal of throughfall, which contains nutrients dissolved from the canopy?

4.4 References

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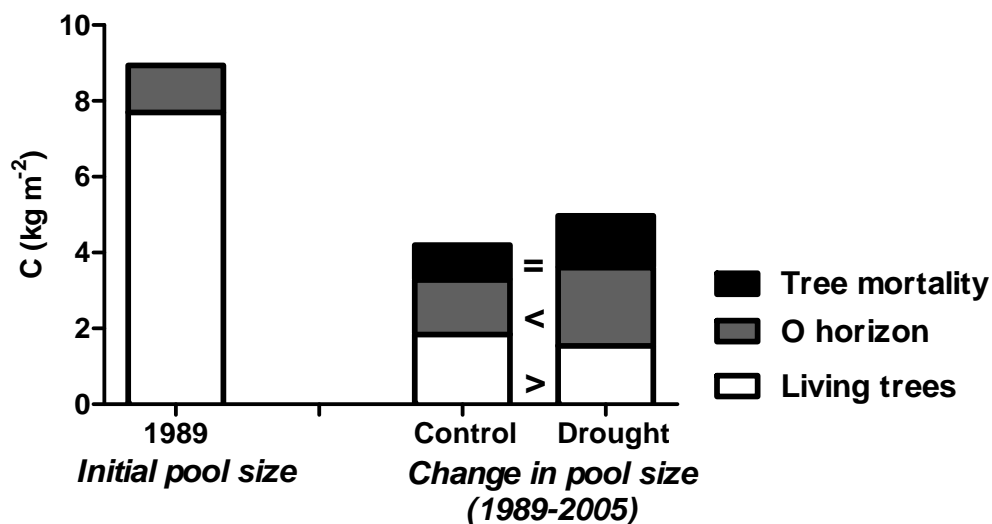


Figure 4.1. Initial C pool size and change in C pools during the study period in upland forests.

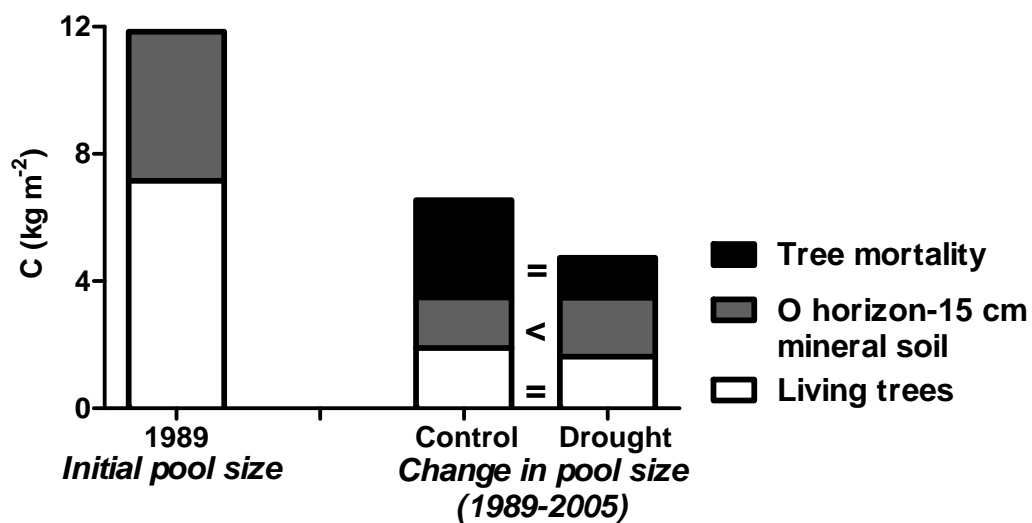


Figure 4.2 Initial C pool size and change in C pools during the study period in floodplain forests.