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Root Production and Herbivory in an Upland Grassland Community in Yellowstone National Park

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Introduction

The synthesis of organic matter by plants via photosynthesis (primary production), is regulated by a complex web of biotic and abiotic feedbacks that occur between trophic levels. Grasslands that support herds of migratory ungulates sustain the highest rates of herbivory among terrestrial ecosystems (Frank et al. 1998) and numerous studies have examined the aboveground interactions between these primary producers and consumers (McNaughton 1976, McNaughton 1984, Frank and McNaughton 1992, Frank and Groffman 1998, Frank et al 2002). In contrast, few studies have examined rates of belowground (root) production and herbivory, despite the long-recognized importance of belowground processes in regulating ecosystem carbon, nutrient, and hydrologic flows (Ares 1976, Nepstad et al. 1994, Jackson et al. 1997, Farrar and Jones 2000). A comprehensive view of both above and belowground processes is needed to provide accurate estimates of terrestrial plant production and to model the responses of terrestrial systems to future environmental perturbations.

Grassland is found on every continent, except Antarctica, comprises 33% of Earth's land surface (Lieth 1978), and provides food and services for approximately 800 million people (FAO 2007). The climate of temperate grassland (known as prairie in North America, steppe in Eurasia, pampas in Argentina and Uruguay, and veldt in South Africa) is semiarid (25-75 cm annual precipitation) and characterized by cold winters and hot summers. Most temperate grassland is dominated by graminoids, supports few shrubs and trees, and possesses organic-rich soil. The fertility of the soil has driven the conversion

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of most natural grasslands to agricultural land (Shantz 1954). Humans depend on converted grasslands to supply all of the major food grains, such as corn, wheat, oats, rice, barley, millet, rye, and sorghum.

In temperate grasslands up to 78% of primary production is allocated to roots (Jackson 1996), and across all ecosystems fine roots (≤ 2 mm diameter) constitute on average 33% of annual net primary productivity (Jackson et al. 1997). Compared to other biomes, temperate grasslands have the greatest fine root biomass per unit area (1.51 kg/m^2) (Jackson et al. 1997). Fine roots are ephemeral in nature, — they grow rapidly, searching out water and nutrients for the plant, but are also consumed rapidly by soil fauna, because they are highly nutritious (low C:N ratio) (Jackson et al. 1997). The rapid turnover (growth and death) of fine roots contributes to the 1477 Gt of organic carbon stored in world's soils (Buringh 1984).

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Temperate grassland soil is home to a diverse assemblage of microfauna that form a tightly coupled community of root herbivores and decomposers (Peterson and Luxton 1982, Anderson 1983). Nematoda, the most abundant multicellular group of microfauna, is found in the greatest densities in temperate grasslands (Peterson and Luxton 1982, Stanton 1988). Other common taxa include Oligochaeta (earthworm), Diptera (fly) larvae, Collembola (springtail), Acari (mite, tick), and Diplopoda (millipede) (Peterson and Luxton 1982). Peterson and Luxton (1982) estimated that soil fauna consume 1-10% of their body weight daily, and Stanton (1988) suggested that root-feeding nematodes may consume more plant biomass than aboveground herbivores. Studies have

shown that root consumers can impact whole plant performance by increasing rates of root mortality (Kosola et al. 1995), decreasing plant seed output (Maron 1998), decreasing live-tiller N content (Moron-Rios et al. 1997), and decreasing total plant biomass (Moron-Rios et al. 1997). Soil microfauna populations respond rapidly to changes in climate (Stanton 1988) and in response to aboveground grazers (Merrill et al. 1994, Frank et al. 2003, Mikola et al 2005).

Although ~~much~~ about how root feeders influence plant growth and death ~~remains~~ unknown, these studies suggest that belowground consumers are important regulators of C and nutrient processes in temperate grassland ecosystems (Blossey and Hunt-Joshi 2003).

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Quantifying the production and consumption of fine roots in the field poses significant methodological challenges. The most common method for estimating seasonal root turnover in the field is to take a monthly soil core, remove the roots from the soil, and find the dry weight of the roots. This provides a measurement of the standing root crop at each date. If there are 100 mg of root mass at time t and 110 mg of root mass at time $t + 1$, root production (growth) would equal 10 mg for the sampling interval. However, the major limitation of this methodology is that it does not provide for roots that simultaneously grow and disappear (by decomposition or herbivory). For example, if during that same time period 20 mg of root grew and 10 mg of root was eaten, production would equal 10 mg and consumption equal 0 mg, clearly an underestimate of both processes. A better estimate of root dynamics would evaluate these processes separately.

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The preferred methodology for estimating seasonal root dynamics in situ is the minirhizotron tube and camera setup (Hendricks et al. 2006) (Fig. 1). The method involves lowering a video camera into a minirhizotron tube, collecting digital images of the roots, and estimating the root lengths from the images.

Unlike soil coring, minirhizotrons allow for the nondestructively measurement of root production and consumption as separate processes (Majdi 1996, Hendrick and Pregitzer 1996). They also provide a more accurate estimate of fine root standing crop than soil coring, due to the difficulty of extracting small root fragments from cores (Hendricks et al. 2006). The major limitation of the minirhizotron technique is that extracting data from the root images is labor-intensive.

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The purpose of this study was to estimate rates of fine root production and consumption in an upland grassland in Yellowstone National Park. I examined the monthly and spatial (depth) variation of root dynamics, and the relationship between root dynamics and monthly average maximum temperature and total precipitation. I also tested whether sampling on a 3-day versus 1-month interval influences estimates of root production and consumption.

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Materials and Methods

Site Description

The study was conducted near Crystal Creek (44⁰54' N, 111⁰19' W, 1909 m. a. s. l.) on the northern winter range of Yellowstone National Park, Wyoming, USA (Fig. 2). The site was located on a flat bench created by glacial deposits. Soils at the site are sandy loam, with a pH of 6.3, bulk density of 1.31 (g/cm³),

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total N content of 0.2% , and 5.4% organic matter, as described by Frank and McNaughton (1992). Vegetation at the site was characterized by common upland grassland species, such as *Festuca idahoensis*, *Carex stenophylla*, *Lupinus sericeus*, *Koeleria cristata*, *Stipa comata*, and *Tetradymia canescens* (C. E. Helquist pers. comm.). The northern range is intensively grazed during the winter and early spring seasons by native ungulates, primarily elk (*Cervus elaphus*), bison (*Bison bison*), and pronghorn (*Antilocapra americana*) (Houston 1982, Frank and McNaughton 1992). Weather data collected at the Tower Falls station (6 km SW of site) indicated that the 1948 – 2006 climate (Western Regional Climate Center, NOAA) was temperate, with long, cold winters (October – March monthly mean temperatures ranged -13 – 2.8°C), and short, dry summers (April – September precipitation was 25 cm),

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Four minirhizotron tubes (90 cm long x 5 cm inside diameter) were installed at an angle of 45° to the soil surface in the spring of 2004, one year prior to data collection, in order to provide sufficient time for the root growth and mortality dynamics to recover from disturbance caused by tube insertion (Hendrick and Pregitzer 1996, Majdi 1996, Joslin and Wolfe 1999, Hendricks et al. 2006). By the first sampling date in 2005 the tubes had settled to an average angle of 28°. The tubes were located > 5 m apart and distributed within a 24 x 24 m plot that was representative of the diversity of the local plant community. The tubes were sealed at the bottom with a rubber stopper, and the portions that extended aboveground were painted and capped to prevent light and water from entering. A piece of insulation that extended approximately 8 cm was fitted into

the top of each tube to minimize large air temperature fluctuations from influencing tube and soil temperature. Prior to installation, 75 numbered image frames (0.9 x 1.3 cm) were sequentially etched into the exterior surface of each tube, and the etchings were painted so that frame outlines could be easily recognized during digitizing. These reference frames allowed me to return to the same frames and follow the same individual roots throughout the season.

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From May – September 2005 digital images from the minirhizotron tubes were collected four times per month at consecutive three day intervals, on the 14th, 17th, 20th, and 23rd of each month. Images of each frame were recorded using a Sony Digital 8 Camcorder. The camcorder was connected to a camera that was attached to a pole, which allowed control of the orientation of the camera in the tube (see fig. 1 – drawing of the field setup). The camera was outfitted with small light bulbs that illuminated the inside of the tube during recordings. All frames were digitized in each tube at each sampling date to a soil depth of approximately 30 cm, because 80-90% of roots in temperate grasslands are found in the upper 30 cm of soil (Lee and Lauenroth 1994, Jackson et al. 1996, Hendricks et al. 2006).

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Image and Data Analysis

Video images of the frames in each minirhizotron tube were converted to JPEG files using Pinnacle Studio V.9.1 video editing software. The images were analyzed with MSU ROOTS Tracer Program 2.2 (Michigan State University, East Lansing, USA) to quantify the length of each root present in a frame using methods developed by Hendrick and Pregitzer (1992, 1993, 1996b). The lengths

of all roots present in even-numbered frames (approximately 35 frames per tube) for each sampling date were traced using a mouse, and all frames were analyzed by one observer to minimize error. These values were written to database files in MSU ROOTS and then converted to Microsoft Excel files using Microsoft Access. Each root was assigned a unique numerical code based on the tube number, the date imaged, the frame number, and the root number (assigned by MSU ROOTS in the order that the root was traced). This code allowed us to compare the lengths of roots in serial sampling dates to determine the rates of root length elongation (growth) and disappearance (mortality) in each frame.

I determined root standing crop and rates of root elongation and mortality for the 0 – 30 cm soil interval for each tube for each month. Database files of root lengths and codes were compiled by minirhizotron and sample date, and the lengths of each root in sequential samples were compared. Standing root crop in a frame was calculated by summing all root lengths present in a frame during a sampling date. Root elongation was defined as either the length of a new root that appeared in a frame between time t and $t+1$ or the growth of a pre-existing root. Root mortality was defined as either the complete or partial loss of a pre-existing root between time t and $t+1$. Values of elongation and mortality for individual roots were summed for each frame, and all of the frames in a tube were summed to find the tube total. I calculated the depth at which each frame was located by using the length of the tube and the angle between the tube and the soil surface. I then found the cumulative elongation and mortality that occurred over three days

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for each 5 cm depth interval and the totals for each tube. The three, three-day estimates of elongation and mortality were averaged for each month.

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I compared estimates of root dynamics from the three-day and one-month sampling intervals. To convert the three-day rates to monthly rates, mean three-day rates of elongation and mortality were first converted to daily rates and then multiplied by the number of days in the month. The three-day estimates were compared to a second set of estimates of root dynamics calculated from observations at one-month sampling intervals. These monthly estimates were derived from values for root growth and disappearance between the last sampling date in one month and the last sampling date in the subsequent month. For example, the June estimates of elongation and mortality were calculated by comparing root images sampled on May 24th to those sampled on June 24th. Both the three-day estimates and 1-month estimates of elongation and mortality were also expressed as percentages of the total standing root crop for each month.

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The effect of observer error on estimates of root length was assessed by re-tracing eleven previously un-analyzed frames, with two weeks between each tracing. Frames were digitized without the aid of previous tracings. Error was calculated by summing the differences in the root lengths between each tracing and dividing this total by the total standing root crop in the eleven frames. By comparing repeated measurements of length, I was able to assess the precision of the methodology (Johnson et al. 2001).

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Statistical Analysis

Sampling replicates within each month were averaged to produce a single three-day estimate of elongation and mortality for each tube. I used paired *t* tests to determine whether rates of elongation and mortality significantly varied between depths in each month. I also used paired *t* tests to determine the monthly variation of rates of root elongation and mortality. In order to determine the effect of sampling interval on estimates of root dynamics, I used a paired *t* test to compare the mean monthly rates of elongation and mortality at three-day and one-month sampling intervals.

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The relationships between local weather variables (monthly mean maximum temperature and total precipitation) with fine root dynamics were examined with regression analysis. Regression analysis was also used to investigate the relationship between the monthly mean maximum temperature : total precipitation ratio, as an index of soil dryness, and the monthly mortality : elongation ratio.

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Results

Temporal changes in root length

Total standing root crop varied through the growing season, with the greatest gains in root length early in the growing season (Fig. 3). Total standing root crop per tube increased from May (369 mm) to June (449 mm) ($P < 0.05$) and did not change from June (446 mm) to September (430 mm) ($P > 0.05$).

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Rates of root elongation per tube varied significantly between all months ($P < 0.05$) except between July and August (Fig. 4a). Root elongation decreased

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slightly from May (338 mm/month/tube) to June (291 mm/month/tube), decreased dramatically in July (68 mm/month/tube), remained constant in August (79 mm/month/tube), and then decreased in September (53 mm/month/tube) (all $P < 0.05$). Root mortality did not vary between months ($P > 0.05$) and was on average 112.45 mm/month/tube (Fig. 4a). Overall rates of root elongation varied temporally whereas rates of mortality did not.

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Effect of sampling interval on elongation and mortality estimates

Rates of elongation and mortality were expressed as percentages of the total monthly standing root crop (Figs. 5a,b). Compared to one-month sampling, rates of elongation derived from three-day sampling were greater in each month ($P < 0.5$), albeit only weakly in June ($P < 0.1$). In June the three-day estimate of elongation as a percent of standing root crop was 69%, whereas the one-month estimate was 22%. Rates of mortality derived from three-day sampling were greater in June and August ($P < 0.05$), weakly greater in September ($P < 0.1$), and not significantly different in July ($P > 0.1$). In June the three-day estimate of mortality as a percent of standing root crop was 28% versus the one-month estimate of 18%.

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Although I did not have data for the one-month estimate of root dynamics in May, June – September data suggest that there would have been a large disparity between the three-day and one-month estimates of root dynamics in May (Fig. 5a). Overall, sampling on a one-month time step underestimated June – September root elongation and mortality by 60% relative to absolute values of

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three-day elongation and mortality ($P < 0.05$). Both time steps showed the same temporal trends in elongation and mortality.

Effect of soil depth on root dynamics

Elongation was greatest in May from 20-25 cm ($P < 0.05$) (Fig. 6a) and in June from 15-20 cm and 25-30 cm ($P < 0.05$) (Fig. 6b). In July, August, and September rates of root elongation did not significantly vary with depth ($P > 0.05$) (Figs. 6c,d,e). A lack of depth effect later in the season was likely due to the overall reduction in root production (Fig. 4a). Early in the growing season elongation was concentrated in intermediate depths, and the effect of depth decreased over the course of the growing season.

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Mortality was greatest in May from 20-30 cm (Fig. 6a), in June from 15-20 cm (Fig. 6b), in July from 10-15 cm interval (Fig. 6c), and in August at all depths greater than 20-30 cm (all $P < 0.05$) (Fig. 6d). Root mortality did not significantly vary with depth in September ($P > 0.05$) (Fig. 6e). Throughout the growing season the greatest rates of mortality shifted from deeper to shallower soil. Similar to rates of elongation, the effect of depth decreased from May – September.

Climatic effects

Monthly mean maximum temperature and total precipitation were not significantly related to either monthly elongation ($P < 0.05$) or mortality ($P < 0.05$). However, the ratio of monthly mean maximum temperature : total precipitation and the ratio of monthly mortality : elongation were positively related ($P < 0.05$, r

= 0.87) (Fig. 7). When the weather was cool and wet in June, few roots disappeared relative to the rate of root growth. When the weather was hot and dry in July, more roots disappeared relative to the rate of root growth. The dramatic difference in the root mortality : elongation ratio between cool, wet June and hot, dry July was primarily caused by the decline in absolute root elongation. This suggests that root production in this grassland was influenced by soil moisture conditions.

Methodological error

The test of observer error indicated that there was 5.6% error in tracing root lengths from one digitizing session to the next. Consequently, conservative estimates of elongation and mortality would be 5.6% lower. This amount of error did not influence the conclusions reported here.

Discussion

Sampling once per month markedly underestimated rates of fine root production and mortality as compared to rates derived from sampling once every three days. Few studies have examined the effects of sampling interval on estimates of root dynamics (Dubach and Russelle 1995, Johnson et al. 2001). Johnson et al. (2001) found that when estimates of fine root dynamics using two, four, and eight week sampling intervals were compared, cumulative root production and mortality were underestimated by 28% with four-week intervals and by 54% with eight-week intervals.

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The most common sampling interval used in minirhizotron studies is once per month, although studies have used intervals ranging from one to sixteen weeks. The range in sampling intervals reflects a trade-off between frequent sampling of few tubes to determine short-term dynamics at few sites, and infrequent sampling of many tubes to examine long-term dynamics at many sites (Johnson et al. 2001). The appropriate sampling frequency also depends on the targeted variable of interest. Estimates of seasonal root production and consumption require frequent, repeated measurements, whereas an estimate of mean annual standing root crop may require less frequent sampling. In a review of minirhizotron methodology, Hendrick and Pregitzer (1996a) emphasized the importance of shortening sampling intervals in order to better understand patterns of root turnover. My results support the recommendations of Hendrick and Pregitzer and suggest that previous estimates of fine root dynamics derived from longer sampling intervals probably underestimated rates of production and consumption. In order to fully capture belowground processes, minirhizotrons must be sampled at a time step that is short enough to match the temporal scale of root dynamics.

A high degree of within-site variation was reflected in the large confidence intervals of ~~monthly estimates of root elongation and mortality~~. For example, the standard deviation for elongation in May was 360 ± 140 mm/month and mortality was 156 ± 119 mm/month. A high degree of ~~fine-grained spatial~~ variability is characteristic of temperate grasslands and ~~has~~ been a confounding factor in minirhizotron studies (Majdi 1996). At two points less than a meter

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apart, soil characteristics such as organic matter, phosphate, potassium, ammonium, and nitrate may be highly variable (Jackson and Caldwell 1993, Augustine and Frank 2001), thus leading to the uneven distribution of fine roots observed both within and between minirhizotron tubes. For this reason, I used paired *t* tests to determine the variation between one tube at time *t* and the same tube at time *t* + 1 and disregarded the effects of spatial (between-tube) variation.

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The variation in root elongation and mortality with depth was likely due to microclimatic differences within the soil column. Root growth was concentrated at intermediate soil depths in May and June when the roots were most productive, suggesting that these depths allowed for the optimal tradeoff between the gains in resources (from the acquisition of nutrients and water) and the costs in energy (due to increased root growth). Root mortality shifted from deeper to shallower soil throughout the growing season, which indicated that root herbivores and decomposers may have shifted their distribution upwards, at least in the 0-30 cm interval.

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The results also indicated that throughout the growing season there was little root activity in the 0-5 cm soil interval, despite evidence from soil coring that maximum root biomass at this site was concentrated near the surface of the soil horizon (D. A. Frank, unpublished data). Reviews of minirhizotron methodology have shown that compaction and desiccation of the shallowest soils limited root growth, which led to underestimates of shallow root dynamics (Majdi et al. 1992, Hendrick and Pregitzer 1996a). Digital images of roots in the 0-5 cm

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depth interval likely underestimated actual root activity, due to effects of minirhizotron tubes on shallow soil microclimate.

Root elongation showed significant seasonal variation, with peaks in root production early in the growing season followed by a rapid decline. The pattern of rapid root growth preceding maximum aboveground production has been previously documented in temperate grasslands (Ares 1976, Fitter 1986).

Maximum aboveground production in 2005 at this site was probably in June,

based on monthly shoot production values from 1999-2001 (Frank 2007). By the end of June, 76% of all root production had already occurred. One possible reason that root growth tends to peak prior to shoot growth is that the plants need to acquire nutrients and water via fine roots before they can begin to produce new shoot growth. This suggests that aboveground production in grasslands may be ultimately limited by fine root production.

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Unlike root production, mortality did not show significant seasonal variation. Other studies also found that shallow, fine root mortality was more evenly distributed across the growing season than root production (Hendrick and Pregitzer 1992, 1996, West et al. 2004). West et al. (2004) suggested that fine root mortality varies independently of root production. Therefore, the mechanisms that directly drive mortality may be distinct from those that drive elongation, although the ultimate drivers (i.e. climate) may be the same.

Root mortality is the consequence of two trophic pathways – herbivory and decomposition. However, most estimates of fine root mortality in the field (Aerts et al. 1989, Hendrick and Pregitzer 1993, 1996b, Katterer et al. 1995, Milchunas

and Lauenroth 2001) have assumed that decomposition is the primary proximate cause of root mortality and that herbivory is inconsequential. This emphasis on decomposition contradicts estimates of rates of fine root decomposition that would suggest much lower rates of root loss. In a review of the application of minirhizotrons, Hendrick and Pregitzer (1996) noted that rates of fine root mortality observed in minirhizotrons were much greater than the rates of decomposition determined by buried bag studies, which estimated that 20-50% of fine root biomass decomposed after one year. Using minirhizotrons tubes in Yellowstone, for example, I found that from May – September total mortality was 64% of total production. However, estimates of rates of decomposition from buried bag studies (Silver and Miya 2001) likely underestimated actual rates, because the methodology required that roots be removed from the microbial community of the rhizosphere (Dornbush et al. 2002). Despite this caveat related to the buried bag technique, I believe that estimates of root turnover derived from the minirhizotron method were greater than those from the buried bag method, because rates of root herbivory were omitted from minirhizotrons estimates.

Yanai and Eissenstat (2002) proposed a model of optimal root turnover that considered root herbivory rather than decomposition to be the major factor in determining root lifespan. My estimates of root mortality were calculated by summing the root lengths that disappeared over three days. Based on estimates of rates of fine root decomposition, it is highly unlikely that a root would completely decompose within that time frame. Therefore, three-day estimates of root mortality should primarily reflect rates of consumption by root herbivores, which

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would suggest that root herbivory rather than decomposition is the principal cause of root mortality.

If estimates of root mortality are attributed primarily to herbivory, rates of belowground herbivory relative to belowground plant biomass may be greater than rates of aboveground herbivory relative to aboveground plant biomass. May - September root mortality as a percent of root production (65%) was greater in magnitude than a previous (1999 -2001) mean estimate of annual aboveground consumption as a percent of aboveground net primary productivity (23%) (Frank 2007). This indicates that root herbivores may have a greater impact on primary production in this grassland than their more conspicuous aboveground, ungulate counterparts.

Similar to my results for an upland grassland in YNP, Gill and Jackson (2000) reported that global patterns of root turnover in terrestrial systems were strongly linked to the ratio of growing season precipitation to maximum monthly temperature. Frank (2007) studied the effects of a three-year drought on grassland primary production in Yellowstone National Park and found that the effect was much more pronounced belowground than aboveground. During the drought belowground net primary productivity declined dramatically, whereas little effect was observed aboveground, indicating that roots were more sensitive to changes in climate than shoots. Other studies have shown that warmer temperatures are linked to greater rates of root mortality (Hendrick and Pregitzer 1993), and it has been suggested that this is due to increased microfauna populations (Gill and Jackson 2000). The tight linkages between precipitation,

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temperature, root growth, and consumption indicate root systems will be particularly responsive to future changes in climate and may determine the limits of productivity of this ecosystem.

Conclusions

Patterns of root production were most likely coupled with aboveground production, whereas mortality may have been driven by herbivore abundance and soil moisture. Sampling on short, three-day time intervals provided greater estimates of root growth and mortality, because the long, one-month interval missed rapid, fine-root dynamics. Root herbivory rather than decomposition is the primary trophic pathway that determines root lifespan, and root consumption is the major form of herbivory in this grassland that supports intense aboveground grazing. I concur with Stanton (1988) that, “Within grasslands it may be the ubiquitous microfauna that ultimately regulate net primary production by their consumption of roots and the microbial biomass.”

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Acknowledgements

I thank A. Risch, V. Green, & M. Wysser for assistance in the field. Thanks to M. Thorne & J. Fridley for helpful comments, and S. Stehman & S. Bagchi for help with statistics. This work was supported by the Ruth Meyer grant & the National Science Foundation grant DEB-0318716.

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References

- Aerts, R., Berendse, F., Klerk, N. M., and Bakker, C. 1989. Root production and root turnover in two dominant species of wet heathlands. *Oecologia* **81**:374-378.
- Anderson, R. V., Gould, W. D., Woods, L. E., Cambardella, C., Ingham, R. E., and Coleman, D. C. 1983. Organic and inorganic nitrogenous losses by microbivorous nematodes in the soil. *Oikos* **40**:75-80.
- Ares, J. 1976. Dynamics of the root system of the blue grama. *Journal of Range Management* **29**:208-213.
- Augstine, D. J. and Frank, D. A. 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. *Ecology* **82**:3149-3162.
- Blossey, B. and Hunt-Joshi, T. R. 2003. Belowground herbivory by insects: Influence on plants and aboveground herbivores. *Annual Review of Entomology* **48**:521-547.
- [Buringh, P. 1984. Organic carbon in soils of the world. Pages 91-109 in Ed. G. M. Woodwell. The role of terrestrial vegetation in the global carbon cycle: Measurement by remote sensing. John Wiley and Sons, New York, New York, USA.](#)
- Dornbush, M. E., Isenhardt, T. M., and Raich, J. W. 2002. Quantifying fine-root decomposition: An alternative to buried litterbags. *Ecology* **83**:2985-2990.
- Dubach, M. and Russelle, M.P. 1995. Reducing the cost of estimating root turnover with horizontally installed minirhizotrons. *Agronomy Journal* **89**:258-263.
- Farrar J. F. and Jones, D. L. 2000. Research Review: The control of carbon acquisition by roots. *New Phytologist* **147**: 43-53.
- Fitter, A. H. 1986. Spatial and temporal patterns of root activity in a species-rich alluvial grassland. *Oecologia* **69**:594-599.
- Frank, D. A. and McNaughton, S. J. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. *Ecology* **73**:2043-2058.
- Frank, D. A. and Groffman, P. M. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. *Ecology* **79**:2229-2241.

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- Frank, D. A., McNaughton, S. J., and Tracy, B. F. 1998. The ecology of the Earth's grazing ecosystems. *BioScience* **48**:513-521.
- Frank, D. A., Kuns, M. M., and Guido, D. R. 2002. Consumer control of grassland plant production. *Ecology* **83**:602-606.
- Frank, D. A., Gehring, C. A., Machut, L. and Philips, M. 2003. Soil community composition and the regulation of grazed temperate grassland. *Oecologia* **137**:603-609.
- Frank, D. A. 2007. Drought effects on aboveground and belowground production in a temperate grazed grassland ecosystem. *Oecologia*. Online First.
- Gill, R. A. and Jackson, R. B. 2000. Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* **147**:13-31.
- Hendrick, R. L. and Pregitzer, K. S. 1992. The demography of fine roots in a northern hardwood forest. *Ecology* **73**:1094-1104.
- Hendrick, R. L. and Pregitzer, K. S. 1993. Patterns of fine root mortality in two sugar maple forests. *Nature* **361**:59-61.
- Hendrick, R. L. and Pregitzer, K. S. 1996a. Applications of minirhizotrons to understand root function in forests and other natural ecosystems. *Plant and Soil* **185**:293-304.
- Hendrick, R. L. and Pregitzer, K. S. 1996b. Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. *The Journal of Ecology* **84**:167-176.
- Hendricks, J. J., Hendrick, R. L., Wilson, C. A., Mitchell, R. J., Pecot, S. D., and Guo, D. 2006. Assessing the patterns and controls of fine root dynamics: and empirical test and methodological review. *The Journal of Ecology* **94**: 40-57.
- Houston, D. B. 1982. *The northern Yellowstone elk: ecology and management*. Macmillan, New York, New York, USA.
- Jackson, R. B. and Caldwell, M. M. 1993. Geostatistical patterns of soil heterogeneity around individual perennial plants. *The Journal of Ecology* **81**:683-692.
- Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., and Schulze, E. D. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**:389-411.

- Jackson, R. B., Mooney, H. A., and Schulze, E.-D. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences* **94**:7362-7366.
- Johnson, M. G., Tingey, D. T., Phillips, D. L., and Storm, M. J. 2001. Advancing fine root research with minirhizotrons. *Environmental and Experimental Botany* **45**:263-289.
- Joslin, J. D. and Wolfe, M. H. 1999. Disturbances during minirhizotron installation can affect root observation data. *Soil Science Society of America Journal* **63**:218-221.
- Katterer, T., Fabiao, A., Madeira, M., Ribeiro, C., and Steen, E. 1995. Fine-root dynamics, soil moisture, and soil carbon content in a *Eucalyptus globulus* plantation under different irrigation and fertilization regimes. *Forest Ecology and Management* **74**:1-12.
- Kosola, K. R., Eissenstat, D. M., and Graham, J. H. 1995. Root demography of mature citrus trees: The influence of *Phytophthora nicotianae*. *Plant and Soil* **171**:283-288.
- Lee, C. A. and Lauenroth, W. K. 1994. Spatial distribution of shrub root systems in the shortgrass steppe. *American Midland Naturalist* **132**:117-123.
- Lieth, H. and Whittaker, R. H. 1975. *Primary productivity of the biosphere*. Springer-Verlag, New York, New York, USA.
- Majdi, H., Smucker, A. J. M., and Persson, H. 1992. A comparison between minirhizotron and monolith sampling methods for measuring root growth of maize (*Zea mays* L.). *Plant and Soil* **147**:127-134.
- Majdi, H. 1996. Root Sampling Methods -- Applications and limitations of the minirhizotron technique. *Plant and Soil* **185**:255-258.
- Maron, J. L. 1998. Insect herbivory above- and belowground: individual and joint effects on plant fitness. *Ecology* **79**:1281-1293.
- McNaughton, S. J. 1976. Serengeti Migratory Wildebeest: Facilitation of Energy Flow by Grazing. *Science* **191**: 92-94
- McNaughton, S. J. 1984. Grazing lawns: Animals in herds, plant form, and coevolution. *The American Naturalist* **124**:863-886
- Merrill, E. H., Stanton, N. L., Hak, J. C. 1994. Response of bluebunch wheatgrass, Idaho fescue, and nematodes to ungulate grazing in Yellowstone National Park. *Oikos* **69**:231-240.

Mikola, J., Nieminen, M., Ilmarinen, K., and Vestberg, M. 2005. Belowground responses by AM fungi and animal trophic groups to repeated defoliation in an experimental grassland community. *Soil Biology and Biochemistry* **37**:1630-1639.

| Moron-Rios, A., Dirzo, R., and Jaramillo, V. J. 1997. Defoliation and below-ground herbivory in the grass *Muhlenbergia quadridentata*: Effects on the plant performance and on the root feeder *Phyllophaga* sp. (Coleoptera: Melolonthidae). *Oecologia* **110**:237-242.

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Nepstad, D. C., Carvalho, C. R., Davidson, E. A., Jipp, P. H., Lefebvre, P. A., Negreiros, G. H., Silva, E. D., Stone, T. A., Trumbore, S. E., and Vieira, S. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* **372**:666-669.

Peterson, H. and Luxton, M. 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos* **39**:288-388.

Silver, W. L. and Miya, R. K. 2001. Global patterns in root decomposition: Comparisons of climate and litter quality effects. *Oecologia* **129**:407-419.

Shantz, H. L. 1954. The place of grasslands in the Earth's cover. *Ecology* **35**:143-145.

Stanton, N. L. 1988. The underground in grasslands. *Annual Review of Ecological Systems* **19**:573-589.

West, J. B., Espeleta, J. F., and Donovan, L. A. 2004. Fine root production and turnover across a complex edaphic gradient of a *Pinus palustris*--*Aristida strictata* savanna ecosystem. *Forest Ecology and Management* **189**:397-406.

Yanai, R. D. and Eissenstat, D. M. 2002. Coping with herbivores and pathogens: A model for optimal root turnover. *Functional Ecology* **16**:865-869.

Appendix A: Figures

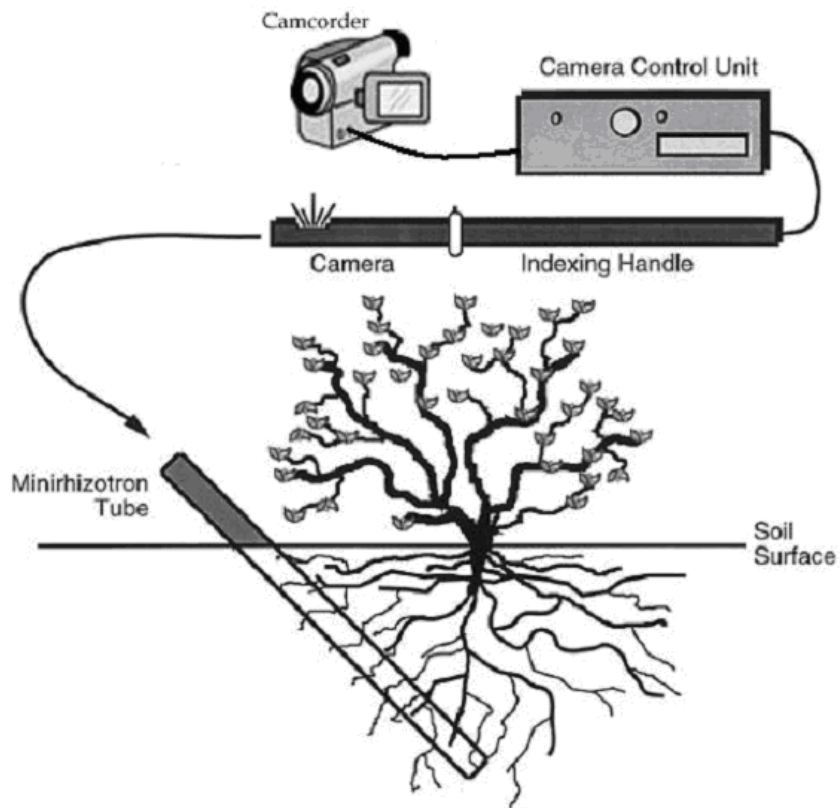


Figure 1. General setup of minirhizotron tube and cameras. Adapted from Johnson et al. 2001.

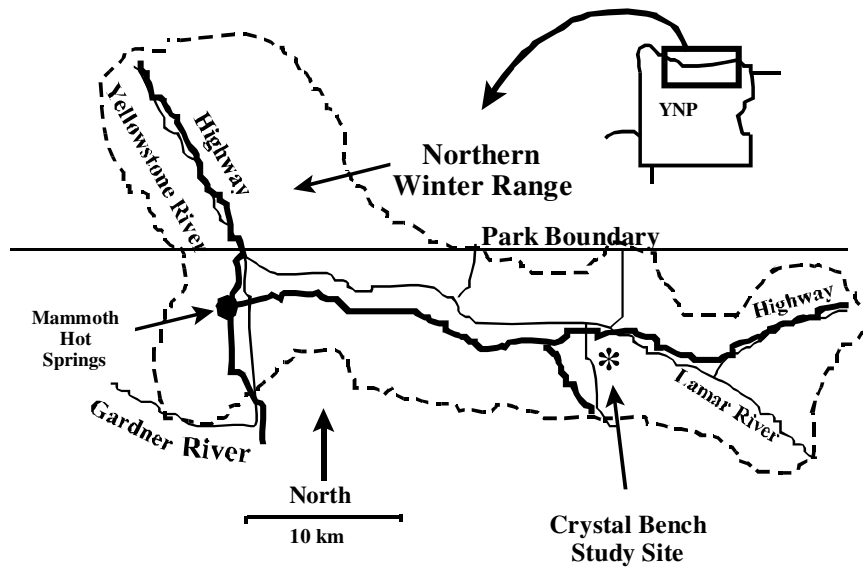


Figure 2. Map of Crystal Bench study site (44⁰54' N and 111⁰19' W, 1909 m above sea level) in the northern winter range of Yellowstone National Park.

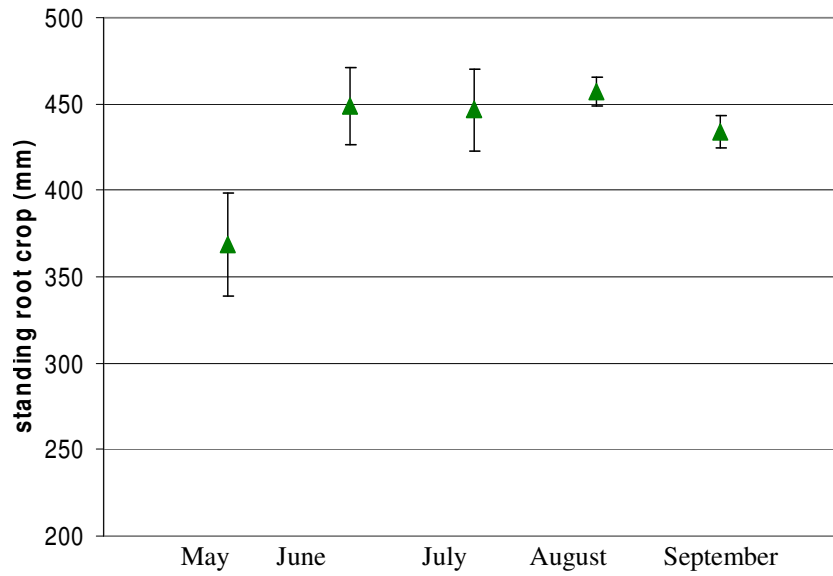


Figure 3. Mean monthly estimates of total standing root crop per tube and 95% confidence intervals. Standing root crop (mm root length) increased significantly from May – June ($P < 0.05$) and remained constant from June – September ($P > 0.05$).

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Figure 4

Mean monthly estimates and 95% confidence intervals of elongation (mm/month) and mortality (mm/month) per tube from 3-day sampling intervals (A) and 1-month intervals (B). In Fig 4a, rates of elongation significantly declined from May to September ($P < 0.05$) except for between the months of July and August ($P > 0.05$). Mortality did not vary with month ($P > 0.05$). In Fig 4b elongation in June was significantly greater than in July – September, and mortality was significantly greater in July (all $P < 0.05$).

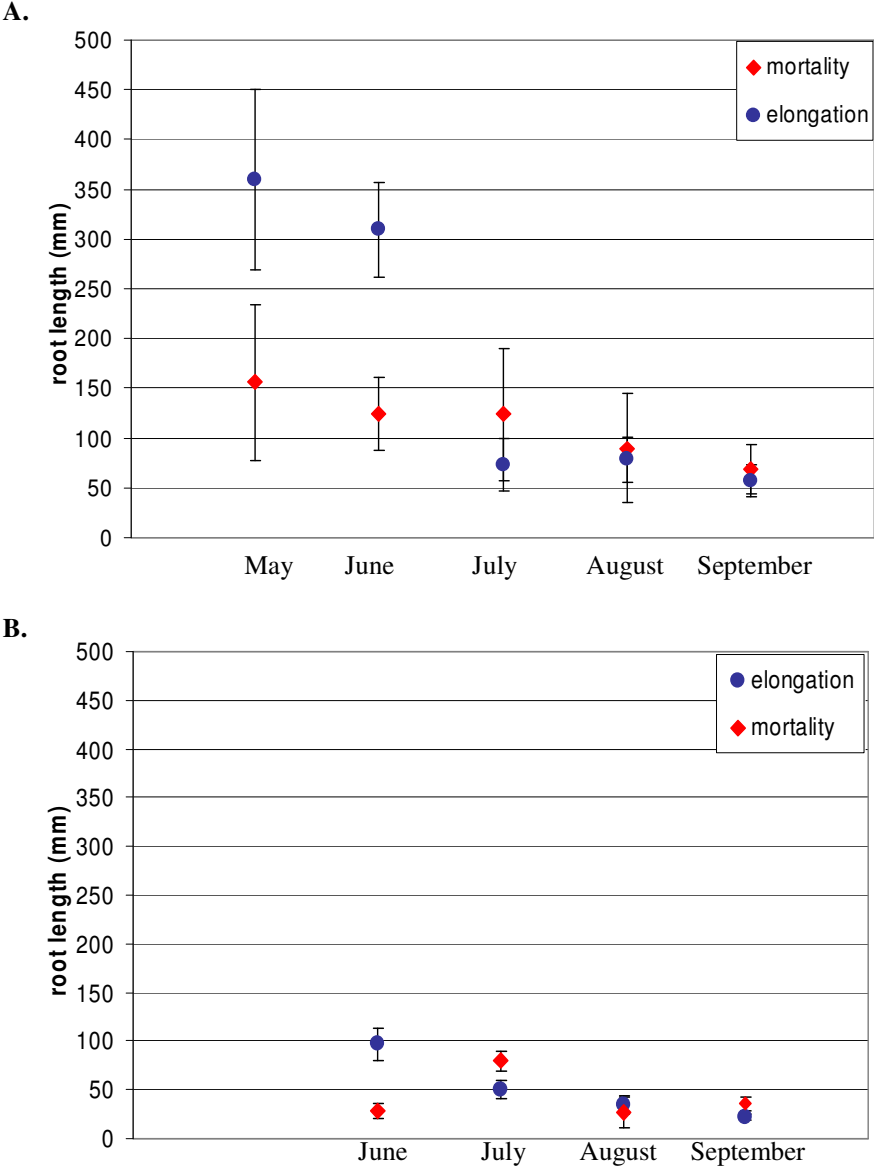
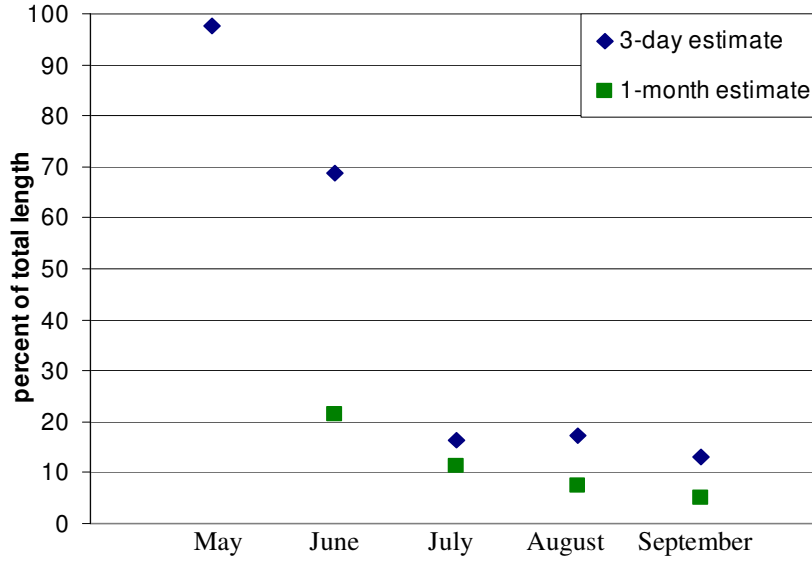


Figure 5

Mean monthly elongation (A) and mortality (B) per tube expressed as a percent of monthly total standing root crop for three-day and one-month sampling intervals. Sampling on a one month interval underestimated total growing season elongation and mortality by approximately 60% relative to sampling on a three-day interval.

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A.



B.

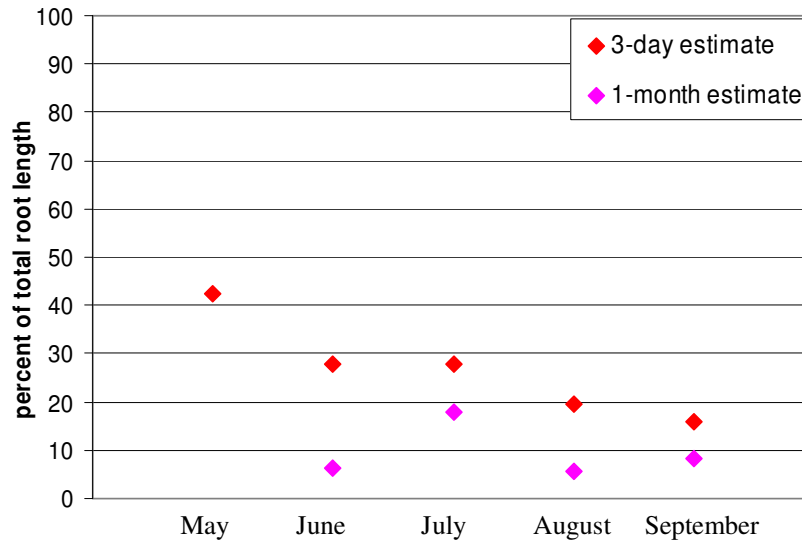
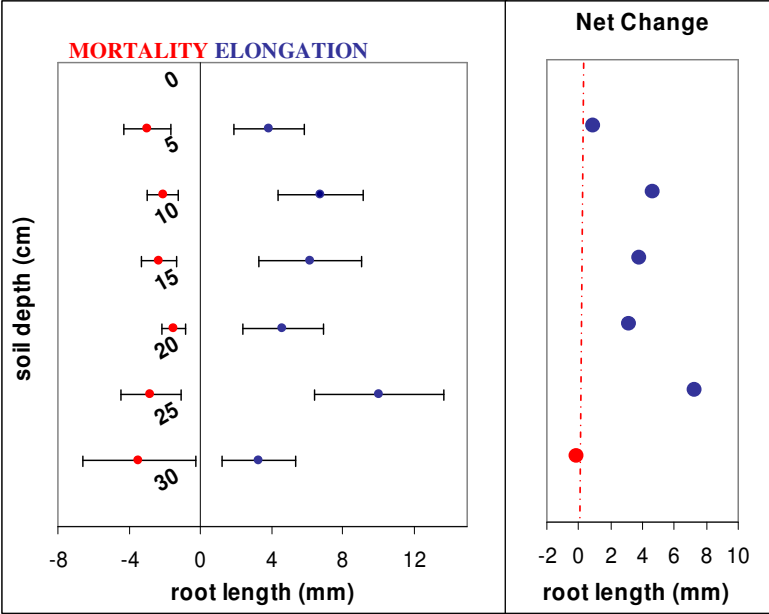


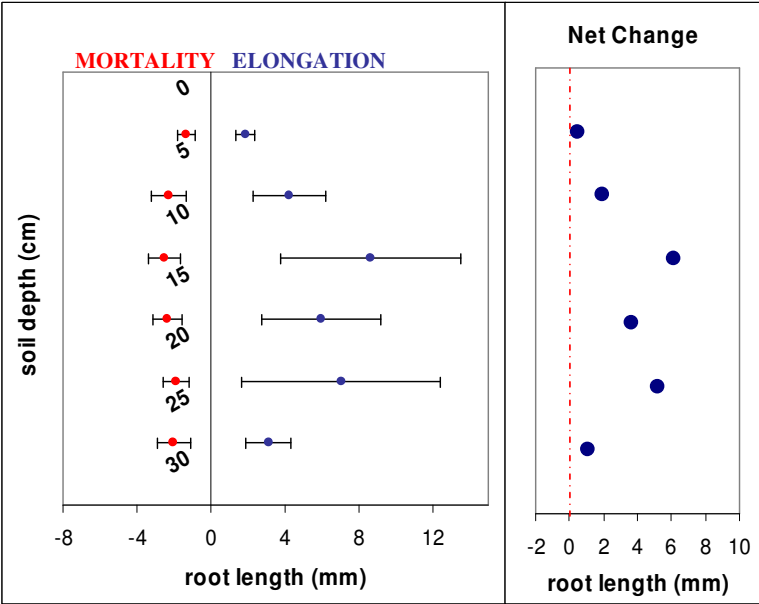
Figure 6

Mean May – September (A – E) root elongation and mortality at 5 cm depth intervals with 95% confidence intervals and the net change in root length at each interval (net change = elongation + mortality). Dashed red lines represent depths where the net change in root length equals zero.

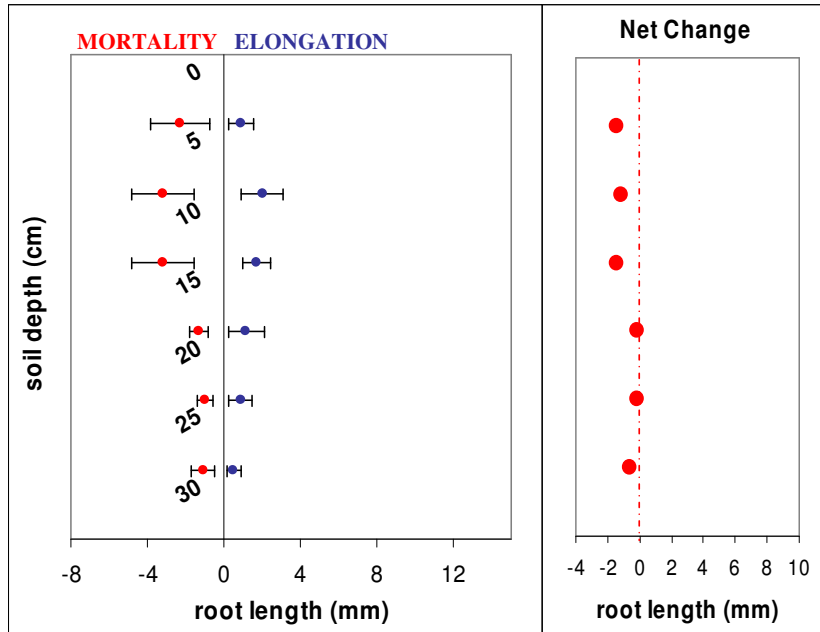
A. May



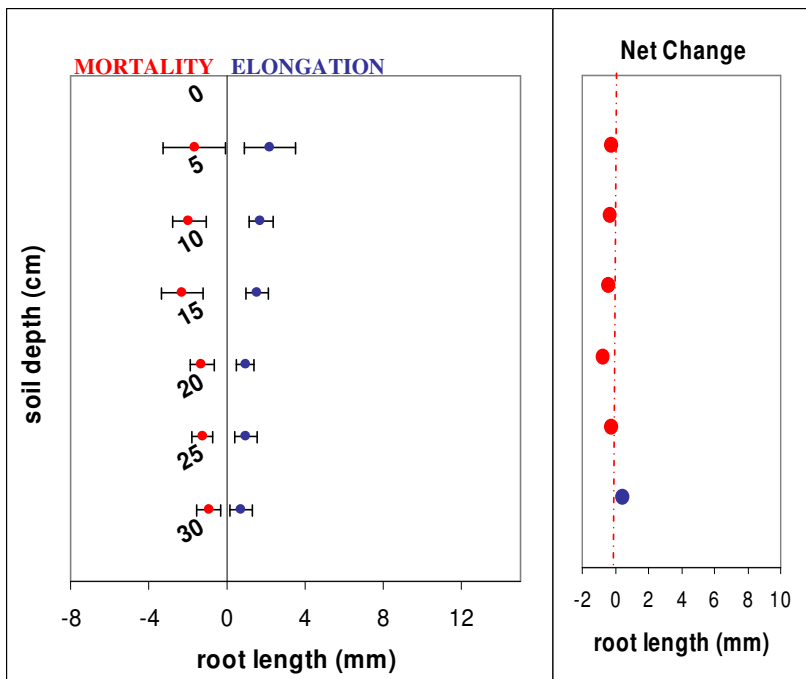
B. June



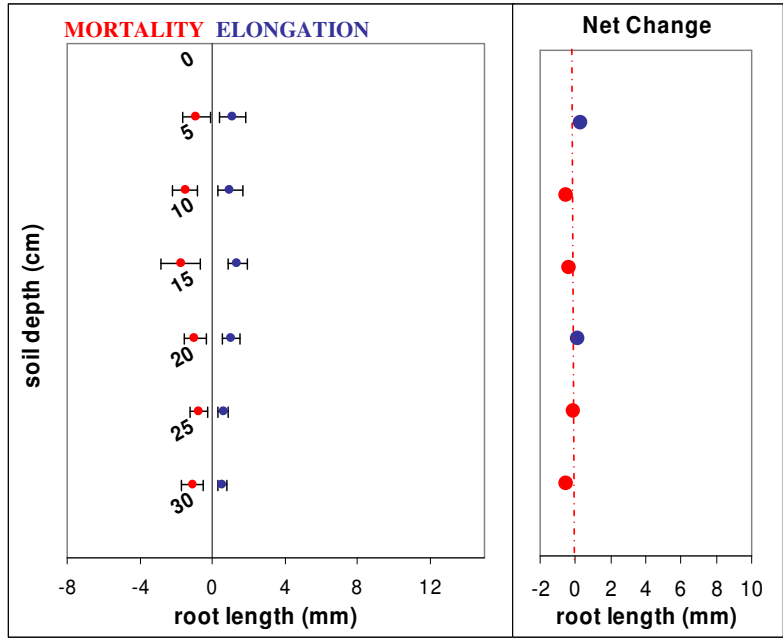
C. July



D. August



E. September



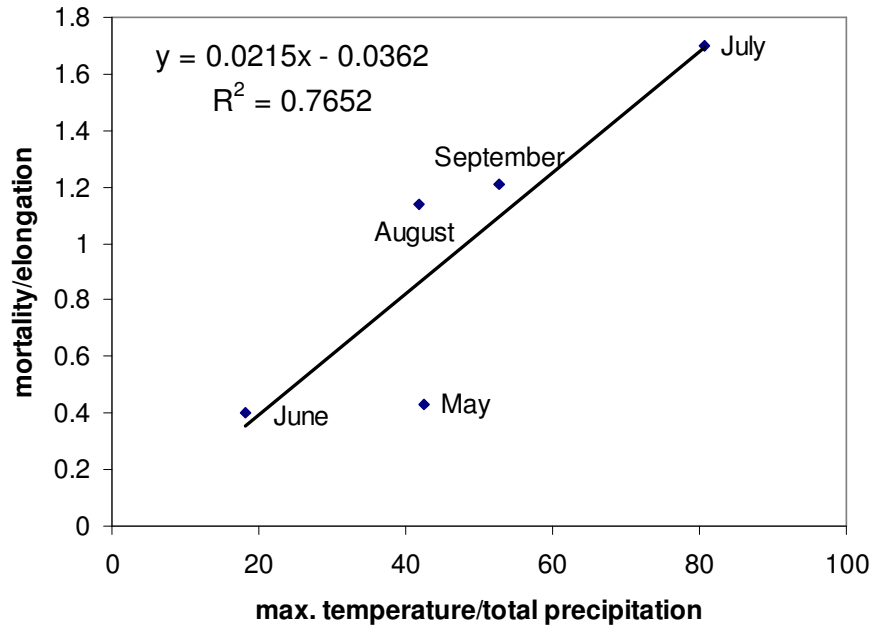


Figure. 7. The relationship between the ratio of mean maximum monthly temperature : monthly total precipitation and the ratio of mean monthly mortality : elongation was statistically significant ($P < 0.05$).