University of Alberta

Trails, Trampling and Scale of Observation in a Rough-Fescue Grassland

by

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CHAPTER 1

THE EFFECTS OF TRAMPLING ON PLANTS

INTRODUCTION

In grassland ecosystems, both plant species and communities respond to both long term and large-scale disturbances such as fire, drought and grazing (Knapp and Seastedt 1998), and to short term, small scale disturbances, such as those caused by non-grazing animal activity (Loucks et al. 1985). These disturbances interact with local processes, including plant competition and insect herbivory, to influence the local plant community (Ricklefs and Schluter 1993, Hartnett and Fay 1998). Historically, research on non-grazing animal activity in grassland systems has focused on gap disturbances, such as those created by pug (hoof) marks, fecal pats, ant hills and small mammal burrowing activity (eg. Taylor and Friend 1984, Coffin and Lauenroth 1988, Bradshaw and Goldberg 1989, Reichman et al. 1993, English and Bowers 1994).

Small scale disturbances generated by animal activity (eg. gopher mounds, badger burrows) influence plant community structure and dynamics in herbaceous systems (Platt 1975, King 1977, Hobbs and Mooney 1985, Bradshaw and Goldberg 1989, Gibson 1989). Species composition in gaps often differs from the surrounding vegetation (eg. Platt 1975, King 1997, Morgan 1988, Williams 1992), and gaps generally have some reduced level of plant cover or areas of bare ground (Bradshaw and Goldberg 1989). Gaps <50cm wide are the most common in productive herbaceous communities (Platt 1975, Goldberg and Gross 1988) and comprise less than 2% of studied areas (Gross and Werner 1982, Tilman 1983, Goldberg and Gross 1988, English and Bowers 1994). Although gaps are relatively rare both spatially and temporally in grasslands, many common species require gaps for establishment from seed and have higher emergence, survival and growth in gaps compared with that in undisturbed vegetation (Gross and Werner 1982, Goldberg and Werner 1983, Goldberg 1987, Aguilera and Lauenroth 1995, Morgan 1998, Kiviniemi and Eriksson 1999). Relatively infrequent disturbances such as gaps that comprise 2% of an area, can have a large role in shaping community structure, especially when the establishment of new individuals is rare in relation to the dominant organism's lifespan (Pickett and White 1985). The size and time of gap formation and the rate at which the gap closes after disturbance influence the availability of gaps for recruitment and colonization events (Williams 1992, Morgan 1998), and the effects can depend on the topographic position of the gap and interactions with other disturbance factors (eg. grazing) (Coffin and Lauenroth 1988).

In grasslands, reduced competition in gaps provide opportunities for less competitive species to colonize (Platt 1975, King 1977, Hobbs and Mooney 1985, English and Bowers 1994). Effects on community structure and dynamics depend not only on the response of species to the characteristics of gaps, but also on the interactions between individuals invading gaps (McConnaughay and Bazzaz 1990). Gaps may provide some resources species are unable to acquire in undisturbed sites; while more light is available in gaps, soil moisture, nutrient levels and organic matter are often lower (Bradshaw and Goldberg 1989, McConnaughay and Bazzaz 1990). Independent of any advantage gained from increased available light, a reduction in root competition may also contribute to the increased plant growth (Cahill and Casper 2002).

In most studies that examine the influence of vegetation gaps caused by animal activities (eg. burrowing) on grassland community dynamics, the animal activity involves the disturbance and exposure of mineral soil and the removal of existing vegetation and litter (Goldberg and Gross 1988). However, not all non-grazing animal activities which create gaps involve disturbances that expose mineral soil. Many trails created by animals using grasslands as conduits to and from feeding and bedding sites disrupt the vegetation and litter layer. While the trampling action of animals can expose some mineral soil (eg. Weaver and Dale 1978, Wilson and Seney 1994), most trails in grasslands created and used by wild animals, are visible as continuous disturbances of the vegetation and litter layer.

Gaps created by the non-grazing animal activity of trampling and trail creation are fundamentally different from those created by burrowing mammals, in that the mineral soil is not disturbed or exposed to the same extent. To date, no studies have directly examined how trails used by wildlife in grasslands act as a localized gap disturbance. Nor have any determined how these small-scale disturbances influence plant community structure and dynamics, although one study characterizes wildlife trails by the presence or absence of certain vegetation types (Taylor and Friend 1984). In systems where light is limited by the dominant vegetation and trampling disrupts it, changes in available light due to trampling may contribute to higher species richness and frequency on trails, as found in *Typha* mats (Hewitt and Miyanishi 1997). Trampling concentrated at feeding and resting sites does influence local composition in several grassland systems and effects are often dependent on the identity of the animal trampler and their local density (Lock 1972, McNaughton 1983, Belsky 1986, Dublin et al. 1990, Plumptre 1993). It is reasonable to suspect that trails, as continuous small scale disturbances, may influence local plant community structure and dynamics by trampling both the vegetation and the litter layer, but not necessarily disrupting mineral soil to the extent of burrowing.

Litter Layer in Grasslands

The litter layer in productive grassland systems can be substantial (Goldberg and Werner 1983, Carson and Peterson 1990). Litter is a fundamental factor in controlling plant community structure and may also influence competition in productive habitats (review see: Xiong and Nilsson 1999). Litter directly suppresses germination, establishment, species richness and diversity and aboveground biomass (Tilman 1993, Xiong and Nilsson 1999). In providing habitat for many invertebrate species (Duffey 1972), litter can increase both the damage to and mortality of seedlings by invertebrates (Facelli 1994). This implies that in communities with abundant litter, vegetation development relies largely on reducing factors such as fast decomposition and disturbances (eg. burning, grazing and trampling) that remove or open up the litter layer (Foster and Gross 1998, Carson and Peterson 1990). Litter also protects seeds from predators (Sydes and Grime 1981), adds nutrients (Facelli and Picket 1991), carries diaspores during water redistribution, and ameliorates stressful conditions by buffering effects from lethal frosts (Watt 1974) and conserving water in dry conditions (Fowler 1986).

Litter has a stronger negative effect on plant germination than establishment, suggesting that disturbances reducing litter will have more of an effect early in the growing season, when they are likely to coincide with germination (Xiong and Nilsson 1999). The inhibitory effect of litter on species richness is attributed to the attenuation of light to very low levels, as litter shades and mechanically impedes seedlings (Goldberg and Werner 1983, Carson and Peterson 1990, Tilman 1993, Foster and Gross 1998). Because fire is currently absent from most grassland landscapes, the rapid accumulation of grass litter may be a unique feature that limits species establishment and diversity (Foster and Gross 1988). Native grassland species that evolved in the presence of fire may lack adaptations for establishment in dense litter (Tilman 1993).

While litter has both positive and negative effects on plants, trampling adds a new dynamic as it crushes and fragments litter, forcing it into the soil matrix (Duffey 1972). Trampling decreases both litter biomass and the number of air spaces within the litter matrix, while also increasing the ratio of fibre to air space (compression value). Trampling also mechanically consolidates nutrients as organic manure is broken into smaller sizes and incorporated into the surface layers of the soil via hoof action (Keen and Cashen 1932, Weir 1971). As litter and nutrients are incorporated into the soil, rates of decomposition and mineralization can increase by increasing the surface area and proximity of plant material to decomposers (Zacheis et al. 2002).

TRAMPLING AND TRAIL CREATION

Just as animals create trails in systems while using them as conduits, humans create trails in natural areas in both recreational (eg. hiking, hunting) and professional (eg. research, surveys) capacities. Humans historically used trails during seasonal migrations (6000-8000 years ago) (Marr and Willard 1970), and pollen spectra identify areas historically trampled in arctic ecosystems (ca. 800 B.P.) (Rasanen 2001, Forbes 1996). Trails develop as plants are first bent, then broken, then killed (Willard and Marr 1971), causing localized environment changes and habitat fragmentation (Kutiel 1999). The amount of trampling that leaves a visually obvious trail is described as the significant threshold of impact (Cole 1993), and once a trail is formed it tends to attract further attention and use by both people (Cole 1993) and animals (Bates 1951, Ganskopp et al. 2000). Trails therefore develop through a positive feedback mechanism that can lead to pronounced impacts on the vegetation and soil (Cole 1993).

Direct impacts to vegetation on trails depend not only on the frequency with which the trail is used, but also on the characteristics of the trampler. In North America, wildlife creating and using trails vary in weight from vole to moose and in locomotory form and weight distribution from hoofed ungulate to pawed bear. Humans create trails in systems in many different ways, while walking, riding bicycles or driving horse carts, cars and all terrain vehicles. Regardless of how the trail is created, the mode of trail creation is trampling, trails are created by the direct damage done to an individual plant as it is stepped on and damaged by hoof, foot or wheel.

Trampling Forces Exerted on Vegetation

Forces exerted by trampling humans and wildlife are different; large ungulates carry more weight per unit area of hoof that touches the ground surface than human feet (Bates 1938). As well, the ungulate foot surface is not flat (Bates 1938) and the depression caused by ungulate hoof prints can provide microsites for seedling establishment (McNaughton 1983). While ungulates of greater mass do cause more damage to vegetation when trampling (Ssemakula 1983, Bennett 1999), it is because they trample a greater area, not because larger and smaller ungulates have different hoof pressures (Cumming and Cumming 2003). Larger herbivores have relatively shorter legs and take relatively shorter steps than smaller herbivores, and therefore trample a greater area of ground per unit distance traveled (Cumming and Cumming 2003). When relationships between body mass, shoulder height, hoof area, stride length and daily ranging distance of African ungulates ranging from 5 to 5000 kg were examined, hoof area scaled linearly to body mass with a slope of unity (Cumming and Cumming 2003). This means that despite a large difference in body mass, the pressures exerted on the ground per unit area by a small antelope and an elephant are identical.

The force exerted by a human foot with bipedal motion differs from quadrupedal motion, as bipedal humans have vertical pressure plus a distinct horizontal and semi-rotary twist as the ball of the foot leaves the ground (Bates 1938). At a normal walking gait, the foot comes down at an angle, with the weight of the entire body placed first on the heel, then rolling towards the toes as the foot is lifted (Palmer 1972). Therefore, the sharp edge of a hard-soled hiking boot causes more vegetation cover loss than soft-soled running shoes (Palmer 1972, Cole 1995d). Running shoes and hiking boots have different effects on cover immediately after trampling stops, as well as one year later (Cole 1995d). Furthermore, a person's weight influences vegetation height, but not vegetation cover (Cole 1995d).

Trails created by bicycles, motorcycles and motorized vehicles also have different characteristics than those created by animals or humans, as the pressures exerted and the mode of action (wheels versus feet) are different (Liddle and Grieg-Smith 1975a, Weaver and Dale 1978, Wilson and Seney 1994). Further discussion of these differences is beyond the scope of this paper, as this review focuses on the effects of non-motorized trails.

Trail Characteristics

Both the species that create and continue to use a trail in the grassland can influence the characteristics of a trail (Table 1.1). Trails made and used by domestic and wild animals tend to lead to a specific destination, such as a watering hole, salt lick, resting place or feeding site (Bates 1951, Oikawa et al. 1981). These trails tend to avoid hazards and follow the route of least resistance, such as a ridge crest or hill base, and tend to be parallel to contour lines, with few perpendicular routes (Bates 1951,Thomas 1959, Oikawa et al. 1981). Humans tend to make trails by following a guiding line made by previous passage, such as footprints in snow or mud on vegetation (Bates 1951), and meander from soft ground or with changes in slope (Bates 1951). Animal trail densities are highest near water sources (Walker and Heitschmidt 1986), and there tend to be more human trails in poorly drained areas (Cole 1985a, Yalden and Yalden 1988). The lateral boundaries of domestic animal trails are sharp, while wild animal and human trails tend to have boundaries that merge gradually into the surrounding vegetation (Bates 1935, 1951). Domestic animal trails are narrower and deeper, and while human trails are wider, their use is often concentrated within the central 10cm of the trail (Thurston and Reader 2001). Due to the higher amounts of bare ground exposed on domestic animal trails, more sediment is exposed for erosion (Deluca et al. 1998).

Trail width and depth increase with use, with the most rapid increases occurring within the first few hundred passes in most systems; moreover the increase is greater when trails are wet, or when made in one day versus over four months (Bayfeild 1973, Weaver and Dale 1978, Hylgaard and Liddle 1981). Width also depends on the local topography, as trails are wider on rough ground surface, on steep slopes and in open habitats (Watson et al. 1969, Dale and Weaver 1974). Width also depends on soil type, as trails are wider on peat soils than gravel, and on clay than sand (Watson et al. 1969).

Once a path has lost vegetation cover, widening may be maintained as much by soil erosion as by trampling, independent of increases in use (Lance et al. 1989). It is important to remember that trampling on trails is not always the single dominant process active on trails, as trail degradation is also a function of landform, climatic and catastrophic events and geomorphological processes (Summer 1986). Erosion of active trails is also related to the type of landform crossed; trails below the crest of a hill can be expected to erode more quickly than trails on other segments of a slope (Summer 1986).

RESPONSES TO TRAMPLING

Early examination of the impacts of trampling on local plants and the abiotic community began with observational studies noting that some plants appeared less able to tolerate the disturbance and that plants were shorter on trails than in adjacent areas (Jeffreys 1917, Shantz 1917). Compositional differences between trails and adjacent areas were examined by both Bates (1935, 1938) and Davies (1938). The first study that involved trampling as a manipulated treatment was designed to examine the effects of trampling on the leaf size and root system of *Trifolium repens*, directly measuring soil compaction and leaf damage (Bates 1934). Later studies investigated the effects of trampling in natural areas by a variety of species, such as sheep (Edmond 1962), horses (Perring 1967), humans with various footwear (Cole 1995d) and artificial devices designed to stimulate recreational foot traffic such as the tamp (Wagar 1964) or the mechanical foot (Bayfield 1971b).

Following the Second World War, increased leisure time and real income led to increased human use of natural areas (Wagar 1964, Goldsmith et al. 1970), and this increased use resulted in attempts to define the carrying capacity of various 'wildland' habitats (eg. Wagar 1964, Dotzenko et al. 1967, Watson et al. 1969). Initially, observations and questionnaires were used to determine the number of people using a particular trail or recreation site, as well as photo-electric and electromagnetic people counters (Goldsmith et al. 1970) to determine the volume of users (Bayfield 1971a). Bayfield (1971a) developed a trampleometer; a series of fine wires projecting from pins at the ground surface, which would bend when stepped upon. By placing pins at different densities on and near trails, researchers could determine where people actually walked and with what frequency.

By the 1980s, the effects of human trampling in recreational settings had been examined enough to warrant an annotated bibliography related to management of wilderness or back country areas (Cole and Schreiner 1981). Cole (1985b) and Liddle

(1975b, 1991) have focused reviews on synthesis across systems, while system specific trampling effects have been reviewed for alpine vegetation (Price 1985), rocky intertidal communities (Jenkins et al. 2002) and coral reefs (Liddle and Kay 1987, Kay and Liddle 1989). A focused review of trampling effects in grassland systems is missing from this literature. In general, experimental trampling studies compare trampled areas with adjacent untrampled areas (Sun and Liddle 1993c) and are based on the assumptions that 1) the vegetation of the whole area was homogenous before trampling (Price 1985), and 2) that changes may be attributed to the effect of trampling, whether direct or indirect (Liddle 1975a).

General Effects of Trampling

In most systems, trampling decreases vegetation cover (eg. Hosier and Eaton 1980, Anderson 1995, Cole 1995b, Cole and Monz 2002, Ikeda 2003), plant height (eg. Cole and Monz 2002, Scott et al. 2002), aboveground biomass (eg. Bell and Bliss 1973, Grabherr 1982, Sun and Liddle 1993d, Whinham and Chilcott 1999), root biomass (Sun and Liddle 1993d) and litter (Gillham 1956, Bayfield 1971b, but see Shaw and Diersing 1990), with increases in the percentage of bare ground (eg. Weaver et al. 1979, Cole 1987, Anderson 1995, Whinham and Chilcott 1999).

Both the short and long-term responses to trampling depend on the direct and indirect effects trampling has, not only on the vegetation damaged, but also on the resources available to damaged, neighbouring and colonizing plants, as well as the local invertebrate and vertebrate communities. Trampling directly affects the plant immediately stepped upon, either by damaging the plant to some degree or killing it. Plants experience mechanical injury to stems and surface roots, as trampling crushes and tears plant tissue, breaks stems, leaves and flower stalks, and can dislodge and bury plants (Willard and Marr 1970, Bayfield 1971b, Watson 1985, Kuss 1986). A plant that survives trampling will often grow bent, twisted and withered (Bowles and Maun 1982), although trampling can stimulate the growth rate of some species (Sun and Liddle 1993b). Trampling decreases the aboveground biomass of plant parts, the number of leaves or tillers, tiller length, tiller diameter, relative growth rate and leaf weight ratio, while the number of broken tillers and leaves increases (Sun and Liddle 1993b, Kobayashi and Hori 1999). Taller plants are more adversely affected by trampling

(Gilham 1956, Goldsmith et al. 1970, Bowles and Maun 1982), and the breaking of stems is the main reason for the reduction in plant height (Sun and Liddle 1993c). Water loss from plants via evapotranspiration also increases with trampling (Scott et al. 2002). Neighbouring plants experience mechanical perturbation. As the aerial parts of plants are moved, mechanically induced stress occurs, and the morphological response is species dependent (Biddington 1986, Jaffe and Forbs 1993).

Trampling directly and indirectly alters available resources. As trampling decreases the height of damaged vegetation (Scott et al. 2002), a gap is created and more light is available for both the damaged plant and its neighbours (Sun and Liddle 1993c, Hewitt and Miyanishi 1997). Variation in vegetation structure and foliage distribution creates spatial variation in transmitted light, which can affect the growth and mortality of seedlings (Montgomery and Chazdon 2001). Trails can also alter this vertical profile indirectly, in adjacent areas. As the sheltering effect of taller vegetation is lost, evaporation could increase with the increased light, air temperature and airflow; however, air temperature and evaporation did not increase with trampling in montane grasslands (Scott et al. 2002).

Soil compaction and penetration resistance increase with trampling intensity (eg. Weaver and Dale 1978, Cole 1987, Gomez-Limon and de Lucio 1995, but see Hosier and Eaton 1980), reaching a threshold at higher intensities (Liddle and Greig-Smith 1975a, Crawford and Liddle 1977). Soil compaction can decrease the permeability and water content of the soil, which can lead to root damage and increased runoff of surface water, thus contributing to erosion (Scott et al. 2002). Soil compaction affects processes critical to the function of root hairs. Compaction decreases overall plant growth and changes root hair morphology, decreasing nutrient and water uptake (Alessa and Earnhart 2002). Compaction affects establishment and seedling emergence both positively and negatively, as some species may perform better at particular levels of compaction, especially in sandy soils (Edmond 1958, Barton et al.1966, Blom 1976, Gomez-Limon and de Lucio 1995, Kobayashi et al.1997).

As trampling increases, bulk density increases (Dotzenko 1967, Grabherr 1982), while total pore space decreases, altering proportions of water and air-filled pores (Burden and Randerson 1972, Lock 1972). Compaction also alters water content, infiltration rates and transmissions within soils; soils can hold less or more water depending on the structural changes and depth from the surface (Tanner and Mamaril 1959, Dotzenko et al. 1967, Chappell et al. 1971, Grabherr 1982, Watson 1985, Tian et al. 1998, Scott et al. 2002).

The presence of a trail may attract further use by local mammals, which can alter adjacent vegetation directly through herbivory (Bolter et al. 1997), as well as indirectly by depositing urine and feces on or near trails (Thomas 1959). This can create resource patches that result in increased aboveground production and changing species composition, as well create focal areas for future grazing events (Day and Dettling 1990, Jaramillo and Detling 1992a, 1992b, Parikesit et al. 1995, Steinauer and Collins 1995). Animals using trails can also act as seed vectors, carrying seeds on their body, or depositing seeds in feces (Wang and Smith 2002, Andresen and Levey 2004).

Changes in the physical structure of the litter layer and soil compaction can also influence local invertebrate populations by disrupting or creating new habitats (Edmond 1962, Chappell et al. 1971, Morris 1971, Duffey 1972, Lock 1972, Kevan et al. 1995, Rivers-Moore and Samways 1996, Stewart and Samways 1998, Samways and Kreuzinger 2001). For example, litter greater than 10cm deep, with open and loose structure and a large number of small spaces, provides shelter and hunting territory for small spiders (Duffey 1972) and acts as an insulating layer below which the soil is warmer and does not freeze with frosts (Chappell et al. 1971). As well, when plant tissue is damaged, chemicals are released that not only attract herbivores (Bolter et al. 1997), but also the predators and parasitoids of the feeding herbivores (Baldwin et al. 2001). The mechanical stimulation experienced by neighbours of trampled plants can also elicit plant resistance to pathogen and insect attacks (Cipollini 1997).

Frequency response and thresholds

Individual plants have thresholds of response that depend on the amount of damage, habitat and immediate conditions at the time the damage occurs. For example, minimal levels of trampling (0,1 and 5 passes at one time) can stimulate tiller number and root biomass of *Phleum pratense*, but any more than 10 passes results in a decrease in tiller number and root and shoot biomass (Bayfield 1971b). Most of the direct damage to vegetation occurs immediately following trampling (Wagar 1964). The greatest degree of change between occurs at trampling frequencies between zero and the first level of use, and the major floristic measures are most affected by the least amount of trampling (Kuss and Hall 1991), with little change at higher frequencies (Sun and Liddle 1993c). The threshold for this greatest degree of change differs with habitat and is greater in grasslands than in forests (Cole 1988).

Extreme levels of disturbance (i.e. soil completely disturbed) eliminate most, if not all, vegetation and litter and the organic layer is worn to the point of exposing the parent material (Gillham 1956, Bayfield 1971b). Exposed mineral soil increases linearly with trampling intensity (Young 1978, Cole 1988) and the effects are additive, as Cole (1988) did not find a limit beyond which further use had little additional effect.

At low levels, trampling can cause little observable damage as trampled plants can spring back into their original position (Palmer 1972). In addition, if trampling does not cause permanent abrasive or crushing damage, evidence may be erased by peak growing season (Willard and Marr 1970). The amount of damage (crushed vegetation) appears to be additional until the threshold is reached, at which point no further damage occurs (Palmer 1972).

Moisture conditions and season

The response of plants to trampling damage depends not only on the species of trampler and local topography, but also on meteorological conditions at the time damage occurs. Damage to soil and vegetation are generally greater when wet (Edmond 1962, Perring 1967, Wilson and Seney 1994), although some species are more tolerant to trampling when wet (Bates 1935, Tanner and Mamaril 1959, Willard and Marr 1970, Bayfeild et al. 1981, Gallet and Roze 2002). Plant tolerance to damage is further related to both the season in which the damage occurs, and the relative life cycle stage of the trampled plant. For instance, cattle trampling during winter seasons can have negative effects on spring growth rates (Sheath and Boom 1997) and plants trampled in both the dormant (winter) and growing (summer) seasons show cumulative effects (grasslands: Harrison 1981). However, a slight (1cm) snow cover can mitigate damage (alpine: Watson et al. 1969, Bayfield 1971b). In permafrost systems, the organic layer compresses with trampling in the summer and experiences less damage than the abrasive effects of winter (Kerfoot 1972). In the winter, more and longer lasting damage occurs on wetter ice rich permafrost than on drier, frozen ground (Willard and Marr 1970, 1971, Rickard and Brown 1974).

Timing of Disturbance

In experiments, trampling can occur within a short period of time (one day to a week) or over single or multiple growing and dormant seasons, depending on the focus of research questions. Studies may focus more on the snapshot response of a community or individual to a set intensity of trampling frequencies, or they may examine the response of a community to persistent trampling. The same number of passes applied in small but cumulative doses is liable to cause greater damage than a one time application of the same number of passes (Bayfield 1971b, Weaver and Dale 1978, Hylgaard and Liddle 1981, Rickard et al. 1994, Kutiel et al. 2000). However, multiple passes versus a one time application may not matter in study periods as short as a week (Rogova 1976) or potentially when the minimum intensity of trampling that occurs at one time exceeds the threshold of damage (Bayfield 1979, Cole 1985b, 1987). Disturbances have different effects at different times during the growing season (Bowles and Maun 1982, Hoffman and Alliende 1982, Armesto and Pickett 1985); the effects depend on how the disturbance changes the vegetation structure and the role and seasonal cycle of the dominant species (Armesto and Pickett 1985). In addition, research questions must also consider the importance of recovery; if trampling intensities are below the damage threshold, vegetation can recover in the absence of further disturbance (Bell and Bliss 1973, Rogova 1976).

Intrinsic Plant Traits

Specific responses of individual plants to frequency and intensity of trampling, moisture conditions, season and timing of disturbance relative to the plant's life cycle, all depend on plant traits.

Resistance and Resilience

The short and long-term responses of the plant community to trampling disturbance depend on how each individual plant directly and indirectly responds to the disturbance, and with responses reflective of their resistance and resilience to the damage caused by trampling. *Resistance* is the relative ability of individual species to withstand damage during trampling events, before being injured or impaired (del Moral 1979, Kuss and Hall 1991, Yorks et al. 1997) and is a quality of an organism which affects the degree of immediate change it experiences as a result of impact (Sun and Liddle 1991). High resistance (or inertia: Westman 1978) allows an organism to remain relatively unchanged even with high impacts; vulnerability is the inverse (Sun and Liddle 1991). Tolerance (Liddle and Thyer 1986), or survival (Sun and Liddle 1991), is the expression of resistance by the damaged plant to the immediate impact of trampling, whether or not it survives the disturbance. Tolerance can also be defined as a measurement of the ability of vegetation to withstand a cycle of disturbance (Cole 1995c). Resistance of vegetation varies with habitat (Cole 1995a); thus the relative tolerance of different species cannot be considered in isolation from the habitat in which they are growing. For example, *Festuca rubra* is considered tolerant in sand dune communities (Liddle and Greig-Smith 1975b), but not as tolerant as other grass species in grasslands (Crawford and Liddle 1977). *Resilience* is the capacity of an individual species to survive or regenerate following the end of the disturbance (Kuss and Hall 1991, Yorks et al. 1997). The three main factors affecting resilience (called tolerance in Liddle 1975b) include plant structure, potential for regrowth and environmental conditions (Liddle 1975b). The definitions for each of these concepts can vary with author (del Moral 1979, Kuss and Hall 1991), and careful examination is often needed for inter-study comparison.

Plant Traits

When trampling disturbance is a continual process, responses of plants in the local community depend on a mixture of their resistance and on going resilience to damage (Yorks et al. 1997). The immediate response of an individual plant to and the subsequent recovery from trampling depends on many factors extrinsic to that plant (eg. local conditions, season, trampling intensity and frequency), as well as on intrinsic traits such as lifeform (eg. Cole 1995c), stem and leaf morphology (Whinam and Chilcott 2003), plasticity of traits (eg. Warwick and Briggs 1978a, 1978b) and rates of regrowth and reproduction (Liddle 1975b). Although extrinsic factors are important, intrinsic factors such as plant morphological characteristics explain more variation in response to trampling than the extrinsic characteristics of altitude, overstorey canopy or total ground layer vegetation cover (Edmond 1964, Cole 1995c).

Plant lifeform is important in influencing the short and long-term responses of plants to trampling (Cole 1995c, Yorks et al. 1997). Distinguishing plant groups that correlate with resistance or resilience can be useful for predicting responses to trampling damage (Yorks et al. 1997). Some lifeforms are more resistant to trampling; that is, they can withstand trampling before exhibiting signs of damage, and are ranked as graminoids, trees, forbs, thallophytes (liverworts, mosses and lichens), shrubs and then climbers (Yorks et al. 1997). Plants with the capacity to survive or regenerate following trampling disturbances, or with more resilience, are ranked as graminoids, forbs, thallophytes, trees and shrubs and cactoids (Yorks et al. 1997). These rankings are based on the response of aboveground parts, and lifeforms exhibit little difference in resistance when examined by their root structure (Yorks et al. 1997). Graminoids are commonly identified in many systems as both resistant and resilient to trampling (Lesko and Robinson 1975, Cole 1995c, Yorks et al. 1997) and tolerate trampling better than other herbaceous (Palmer 1972) and woody species (Cole 1993).

While lifeform is important in predicting resistance and resilience, other traits can be equally important. For example, not all growth forms of graminoids tolerate trampling, but those that grow in dense tufts (caespitose) do (Cole 1995c). Plants that are low to the ground, such as those that are prostrate, creeping (Gillham 1956) or in rosette form (Burden and Randerson 1972, Aspinall and Pye 1987), or with dense bases (Lock 1972) tend to tolerate trampling. Some plants grow in habitats that enable their ability to tolerate trampling, such as mosses protected by soil encrustation (Studlar 1983). Plants with basal apices and well-protected meristems tolerate trampling better than those with perennating buds above the ground surface (Bates 1935, 1938, Bayfield 1971b, Lock 1972, Liddle and Greig-Smith 1975b, Aspinall and Pye 1987).

The stem and leaf morphology of the plant directly damaged or brushed by trampling also influences the immediate response. Trampling resistance is often associated with flexible stems, stolons or tillers (Sun and Liddle 1993a) that are often tough and fibrous and do not snap if bent (Bates 1935). Plants with tall succulent stems, or with extensive branching (Rogova 1976) and stems and branches that detach easily with damage are less tolerant (Bayfield 1971b). As well as morphology, the number of tillers present at the time of disturbance is also important; resistance of tussock grass species increases as the number of tillers increase (Sun and Liddle 1993b). Leaf size decreases with trampling and damage to leaves is visible as scars and necrotic patches (Goryshina 1983). Plants with finely dissected leaves are generally more tolerant to the direct damage caused by trampling (Bates 1935), while wide leaves are not (Grabherr 1982, Sun and Liddle 1993c, 1993d). The physical damage to leaves and the inhibition of leaf growth may be reasons for reduction in width; length and width decrease as trampling increases (Sun and Liddle 1993c, 1993d). Leaf thickness responses to trampling vary with trampling intensity, species and local conditions (Sun and Liddle 1993c).

Stem flexibility is more important than tensile leaf strength with respect to resistance and survival of plants (Sun and Liddle 1993a); species on heavily trampled areas have higher resistance to tear stress and a better recovery after shoot damage (Engelaar and Blom 1995). The tensile strength of *Poa annua* organs and inflorescences varies with trampling regimes, suggesting plasticity in leaf structure (Kobayashi and Hori 1999). Plants from the same parent change from erect to prostrate when trampled, and round tufted grasses become elliptical (Edmond 1958). Frequent damage by trampling to terminal buds can cause stunted growth and individuals with more extensive branching (Goryshina 1983).

Recovery from Disturbance

Recovery is the growth rate of an organism after a given amount of damage, which may be expressed as the proportion of the growth rate of an undamaged organism (elasticity: Westman 1978, Sun and Liddle 1991). The recovery of the system after the disturbance implies the re-establishment of the original plant stand in terms of the chosen floristic measures, such as species composition, density or relative abundance (Kuss and Hall 1991). Recovery rates depend on the identity and resiliency of the individuals damaged and on their capacity for rapid increase in cover (Cole 1988, Arnesen 1999). Recovery is slow in habitats where the growth rate of the dominant species is slow (sand dunes: Carlson and Godfrey 1989, higher altitudes Bayfield 1979). For example, the vegetation may take years to recover from a single disturbance episode in desert or sand dune communities (Bowles and Maun 1982, Lathrop 1983, Webb et al. 1983). Plants that experience less initial damage when trampled (eg. graminoids or low growing forbs) can exceed pre-disturbance conditions during recovery; while plants with higher initial damage (eg. erect forbs) experience less recovery (Marion and Cole 1996).

Recovery rate also depends on trampling intensity and the amount of damage to the existing vegetation and soil once the disturbance stops (Webb et al. 1983). Species richness can increase when trampling stops temporarily within a growing season (van der Maarel 1971) or between seasons (Marion and Cole 1988). Recovery rates appear to be greater in the first few years following disturbance than in the subsequent years required for full recovery (Hartley 2000). The full time required for recovery from disturbance depends on the type of soil present, the magnitude of soil compaction, the propagation of surviving vegetation, the amount and temporal distribution of rainfall, the severity of the winter climate and the degree to which the area is left undisturbed from additional trampling disturbances (Webb et al. 1983).

COMMUNITY DYNAMICS AND TRAMPLING DISTURBANCE

Factors both intrinsic to plants (eg. traits that influence tolerance to trampling) and extrinsic (eg. moisture, season, local topography, duration and intensity of disturbance) all influence how an individual plant can respond directly and indirectly to trampling. Ecologists often use measures such as richness or evenness and changes in composition to describe how the local plant community responds to a treatment or disturbance. This section focuses on the known effects of trampling upon two common measures of plant responses to trampling in the local communities: species richness and composition, as well as potential mechanisms of change in productive grassland systems.

In most vegetation types (eg. various forests and grasslands) and conditions extrinsic to plants, species richness decreases as trampling intensity increases, to a threshold where only a small number of specialized plants can survive (Grime 1979). The relationship is curvilinear (Figure 1.1 "A"), and less curvilinear in systems that are relatively more resistant to trampling damage (Cole 1987, Cole 1995b). This decrease in richness is reported in systems where initial diversity is relatively high and the dominant canopy species are not disturbed, such as forests (Kuss and Hall 1991, Cole 1993). Richness also decreases with trampling intensity in systems comprised of species intolerant to trampling (alpine: Hoffman and Alliende 1982; 1 year old-fields: Armesto and Pickett 1985, Ikeda 2003), or where growth substrate takes a relatively long time to develop (cliff plant communities: Camp and Knight 1998, sand dunes: Kutiel et al. 2000). For example, once plants are removed from the cracks and ledges of cliffs, rain and wind action and continued use wash away the sparse soil that has accumulated, decreasing the amount of suitable growing sites for plants (Camp and Knight 1998).

However, low levels of trampling in some systems initially increases richness, and is eventually followed by a decrease as trampling intensity increases further (Figure 1.1 "B"). This tends to occur in systems dominated by a few species that form a dense canopy or mat (perennial dominated old field: Armesto and Pickett 1985, shaded forests: Kobayashi et al. 1997, *Typha* marshes: Hewitt and Miyanishi 1997), or where many species within the community are trampling tolerant (alpine cushion/ graminoid: Hoffman and Alliende 1982). If the trampling treatment creates bare ground or exceeds the potential threshold for a positive response (coastal grasslands: Hosier and Eaton 1980, fens: Arnessen 1999), or if trails were already established at study initiation (tropical and subtropical vegetation: Sun and Liddle 1993c, coastal grasslands: Anderson 1995, valley grasslands: Gomez-Limon and de Lucio 1995), richness decreases with trampling intensity. With those limitations, however, it is not possible to determine if these studies represent the decrease associated with Figure 1.1 "A" or "B".

In productive grasslands, the dominant graminoids can form dense mats of litter in the absence of disturbance, and vegetation development relies largely on litter reducing factors that remove or open up the litter layer (Carson and Peterson 1990, Foster and Gross 1998). This process may initiate changes in composition that increase richness as seen in Figure 1.1 "B". Trail creation through trampling both removes the dominant vegetation (Hewitt and Miyanishi 1997) and changes the structure of the litter layer (Duffey 1972), creating an opportunity for change in species composition (Figure1.2 "a"). The removal of the dominant vegetation provides an opportunity for colonization by otherwise less competitive species (Connell 1978, Grime 1979, Armesto and Pickett 1985, Sun and Liddle 1993c, Kobayashi et al. 1997), as trampling directly reduces the competitive dominance of some species (Pradhan and Tripathi 1983, Ikeda and Okutomi 1992, 1995). As gaps within the matrix open, more light becomes available to neighbours of the trampled species (Sun and Liddle 1993c). Many common grassland species require gaps to establish from seed (Goldberg 1987) and many species have higher emergence, survival and growth in gaps (Goldberg 1987, Gross and Werner 1982). Litter attenuates light to low levels and mechanically impedes seedlings (Goldberg and Werner 1983, Carson and Peterson 1990, Tilman 1993, Foster and Gross 1998).

Community composition is now different than at the initiation of the trampling disturbance; competitive relationships between existing species have changed, responding to the change in resources in the gap. As the trampling disturbance continues, composition can again change, as the disturbance removes species that are intolerant to trampling (Figure 2.2 "b") while the performance of trampling tolerant plants improves (Figure 2.2 "c") (Perring 1967, Dawson et al. 1978, Young 1978, Bayfield 1979, Jim 1987, Ikeda and Okutomi 1990, Shaw and Diersing 1990, Ikeda 2003). If trampling continues at a low enough frequency to prevent elimination of most species, the disturbance should continue to influence composition in this manner, with fluctuations depending on the frequency and intensity of trampling, the timing of disturbance events relative to plant growth cycles and local conditions at the time of disturbance. When disturbance creates conditions of physical stress, composition changes likely reflect both competitive reduction processes (removal of dominant biomass and gap creation) and changes to competitive hierarchy (Suding and Goldberg 2001). These proposed processes influencing community change are not restricted to a specific time period after the initiation of disturbance, but begin to some degree with trampling initiation.

RESEARCH FOCUS

The main focus of this research is to determine how trails influence local plant community dynamics in a rough-fescue system. Within this framework, this project examines the influence of two types of trails, "old" wildlife and "new" human, on the local plant community, by comparing responses of community composition and production at varying distances from trails.

This study also examines how the active use of these trails in a rough-fescue grassland influences the local community. Specifically, it examines how the use of "old" wildlife trails by humans changes the local community, by comparing responses of composition and production at varying distances from wildlife trails used by humans to those without human disturbance. Similarly, it examines how the use of older wildlife trails compares to the use of newer human trails.

Finally, these questions were addressed at three spatial scales over two growing seasons. The spatial scale of analyses, how data are aggregated and patterns examined can influence the form of relationships (Gross et al. 2000). Thus, the spatial extent of older wildlife trails was estimated to determine 1) the total area within this study site affected by trails, and 2) the area potentially affected by the presence and/or continuous use of trails.

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Table 1.1. Characteristics of trails made by humans and wild and domestic animals.

Characteristic	Animal Trail	Human Trail
Creation	Lead to a specific destination (watering hole, salt lick, resting place)[1,2]	Follow a guiding line made by previous passages (eg foot prints in snow)[1]
	Avoid hazards, follow route of least resistance (ridge crest, hill base, parallel to contours)[3]	Meander from soft to hard ground, changes in slope[1]
Density	High density of trails near water sources[4]	More trails in poorly drained areas[5,6]
Lateral Boundary	Domestic: sharp edges[1,7]	Merge gradually into surrounding vegetation[1,7]
	Wild: merge gradually into surrounding vegetation	
Dimensions	Domestic: narrower and deeper[8]	Wider; but use concentrated in central 10cm[8]
Erosion	Domestic: create more sediment for erosion[9]	

Citations: [1]Bates 1951, [2]Oikawa et al. 1981, [3]Thomas 1959, [4]Walker and Heitschmidt 1986, [5]Cole 1985a, [6]Yalden and Yalden 1988, [7]Bates 1935, [8]Thurston and Reader 2001, [9]Deluca et al. 1998

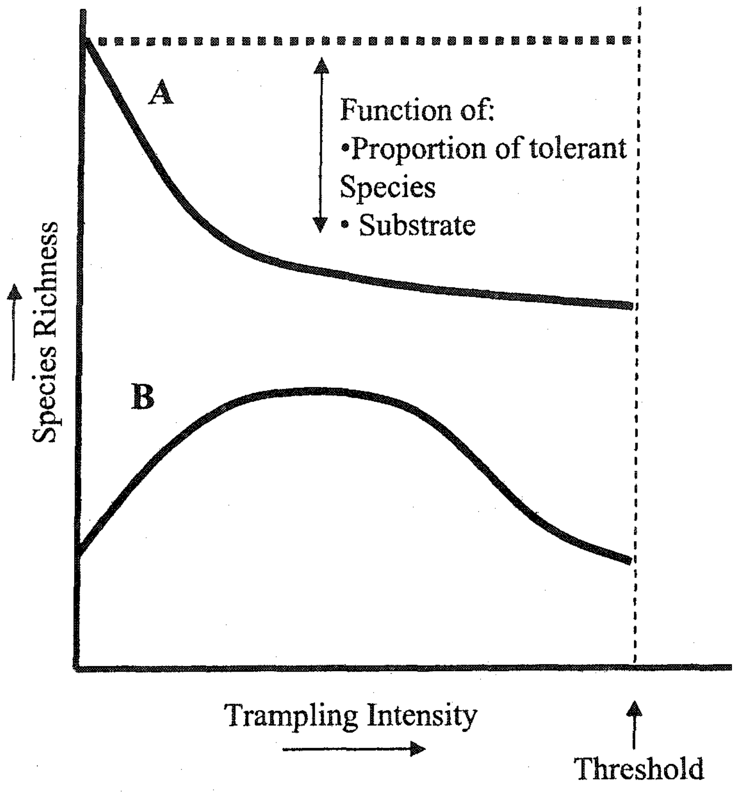

Figure 1.1. The relationship of species richness and trampling intensity, where both scenarios **A** and **B** reach a threshold to where either bare ground is exposed or only a small number of specialized species can survive. In **A**, species richness decreases curvilinearly as trampling intensity increases; and the degree of curvilinearity depends on factors such as proportion of trampling tolerant species and substrate.

In **B**, species richness initially increases at low intensities of trampling, then decreases at further intensities.

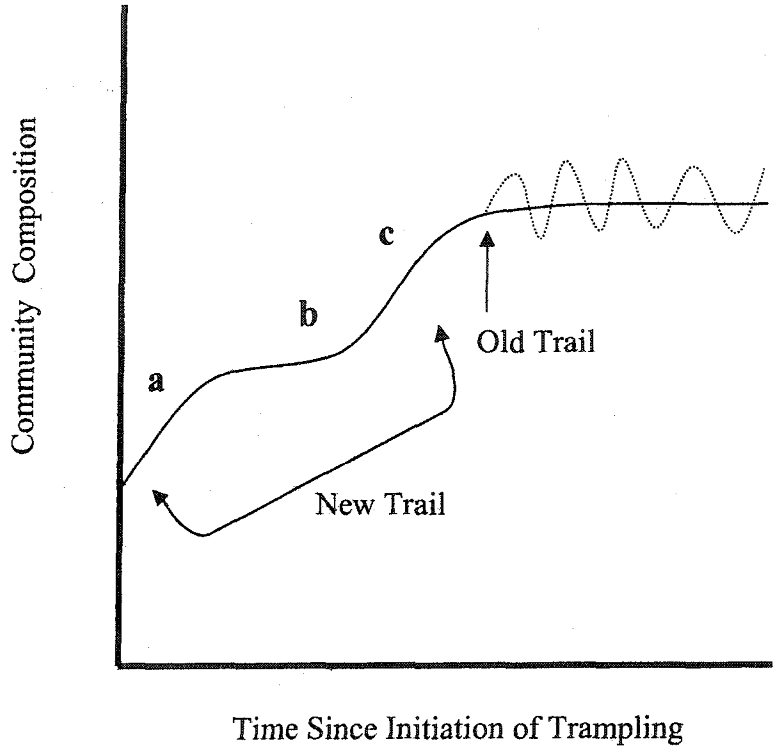

Figure 1.2. Changes in composition with time since initiation of trampling disturbance. At **a**, species composition changes as dominant graminoids and litter disturbed, new species colonize gap, competitive relationships change. At **b**, species intolerant of continuous trampling disappear or decrease in abundance and competitive relationships change. At **c**, performance trampling tolerant species improves. See text for references and details. The change in composition is not a scale of increase or decrease, it is simply a scale of change.

CHAPTER 2

COMMUNITY RESPONSE TO TRAILS AND TRAMPLING

INTRODUCTION

Fire, drought and grazing are important determinants of large-scale grassland community structure (Knapp and Seastedt 1998). These factors interact with local processes, including plant competition, insect herbivory and non-grazing animal activity to influence local plant community structure (Ricklefs and Schluter 1993, Hartnett and Fay 1998). Historically, the primary research focus on non-grazing animal activity in grassland systems has been on gap disturbances, such as pug (hoof) marks, dung pats, burrows and gopher mounds (eg. Taylor and Friend 1984, Goldberg 1987, Reichman et al. 1993, English and Bowers 1994, Suding and Goldberg 2001). Small-scale disturbances generated by this type of animal activity influence plant community structure and dynamics in herbaceous systems (Platt 1975, King 1977, Hobbs and Mooney 1985, Bradshaw and Goldberg 1989, Gibson 1989), and gaps of this nature often have some reduced level of plant cover and exposed soil or parent material (Bradshaw and Goldberg 1989).

However, trails in grasslands are also small-scale gap disturbances and can differ from the disturbances caused by burrows and mounds in that the parent material is often largely intact, and only the vegetation and litter layer are disturbed. Trails are created in grasslands by wildlife using them as conduits (eg. to and from feeding and bedding sites), and how these types of trails influence local community dynamics is not understood. Humans also create trails in grasslands in recreational (eg. hunting and hiking) and professional (eg. research and surveys) capacities. The impacts of human recreation trails in many systems with various trampling frequencies are well studied (eg. for reviews see: Liddle 1975, Kuss 1986, Liddle 1991, Yorks et al. 1997), and the notion of trail creation and its consequences is commonplace for recreational activities. However, the consequences of trail creation while conducting ecological research are seldom explored. Trails are created and continually used when visiting a bird nest, focal plant or mammal trap in a system and have the potential to influence local plant community dynamics. The scope of this issue differs from that concerning recreation trails because research trails, by altering plant community dynamics adjacent to trails, may inadvertently alter observed plant responses, and thus experimental or research outcomes.

Trampling is a common element to trails made and used in grassland systems as the method of trail creation. While the end result, the creation of a trail, is similar, the forces exerted by human feet and ungulate hooves are different. Bipedal motion differs from quadrupedal, and large ungulates carry a much greater weight per unit area of hoof that touches the ground than do humans (Bates 1938). As well, the ungulate foot surface is not flat (Bates 1938), and hoof prints often create microsites for seedling establishment (McNaughton 1983). Plant community dynamics on and near wildlife and human trails may therefore respond differently to human use.

Both the short and long-term responses of individual plants depend on the direct and indirect effects trampling has, not only on the vegetation damaged, but to neighbouring and colonizing species, as well as the local vertebrate and invertebrate communities. Directly, trampling affects the plant immediately stepped on by either damaging the plant to some degree or killing it. Plants experience mechanical injury to stems and surface roots, as trampling crushes and tears plant tissue, breaks stems, leaves and flower stalks and can dislodge and bury plants (Willard and Marr 1970, Bayfield 1971, Watson 1985, Kuss 1986). A plant that survives trampling will often grow bent, twisted and withered (Bowles and Maun 1982), although trampling can stimulate the growth rate of some species (Sun and Liddle 1993b). The response of an individual plant to the damage caused by trampling is largely dependent on factors both intrinsic and extrinsic to the plant. Intrinsic factors that govern a plant's resistance, tolerance and resilience to trampling damage include life and growth form (eg. Cole 1995b), morphology (Whinham and Chilcott 2003), and trait plasticity (Liddle 1991). Plants that resist damage are often rosettes, with protected buds, and plants with flexible stems composed of small cells (Sun and Liddle 1993a, Liddle 1991). Extrinsic factors include the frequency, intensity and duration of the trampling disturbance (eg. Cole 1987, Kuss and Hall 1991), the local topography (Weaver and Dale 1978), identity of trampler (Weaver et al. 1979), local moisture conditions at the time of damage (Edmond 1962, Wilson and Seney 1994, Gallet and Roze 2002), and the timing of disturbance in relation to the plant's life cycle (eg. Bayfield 1971, Weaver and Dale 1978, Rickard et al. 1994, but see Rogova 1976, Bayfield 1979, Cole 1987).

Indirectly, trampling and trail creation also influence local communities by altering the vertical light profile, available nutrients, local insect populations, and by stimulating thigmomorphogenic responses as well as responses to the presence of the trampler. Variation in vegetation structure and foliage distribution creates spatial variation in transmitted light, which can affect the growth and mortality of seedlings in forests (Montgomery and Chazdon 2001) and trails can alter this vertical profile in adjacent areas. Nutrients available to plants can change, as animals deposit urine and feces directly on or near the trail. This can directly kill vegetation (Collins and Steinauer 1998), and also create resource patches resulting in increased aboveground production and changing species composition, as well as acting as focal areas for future grazing events (Day and Dettling 1990, Jaramillo and Detling 1992a, 1992b, Steinauer and Collins 1995). Animals using trails can also act as seed vectors, carrying seeds on their body, or depositing seeds in feces (Wang and Smith 2002, Andresen and Levey 2004).

Locally, the change in the physical structure of the litter layer can disrupt or create new habitats for invertebrate populations (Chappell et al. 1971, Duffey 1972, Rivers-Moore and Samways 1996, Stewart and Samways 1998, Samways and Kreuzinger 2001). Additionally, when trampling damages plant tissue, chemicals are released that not only attract invertebrate herbivores (Bolter et al.1997), but also the predators and parasitoids of the feeding herbivores (Baldwin et al. 2001). Mechanical stimulation can also elicit plant resistance to pathogen and insect attacks (Cipollini 1997).

Neighbouring plants can also experience mechanical perturbation. As the aerial parts of plants are moved, as trampling bends stems or brushes shoots, mechanically induced stress occurs and the resulting morphological responses are species dependent (Biddington 1986, Jaffe and Forbes 1993). The physical presence of a trampler may also indirectly affect plant success, as evidence suggests that repeated visitation of focal plants can influence the success of the surrounding community (Cahill et al. 2001, 2002, Hik et al. 2003, but see Schnitzer et al. 2002). Factors both intrinsic and extrinsic to plants interact to influence how an individual plant responds, both directly and indirectly, to trampling.

Directly on trails in grasslands, trampling decreases cover of vegetation (eg; coastal: Hosier and Eaton 1980, Anderson 1995, montane: Cole 1995a, subalpine: Cole and Monz 2002; old field: Ikeda 2003), height (eg. subalpine: Cole and Monz 2002, montane: Scott et al. 2002), aboveground biomass (eg. high altitude: Grabherr 1982, tropical: Sun and Liddle 1993c), root biomass (eg. tropical: Sun and Liddle 1993c) and litter (eg. Bayfield 1971, but see Shaw and Diersing 1990), with increases in percentage of bare ground (Weaver et al. 1979, Cole 1987, Anderson 1995), soil compaction and penetration resistance (eg. Weaver and Dale 1978, Cole 1987, but see Hosier and Eaton 1980). In most vegetation types, species richness decreases as trampling intensity increases, up to a threshold where only a number of specialized plants can survive (Grime 1979). This decrease is reported in systems where initial diversity is relatively high and the dominant canopy species are not disturbed (forests: Kuss and Hall 1991, Cole 1993, 1 year old fields dominated by annuals: Armesto and Pickett 1985, Ikeda 2003). The relationship is curvilinear (Figure 2.1 "A"), with the degree of curvilinearity depending on the proportion of trampling resistant species present (Cole 1987) and the growth substrate (eg. cliff plant communities: Camp and Knight 1998, sand dunes: Kutiel et al. 2000). At low levels of trampling, however, species richness initially increases, eventually followed by a decrease as trampling intensity further increases (Figure 2.1 "B"). This tends to occur in systems dominated by a few species that form a dense canopy or mat (perennial dominated old field: Armesto and Pickett 1985, *Typha* marshes: Hewitt and Miyanishi 1997), or where many species within the community are trampling tolerant (alpine cushion/ graminoid: Hoffman and Alliende 1982).

In grassland systems with large amounts of litter, continual trampling is likely to initiate a series of changes in the local composition both directly on trails and in the adjacent vegetation. For example, in *Typha* mats, species richness and frequency are greater directly on wildlife trails than 2m from trails (Hewitt and Miyanishi 1997). We could expect grassland systems to respond similarly, as the main mechanism in the *Typha* marsh was thought to be a response to the increase in available light as the dominant vegetation was disturbed (Hewitt and Miyanishi 1997). In productive grasslands, vegetation development relies largely on disturbance factors that remove litter or open up the litter layer (Carson and Peterson 1990, Foster and Gross 1988). The removal of the dominant vegetation provides an opportunity for colonization of otherwise less competitive species (Connell 1978, Grime 1979, Armesto and Pickett 1985, Kobayashi et al. 1997), and can create conditions for common species to establish from seed (Goldberg 1987) and for increased emergence, survival and growth in gaps (Goldberg 1987, Gross and Werner 1982). Because of the trampling disturbance, community composition on trails is different than before the disturbance began (Figure 2.2 "a"). As the trampling disturbance continues, composition may continue to change as the disturbance removes species that are intolerant to trampling (Figure 2.2 "b") while the performance of trampling tolerant plants improves (Figure 2.2 "c") (Perring 1967, Dawson et al. 1978, Young 1978, Bayfield 1979, Jim 1987, Ikeda and Okutomi 1990, Shaw and Diersing 1990, Ikeda 2003). Community composition continues to change as time since the initiation of the disturbance (trampling) increases, and changes likely reflect both the competitive reduction processes (i.e.removal of the dominant biomass and gap creation) and changes to the competitive hierarchy (eg. trampling tolerant and intolerant plants) (Suding and Goldberg 2001).

Research Focus

The main focus of this research is to determine how trails influence local plant community composition and dynamics in a rough-fescue system. Within this framework, this project examines the influence of two types of trails ("old" wildlife and "new" human) on the local plant community, by comparing responses of community composition and production at varying distances from trails.

This study also examines how the active use of these trails in a rough-fescue grassland influences the local community. Specifically, it examines how the use of "old" wildlife trails by humans changes the local plant community, by comparing responses of composition and production at varying distances from wildlife trails used by humans to those without human disturbance. Similarly, it examines how the use of older wildlife trails compares to the use of newer human trails.

These questions were addressed at three spatial scales over two growing seasons. The spatial scale of analyses and how data are aggregated and patterns examined can influence the forms of relationships (Gross et al. 2000). The spatial extent of older wildlife trails was estimated to determine 1) the total area within this study site affected by trails, and 2) the area potentially affected by the presence and/or continuous use of trails.

MATERIALS AND METHODS

Study Area

This study was conducted within the Rough Fescue grasslands in the Aspen Parkland ecoregion of central Alberta. The boundaries of this ecoregion are based on the Black/Dark Brown Chernozem soil boundary and the eastern extent of aspen (Strong and Leggat 1992). The study site (roughly 53°N latitude and 111°W longitude, elevation 705m) consisted of two quarter sections (about 1.30 km^2 total) of parkland belonging to Ducks Unlimited in the counties of Beaver and Wainright, approximately 150km southeast of Edmonton, Alberta (Twp 48 Rg11, 17 SE and SW). After observation of numerous candidate field sites, this location was chosen because: 1) it had not been developed agriculturally; 2) it was not grazed since 1992, and deeply grooved cattle trails were absent (not grazed since 1992 (Hauser, personal communication)); and 3) access was restricted and activity primarily limited to foot traffic (Shewchuk, personal communication).

Within the study site, the dominant graminoid species were plains rough fescue (*Festuca hallii* (Vasey) Piper) (Pavlick and Looman 1984) and western porcupine grass (*Stipa curtiseta* (A.S. Hitchc.) Barkworth). Common non-graminoid herbaceous species included common yarrow (*Achillea millefolium* L.), prairie sagewort (*Artemesia ludoviciana* Nutt.) and prairie smoke (*Geum triflorum* Pursh), with the common woody species prairie rose (*Rosa arkansana* Porter) (Little 1942) and western snowberry (*Symphoricarpos occidentalis* Hook). Nomenclature for the complete species list (Appendix A) follows Moss (1983), unless otherwise noted.

The presence of large mammals in this system was identified by scat and visual observation. They included white-tailed and mule deer, moose, coyotes, black bears, wolves and rabbits (Brown, personal observation).

Precipitation and Drought

The field experiment was conducted from June 2001 to August 2002. Mean annual temperature was 4°C in 2001 and 3.2°C in 2002, with a July mean of 17.3°C in 2001 and 19.6°C in 2002 (Environment Canada). This study occurred during a drought, and total annual precipitation was 227.8mm in 2001 and 231.4mm in 2002, which was 53 and 54% of the 1971-2000 mean (Environment Canada). Total growing season (May to August) precipitation was 158.7 mm in 2001 and 113.1mm in 2002 (61 and 44% of the 1971-2000 average). The distribution of precipitation indicates the drought was most severe in the 2002 growing season. From January to June 2001, average precipitation was 21.15mm, and 16.82mm from July to December, with a January to June 2002 average of 13.52mm (July to December =25.05mm).

A study conducted in the same area (within 3km) found decreases in standing shoot biomass (78%) and species richness (36%) in 2002 relative to 2001 measures (Coupe, unpublished data). However, both biomass and richness returned to 2001 measures in 2003, indicating that drought stress was most severe in 2002. Drought in 2002 made July field identification of vegetation difficult, as many species did not flower. As a result, plant species richness and evenness are likely under-represented for this time period.

Trails

Two types of trails were visually evident in this grassland community: 1) those >20cm wide, created and used by larger-bodied mammals, such as deer, coyotes and humans; and 2) those <20cm wide, created and used by smaller-bodied mammals, such as rabbits. While the time and species responsible for the creation and continued use of each trail were not known, trail selection for inclusion in this study was standardized. Within this system, trails were visually obvious as distinct paths of flattened vegetation. They were distinct in that the dominant graminoid matrix (about 10-15cm deep) was heavily disturbed. Trails were chosen only if they were paths of flattened vegetation greater than 20cm wide and visually distinct from the surrounding matrix. Areas were avoided in which the presence of the trail was ambiguous. The presence of scat and visual observation indicated these trails were actively used by wildlife. It is also likely that humans use these trails are used recreationally (eg. hikers, hunters).

Although trails are relatively rare on the landscape, their absolute abundance is rarely measured (Hewitt and Miyanishi 1997), and is of particular importance here because once the abundance of trails is known, the full extent of their influence can be determined. To assess their abundance, the percentage of trails within the grassland was estimated. Percentage was determined in all grassland areas within the study site, excluding those designated as blocks, in order to minimize disturbances. Transects were placed at 10m intervals within the grassland areas and each time a transect crossed a trail (same selection criteria as those used in the study), its length was recorded. In total, there were 56.2m of trails on the 2590m of linear transects walked; thus trails occupy about 2.2% of the grassland area in this system. The value is similar to that reported to be caused by gopher mounds (Tilman 1993), and is within the range (0.1-10%) of areas caused by other animals disturbances (Goldberg and Gross 1988).

Experimental Design and Definition of Treatments

A randomized block design was used, with 10 replicate blocks. Blocks were placed within the grassland portions of the parkland study site (Figure 2.3), separated by 0.1- 1.0 km. Block locations were chosen based on a minimum grassland size requirement and local trail density. Each block was approximately 75 x 65m, and the spatial extent of this study was approximately 38% (area used/ site area=0.4875/1.30 km^2). Each block enclosed a portion of an existing trail, and each of the 10 replicate blocks consisted of four plots (8x 9m), which were at least 5m from each other and placed in similar areas with regard to dominant vegetation, aspect and slope. The slope and aspect (eastness and northness) were not significantly different among treatment plots ($n=40$; $p>0.05$), suggesting no topographic difference among locations.

One of each of the four plots was used for one of four treatments, which included three different types of trails, plus an untrailed control (Figure 2.3). As each block enclosed a portion of a continuous wildlife trail, two treatment plots included this trail, while two were offset 5m from the trail in untrailed grassland (Figure 2.3). The human trampling treatment (weekly or none) was randomly assigned to one plot with a wildlife trail and one plot in the grassland, resulting in four treatment combinations (Figure 2.3).

Plant response to trails and human trampling was examined using three belt transects perpendicular to the trails (or similar area in controls) (Figure 2.4). The central transect was used for nondestructive cover measures, with the other two used for biomass sampling (Figure 2.4).

Human Trampling

The human trampling treatment consisted of 5 passes per week for 13 weeks (6 June to 29 August) in the 2001 season and for 9 weeks (13 June to 7 August) in the 2002 season. The shorter duration in the 2002 season reflects the early senescence of the vegetation associated with the drought. Within a week, all 5 passes occurred successively in 1 day, where a pass was defined as a 1-way walk along the trail, at a natural gait by a person (approximately 60kg) wearing rubber-soled shoes. A trail of flattened vegetation was visibly obvious in the grassland after 5 passes through this system (Brown, personal observation). This frequency, 5 passes per week, has been previously identified as the minimum number of passes needed to create lasting damage in alpine communities (Bell and Bliss 1973). However, with consistent effort made to choose a different route, plants can return to their normal appearance after four days (Bell and Bliss 1973). Five passes is also the minimal threshold for plant response identified by recreation ecologists examining the effects of human trampling (Bayfield 1971, Palmer 1972).

The human trampling component was designed to simulate the level of disturbance grassland systems experience during a typical ecological experiment. To determine if the trampling treatment is representative of the common practice of use by the ecological community, a survey was submitted to a non-random sampling of ecologists conducting research in grasslands (Appendix B). Researchers were selected for contact from lead authors of papers published between 1985 and 2002 in databases in which grassland was the key search term; 92 were contacted and 33 responses were returned. In the survey, I asked each researcher to estimate: 1) the number of visits experimental plots received; 2) the number of people at each plot during the visit; and 3) the duration of the study. The number of visits per week ranged from 0.02 to 7, with a median response of 1 visit (Appendix B: Table 1). The numbers of people present at each visit ranged from 1 to 4.5, with a median of 2. The durations of studies varied greatly, from less than 1 week to 52 weeks, with 30% of studies lasting more than one year. Thus the treatment of 5 passes used in this study is representative of the common practice of 4 passes per week used by the ecological community.

Response Variables

Community Composition

Percent cover of all plant species was estimated with quadrats along the cover transect, with both contiguous 0.2 x 0.5m quadrats for 5m and 0.1 x 0.1m quadrats for 2m (Figure 2.4). Most studies examining responses as a function of distance to trail do not examine distance as a continuous variable, but instead predetermine where change may occur by looking on and immediately next to the trail, and then at some distance described as a control in vegetation not directly trampled (Dale and Weaver 1974, Liddle and Greig-Smith 1975b, Cole 1978, Parikesit et al. 1995, Bright 1986, Hall and Kuss 1989, Boucher et al. 1991, Patel and Rapport 2000, but see Hartley 2002). This approach has the potential to reflect patterns due to sampling method instead of pattern withins the vegetation.

Cover estimates were taken from the same plots on 27-31 July 2001 and 23-29 July 2002. Species area curves generated from the July 2001 cover data using EstimateS (Colwell 1997) indicated that doubling the number of samples taken at the 5m scale would increase measured species richness by 13-25% (mean:16%). Therefore, in July 2002 cover measures are the average of two 5m transects, the original cover transect and an adjacent transect offset by 60cm in undisturbed vegetation. Space constraints within treatment blocks limited increased sampling. Doubling (n=1600) or tripling (n=2400) the number of quadrats on the 2m scale was not feasible and therefore likely under-represents true species diversity.

In 2001, cover was estimated using the Braun-Blanquet cover scale (Kent and Coker 1992). In 2002, percent cover (maximum 100%) was estimated using actual percents in order to obtain more precise information. In 2001 the area covered by bare ground and vegetation was classified, but the living and dead vegetation were not estimated separately. To improve the census technique in the 2002 growing season, estimates of bare ground and percent of live and dead vegetation were obtained for each quadrat.

Plant community response to trail type and human trampling was described by examining species richness, evenness and total live cover and dead plant matter at three scales: 1) plot-level (5 x 8m); 2) mid-scale within 5m of trails (0.5 x 8m); and 3) fine-scale within 2m of trails (0.1 x 8m). Definitions of scale are specific to this study, and are not intended for direct comparisons to other studies. Plot-level measures examined the diversity of each treatment plot (2001n=10, 2002n=9). Mid-scale measures examined localized responses as a function of proximity to trails (and use) in the maximum distance available due to the spatial organization of trails in this system (2001n=400, 2002n=360). At the fine-scale, measures examined the response of the vegetation immediately adjacent (within 2m) to trails (2001n= 800, 2002n=720). Within 2m of trails and within the relatively short examination time (2 growing seasons), changes in relative abundance are most likely to be detected in response to the trampling disturbance. Previous research suggests vegetation within 2m of trails is most affected by the presence and use of a trail (Dale and Weaver 1974, Taylor et al. 1993). In 2002 measures, one block of four treatment plots was excluded from analyses, as the position of the trail shifted in the second season.

Community Production

To examine change in standing shoot and root biomass (g m^{-2}) destructive samples were taken at 0, 1, 2, 3 and 4m (and 5m for root biomass) from the trail centre (Figure 2.4). Shoot biomass was sampled by clipping vegetation 2cm from the ground in a 0.2 x 1m area (long axis of quadrat parallel to trail) 3-7 August 2001, after 9 weeks of trampling and 26-29 July 2002, after 7 weeks of trampling in the second year (20 weeks cumulative 2001-02). Vegetation was sorted into living and dead, with the living vegetation further sorted into graminoids, woody species and forbs, and to species when possible. All samples were oven-dried to a constant mass and weighed. In 2002, soil cores (5 x 15 x 10cm) were taken (22-24 July), roots were separated from the soil using a root washer (Delta-T Devices Ltd 1995), dried to a constant mass and weighed. Biomass response to the treatments was analyzed at both the plot-level (standing 2001 and 2002 n=10, root 2002n=9), and the mid-scale (standing 2001 and 2002 n=200, root 2002n=216). Root biomass samples were obtained in 2002 for 9 blocks as the soil corer broke and a replacement was not readily available.

Light

Changes in the amount of available light as a response to trails and trampling were measured in 2002, by measuring the amount of photosynthetically active radiation (PAR; μmol m^{-2} s^{-1}), with the AccuPAR Light Interception Device, Model PAR-80

(Decagon Devices Inc. 1999). Measurements were taken in 10cm contiguous intervals along the cover transect (Figure 2.4) immediately below vegetation surveyed for percent cover estimates. PAR was measured both above and below the litter layer (>2cm deep) in July 2002. Measurements of PAR above standing vegetation were also obtained at each interval to determine percent transmission of PAR above the litter layer (PARa) and below the litter layer (PARb). Percent transmission is defined as the proportion of light above the standing vegetation that reaches below or above the litter layer. As with percent cover, PAR transmission was analyzed at three scales: plot-level, mid-scale and fine-scale (2001 and 2001n same as percent cover).

To determine differences in the vertical distribution of light as a function of trail type and proximity, the vertical light profile was determined both on the trail and at distances of 1, 2, 3, 4 and 5m, from the trail on 7-8 August 2002. A ladder was constructed with rungs at 5cm intervals and oriented so measurements would be parallel to the existing trail. At each location, PAR transmission was determined at 5cm vertical intervals, beginning flush to the ground surface and ending above the tallest standing vegetation.

Data Analysis

Multivariate Analyses

Blocked multiple response permutations procedure (MRBP; Mielke 1991) was used to test for compositional differences of plant species between treatment groups. All MRBPs were conducted using PC-ORD Version 4.14 (McCune and Medford 1999), with the species percent cover values matrix, for cover values obtained in July 2001 and 2002. This study occurred in a mature grassland with long-lived plants and low species entry, and for a relatively short duration (2 growing seasons). Changes due to trampling are therefore more likely to be reflected with abundance information rather than with presence/absence data. In 2002, drought conditions hindered species identification, and as a result, true species richness is likely under-represented.

The MRBPs were performed to test four null hypotheses, that species composition was not significantly different: 1) on and near wildlife trails than in control areas; 2) on and near trails created and used weekly by humans than in control areas; 3) on and near wildlife trails that are and are not trampled weekly by humans; and 4) on and near either wildlife trails trampled by humans or human trails trampled by humans. Within the MRBPs' medians were aligned to zero for all blocks in order to focus the analyses on within-block differences among hypotheses and therefore Euclidean distances were used (Peterson and McCune 2001, Ponzetti and McCune 2001, McCune and Grace 2002).

Multivariate analyses were conducted at the plot-level, mid-scale and fine-scale. At the plot-level, cover data from the contiguous 0.2 x 0.5m plots were averaged across all plots. At the mid-scale, cover values were examined at four distance intervals from trails: 0-0.5m, 0.5-1.0m, 2.5-3.0m, and 4.5-5.0m. At the fine-scale, cover values within 10cm^2 quadrats were averaged to create the following distance intervals: 0-20cm; 20-40cm; 40-80cm; 80-120cm; 120-160cm; and 160-200cm. These distance intervals were chosen on the basis of patterns from preliminary analyses and separate MRBPs were conducted at each interval.

When a difference between each group was detected, indicator species analyses (ISA; Dufrene and Legendre 1997) determined which species were characteristically found in each of the treatment plots compared using PC-ORD Version 4.14 (McCune and Medford 1999). This method assigns a value or percent group indication to each species, based on the pre-defined groups. The relative frequency and abundance of each species were combined to calculate the indicator value (100%= a species occurs in all sample units of one group). The significance of the indicator value for each species was tested with a Monte Carlo procedure, with 10 000 randomizations.

Univariate Analyses

Univariate response variables were analyzed with a general linear model using Proc Mixed with the SAS System for Windows V8 (1999). In the model, distance from trail centre (continuous), wildlife trail (presence or absence) and human trampling (weekly or none) are fixed factors (Appendix C). The Satterthwaite approximation was applied to determine the correct degrees of freedom for all estimated and test statistics (Littell et al. 1996). Block and plot (treatment) nested within the trail*block*trampling interaction term served as random factors. These fixed factors and random effects define the global model, which includes all potentially relevant effects that reflect potential mechanisms judged as important from an *a priori* consideration of the objectives and experimental design (Burnham and Anderson 2002).

Any distance effect is assumed to be linear, an assumption not likely globally true. To test for non-linearity, a set of plausible candidate models was developed from the global model, in which quadratic and tertiary distance terms were added sequentially (Appendix C). SAS System for Windows V8 (1999) offers four selection criteria to choose the best candidate model or models: -2 Residual Log Likelihood; BIC (Bayesian Information Criteria); AIC (Akaike's Information Criterion); and AIC_C (second order AIC, for small samples). Fisher's likelihood theory, upon which the –2 Residual Log Likelihood method (sequential deletion of random effects based on subjective α levels) is based, assumes that the model structure, or 'true model', is known, and that only the parameters in that model are to be estimated (Burnham and Anderson 2002). Given the appropriate model with a large sample size, maximum likelihood provides estimators of parameters that are consistent, fully efficient and normally distributed, but in reality, it works best in simple problems (Burnham and Anderson 2002). To use this method, the model and its parameters must be known in advance, but in this study, the best model (linear, quadratic or cubic) is not known, and the small sample size (10 replicates per data point) may lead to a small sample bias (Burnham and Anderson 2002). Therefore the –2 residual method is not appropriate. Similarly, BIC methods were also inappropriate, as they can be difficult to understand and may select a model that fits the data poorly, while issues also arise with its dimension consistent property and valid inference of the target model as truth (Burnham and Anderson 2002). As a result, I used Akaike's Information Criterion (AIC) as the model selection criteria (Burnham and Anderson 2002).

Unless the data clearly (difference >3) support only a single model to fit the data, when competing models have AIC values close to the minimum, inference will be based on more than one model (Burnham and Anderson 2002). AIC provides an estimate of the expected, relative distance between the fitted model and the unknown true mechanism that actually generates the observed data (Burnham and Anderson 2002). As well, it is not the absolute size of the AIC value, but the difference between AIC values that is important (Burnham and Anderson 2002). Since the sample size is not large with respect to the number of estimated parameters in the global model, a second order AIC, AIC_C, was used to account for the relatively small sample size (Burnham and Anderson 2002).

A Priori Comparisons

A priori pairwise comparisons were used to further describe significant interaction terms. When a response variable varied as a function of a distance interaction (distance*trampling, distance*trail, distance*trail*trampling), means of the treatment effects were compared separately at each distance interval (0.5m for mid-scale; 0.1m for fine-scale) using the Estimate statements within the Proc Mixed Model (Appendix C). Means are presented graphically with error bars representing the standard error of the mean, and significance of difference is indicated.

When several tests of significance are carried out simultaneously, the probability of a Type I error becomes larger than the nominal value of α, and one option is to adjust the overall α of 0.05 using a Bonferroni correction (Legendre and Legendre 1998). However, debate exists over the use of Bonferroni corrections in interpreting ecological data (eg. Cabin and Mitchell 2000, Moran 2003). While it controls the Type I error problem, it can also increase Type II error rates, and the choice of which problem to control is subjective, unclear and not generally agreed upon (Cabin and Mitchell 2000). Moran (2003) points out mathematical and logistic problems with these corrections, reminding scientists that several relatively high p values can be stronger evidence than one moderately low value. On the basis of the recommendations of Cabin and Mitchell (2000) and Moran (2003), both corrected and actual α levels are presented in these results to allow the freedom of trend detection (Bonferroni corrected α levels are e.i. $p<0.05/n$, where n is the total number of comparisons). Interpretations are based upon assumptions made, limitations of the experimental design, biological significance and logic, with consideration given to alternate interpretations.

Transformations

Transformations to meet the assumptions of normality in 2001 included: 1) above ground biomass of all species (square root) and biomass woody species (natural log) at plot-level; 2) above ground biomass of all species (natural log) and biomass of forb species (square root) at mid-scale; and 3) species richness (square root) and percent PAR transmission below litter (square root) at fine-scale. In 2002, plot-level square root transformations included total cover of living plants and standing biomass of graminoid and forb species, while standing biomass of all living species and woody species were natural log transformed. Mid-scale square root transformations included standing woody species biomass, forb biomass, root biomass and PAR transmission above the litter layer, while natural log transformations included standing biomass of all living species, graminoid species and PAR below the litter layer. Fine-scale square root transformations included species richness, total cover of living plants and PAR above the litter layer; while PAR below the litter layer was natural log transformed. All PAR measures for the vertical distribution of light were arc-sine transformed.

RESULTS

Community Composition

Plot-Level

At the plot-level (5 x 8m), community composition did not differ between any of the 4 treatments in 2001 or 2002 (MRBP: Table 2.1A). Species richness decreased by 17% with trampling in 2001 (Mean±SE; Trampled by Humans=13.85 ± 0.60 species, Untrampled by Humans=16.65 ± 0.76 species), while trail type and use had no effect on richness in 2002 (Table 2.1B, Figure 2.5a). Trampling also decreased evenness in 2001 (Mean±SE; Trampled=0.69 ± 0.03, Untrampled=0.74 ± 0.03), but trail type and use had no effect in 2002 (Table 2.1B, Figure 2.5b).

Mid-Scale

At the mid-scale (0.5 x 8m), proximity to both human trails and wildlife trails influenced richness (2001). Human trampling decreased richness on wildlife trails and further depressed richness on human trails (2001). Trampling decreased evenness (2001), but species composition did not differ between treatments.

Species Composition

Community composition was not different between treatments at the mid scale in 2001 or 2002 (Table 2.2A), with one exception in 2002. From 0-0.5m, composition near trampled human trails, while not different from control areas, differs from trampled wildlife trails.

Richness

Trail proximity and trampling on human and wildlife trails influenced mid scale (0.5 x 8m) richness in both 2001 and 2002. In 2001, species richness varied with distance, trail type, the distance*trail interaction, trampling and the distance*trampling interaction (Table 2.2B). Candidate models did not clearly support a single model to fit the data, thus inference was based on all three models (AIC$_C$ linear=1544.9, quadratic=1542.3, tertiary=1545.2). In general, richness did not differ between wildlife trails and control areas within the first meter, but was reduced on wildlife trails after the first meter (1.0-1.5m: Figure 2.6a). Human trails decreased richness relative to controls for at least the first 2m (Figure 2.6b). While richness was greater near all wildlife trails than far from them, human use of wildlife trails decreased richness within the first meter of wildlife trails (Figure 2.6c). Similarly, trampling on newer human trails decreased richness more within the first meter than did trampling on older wildlife trails (Figure 2.6d).

In July 2002, richness varied with distance, the distance*trail interaction, trampling and the distance*trail*trampling interaction (Table 2.2B). The candidate model with the quadratic distance term supported a single model (AIC$_C$ linear=1474.8, quadratic=1465.8, tertiary=1470.3). Visual inspection indicated qualitatively similar responses for wildlife trails and control areas and for human trails and control areas. General patterns are the same as in 2001, while the strength of significance is not (Figures 2.6 and 2.7 a, b). As in 2001, richness is greater near all wildlife trails than far from them, but trends indicate human use of wildlife trails decreases richness within 2m of trampled wildlife trails, 1m further than in 2001 (Figure 2.7c). While richness is higher near both old wildlife and new human trails, the effects of weekly trampling on either trail are not discernable (Figure 2.7d).

Evenness

In 2001, species evenness varied with distance and trampling (Table 2.2B); the candidate model and AIC$_C$ values supported the linear and quadratic models (AIC$_C$ linear= 364.5, quadratic=-365.9, tertiary=-351.9). Trampling decreased species evenness (Mean±SE; Trampled=0.69 ± 0.01, Untrampled=0.74 ± 0.01).

In July 2002, evenness varied with distance and the distance*trail type interaction, with support for the linear candidate model (AIC$_C$ linear=-525.4, quadratic= -516.0, tertiary=-506.4). Mean evenness was not significantly different at any distance interval between wildlife trails and control areas (Figure 2.8a), or between trampled wildlife and human trails (Figure 2.8b).

Fine-Scale

In 2001, proximity and use of all trails influenced richness, but not composition or evenness at the finest (0.1 x 8m) scale. However, in 2002, only proximity to wildlife trails influenced richness, while both composition and evenness were influenced by proximity and use of all trails.

Species Composition

Within the fine-scale examination of the adjacent vegetation (2m from trails), community composition was not different among treatments at any of the distances examined in 2001 (one exception: Table 2.3A), but was in 2002. In 2002, the community composition within 120cm of wildlife trails was different than control areas. Indicator species analyses identify one species, *Festuca hallii*, as characteristic of wildlife trails (0-20cm: wildlife trails: 61%, control areas 39%, p=0.024). However, composition (MRBP) within 2m of human trails is not different from control areas.

Human use of wildlife trails influences composition within 20cm differently when compared to untrampled wildlife trails, with *F. hallii* again identified as characteristic of wildlife trails (ISA: wildlife trails: 61%, trampled wildlife trails: 39%, p=0.050). Human trampling does not affect composition differently within 0-20cm of older wildlife trails and newer human trails, but does from 20-160cm. *F. hallii* again characterizes trampled wildlife trails (80-100cm: trampled wildlife trails: 65%, trampled human trails:35%, p=0.006). These findings are supported by evidence of a difference at both the fine scale in 2001 (40-80cm: Table 2.3A) and at the mid scale in 2002 (0-50cm: Table 2.2A).

Richness

Species richness is affected by the distance* trail*trampling interaction in 2001, but only by the distance*trail interaction in 2002. In 2001, richness varied with distance, trail and the distance* trail and distance* trail* trampling interactions (Table 2.3B), with AIC_C values supporting the linear candidate model (AIC_C linear=500.6, quadratic=516.7, tertiary=547.6). As indicated with mid scale analyses, richness is the same within the first meter of wildlife trails and control areas, but lower after that point from wildlife trails (Figure 2.9a). Richness tends to decrease with distance from new human trails; trends indicate it is lower after the first meter away from human trails compared to control areas (Figure 2.9b). As at the mid scale, fine scale richness is greatest near all wildlife trails, and tends to decrease with distance, although human trampling on wildlife trails does not affect richness differently at this scale (Figure 2.9c). However, human trampling on older wildlife trails and newer human trails has different effects on the number of species (Figure 2.9d). Richness is higher on (0-10cm) and within 60-130cm of wildlife trails than on and near human trails.

In July 2002, fine scale species richness varied with distance and the distance*trail interaction (Table 2.3B); AIC_C values supported the linear candidate model (AIC_C linear=117.4, quadratic=137.6, tertiary=167.1). Richness is higher within 20cm of wildlife trails than in control areas (Figure 2.10a) and weekly trampling does not affect richness differently on or near wildlife trails than on or near human trails (Figure 2.10b).

Evenness

In July 2001, species evenness in the adjacent vegetation at the fine scale did not vary with any factors (Table 2.3B); AIC_C values supported the linear candidate model (AIC_C linear=5.4, quadratic=26.7, tertiary=56.4). In 2002, however, evenness varied with distance, trail type, the distance*trail type interaction, trampling and the distance* trail type*trampling interaction (Table 2.3B): AIC_C values supported the linear candidate model (AIC_C linear=-235.1, quadratic=-212.3, tertiary=-181.1). Evenness increased with distance from wildlife trails and was lower within 70cm of untrampled wildlife trails than in undisturbed grassland (Figure 2.11a). Weekly use of a human trail did not influence evenness differently from control areas (Figure 2.11b). Trampling on wildlife trails did not affect richness differently from untrampled wildlife trails (Figure 2.11c), nor were the effects of trampling different on human or wildlife trails (Figure 2.11d).

Community Cover and Production

Plot-Level

Percent cover of all living species in 2001 and 2002 (Figure 2.12a) and all dead species in 2002 (Figure 2.12b) did not vary with trail type, trampling or the trail type *trampling interaction at the plot-level (Table 2.4, Figure 2.12). Human trampling decreased forb biomass 32% in 2001 (Mean±SE; Trampled=54.70 ± 6.74, Untrampled= 72.40 ± 6.07 gm^{-2}) and 38% in 2002 (Mean±SE; Trampled =8.05 ± 1.09, Untrampled= 13.03 ± 1.68gm^{-2}) (Figure 2.13 c). Other measures of standing biomass, including total living (Figure 2.13a), living graminoid (Figure 2.13b), living woody (Figure 2.13d), total dead (Figure 2.13e) did not vary in 2001 or 2002; nor did root biomass vary in 2002 (Table 2.4, Figure 2.13f). In 2002, drought stress is evident in control plots, as graminoid biomass and forb biomass decreased, while biomass of woody and dead plant matter increased (Figure 2.13).

Mid-Scale

Cover

Cover of living vegetation varied with distance in 2001;AIC$_C$ values supported the quadratic and tertiary candidate models (AIC$_C$ linear=3493.6, quadratic=3490.3, tertiary=3490.1) (Table 2.5). In 2002, living cover varied with distance, trail type and the distance*trail interaction, with quadratic and tertiary candidate models (AIC$_C$ linear=2654.2, quadratic=2643.7, tertiary=2644.8) (Table 2.5). Plant cover was slightly higher on wildlife trails than far from them, but was not different (Figure 2.14a). Human trampling had different effects on and near older wildlife trails and newer human trails and cover was higher within 0-1m of trampled wildlife trails (Figure 2.14b).

Percent cover of dead plants also varied with distance, trails and the distance*trail interaction in 2002 (Table 2.5), with quadratic and tertiary candidate models (AIC$_C$ linear=2552.7,quadratic=2546.3, tertiary=2547.8). Cover of dead vegetation was lower directly on wildlife trails than far from them, but not different from control areas (Figure 2.14c). Human trampling also had different effects within 0-1m of older wildlife and new human trails, and cover of dead plants was lower on wildlife trails (Figure 2.14d).

Biomass

In 2001, standing living total and woody species biomass at the mid-scale were not influenced by proximity to trail, trail type or trampling, while standing biomass of all living forbs, graminoids and dead species were (Table 2.5). Trampling decreased forb biomass 33% (Mean±SE; Trampled=49.88 ± 3.70, Untrampled=74.22 ± 5.54 gm^{-2}), and AIC$_C$ values supported the linear distance model (AIC$_C$ linear=662.4, quadratic=666.7, tertiary=670.4). Both standing living graminoid and total dead biomass had a general distance response (Table 2.5), and both had tertiary models (graminoid AIC$_C$ linear=1487.8, quadratic=1486.4, tertiary=1481.7; dead AIC$_C$ linear=1604.7, quadratic=1600.2, tertiary=1595.5). Standing living graminoid and total dead biomass tended to increase from 0-1m and then again at 3m.

In 2002, total living biomass varied with trampling and the distance*trampling interaction, with the linear candidate model (AIC$_C$ linear=389.9, quadratic=394.8, tertiary=400.0). Biomass increased with distance from human trails; trends though not significant, suggest biomass was lower near human trails than in control areas. Trampling on wildlife trails decreased total biomass directly on the trail, as mean biomass was greater at 0m on untrampled wildlife trails than trampled.

Forb biomass varied in 2002 with distance and the distance*trail*trampling interaction, with all three candidate models (AIC$_C$ linear=386.5, quadratic=387.4, tertiary=390.0) (Table 2.5). Wildlife trails and undisturbed grasslands did not affect forb biomass differently, except at 4m from the trail, where biomass was higher in undisturbed plots than in wildlife trails (Figure 2.15a). Trampling increased forb biomass on human trails, and after 1m, biomass was lower near human trails than in control areas (Figure 2.15b). While biomass decreased with distance from all wildlife trails, human trampling did not affect biomass differently on wildlife trails (Figure 2.15c). Trampling had the same effect on older wildlife and newer human trails; biomass was highest directly on both (Figure 2.15d).

Graminoid biomass varied at the mid-scale with distance, trampling, the interactions of distance*trampling, trail* trampling and distance*trail*trampling (Table 2.5) with the linear candidate model (AIC$_C$ linear =288.2, quadratic=291.1, tertiary=295.6). Biomass was higher 1m from wildlife trails than in undisturbed grasslands (Figure 2.16a). The creation and use of a human trail for two growing seasons decreased graminoid biomass directly on the human trail, with biomass lower on human trails than in undisturbed grasslands (Figure 2.16b). Weekly human trampling on wildlife trails decreased graminoid biomass directly at 0 and 1m from trails (Figure 2.16c). Trampling had the same effect on wildlife and human trails; biomass was lowest on trails and increased with distance (Figure 2.16d).

Biomass of total dead plant matter varied with distance and trampling in 2002, with the tertiary candidate model (AIC$_C$ linear=1799.8, quadratic=1781.2, tertiary=1770.6) (Table 2.5). Trampling decreased mean biomass of dead plant matter 9% (Mean$\pm$SE; Trampled=312.03 $\pm$ 13.65, Untrampled=341.61 $\pm$ 12.92).

Mid scale root biomass did not vary with any factors in July 2002; AIC_C values supported the linear candidate model (linear=123.4, quadratic=130.2, tertiary=136.2) (Table 2.5).

Fine-Scale

Cover

Fine scale (0.1 x 8m) cover of living vegetation varied with distance and the distance*trampling interaction in 2001;AIC_C values supported the linear candidate model (linear=6669.1, quadratic=6683.8, cubic=6706.5) (Table 2.6). While percent cover of living plants is generally the same near human trails and controls, trends indicate cover is higher 180-200cm from human trails than in control areas (Figure 2.17a). Trampling on wildlife trails does not affect cover differently within the first meter of trails, but cover of living vegetation is higher 120-150cm from trampled wildlife trails compared to those not trampled (Figure 2.17b).

In 2002, the percent cover of both living and dead vegetation varied with distance, trail type, the distance*trail interaction, trampling and the distance*trampling interaction (Table 2.3B). AIC_C values supported the linear candidate models for both variables (living: AIC_C linear=2620.1, quadratic=2639.6, cubic=2664.8, dead: AIC_C linear=5886.8, quadratic=5902.2, cubic=5921.5). Percent cover of living vegetation decreases with distance from wildlife trail and was higher near wildlife trails than in undisturbed grasslands (Figure 2.18a). As well, trends suggest cover of living plants may be higher in undisturbed grasslands than within 1m of human trails (Figure 2.18b). Human trampling on wildlife trails decreases cover of living plants and is lower on trampled wildlife trails (0-20cm) than on wildlife trails not actively trampled (Figure 2.18c). Trampling has a more deleterious effect on living cover of plants 60-120cm from human trails than wildlife trails; mean cover is higher 60cm from wildlife trails than from human trails (Figure 2.18d).

Mean percent cover of dead vegetation is lower immediately near (0-20cm) wildlife trails than in undisturbed grasslands (Figure 2.19a). Dead cover is not different near human trails and undisturbed grasslands, although the area covered by dead plant matter is generally higher on and near human trails (Figure 2.19b). Human trampling on wildlife trails increases dead plant matter, as mean cover of dead plant matter is higher immediately (0-20cm) on trampled wildlife trails than on those without weekly human trampling (Figure 2.19c). Weekly human trampling affects plants differently on wildlife trails than human trails; mean cover is higher within the first 120cm of human trails than wildlife trails (Figure 2.19d).

Available Light

Plot- Level

At the plot-level, differences among treatments in PAR transmission were detected both below and above the litter layer in 2002. Transmission below the litter layer varied with trail and trampling (Table 2.7); trampling increased PAR transmission by 109% below the litter layer (Mean±SE; Trampled=7.80 ± 0.87, Untrampled=3.74 ± 0.55) and 38% more light was available on older wildlife trails than on human trails and control areas (Mean±SE; Wildlife=6.64 ± 0.85, Human+ Control=4.89 ± 0.86) (Figure 2.20). Above the litter layer, trampling increased transmission by 32% (Mean±SE; Trampled=24.72 ± 1.75, Untrampled=18.77 ± 1.37), however, unlike the response below litter, it is the trampling on wildlife trails (versus those not trampled) that drives this pattern (Figure 2.20).

Mid-Scale

Proximity to trail and human trampling influenced both below and above litter PAR transmission. Transmission below the litter layer varied with distance and trampling; AIC_C values supported the tertiary candidate model (linear=1377.7, quadratic=1365.0, tertiary=1334.2) (Table 2.7). Trampling increased mid scale transmission by 123% below the litter layer (Mean±SE; Trampled=8.33 ± 1.29, Untrampled=3.74 ± 0.58).

Above the litter layer, transmission varied with distance, trampling, and the distance*trampling interaction (Table 2.7); AIC_C values supported the tertiary candidate model (linear=-161.4, quadratic=-169.6, tertiary=-187.1). Transmission was greater within 0.0-0.5m of human trails than controls, but less within 0.5-1.0m (Table 2.21a). Transmission was also greater directly on wildlife trails than far from them; trends indicate more light was available within 2.5m of trampled wildlife trails than on those not trampled (Figure 2.21b).

Fine-Scale

PAR below the litter layer varied with distance, trail type and the distance*trail interaction, with both linear and tertiary candidate models (AIC_C linear=2803.5, quadratic=2812.1, tertiary=2805.9) (Table 2.7). Transmission was greater on wildlife trails (0-10cm) than in control areas (Figure 2.22a). Trampling had similar effects on older wildlife trails and newer human trails, with 40% more light directly on trails (0-10cm) than on the area directly adjacent (Figure 2.22b).

Above litter patterns were similar to mid-scale patterns and are only presented graphically (Figure 2.22c,d).

Vertical Light Profile

At the trail centre (0m) the amount of light reaching the soil surface (0cm) was similar on undisturbed wildlife trails and in control areas (Figure 2.23). Human trampling on either human or wildlife trails increased light penetration. At 5cm from the ground surface, light transmission was greater on wildlife trails than control areas and on trampled human trails than control areas. Trampling did not significantly increase the amount of light available on wildlife trails compared to those not trampled, nor did trampling affect transmission differently on human or wildlife trails. After 5cm, the difference in mean PAR was not significant between any treatments, except at 30cm, where more light was available on trampled wildlife trails than those not disturbed.

One meter from trails, the amount of light available within the vertical profile was influenced by the presence of an established wildlife trail; in addition trampling increased light more on human trails than wildlife trails. The presence of wildlife trails decreases the transmission of PAR within 5-15cm of the vertical profile, relative to control areas (Figure 2.24). However, the creation and use of human trails did not affect the vertical light profile differently from control areas. It also appears that further use of wildlife trails by humans does not alter the amount of light in the vertical profile when compared to wildlife trails not used by humans. However, trampling has different effects on human and wildlife trails; the use of an existing wildlife trails decreases the amount of light in the profile 10-15cm from the ground surface.

Trampling on trails decreased light two meters from trails within the vertical profile when compared to those without human use, and trampling on human and wildlife trails may affect the profile differently. At this distance (2m), neither the presence of a wildlife trail, nor the presence and use of a human trail, affects the vertical light profile differently than in control areas (Figure 2.25). However, human trampling on wildlife trails decreased the amount of light within 5-25cm of the ground surface, relative to wildlife trails not used. Human trampling on wildlife trails may decrease light more than on human trails, as trends indicate mean PAR was greater near human trails within 0-25cm of the soil surface, with the difference significant only at 10cm.

Changes in the vertical light profile were not significantly different between treatments at distances of 3, 4, and 5m from trail centres.

DISCUSSION

Responses to trail type and use vary with scale, year of observation and comparison made. Due to the volume of information presented, the discussion is organized in the following manner. In the first section, discussion of the major patterns focuses on scale of observation. In the second section, patterns and proximity relationships are explored individually for 1) wildlife trails, 2) human trails, and 3) human use of old and new trails. The third section considers the implications of study findings, and addresses key areas for future research.

Patterns at Plot-Level, Mid and Fine-Scales

Plot-Level

At the largest scale of observation, human trampling decreases species richness and evenness, as well as forb biomass (Summary Table 2.8). Creating and using human trails appears to have the same effect as trampling on older wildlife trails in 2001(Figure 2.5, 2.13c). Even at the largest level of observation, the weekly use of a new or old trail will influence local dynamics. The losses in richness, evenness and forb biomass are primarily a response to the damage from the repeated trampling disturbance. Trampling disrupts the dominant vegetation and litter layer, and more light is available both at the ground surface and above the remaining litter layer in plots with human trampling (Figure 2.17). Although these changes in the structure of the vegetation and resources within these gaps can provide opportunities for the colonization of otherwise less competitive species (Connell 1978, Grime 1979, Armesto and Pickett 1985, Ikeda and Okotumi 1990, 1992, 1995, Kobayashi et al. 1997) and increased emergence, survival, growth and establishment from seed (Goldberg 1987, Gross and Werner 1982), it appears that only a few species are able to survive the disturbance of repeated trampling. As well, evenness decreases, indicating proportions of trampling resistant species may be much greater than those of non-resistant species. Time since initiation of trampling must also be considered. While richness, evenness and forb biomass decreased with trampling, changes in species composition were not detected. This may either reflect a delay in the establishment of trampling resistant species or be a reflection of scale, as compositional differences were detected at the two finer scales.

While trampling decreased plot level richness in 2001, it did not in 2002. In the absence of continued trampling in the second year, richness may have begun to increase as new species colonized the trail, since removal of the dominant vegetation provides an opportunity for colonization of less competitive species (Connell 1978, Grime 1979, Hewitt and Miyanishi 1997) and the litter reducing disturbance opens up the litter layer (Carson and Peterson 1990, Foster and Gross 1988). However, in one growing season, richness still would not likely recover.

The absence of a trampling effect in 2002 may also be due to drought, as drought stress decreases species richness by 28%. Similar decreases due to drought have been reported both in the literature (Tilman and El Haddi 1992, Hobbs and Mooney 1991, but see Bollinger et al. 1991) and in an unpublished study conducted within the same area (Coupe, unpublished data). If drought sensitive species are also the same species that are sensitive to trampling, then we would not expect to see a trampling effect in 2002. Trampling tolerant and drought tolerant species share many traits, although trampling tolerant plants are not always adapted to low moisture conditions (Kobayashi and Hori 1999). Plants tolerant to both disturbances are often plants with protected meristems or meristems close to the ground (drought: Walter et al. 1999, McWillaims and Kramer 1968, trampling: Bates 1935, 1938, Liddle and Grieg-Smith 1975) and plants with greater basal areas (drought: Boschma et al. 2003, trampling: Holmes and Dobson 1976, Cole 1987). As well, a greater number of tillers increases tolerance to both trampling and drought (drought: Boschma et al. 2003, trampling: Sun and Liddle 1993b). The species that survive both disturbances (drought and trampling) are similar; they are often perennial grasses and forbs, legumes and woody plants (drought: Herbel et al. 1972, Tilman and El Haddi 1992, trampling: Palmer 1972, Cole 1993).

We might expect grassland plants to have similar tolerances and sensitivities to both disturbances, as this system has likely evolved under both disturbances. Grasslands have evolved in the presence of periodic drought, fire and animal grazing (Hartnett and Fay 1998, Knapp and Seastedt 1998) and trampling is an animal activity associated with animal grazing (eg. Dublin et al. 1990, Plumptre 1993). It is not surprising, therefore, that richness does not change. However, trampling does decrease forb biomass (Figure 2.5). In addition to the biomass lost as plants are crushed and torn, one explanation for the observed decrease in biomass in the absence of a decrease in richness and evenness involves drought stress. Many forb species that persisted in the drought were likely under stress. The partially desiccated brittle plant parts would be more likely to break when trampled, as water stressed plants are more easily damaged than plants with adequate moisture (Thomas and Wilson 1997). However, as only a portion of the plant is removed instead of the whole plant, neither richness, evenness nor composition change, but biomass does. Many ecological processes are correlated (eg. Turner 1988, Kobayashi and Hori 1999, Boschma et al. 2003), and many ecologists stress the necessity of understanding interactions in order to understand the dynamics involved in plant responses to disturbance (eg. Turner 1988, Gibson 1989, Ikeda and Okotumi 1992, Thomas and Willson 1992, Weisberg and Bugman 2003). We know, for example that large scale disturbances such as grazing and fire interact with local disturbances such as trampling (Liddle and Thyer 1986, Turner 1988, Gross et al. 1998). Therefore, exploring interactions between large and small-scale disturbance events will further increase our understanding of relationships at localized scales.

Mid-Scale

At the middle scale of observation (0.5 x 8m), the proximity to both trails and trampling influenced richness in 2001 (Summary Table 2.9, Figure 2.26). In control plots we see little change in richness with distance; there are a few fluctuations, but no strong patterns. However with trails and their use we see some deviations within the first two meters. Trampling suppresses richness, with the largest effects occurring within 2m of new human trails. Richness is higher on older wildlife trails than new human trails, and human use of wildlife trails further decreases richness. These patterns at the mid-scale support those at the plot-level, but provide more information about where trampling effects are most concentrated, within the first 1 to 2m from trails. Additionally, information at this scale indicates that wildlife trails do, in fact, influence the local plant community and that trails in grasslands are similarly important to other localized disturbances, such as woodchuck burrows and gopher mounds (English and Bowers 1994, Hobbs and Mooney 1985).

Clearly, the vegetation directly on and near trails is affected by the presence and use of trails, and the effect is different on new and old trails. Richness is lower near human trails than near both wildlife trails. On new human trails, in addition to changing the structure of trail vegetation, trampling can alter composition, by removing some species that are not tolerant to the disturbance (eg. Burden and Randerson 1972, Liddle and Greig-Smith 1975, Hall and Kuss 1989). However, composition on is the same, suggesting that in all blocks, enough individuals of each species survive within the chosen distance class of 0-0.5m. Composition differences are detected between human trails and trampled wildlife trails at the finest scale of observation, from 40-80cm (Table 2.10). Scale of observation is important for detecting compositional differences, as is the chosen distance class. The difference in richness and composition reflects changes in relation to the time since initiation of disturbance (Figure 2.2). Thus, even though changes in structure create both a gap in which new species can colonize (Connell 1978, Grime 1979) and create conditions for increased establishment, emergence, survival and growth (Goldberg 1987, Gross and Werner 1982), continuous trampling at the set frequency (5 passes per week) depresses richness (Figure 2.1A).

Compared with trails that are trampled, richness is higher on and near older wildlife trails without the weekly trampling component. While the frequency with which these trails were actually used by wildlife is not known, the mode of action of ungulates and humans using the trails is different. Within the human trampling component, each step followed the next (toe to heel), while subsequent ungulate steps would be much further apart. As a result, within the same section of a trail, human trampling would likely directly trample more plants.

Boucher et al. (1991) found a similar pattern in a tropical forest, diversity and cover were higher on the older trail that was not currently in use than either the older or newer trail in use, nor were diversity and cover different between either of the two actively used trails. As the trails create gaps in the dominant vegetation structure, resource gaps open and create sites for colonization, increased seedling survival and emergence (Connell 1978, Grime 1979, Goldberg 1987, Gross and Werner 1982). In the absence of frequent human trampling, richness on wildlife trails increases (increase in Figure 2.1 "B"). However, we might expect richness to decrease as the damage caused by further trampling reaches a threshold level (decrease in Figure 2.2 "B"). We see evidence of trampled wildlife trails approaching this decrease, as richness is lower, although not significantly, on trampled wildlife trails than on those undisturbed (Figure 2.26). The frequency (5 passes/week) of trampling reduces richness on trails and similar to the plot-level, trampling reduces evenness and forb biomass (Table 2.9). Vegetation can recover relatively quickly in the absence of frequent disturbance (van der Maarel 1971, Marion and Cole 1988, Boucher et al. 1991)

Unlike at the plot-level, responses to trampling and trail effects are detected at the mid-scale of observation in the drought year for most of the response variables (Table 2.9). Trail and trampling effects are detected despite the drought, although most likely the effects of both disturbances are interacting. Patterns in richness in 2002 are similar to 2001 and most deviations occur within the first meter of trails. Again, in control plots, we see little change with distance, although mean richness is lower in 2002. However,in 2002 richness is depressed only 1m from human trails, versus two meters in 2001. The difference in the decrease between human trails and trampled wildlife trails is not as great directly on trails.

The presence of a trail may ameliorate drought stress. When an old trail is present, but trampling is not, richness is higher during the drought. If trampling is introduced to the old trail, richness decreases; if trampling occurs on a new trail, richness is lowest (Figure 2.27; 0m). Cover of living vegetation is higher on older wildlife trails than in control areas and on trampled older trails than newer human trails (Figure 2.14a,b). This suggests different types of plants grow here, and these plants may be more resistant to both disturbances, due to traits such as protected meristems, greater basal areas, and greater numbers of tillers (drought: Walter et al. 1999, McWilliams and Kramer 1968, Boschma et al. 2003, trampling: Bates 1935, 1938, Liddle and Grieg-Smith 1975, Holmes and Dobson 1976, Cole 1987, Sun and Liddle 1993b). Different types of plants are present on both trampled trails, than in control areas or on untrampled wildlife trails, as biomass the dominant lifeforms, graminoids and their associated litter are lower (Figure 2.16). However, composition is different (0-0.5m) on and near active wildlife and human trails, characterizing species responses to trampling over time.

Fine-Scale

While examining fine-scale patterns can offer insight into details of responses to treatments, it also has the potential to distort information. Patterns measured at relatively small scales do not necessarily reflect patterns at larger scales (Wiens 1989, Schnieder 2001). For example, when comparing fine-scale richness in 2001 (Figure 2.9) in control plots to wildlife and human trails, it appears richness is considerably higher in the last meter. However, though that holds true for this scale of observation, mid-scale data points for the same distance (1.0-1.5, 1.5-2.0) indicate that while richness is a bit higher, it is not out of the normal range (Figure 2.26). Scale dependent relationships are common in ecology (Gross et al. 2000, Schneider 2001), and often arise because different processes operate at different scales (Crawley and Harral 2001, Dixon et al. 2002). Fine scale observations can offer greater detail about biological mechanisms underlying patterns, while broader scales are more likely to provide generalizations (Wiens 1989); thus, it is important to examine multiple scales (Gross et al. 2000). As well, the assignment of fine and broad scales is relevant only within the context of a particular study, and it has been suggested that even 10 x 10cm quadrats (fine scale of this study) are larger than the scale at which interactions between plants are likely to occur within grasslands (Purves and Law 2002). To date, few studies exist that examine how consistent vegetation response is to trampling on different temporal and spatial scales (but see Taylor et al. 1993, Ikeda 2003).

Within this study, patterns at the fine-scale indicate that richness is higher near both types of wildlife trails than far from them (Figure 2.9c), but that directly on wildlife trails, human trampling does not have a consistent effect on richness at this scale. We do see evidence for an influence on cover, as trampling on wildlife trails decreases cover of living vegetation 60-100cm from trails, while cover increases 100-150cm from them (Figure 2.17b). Trends suggest richness is generally lower on and near human trails than wildlife trails (Figure 2.9d) and composition is different 40-80 cm from both trails. In

2001, fine scale patterns alone do not offer much insight into the responses of this system to trampling on trails.

In 2002, fine-scale patterns reveal changes in composition as a response to trail type and use. Composition on and near (0-120cm) wildlife trails is different than in control areas. Plants on the trail could influence the adjacent vegetation; species on trails could act as sources for colonization, by seed or vegetative means, and plants on trail edges have been noted to flower more (Liddle 1991). As well, structural changes may alter local microsite conditions, and animals using the trails can also act as seed vectors (Wang and Smith 2002, Andresen and Levey 2004).

In contrast compositional differences are not detected between new human trails and control areas, further illustrating species' responses to trampling over time (Boucher et al. 1991). Only the area directly trampled on actively used wildlife trails (0-20cm) differs in composition from that of unused wildlife trails, suggesting plants intolerant to this frequency of trampling are removed. It appears that trampling removes similar species in this drought year, regardless of the age of the trail, as composition in the central area (0-20cm) of old and new trails is the same, and trampling similarly reduces cover of living vegetation (Summary Table 2.10, Figure 2.18d). There is a difference, however, in composition 20-120cm from these active trails. A change in composition in the adjacent vegetation as a response to the presence of a new trail takes longer than two growing seasons, although the time needed for response may be shorter in the absence of drought.

Wildlife Trails, Human Trails and Trampling

Wildlife Trails: Animal Generated Disturbance

Wildlife trails do not have much influence on plot-level dynamics, but do influence the local plant community at the two smaller scales in both study years (Table 2.9). In 2001, richness is higher on and near wildlife trails than further from them (Figure 2.6a, 2.9a). Mid-scale examination indicates richness is higher within the first meter (Figure 2.6a), or possibly 80cm at the fine-scale (Figure 2.9a). This is expected, as trails of this nature disrupt the structure of the dominant graminoids and their litter layer and vegetation development in productive grassland relies largely on litter reducing factors that remove or open up the litter layer (Carson and Peterson 1990, Foster and

Gross 1988). As more species both colonize in the gap created by the trail and establish from seed or increase in emergence, survival and growth (Connell 1978, Grime 1979, Gross and Werner 1982, Goldberg 1987), more species become available for colonization of adjacent areas. Less light is available 5-15 cm from the ground surface at a distance of 1m from wildlife trails relative to control areas (Figure 2.22), indicating that structural changes occurring on the wildlife trail influence light conditions 1m away. Vegetation at the edge of trails may respond with increased height to the increased light, essentially forming a wall of vegetation that alters light distribution within the vertical profile up to 1m away. Although vegetation height was not directly examined in this study, other studies have documented the increased height of vegetation at trails edges (Thomas 1959, Pradhan and Tripathi 1983, Studlar 1983, Liddle 1991).

After one meter (1.0-1.5m), richness may be lower near wildlife trails than in control areas in 2001 (Figure 2.6a), although the significance may be spurious. We see the same pattern in 2002 (Figure 2.7a), although the difference is not as great, likely influenced by the general decrease in production and richness associated with the drought. This decrease is accompanied by an increase in graminoid biomass (Figure 2.16a). Therefore, it seems that at the edge of a wildlife trail the increased vegetation height causes a decrease the available light within 5-15cm of the vertical profile 1 meter away from the trail (Figure 2.24), thereby exacerbating light competition. The decrease in richness and the corresponding increase in graminoid biomass support this idea. While the decrease in light resources is one explanation for this pattern, we must also consider potential influences of animals using these trails, as English and Bowers (1994) consider selective herbivory near burrows. Mammalian herbivores move and forage at the same time (Jiang and Hudson 1993, Fortin et al. 2004) and large ungulates often turn their heads aside to reach for bites while walking (Jiang and Hudson 1993). Mammals using this system may be preferential foragers, as ungulates are known to exhaust highly preferred foods before switching to lower ranked ones (Gillingham and Bunnell 1989). Such selective feeding can modify both the structure and composition of plant communities (Pastor and Naiman 1992, Pastor et al. 1988). In an area near this study site, ungulates tend to select young leaves of species such as *Geum triflorum*, *Aster* and *Viola* species, and *Rosa arkansana* (Didkowsky, personal observation). Therefore, animals using these trails may selectively forage for some non-graminoid herbaceous species, decreasing localized abundance near trails, since they may be more likely to encounter preferred plants near trails than in the rest of the grassland.

In 2002, information from the fine-scale again appears to provide insight into what is happening at the individual plant level. Fine-scale composition is different within 120cm of wildlife trails than in control areas, and *Festuca hallii* characterizes these wildlife trails (0-20cm) (Table 2.9). Evenness is lower within the first meter of wildlife trails (Figure 2.11a), although richness does not change much, except from 10-20cm (Figure 2.10a). This illustrates the importance of using measures of equitability in conjunction with measures of abundance; others have also documented changes in evenness with little or no changes in richness (see Wilsey and Potvin 2000). While biomass estimates are not directly available for this scale, changes in cover provide some insight. Cover of living vegetation is higher near wildlife trails than far from them, and within the first 40cm is higher than in control areas (Figure 2.18a). The area that has the most direct contact with hooves or feet (0-20cm) also has less cover of dead vegetation. This is logical, as the trampling action of hooves and feet breaks the dead portions of plants and can both work them into the soil matrix (Keen and Cashen 1932, Weir 1971, Zacheis et al. 2002) and make more pieces available for wind distribution. It is also important to note that on older trails (possibly in recovery phase) that are trampled at a very low intensity, if at all, light levels directly below and above the litter layer are not much different than in control areas (Table 2.9-2.11). At the fine-scale, there is more below the litter layer directly on the wildlife trails (0-10cm), while at the plot-level 38% more light is available to plants near active and recovering wildlife trails. Within this grassland, changes in the composition may be partially dependent on litter reducing disturbances, such as trampling. Litter reducing disturbances may have more of an effect early in the growing season (Xiong and Nilsson 1999), when removing the litter layer can increase light to seedlings, as litter shades and mechanically impedes seedlings (Gross and Werner 1983, Carson and Peterson 1990, Tilman 1993, Foster and Gross 1998). As trampling breaks down the litter layer, the surface area and proximity of plant material to decomposers increases (Zacheis et al. 2002); thus more nutrients may become available to plants directly on trails and in the adjacent vegetation.

Numerous studies examine other small scale disturbances created by animal activity, such as ant hills, badger and gopher mounds, mole and vole burrows, bison wallows, or fecal and urine patches, and generally conclude that such disturbances are important for grassland vegetation dynamics (Platt 1975, King 1977, Hobbs and Mooney 1985, Bradshaw and Goldberg 1989, Gibson 1989, Day and Detling 1990, Reichman et al. 1993, English and Bowers 1994). The area directly disturbed by these activities ranges from 0.01% to 10% (Goldberg and Gross 1988), and the area directly disturbed by trails in this study site is 2.2%. In this study site, trails may influence the local plant community up to 1.5m away from them, meaning that at the upper bounds, these trails can influence up to 28% of grasslands. This influence is not static, since the strength and specific measured responses differ in growing seasons and some of these differences may be due to drought stress, changes in frequency of use by animals and recovery of vegetation. These trails are a different type of disturbance than the burrows and mounds created by animal activity. Burrows and mounds involve the exposure of mineral soil as well as the removal of existing perennial vegetation and litter (Goldberg and Gross 1988), but on trails of this nature, mineral soil is rarely exposed. Clearly, these types of trails are important for grassland vegetation dynamics and research into this type of small-scale disturbance should reflect that of other animal activities.

Human Trails: Their Presence and Use

When we examine how human trails influence local plant community dynamics, we are considering two important concepts. Firstly, as new trails, we are able to directly compare their composition and production with that of older wildlife trails, gaining insight into how changes that make a trail different from the surrounding matrix occur. Secondly, as these trails are representative of those created by ecological research in grassland systems, we can better understand our influence upon the systems we study. Outside of plant ecology, handling and mark/recapture effects, such as those used by animal ecologists, are well known (eg. Mallet et al. 1987, Wenny 2002), as are the effects upon predation of trail proximity to bird nests (Hickman 1990, Riffell et al. 1996, Miller et al. 1997, Olson and Rohwer 1998, Miller and Hobbs 2000). Some mammalian species are known to avoid human trails, and others to use them preferentially over predator trails (Pepin et al. 1996, White et al. 2003). Within plant ecology, thigmomorphogenic responses to human touch are well documented (eg. see Klaring 1999) and evidence is emerging indicating touching plants can alter rates of herbivory (Cahill et al. 2001, 2002, Hik et al. 2003, but see Schnitzer et al. 2002, Bradley et al. 2003) and pathogen damage (Schnitzer et al. 2002). However, how the presence of a researcher can influence plant success in the absence of contact is unclear (Cahill et al. 2002). Examining the relationship of plant proximity to new human trails may provide more insight into how researcher visitation effects occur, and consequently, how the methodology used by grassland ecologists may influence plant responses.

Within 2m, the creation and use of a new human trail depresses richness after one season (Figure 2.6b). We also see evidence for a similar effect in 2002 (Figure 2.7b), but it is likely masked by drought. Directly on new trails, we expect this decrease in richness as plants respond directly to the damage caused by trampling (eg. Willard and Marr 1970, Bayfield 1971, Watson 1985, Kuss 1986). Although the disruption of the dominant graminoids and litter increases light available on trails and creates conditions for competitive inferiors to both establish and increase in emergence, survival and growth (Connell 1978, Grime 1979, Gross and Werner 1982, Goldberg 1987), plant response is primarily a function of trampling damage. In conjunction with continuous trampling, one growing season is not enough time for the establishment of new species that tolerate trampling, as highlighted by the absence of change in either evenness or composition at the fine scale (Table 2.10). Recovery rates depend both on the identity and resiliency of the individuals damaged, their capacity for rapid increase in cover (Cole 1988, Arnesen 1999) and the amount of damage initially received (Marion and Cole 1996).

Processes responsible for patterns directly on new trails are easier to understand, but explanations for the decrease observed in richness 0.5-2m from new trails are more complex. While mechanisms responsible for the decrease are not directly offered by this study, there are a few possible explanations. Structural changes to the vegetation on and immediately next to the trail could contribute to the decrease in richness. While more light is available above the litter layer directly on trails, we also see that less light is available 0.5-1m from them (Figure 2.21a), suggesting that competition for light could be exacerbated. Changes that occur within the structure of the vegetation as the trail is created may also indirectly contribute to species loss near trails by influencing local populations of vertebrate and invertebrate herbivores. Disturbances such as trails creation can lead to favorable microclimates and foraging conditions for grasshoppers (Corcket et al. 2003). Finally, Fecal pellets were found on new human trails (Brown, personal observation), indicating use by local mammals. As previously discussed, it is reasonable to assume that these vertebrates could also be selectively foraging near trails, contributing to species loss.

The direct damage caused by trampling also has the potential to influence local invertebrates. Chemicals released from damaged plant tissue can attract insect herbivores (Bolter et al. 1997) and their attraction to the damaged plants may make a discovery of neighbouring plants more likely. If this was the case, we might then expect to see evidence of insect herbivory not only on plants located directly on trails, but on plants near trails as well. In forests, the proportion of leaves on trees with foliar damage due to insect herbivory was not related to distance from trail edge (Patel and Rapport 2000). However, in this grassland system, evidence for such a relationship exists from a sub-study that examined the damage cause by both insect herbivory and other factors on a subset of plant species within this study site, conducted within the constraints of the larger study (Appendix D). Preliminary analyses (Appendix Table D.1) indicate damage due to insect herbivory is related to the proximity to human trails, as evidence of insect herbivory is higher near trails and decreases with distance (Appendix Figure D.1). Further evidence indicates that damage due to other factors, such as pathogens and drought stress, is also higher on and near human trails than far from them (Appendix Figure D.2). Schnitzer et al. (2002) also found evidence suggesting human visitation caused slightly higher pathogen damage. Finally, drought stress can promote outbreaks of plant-eating fungi and insects (Mattson and Haak 1987). Leaf yellowing is included within the estimates of other damage; and with leaf yellowing, higher temperatures and greater infrared reflectance of drought-stressed plants may make them more attractive to insects (Mattson and Haak 1987). Positive interactions have been found between damage due to drought stress and insects (Wilis et al. 1993). Drought-stressed plants may be more suitable for insect growth, and survival of as plant nutrients may be more concentrated, and insect outbreaks are associated with droughts (Mattson and Haak

1987). It is likely that all three of these processes, trampling, drought stress and insect herbivory, are interacting, and thereby influencing the local plant community.

Human Trampling on Old and New Trails

Trampling on Old Wildlife Trails

Human trampling on older wildlife trails decreases richness near trails. In 2001, the extent of influence at the mid scale is about 1m, while in 2002 it reaches further to 2m (Figures 2.6 and 2.7c). The difference in richness is greatest after 0.5m, indicating that human use of trails suppresses richness in adjacent vegetation. It seems that directly on the trail, trampling has little effect, although we might expect the disturbance to remove trampling intolerant species (Perring 1967, Dawson et al. 1978, Young 1978, Bayfield 1979, Jim 1987, Ikeda and Okutomi 1990, Shaw and Diersing 1990, Ikeda 2003). One growing season may not provide enough time to see a change in richness, as the trail community likely already contained many trampling tolerant species. However, one growing season was enough time to detect changes in both forb biomass and evenness, which were lower in all trampled trails at this scale (Summary Table 2.9). Therefore we might have expected an effect directly on the trails in 2002, however, in combination with the species loss due to drought stress an effect we did not (Figure 2.7c). At the fine-scale, we do see a change in composition along with a decrease in living cover on (0-20cm) trampled wildlife trails in 2002 (Summary Table 2.10, Figure 2.18c), and *Festuca hallii* is associated with wildlife trails not trampled. Trends also suggest evenness is higher within 70cm of wildlife trails (Figure 2.11c). Here, scale of observation is important for detecting changes at the plant level.

Another possibility is that the increased light below the litter layer on trampled trails (Figure 2.23) creates conditions that allow enough species to establish in the presence of this trampling regime. In the absence of trampling, wildlife trails may ameliorate drought stress. Trails, as depressions in the existing grassland matrix and soil, may act as places of water collection during precipitation events. This pooling effects, in combination with the changes the gap created by the trail provides (Gross and Werner 1982, Goldberg 1987) and the influence of animals using these trails (seed vectors, litter incorporation, nutrient deposition) (Keen and Cashen 1932, Weir 1971, Day and Dettling 1990, Wang and Smith 2002, Andresen and Levey 2004) may help to ameliorate drought stress. We see evidence for amelioration on wildlife trails in 2002; richness is higher on trails than far from them. As well, total living biomass and standing biomass are higher on untrampled trails in 2002 (Figure 2.16c).

How trampling can depress richness near older wildlife trails is an interesting question, and while all possible mechanisms were not directly examined in this study, there are a few probable explanations. First, we know that more light reaches the vegetation above the litter layer within the first 2m of trampled trails (Figure 2.21b). It is, however, important to consider that this measurement was taken above the standing graminoid litter layer, but not at a constant height. Information from the vertical light profile is constant, and 2m from these trails, less light is available within the vertical profile (5-20cm) near trampled wildlife trails (Figure 2.25). This suggests that, somehow, trampling on trails indirectly decreases the light available to surrounding vegetation. One explanation is that vegetation at the edge of the trail is able to grow taller (Liddle 1991), thereby suppressing the light available in the vertical profile, which increases competition for light and depresses richness in the surrounding vegetation. Other mechanisms to consider are how trampling and human visitation may alter local insect populations, and their interactions with drought, as previously discussed. Preliminary evidence from the sub-study (Appendix D) indicates trampling on wildlife trails increases damage related to other factors for *Festuca hallii* and *Artemesia ludoviciana*.

Trampling on Old and New Trails

When we compare trampling effects on new human trails and older wildlife trails, plant responses are primarily a function of compositional differences. These compositional differences are related both to the relative age of the trail, as well as the history of use. The history of use includes factors such as the frequency with which trails are used, as well as which species (animals, humans) predominantly use them and when. For example, trampling in both the dormant and growing seasons has cumulative effects (Sheath and Boom 1997), and it is likely many of the wildlife trails in this system are used continuously throughout the year. As well, animals using wildlife trails can also influence the vegetation directly on and adjacent to trails, by acting as seed vectors (Wang and Smith 2002, Andresen and Levey 2004), depositing nutrients as well as working them into the soil (Keen and Cashen 1932, Wier 1971, Day and Dettling 1990), and through selective foraging (Jiang and Hudson 1993, Fortin et al. 2004). Directly comparing the effects of human trampling on both old and new trails allow us 1) to examine the differences and similarities in composition, and 2) to identify potential mechanisms involved in community change.

Trampling on new human trails depresses richness more than trampling on older wildlife trails. At the mid- scale in 2001, we see this depression within the first meter (Figure 2.6d) and composition is different within 40-80cm of both trails at the fine scale (Summary Table 2.10). The difference in composition in adjacent areas reflects the age of the trails, as new species have had more time to establish on older trails and establish in the surrounding vegetation. One growing season, however, is insufficient time to detect changes in composition on the trails themselves.

In 2002, drought stress likely masks differences in richness (Figure 2.7d), trampling appears to have similar effects directly on both trails, forb biomass is higher (Figure 2.15d), graminoid biomass (Figure 2.16d) is lower and more light reaches below the litter layer directly on trails (Figure 2.22b). These effects are likely due to both of the disturbances and whether the responses would have been similar in a second trampling season in absence of drought is not known. However, even with drought stress, we find evidence of differences in composition in areas adjacent to trails. At the mid-scale of observation, composition is different within 0-0.5m of both trails (Summary Table 2.9). However, at the fine-scale, this difference in composition does not occur directly on the trails (0-20cm), but in the area adjacent to the trail (20-120cm) (Summary Table 2.10). *Festuca hallii* is associated with wildlife trails, but not human trails. Patterns for greater living cover near wildlife trails and less dead cover are similarly supported at both scales (Figures 2.14d, 2.18d, 2.19d).

However, the time needed for the trail community to establish and disperse appears to be more important in than available light in this season, although the effects of drought stress must be considered. Even though more light is available within the vertical profile of plants 1 and 2m from human trails than wildlife trails (Figures 2.24, 2.25), richness does not change. While the ability of new species to establish and colonize may be hindered by both time and drought, topographical differences in positions of new human and old wildlife trails might also contribute to responses. However, neither the slope of cover transects, nor aspect (eastness or northness) was significantly different among all treatment plots, suggesting locations were topographically similar. While plots are topographically similar, consideration must be given to the selection criteria used by animals when creating and using a trail. While selective foraging may offer a possible mechanism to explain the association of *Festuca hallii* with wildlife trails, it is also possible trails were intentionally located in areas in which *F. hallii* is locally abundant.

Implications and Ideas for Future Research

Implications

The results of this study further highlight the importance of using multiple scales, both spatially and temporally, to examine relationships in plant communities. Spatially, broader scales can provide generalizations, while finer scales can provide details about potential biological mechanisms (Wiens 1989). In this study, scale-dependent processes may be responsible for the different patterns observed. At the largest scale, plot-level richness, evenness and forb biomass are suppressed by human trampling. At the mid-scale, we see the extent of influence within the local community near trails, and at the fine-scale we find evidence for compositional shifts in response to trampling and trail proximity. Temporal scales are also important in this study. While this study occurred over a relatively short time period (2 growing seasons), the severe drought in the second season provided a unique opportunity to consider the interacting effects of trampling and drought, both of which are common disturbances in grassland systems.

Wildlife trails are arguably as influential on local plant community dynamics as other types disturbances caused by non-grazing animal activity in grasslands. Approximately 2.2% of grassland within this study site is directly covered by wildlife trails. While this may seem like a relatively minor disturbance, these trails may influence 1.5m of the surrounding vegetation. If the effects are similar on both sides of trails (not addressed here), then at the upper extent 28% of the total area is influenced by trails. This study is one of two that directly examines how wildlife trails influence local plant dynamics and the only study conducted in grasslands (*Typha* marshes: Hewitt and Miyanishi 1997). In comparison to studies that examine other non-grazing animal activities, knowledge about the spatial and temporal abundance and distribution of wildlife trails, as well as effects on local dynamics is severely under-represented. Recently, Weisberg and Burgmann (2003) stressed the need for ecologists to move beyond single factor studies to embrace the complexity of ungulate-vegetation interactions at multiple scales. Conclusions from this study indicate the importance of examining the interactions of both the larger disturbance factors, such as drought, and the smaller disturbance factors of wildlife trails.

Another implication of this study relates to conservation issues. Human use of either old or new trails at relatively low levels (5 passes once a week) suppresses species richness, evenness and forb biomass as the largest (5 x 8m) scale of observation. The response of land managers to loss in species richness is dependent upon which species are lost with human trampling at this low frequency. If the component species are sensitive to trampling, their loss can influence system functioning, and alter local processes such as plant-plant interactions. For example, the association of a plant with an unpalatable neighbour may help to protect it from herbivory (Callaway et al. 2000), an interaction lost if the unpalatable species is trampling sensitive. If the rare species in the system are trampling sensitive, land managers risk losing local populations, important for maintaining genetic variation and preventing inbreeding and genetic drift (Neel and Ellstrand 2003). As well, the local extinction of any species, component or rare, would have continuing effects on subsequent trophic levels (Duffy 2003). The use of either old or new trails in this grassland system depresses richness, evenness and forb biomass, and prevention may necessitate human access restriction.

As well, *Festuca hallii*, the Alberta provincial grass, is associated with wildlife trails, and particularly those not trampled by humans. While wildlife may create trails in rough-fescue dense areas, the movement and selective foraging of larger wildlife within this system may also influence the distribution of this species. Both the presence of wildlife trails and the frequency with which they are used are important for local distribution of this species. This study did not directly monitor the use of the untrampled wildlife trails by other species or humans, but the detection of a relationship between *F. hallii* and wildlife trails suggests further study is warranted.

In a single growing season the creation and use of a new human trail decreases richness within 2m of the trails. Directly on the new trails, we are able to compare composition and production with older trails, gaining insight into how changes occur that distinguish a trail from the surrounding matrix. During the first season, the response on the trails appeared to be primarily a function of trampling damage, as richness was lower. In the second season, drought and trampling interactions made it difficult to detect compositional changes in response to the disturbance of the dominant graminoids. The extent of influence (2m) of these human trails raises challenging methodological questions for grassland ecologists and may provide insight into how researcher visitation effects occur. The extent of the influence of these researcher trails (2m) suggests it is difficult to repeatedly reach an area in an unbiased manner. However, while these methodological implications arise from a single ungrazed field site, with a large litter component, thus potentially representing the worst case scenario, they still warrant serious consideration.

Future research

The results of this research project clearly show that trails affect plant community dynamics in this grassland. As well, we know that human trampling has different effects on old and new trails and that influences on the local plant community are both temporally and spatially dependent. To further understand how widespread the affects of wildlife trails are, detailed studies of wildlife trail densities and the extent of their influence are required in a wider variety of plant communities. Beyond gaining an understanding of the generality of their influence, future studies must attempt to directly examine potential mechanisms for plant responses. While studies of this nature are difficult to design, it is important to examine multiple interactions. Monitoring both the frequency with which trails are actually used by wildlife, as well as foraging behaviour while on trails are important, as it is likely that those actions interact with the changes in structure and composition that accompany the presence of a trail. Furthermore, the presence and use of trails is also likely to influence local invertebrate populations; the links between trails, their use by humans and wildlife and their direct effects on insect herbivores are not known. Expanding the temporal scale when comparing trampling effects on new and old trails in combination with multiple spatial scales, especially those relevant to the individual plant, may reveal mechanisms of compositional changes. Longer term studies may also help to tease apart responses to drought and trampling disturbances, especially with attention to structural changes in vegetation and light within the vertical profile.

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Table 2.1. Plot-level (5 x 8m) community composition analyses in July 2001 and 2002. **A)** Blocked multiple response permutation procedures test statistics comparing species composition among treatment groups. Where W= wildlife trails not trampled by humans, WH= wildlife trails trampled by humans, H = trampled human trails, and C= control. The MRBP test statistic A, the chance corrected within-group agreement is presented with corresponding *p* values in brackets. For **B)** species richness and evenness, fixed factors are reported for the general linear model, with corresponding *p* values and with F statistic and degrees of freedom (numerator, denominator): P;$F_{\text{DF num, DF den}}$. All *p* values are in bold font when p<0.05.

A)	W=C	H=C	W=WH	H=WH
2001	$0.002_{(0.385)}$	$0.022_{(0.201)}$	$-0.029_{(0.754)}$	$-0.003_{(0.408)}$
2002	$-0.015_{(0.662)}$	$-0.034_{(0.708)}$	$-0.003_{(0.447)}$	$0.005_{(0.332)}$

B)	Year	Trail	Trampling	Trail* Trampling
Richness	2001	0.513	**0.002**	0.372
		$0.44_{1,27}$	$\mathbf{11.27}_{1,27}$	$0.82_{1,27}$
	2002	0.282	0.282	0.428
		$1.21_{1,24}$	$1.21_{1,24}$	$0.65_{1,24}$
Evenness	2001	0.681	**0.017**	0.620
		$0.17_{1,27}$	$\mathbf{6.50}_{1,27}$	$0.25_{1,27}$
	2002	0.929	0.349	0.419
		$0.01_{1,24}$	$0.91_{1,24}$	$0.68_{1,24}$

Table 2.2. Mid-scale (0.5 x8m) community composition analyses in July 2001 and 2002. **A)** Blocked multiple response permutation procedures test statistics comparing species composition among treatment groups. Where W= wildlife trails not trampled by humans, WH= wildlife trails trampled by humans, H = trampled human trails, and C= control. The MRBP test statistic A, the chance corrected within-group agreement is presented with corresponding *p* values in brackets. For **B)** species richness and evenness, fixed factors are reported for the general linear model, with corresponding *p* values and with F statistic and degrees of freedom (numerator, denominator): P;$F_{DF\ num,\ DF\ den}$. All *p* values are in bold font when p<0.05. Of all candidate models (where distance is L=linear, Q=quadratic and T=tertiary), only the model(s) with the lowest AIC_C values are presented.

A)	2001				2002			
Distance (m)	W=C	H=C	W=WH	H=WH	W=C	H=C	W=WH	H=WH
0.0-0.5	-0.009$_{(0.535)}$	-0.028$_{(0.789)}$	0.002$_{(0.372)}$	-0.011$_{(0.604)}$	0.061$_{(0.086)}$	-0.004$_{(0.499)}$	-0.037$_{(0.837)}$	**0.042$_{(0.002)}$**
0.5-1.0	-0.028$_{(0.791)}$	0.025$_{(0.179)}$	-0.026$_{(0.620)}$	-0.004$_{(0.459)}$	0.001$_{(0.401)}$	0.009$_{(0.315)}$	-0.001$_{(0.390)}$	0.052$_{(0.149)}$
2.5-3.0	0.009$_{(0.320)}$	0.001$_{(0.389)}$	0.019$_{(0.233)}$	-0.005$_{(0.456)}$	-0.029$_{(0.719)}$	-0.051$_{(0.837)}$	0.021$_{(0.210)}$	-0.035$_{(0.829)}$
4.5-5.0	0.031$_{(0.131)}$	0.028$_{(0.171)}$	-0.021$_{(0.650)}$	-0.026$_{(0.830)}$	-0.014$_{(0.667)}$	-0.021$_{(0.774)}$	0.028$_{(0.169)}$	0.002$_{(0.378)}$

B)	Year Model		Distance	Trail	Distance* Trail	Trampling	Distance* Trampling	Trail* Trampling	Distance* Trail* Trampling	Distance^2	Distance^3
Richness	2001	L	**0.001** **10.45** $_{1,356}$	**0.041** **4.34** $_{1,67.2}$	**0.001** **11.44** $_{1,356}$	**0.000** **16.08** $_{1,67.2}$	**0.009** **6.99** $_{1,356}$	0.122 2.45 $_{1,67.2}$	0.867 0.03 $_{1,356}$	- - -	- - -
		Q	**0.001** **11.94** $_{1,355}$	**0.041** **4.36** $_{1,66.4}$	**0.001** **11.63** $_{1,355}$	**0.000** **16.18** $_{1,66.4}$	**0.008** **7.11** $_{1,355}$	0.121 2.47 $_{1,66.4}$	0.866 0.03 $_{1,355}$	**0.008** **7.15** $_{1,355}$	- - -
		T	**0.005** **7.83** $_{1,354}$	**0.040** **4.37** $_{1,66.3}$	**0.001** **11.67** $_{1,354}$	**0.000** **16.20** $_{1,66.3}$	**0.008** **7.13** $_{1,354}$	0.121 2.47 $_{1,66.3}$	0.866 0.03 $_{1,354}$	0.063 3.49 $_{1,354}$	0.157 2.01 $_{1,354}$
	2002	Q	**<0.00** **16.02** $_{1,319}$	0.239 1.42 $_{1,58.5}$	**0.002** **9.77** $_{1,319}$	**0.004** **8.83** $_{1,58.5}$	0.091 2.87 $_{1,319}$	0.292 1.13 $_{1,58.5}$	**0.009** **6.94** $_{1,319}$	**0.000** **13.49** $_{1,319}$	- - -
Evenness	2001	L	**0.004** **8.61** $_{1,356}$	0.745 0.11 $_{1,112}$	0.955 0.00 $_{1,356}$	**0.009** **7.03** $_{1,112}$	0.215 1.55 $_{1,356}$	0.617 0.25 $_{1,112}$	0.248 1.34 $_{1,356}$	- - -	- - -
		Q	0.632 0.23 $_{1,355}$	0.745 0.11 $_{1,112}$	0.955 0.00 $_{1,355}$	**0.009** **7.03** $_{1,112}$	0.214 1.55 $_{1,355}$	0.617 0.25 $_{1,112}$	0.247 1.34 $_{1,355}$	0.186 1.75 $_{1,355}$	- - -
	2002	L	**0.004** **8.53** $_{1,320}$	0.350 0.89 $_{1,39.6}$	**0.031** **4.68** $_{1,320}$	0.684 0.17 $_{1,39.6}$	0.364 0.83 $_{1,320}$	0.775 0.08 $_{1,39.6}$	0.358 0.85 $_{1,320}$	- - -	- - -

Table 2.3. Fine-scale (0.1 x8m) community composition analyses in July 2001 and 2002. **A)** Blocked multiple response permutation procedures test statistics comparing species composition among treatment groups. Where W= wildlife trails not trampled by humans, WH= wildlife trails trampled by humans, H = trampled human trails, and C= control. The MRBP test statistic A, the chance corrected within-group agreement is presented with corresponding *p* values in brackets. For **B)** species richness and evenness, fixed factors are reported for the general linear model, with corresponding *p* values and with F statistic and degrees of freedom (numerator, denominator): P;$F_{\text{DF num, DF den}}$. All *p* values are in bold font when p<0.05. Of all candidate models (where distance is L=linear, Q=quadratic and T=tertiary), only the model(s) with the lowest AIC_C values are presented.

A)	2001				2002			
Distance (cm)	W=C	H=C	W=WH	H=WH	W=C	H=C	W=WH	H=WH
0-20	$0.041_{(0.158)}$	$-0.000_{(0.390)}$	$0.024_{(0.197)}$	$0.005_{(0.380)}$	**$0.283_{(0.004)}$**	$0.051_{(0.126)}$	**$0.151_{(0.028)}$**	$0.047_{(0.174)}$
20-40	$0.025_{(0.206)}$	$-0.023_{(0.768)}$	$0.046_{(0.111)}$	$-0.005_{(0.503)}$	$0.077_{(0.080)}$	$-0.015_{(0.646)}$	$-0.028_{(0.611)}$	$0.038_{(0.077)}$
40-80	$0.025_{(0.239)}$	$-0.000_{(0.383)}$	$0.052_{(0.122)}$	**$0.059_{(0.039)}$**	**$0.118_{(0.036)}$**	$0.046_{(0.166)}$	$0.027_{(0.227)}$	**$0.128_{(0.040)}$**
80-120	$0.048_{(0.155)}$	$0.026_{(0.201)}$	$0.004_{(0.357)}$	$0.042_{(0.132)}$	$0.093_{(0.058)}$	$0.039_{(0.188)}$	$-0.048_{(0.755)}$	**$0.456_{(0.002)}$**
120-160	$0.025_{(0.201)}$	$0.050_{(0.075)}$	$-0.035_{(0.824)}$	$0.009_{(0.297)}$	$-0.279_{(0.774)}$	$-0.016_{(0.536)}$	$0.015_{(0.299)}$	$0.020_{(0.209)}$
160-200	$-0.026_{(0.729)}$	$0.012_{(0.304)}$	$-0.022_{(0.577)}$	$0.039_{(0.127)}$	$-0.041_{(0.923)}$	$-0.045_{(0.950)}$	$-0.035_{(0.797)}$	$-0.016_{(0.506)}$

B)	Year	Model	Distance	Trail	Distance* Trail	Trampling	Distance* Trampling	Trail* Trampling	Distance* Trail* Trampling	$Distance^2$	$Distance^3$
Richness	2001	L	**0.000** **$14.76_{1,756}$**	**0.012** **$6.93_{1,44.6}$**	**0.000** **$14.68_{1,756}$**	0.356 $0.87_{1,44.6}$	0.397 $0.72_{1,756}$	0.759 $0.10_{1,44.6}$	**0.016** **$5.84_{1,756}$**	- - -	- - -
	2002	L	**0.042** **$4.15_{1,680}$**	0.095 $2.92_{1,42.2}$	**0.029** **$4.78_{1,680}$**	0.173 $1.92_{1,42.2}$	0.517 $0.42_{1,680}$	0.834 $0.04_{1,42.2}$	0.078 $3.12_{1,680}$	- - -	- - -
Evenness	2001	L	0.112 $2.53_{1,756}$	0.283 $1.18_{1,47.3}$	0.845 $0.04_{1,756}$	0.137 $2.28_{1,47.3}$	0.669 $0.18_{1,756}$	0.544 $0.37_{1,47.3}$	0.571 $0.32_{1,756}$	- - -	- - -
	2002	L	**0.046** **$4.00_{1,680}$**	**0.001** **$11.96_{1,38.5}$**	**<0.000** **$17.63_{1,680}$**	**0.043** **$4.36_{1,38.5}$**	0.054 $3.74_{1,680}$	0.186 $1.82_{1,38.5}$	**0.009** **$6.95_{1,680}$**	- - -	- - -

Table 2.4. Plot-level (5x 8m) total cover (alive and dead) and biomass (standing and root) in July 2001 and 2002. Fixed factors are reported for the general linear model, with corresponding p values and with F statistic and degrees of freedom (numerator, denominator): P;$F_{\text{DF num, DF den}}$. All p <0.05 in bold font

Measure		Year	Trail	Trampling	Trail* Trampling
Cover	Alive	2001	0.229	0.153	0.681
			1.51 $_{1,27}$	2.16 $_{1,27}$	0.16 $_{1,27}$
		2002	0.585	0.251	0.169
			0.31 $_{1,24}$	1.38 $_{1,24}$	2.01 $_{1,24}$
	Dead	2002	0.282	0.345	0.145
			1.21 $_{1,24}$	0.93 $_{1,24}$	2.27 $_{1,24}$
Standing Biomass	All Living	2001	0.790	0.102	0.484
			0.07 $_{1.27.3}$	2.87 $_{1,27}$	0.50 $_{1,27.3}$
		2002	0.692	0.402	0.819
			0.16 $_{1,27}$	0.72 $_{1,27}$	0.05 $_{1,27}$
	Living Woody	2001	0.653	0.154	0.531
			0.21 $_{1,27.3}$	2.15 $_{1,27}$	0.40 $_{1,27.3}$
		2002	0.094	0.382	0.293
			3.01 $_{1,27}$	0.79 $_{1,27}$	1.15 $_{1,27}$
	Living Forb	2001	0.054	**0.033**	0.709
			3.98 $_{1,36}$	**4.92 $_{1,36}$**	0.14 $_{1,36}$
		2002	0.365	**0.019**	0.172
			0.85 $_{1,27}$	**6.21 $_{1,27}$**	1.97 $_{1,27}$
	Living Graminoid	2001	0.086	0.139	0.986
			3.17 $_{1.27.7}$	2.33 $_{1.26.9}$	0.00 $_{1,27.7}$
		2002	0.184	0.094	0.387
			1.86 $_{1,27}$	3.02 $_{1,27}$	0.77 $_{1,27}$
	All Dead	2001	0.793	0.275	0.170
			0.07 $_{1.27.1}$	1.24 $_{1.27}$	1.99 $_{1,27.1}$
		2002	0.459	0.089	0.906
			0.57 $_{1,27}$	3.12 $_{1,27}$	0.01 $_{1,27}$
Root Biomass		2002	0.775	0.994	0.597
			0.08 $_{1,32}$	0.00 $_{1,32}$	0.28 $_{1,32}$

Table 2.5. Mid-scale (0.5x 8m) total cover (alive and dead) and biomass (standing and root) in July 2001 and 2002. Fixed factors are reported for the general linear model, with corresponding *p* values and with F statistic and degrees of freedom (numerator, denominator): $P;F_{\text{DF num, DF den}}$. All *p* values are in bold font when $p<0.05$, and only the model(s) with the lowest AICC value(s) are presented.

Measure	Year	Model	Distance	Trail	Distance* Trail	Trampling	Distance* Trampling	Trail* Trampling	Distance* Trail* Trampling	Distance^2	Distance^3
Cover Alive	2001	Q	**0.006**	0.119	0.324	0.073	0.281	0.421	0.434	0.094	- - -
			$7.76_{1,355}$	$2.49_{1,74.3}$	$0.98_{1,355}$	$3.31_{1,74.4}$	$1.17_{1,355}$	$0.66_{1,74.3}$	$0.61_{1,355}$	$2.82_{1,355}$	
		T	0.413	0.119	0.324	0.073	0.281	0.421	0.434	0.881	0.652
			$0.67_{1,354}$	$2.49_{1,74.4}$	$0.97_{1,354}$	$3.31_{1,74.4}$	$1.16_{1,354}$	$0.66_{1,74.4}$	$0.61_{1,354}$	$0.02_{1,354}$	$0.20_{1,354}$
	2002	Q	**0.002**	**0.021**	**0.000**	0.441	0.727	0.564	0.162	**0.001**	- - -
			$9.99_{1,319}$	**$5.74_{1,40.1}$**	**$14.64_{1,319}$**	$0.61_{1,40.1}$	$0.12_{1,319}$	$0.34_{1,40.1}$	$1.97_{1,319}$	**$11.54_{1,319}$**	
		T	0.312	**0.021**	**0.000**	0.441	0.727	0.564	0.162	0.906	0.626
			$0.91_{1,318}$	**$5.73_{1,40.2}$**	**$14.61_{1,318}$**	$0.61_{1,40.2}$	$0.12_{1,318}$	$0.34_{1,40.2}$	$1.96_{1,318}$	$0.01_{1,318}$	$0.24_{1,318}$
Cover Dead	2002	Q	**0.004**	**0.012**	**0.000**	0.437	0.856	0.340	0.377	**0.006**	- - -
			$8.26_{1,319}$	**$7.00_{1,36.5}$**	**$14.34_{1,319}$**	$0.62_{1,36.5}$	$0.03_{1,319}$	$0.94_{1,36.5}$	$0.78_{1,319}$	**$7.69_{1,319}$**	
		T	0.337	**0.012**	**0.000**	0.437	0.856	0.340	0.377	0.875	0.737
			$0.93_{1,318}$	**$7.00_{1,36.6}$**	**$14.30_{1,318}$**	$0.62_{1,36.6}$	$0.03_{1,318}$	$0.93_{1,36.6}$	$0.78_{1,318}$	$0.02_{1,318}$	$0.11_{1,318}$
Total Living Biomass	2001	L	0.448	0.983	0.649	0.163	0.567	0.218	0.442	- - -	- - -
			$0.58_{1,156}$	$0.00_{1,55.7}$	$0.21_{1,156}$	$2.00_{1,55.7}$	$0.33_{1,156}$	$1.55_{1,55.7}$	$0.59_{1,156}$		
		Q	0.141	0.983	0.649	0.163	0.566	0.218	0.441	0.190	- - -
			$2.19_{1,155}$	$0.00_{1,55.6}$	$0.21_{1,155}$	$2.00_{1,55.6}$	$0.33_{1,155}$	$1.55_{1,55.6}$	$0.60_{1,155}$	$1.73_{1,155}$	
		C	0.066	0.983	0.648	0.162	0.565	0.217	0.440	0.126	0.183
			$3.44_{1,154}$	$0.00_{1,55.4}$	$0.21_{1,154}$	$2.01_{1,55.4}$	$0.33_{1,154}$	$1.56_{1,55.4}$	$0.60_{1,154}$	$2.37_{1,154}$	$1.79_{1,154}$
	2002	L	0.295	0.600	0.848	**0.015**	**0.004**	0.403	0.147	- - -	- - -
			$1.11_{1,156}$	$0.28_{1,65.8}$	$0.04_{1,156}$	**$6.20_{1,65.8}$**	**$8.70_{1,156}$**	$0.71_{1,65.8}$	$2.13_{1,156}$		
Woody Living Biomass	2001	L	0.865	0.482	0.371	0.982	0.632	0.221	0.593	- - -	- - -
			$0.03_{1,156}$	$0.50_{1,50.8}$	$0.80_{1,156}$	$0.00_{1,50.8}$	$0.23_{1,156}$	$1.53_{1,50.8}$	$0.29_{1,156}$		
		Q	0.388	0.482	0.371	0.982	0.633	0.221	0.593	0.342	- - -
			$0.75_{1,155}$	$0.50_{1,50.8}$	$0.80_{1,155}$	$0.00_{1,50.8}$	$0.23_{,155}$	$1.53_{1,50.8}$	$0.29_{1,155}$	$0.91_{1,155}$	
		T	0.564	0.482	0.371	0.982	0.632	0.221	0.593	0.371	0.286
			$0.33_{1,154}$	$0.50_{1,50.7}$	$0.81_{1,154}$	$0.00_{1,50.7}$	$0.23_{1,154}$	$1.54_{1,50.7}$	$0.29_{1,154}$	$0.80_{1,154}$	$1.15_{1,154}$
	2002	L	0.209	0.140	0.915	0.987	0.401	0.523	0.604	- - -	- - -
			$1.59_{1,156}$	$2.23_{1,69.3}$	$0.01_{1,156}$	$0.00_{1,69.3}$	$0.71_{1,156}$	$0.41_{1,69.3}$	$0.27_{1,156}$		

Table 2.5 Continued.

Measure	Year Model		Distance	Trail	Distance* Trail	Trampling	Distance* Trampling	Trail* Trampling	Distance* Trail* Trampling	Distance^2	Distance^3
Forb Living Biomass	2001	L	0.426 0.64 $_{1,156}$	0.070 3.37 $_{1,86.8}$	0.650 0.21 $_{1,156}$	**0.018** **5.86** $_{\mathbf{1,86.8}}$	0.683 0.17 $_{1,156}$	0.813 0.06 $_{1,86.8}$	0.516 0.42 $_{1,156}$	- - -	- - -
	2002	L	0.694 0.16 $_{1,156}$	0.176 1.87 $_{1,82.1}$	0.325 0.97 $_{1,156}$	0.322 0.99 $_{1,82.1}$	0.205 1.62 $_{1,156}$	0.237 1.42 $_{1,82.1}$	**0.000** **15.06** $_{\mathbf{1,156}}$	- - -	- - -
		Q	**0.027** **4.98** $_{\mathbf{1,155}}$	0.174 1.88 $_{1,80.9}$	0.319 1.00 $_{1,155}$	0.320 1.00 $_{1,80.9}$	0.200 1.66 $_{1,155}$	0.235 1.43 $_{1,80.9}$	**0.000** **15.44** $_{\mathbf{1,155}}$	**0.029** **4.88** $_{\mathbf{1,155}}$	- - -
		T	**0.010** **6.84** $_{\mathbf{1,154}}$	0.173 1.89 $_{1,80.2}$	0.316 1.01 $_{1,154}$	0.319 1.01 $_{1,80.2}$	0.196 1.69 $_{1,154}$	0.234 1.44 $_{1,80.2}$	**0.000** **15.67** $_{\mathbf{1,154}}$	**0.034** **4.64** $_{\mathbf{1,154}}$	0.072 3.27 $_{1,154}$
Graminoid Living Biomass	2001	T	**0.007** **7.36** $_{\mathbf{1,154}}$	0.772 0.08 $_{1,87.8}$	0.133 2.28 $_{1,154}$	0.652 0.20 $_{1,87.8}$	0.613 0.26 $_{1,154}$	0.787 0.07 $_{1,87.8}$	0.861 0.03 $_{1,154}$	**0.020** **5.50** $_{\mathbf{1,154}}$	**0.031** **4.76** $_{\mathbf{1,154}}$
	2002	L	0.133 2.28 $_{1,156}$	0.671 0.18 $_{1,69.3}$	0.131 2.31 $_{1,156}$	**<0.000** **17.99** $_{\mathbf{1,69.3}}$	**<0.000** **20.49** $_{\mathbf{1,156}}$	**0.037** **4.55** $_{\mathbf{1,69.3}}$	**0.014** **6.24** $_{\mathbf{1,156}}$	- - -	- - -
Dead Standing Biomass	2001	T	**0.002** **9.62** $_{\mathbf{1,154}}$	0.109 2.63 $_{1,81.1}$	0.111 2.57 $_{1,154}$	0.867 0.03 $_{1,81.1}$	0.605 0.27 $_{1,154}$	0.096 2.84 $_{1,81.1}$	0.712 0.14 $_{1,154}$	**0.018** **5.69** $_{\mathbf{1,154}}$	**0.039** **4.32** $_{\mathbf{1,154}}$
	2002	T	**<0.000** **29.57** $_{\mathbf{1,154}}$	0.134 2.27 $_{1,125}$	0.186 1.76 $_{1,154}$	**0.028** **4.92** $_{\mathbf{1,125}}$	0.155 2.04 $_{1,154}$	0.697 0.15 $_{1,125}$	0.686 0.16 $_{1,154}$	**0.000** **13.85** $_{\mathbf{1,154}}$	**0.003** **9.26** $_{\mathbf{1,154}}$
Root Biomass	2002	L	0.641 0.22 $_{1,176}$	0.201 1.65 $_{1,145}$	0.108 2.61 $_{1,176}$	0.740 0.11 $_{1,145}$	0.700 0.15 $_{1,176}$	0.346 0.89 $_{1,145}$	0.542 0.37 $_{1,176}$	- - -	- - -

Table 2.6. Fine-scale (0.1 x 8m) cover (alive and dead) analyses in July 2001 and 2002. Fixed factors are reported for the general linear model, with corresponding *p* values and with F statistic and degrees of freedom (numerator, denominator): P;$F_{\text{DF num, DF den}}$. All *p* values are in bold font when p<0.05. Of all candidate models (where distance is L=linear, Q=quadratic and T=tertiary), only the model(s) with the lowest AIC_C values are presented.

Cover	Year Model	Distance	Trail	Distance* Trail	Trampling	Distance* Trampling	Trail* Trampling	Distance* Trail* Trampling	Distance^2	Distance^3
Alive	2001 L	**0.004** **8.45** $_{1,756}$	0.842 0.04 $_{1,143}$	0.779 0.08 $_{1,756}$	0.652 0.20 $_{1,134}$	**0.029** **4.78** $_{1,756}$	0.348 0.89 $_{1,134}$	0.447 0.58 $_{1,756}$	- - -	- - -
	2002 L	**0.002** **9.90** $_{1,680}$	**<0.00** **27.44** $_{1,66.6}$	**<0.000** **17.06** $_{1,680}$	**0.002** **10.24** $_{1,66.6}$	**0.013** **6.18** $_{1,680}$	0.296 1.11 $_{1,66.6}$	0.864 0.03 $_{1,680}$	- - -	- - -
Dead	2002 L	**0.002** **9.97** $_{1,680}$	**<0.000** **37.80** $_{1,71.4}$	**<0.000** **21.92** $_{1,680}$	**0.001** **11.11** $_{1,71.4}$	**0.001** **10.63** $_{1,680}$	0.276 1.20 $_{1,71.4}$	0.454 0.56 $_{1,680}$	- - -	- - -

Table 2.7. Photosynthetically active radiation, reported as percent transmission below and above the litter layer (July 2002) at three scales (plot, mid, fine) of observation. Fixed factors are reported for the general linear model, with corresponding *p* values and with F statistic and degrees of freedom (numerator, denominator): $P;F_{DF\ num,\ DF\ den}$. All *p* values are in bold font when $p<0.05$. Of all candidate models (where distance is L=linear, Q=quadratic and T=tertiary), only the model(s) with the lowest AIC_C values are presented.

PAR	Scale	Model	Distance	Trail	Distance *Trail	Trampling	Distance* Trampling	Trail* Trampling	Distance* Trail* Trampling	Distance^2	Distance^3
Below Litter	Plot		---	**0.044** **4.50 $_{1,24}$**	---	**<0.000** **24.31 $_{1,24}$**	---	0.477 0.52 $_{1,24}$	---	---	---
	Mid	T	**<0.000** **59.71 $_{1,315}$**	0.223 1.50 $_{1,142}$	0.779 0.08 $_{1,315}$	**0.013** **6.28 $_{1,142}$**	0.134 2.26 $_{1,315}$	0.831 0.05 $_{1,142}$	0.619 0.25 $_{1,315}$	**<0.000** **46.44 $_{1,315}$**	**<0.000** **37.60 $_{1,315}$**
	Fine	L	**0.001** **10.61 $_{1,666}$**	**0.004** **8.83 $_{1,76.5}$**	**0.003** **8.65 $_{1,666}$**	0.349 0.89 $_{1,76.5}$	0.500 0.46 $_{1,666}$	0.709 0.14 $_{1,76.5}$	0.588 0.29 $_{1,666}$	---	---
		T	**<0.000** **50.50 $_{1,663}$**	**0.003** **9.16 $_{1,71.8}$**	**0.003** **9.12 $_{1,664}$**	0.364 0.83 $_{1,71.8}$	0.510 0.44 $_{1,664}$	0.668 0.19 $_{1,71.8}$	0.604 0.27 $_{1,664}$	**<0.000** **40.79 $_{1,663}$**	**<0.000** **34.59 $_{1,663}$**
Above Litter	Plot		---	0.714 0.14 $_{1,16}$	---	**0.021** **8.23 $_{1,8}$**	---	0.161 2.16 $_{1,16}$	---	---	---
	Mid	C	**<0.000** **47.13 $_{1,318}$**	0.366 0.82 $_{1,137}$	0.425 0.64 $_{1,318}$	**<0.000** **19.65 $_{1,137}$**	**<0.000** **15.55 $_{1,318}$**	0.261 1.28 $_{1,137}$	0.815 0.05 $_{1,318}$	**<0.000** **35.49 $_{1,318}$**	**<0.000** **27.83 $_{1,318}$**
	Fine	L	**0.002** **9.48 $_{1,680}$**	0.421 0.65 $_{1,106}$	0.724 0.12 $_{1,680}$	**0.041** **4.26 $_{1,106}$**	**0.011** **6.48 $_{1,680}$**	0.230 1.46 $_{1,106}$	0.247 1.34 $_{1,680}$	---	---
		T	**<0.000** **59.15 $_{1,678}$**	0.412 0.68 $_{1,98.8}$	0.714 0.13 $_{1,678}$	**0.038** **4.44 $_{1,98.8}$**	**0.008** **7.00 $_{1,678}$**	0.221 1.52 $_{1,98.8}$	0.229 1.45 $_{1,678}$	**<0.000** **55.51 $_{1,678}$**	**<0.000** **52.18 $_{1,678}$**

Table 2.8. Summary table of results at the plot-level (5 x 8m) for community composition (MRBP), community diversity, production and light resources (general linear models) (Tables 2.1, 2.4 and 2.7 for test statistics). Where W =wildlife trails, H= human trails, WH= human trampling on wildlife trails and C= control, and a dashed line (---) indicates no effect. Significant interactions from the general linear models are abbreviated as; HT (human trampling), TR (trail type). When applicable, (-) indicates a decrease, and (+) an increase.

Response Variable	Year	Wildlife Trails vs. Control	Human Trails vs. Control	Trampling on Wildlife Trails	Trampling on Wildlife & Human
Composition	01	---	---	---	---
	02	---	---	---	---
Richness	01	---	HT-	HT-	---
	02	---	---	---	---
Evenness	01	---	HT-	HT-	---
	02	---	---	---	---
Alive Cover	01	---	---	---	---
	02	---	---	---	---
Dead Cover	02	---	---	---	---
Total Alive BM	01	---	---	---	---
	02	---	---	---	---
Woody BM	01	---	---	---	---
	02	---	---	---	---
Forb BM	01	---	HT-	HT-	---
	02	---	HT-	HT-	---
Graminoid BM	01	---	---	---	---
	02	---	---	---	---
Dead BM	01	---	---	---	---
	02	---	---	---	---
Root Biomass	02	---	---	---	---
PAR Below	02	TR +	HT +	HT+	TR+
PAR Above	02	---	HT+	HT +	---

Table 2.9. Summary table of results at the mid-scale (0.5x 8m) level for community composition (MRBP), community diversity, production and light resources (general linear models) (Tables 2.2, 2.5 and 2.7 for test statistics). Where W =wildlife trails, H= human trails, WH= human trampling on wildlife trails and C= control, and a dashed line (---) indicates no effect. Significant interactions from the general linear models are abbreviated as; HT (human trampling), TR (trail type), D (distance), and * indicates a general distance effect. When applicable, - = decrease, and + = increase.

Response Variable	Year	Wildlife Trails vs. Control	Human Trails vs. Control	Trampling on Wildlife Trails	Trampling on Wildlife & Human
Composition	01	---	---	---	---
	02	---	---	---	0.0-0.5
Richness	01	D x TR $W<C_{1-1.5m}$	D x HT $H<C_{0-2m}$	D x HT $W>WH_{0-1m}$	D x TR $H<WH_{0-1m}$
	02	D x TR x HT	D x TR x HT	D x TR x HT $W>WH_{0-2m}$	D x TR x HT
Evenness	01*	---	HT-	HT-	---
	02	D x TR	---	---	D x TR
Alive Cover	01*	---	---	---	---
	02	D x TR $W>C_{0-1m}$	---	---	D x TR $H<WH_{0-1m}$
Dead Cover	02	D x TR $W<C_{0-1m}$	---	---	D x TR $H>WH_{0-1m}$
Total Alive BM	01	---	---	---	---
	02	---	D x HT	D x HT $W>WH_{0m}$	---
Woody BM	01	---	---	---	---
	02	---	---	---	---
Forb BM	01	---	HT-	HT-	---
	02	D x TR x HT	D x TR x HT $H<C_{1-4m}$	D x TR x HT	D x TR x HT H<WH
Graminoid BM	01*	---	---	---	---
	02	D x TR x HT	D x TR x HT $H<C_{0m}$	D x TR x HT $W>WH_{0-1m}$	D x TR x HT
Dead BM	01*	---	---	---	---
	02*	---	HT-	HT-	---
Root Biomass	02	---	---	---	---
PAR Below	02*	---	HT+	HT+	---
PAR Above	02	---	D x HT $H>C_{0-0.5m}$ $H<C_{0.5-1m}$	D x HT $W<WH_{0-2.5m}$	---

Table 2.10. Summary table of results at the fine-scale for community composition (MRBP), community diversity, production and light resources (general linear models) (Tables 2.1, 2.4 and 2.7 for test statistics). Where W =wildlife trails, H= human trails, WH= human trampling on wildlife trails and C= control, and a dashed line (---) indicates no effect. Significant interactions from the general linear models are abbreviated as; HT (human trampling), TR (trail type). When applicable, - = decrease, and += increase.

Response Variable	Year	Wildlife Trails vs. Control	Human Trails vs. Control	Trampling on Wildlife Trails	Trampling on Wildlife & Human
Composition	01	---	---	---	40-80cm
	02	0-120cm	---	0-20cm	20-120cm
Richness	01	D x TR x HT $W<C_{\text{after 1m}}$	D x TR x HT $H<C_{\text{after 1m}}$	D x TR x HT	D x TR x HT $WH>H_{\text{0-10cm}}$
	02	D x TR $W>C_{\text{10-20cm}}$	---	---	D x TR
Evenness	01	---	---	---	---
	02	D x TR x HT $W<C_{\text{0-70cm}}$	D x TR x HT	D x TR x HT	D x TR x HT $WH<H_{\text{10-20 cm}}$
Alive Cover	01	---	D x HT	D x HT	---
	02	D x TR $W>C_{\text{10-40cm}}$	D x HT	D x HT $W>WH_{\text{10-20cm}}$	D x TR $WH>H_{\text{50-140 cm}}$
Dead Cover	02	D x TR $W<C_{\text{0-20cm}}$	D x HT	D x HT $W<WH_{\text{0-20cm}}$	D x TR $WH<H_{\text{70-140 cm}}$
PAR Below	02	D x TR $W>C_{\text{0-10cm}}$	---	---	D x TR
PAR Above	02	---	D x HT $H>C_{\text{0-10cm}}$	D x HT $W<WH_{\text{0-10cm}}$	---

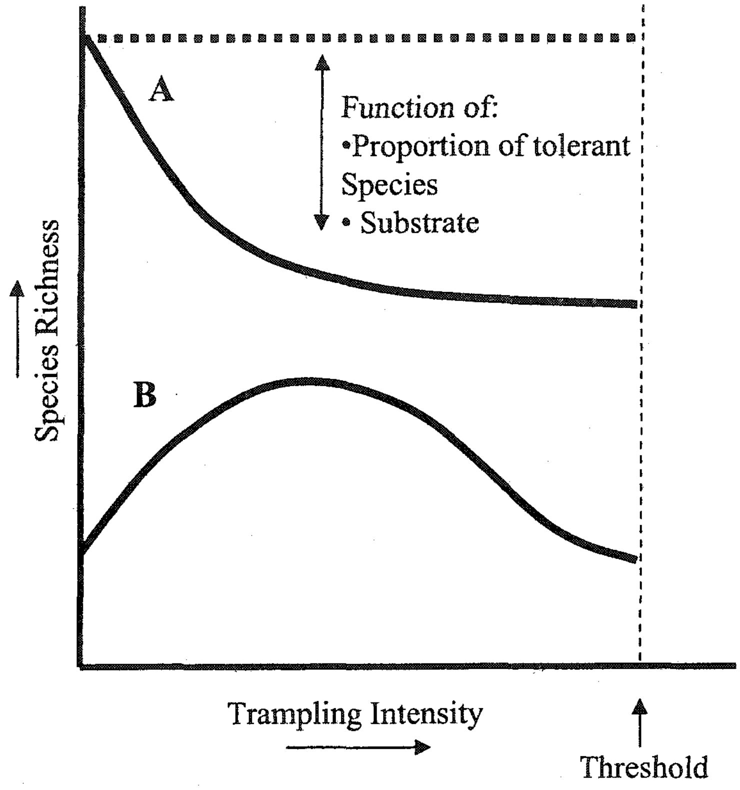


Figure 2.1. The relationship of species richness and trampling intensity, where both scenarios **A** and **B** reach a threshold to where either bare ground is exposed or only a small number of specialized species can survive. In **A**, species richness decreases curvilinearly as trampling intensity increases; and the degree of curvilinearity depends on factors such as proportion of trampling tolerant species and substrate.
In **B**, species richness initially increases at low intensities of trampling, then decreases at further intensities.

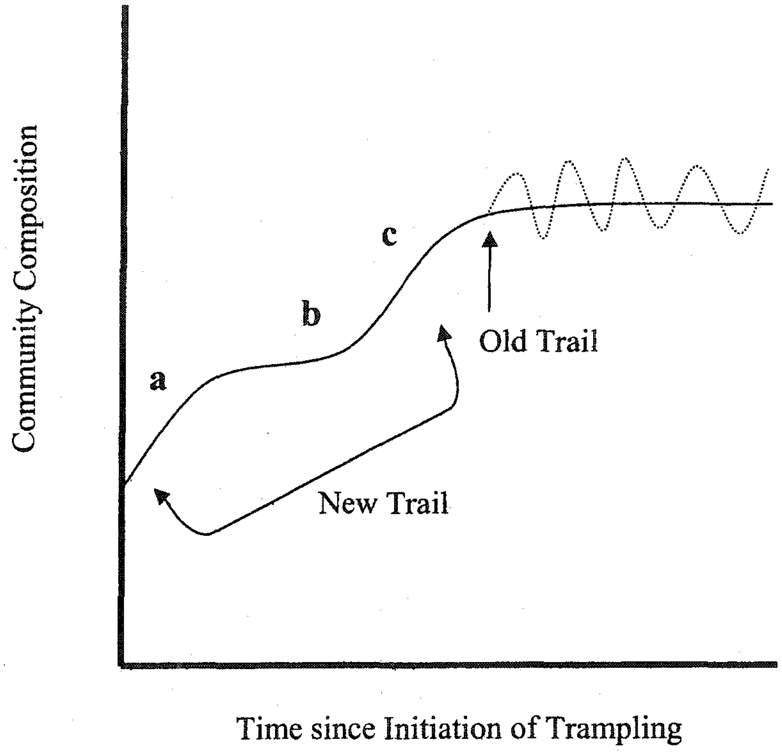


Figure 2.2. Changes in composition with time since initiation of trampling disturbance. At **a**, species composition changes as dominant graminoids and litter disturbed, new species colonize gap, competitive relationships change. At **b**, species intolerant of continuous trampling disappear or decrease in abundance and competitive relationships change. At **c**, performance trampling tolerant species improves. See text for references and details. The change in composition is not a scale of increase or decrease, it is simply a scale of change.

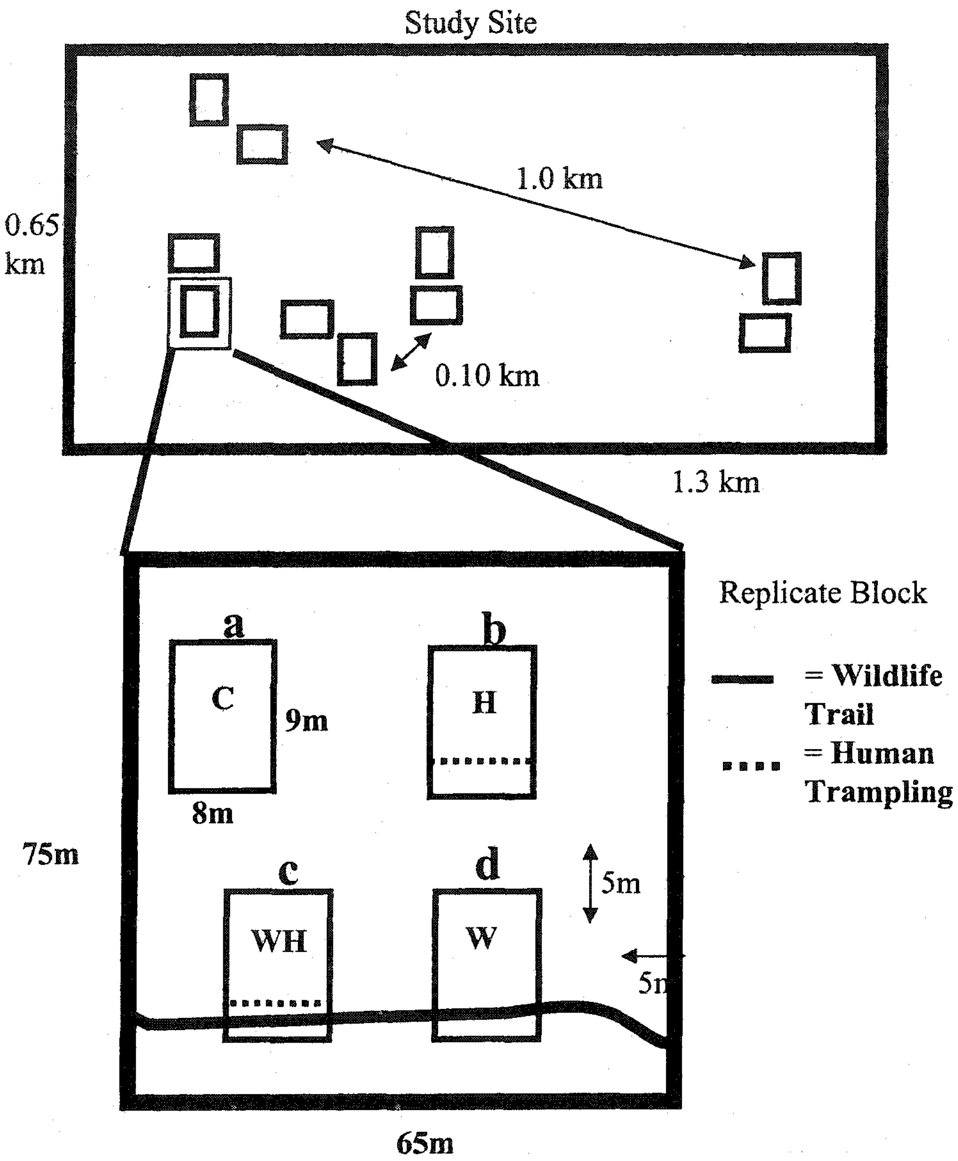


Figure 2.3. Schematic of study site and experimental design. The study site has 10 replicate blocks, separated by 0.1-1km.
Four treatment plots are within one replicate block, where **WH**= wildlife trails with human trampling, **W**= wildlife trail without human trampling, **H**: new trail created by human trampling and **C**= control area without wildlife trails or human trampling. WH and W were randomly assigned to c and d, and H and C were randomly assigned to a and b. Human trampling occurred directly on the wildlife trail (WH), and is offset here solely to illustrate the human trampling component.

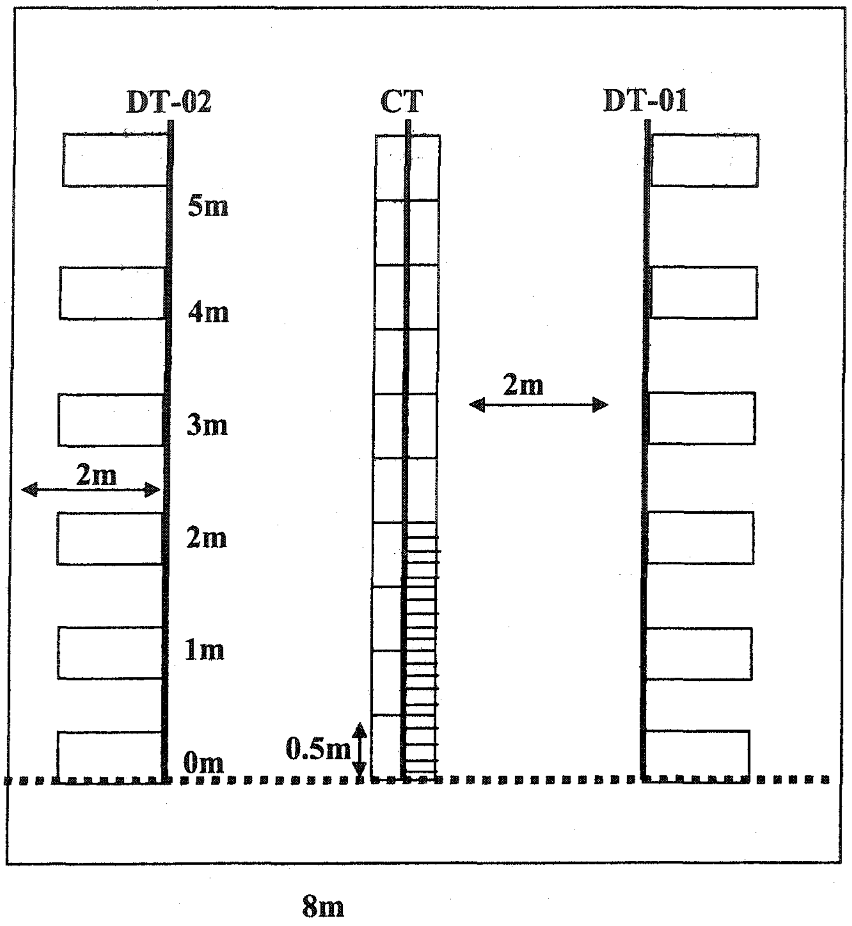


Figure 2.4. Experimental Design: One treatment plot with cover transect (CT) and transects for destructive sampling (DT). Position of DT (01 or 02) And side of sampling randomly determined in 2001. Transects start at trail center, represented by the broken line. Cover estimates are taken at two scales; **5m** in 20x 50 cm quadrats and **2m** in 10x 10cm quadrats. Along the destructive transect, standing biomass is sampled in 20 x100cm quadrats.

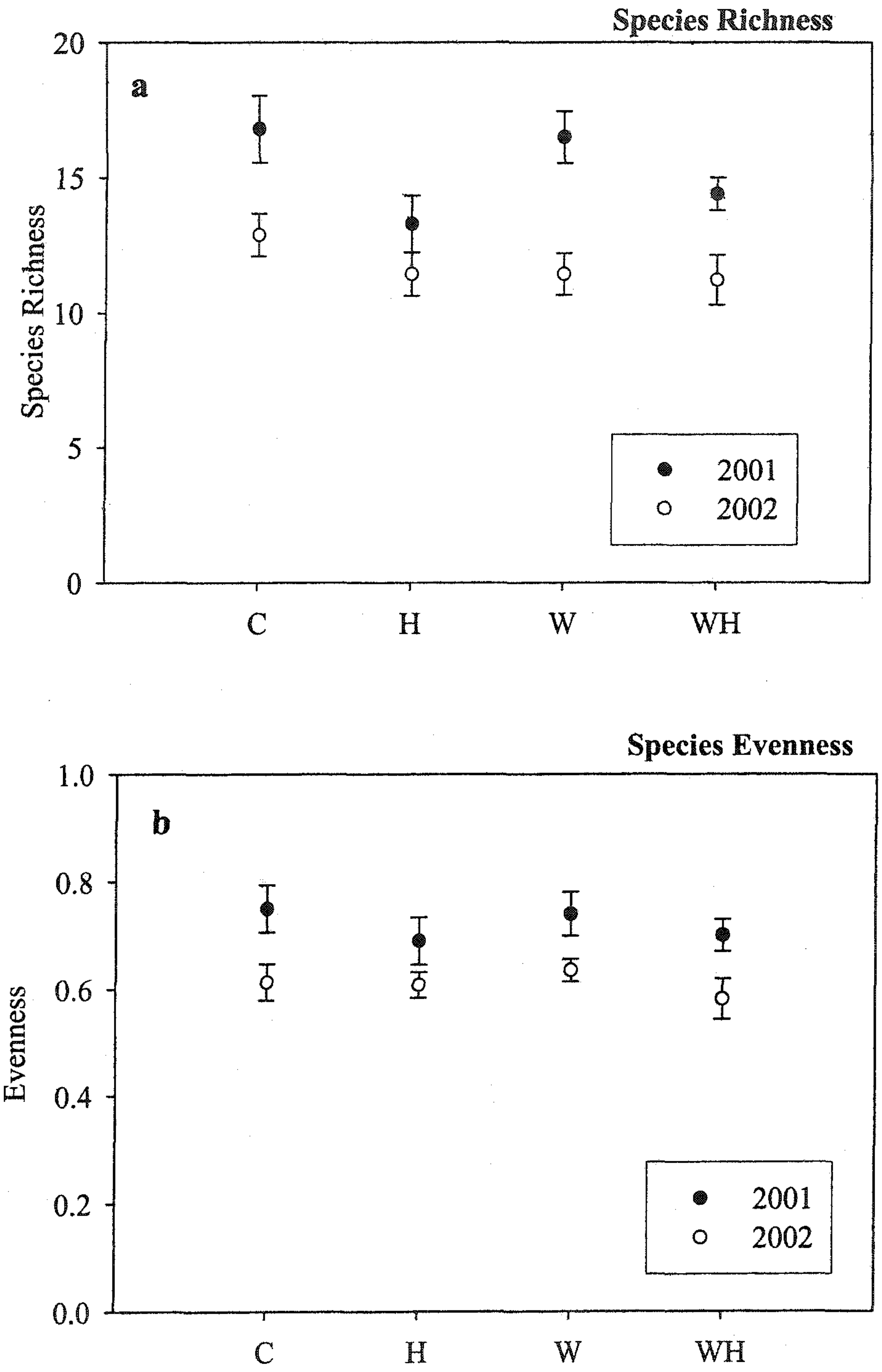


Figure 2.5. Plot-level means for species richness(a) and evenness(b) in July 2001 and 2002. Symbols represent means ± 1 SE, and C= control areas, H= human trails, W= wildlife trails not trampled, and WH= wildlife trails with weekly human trampling.

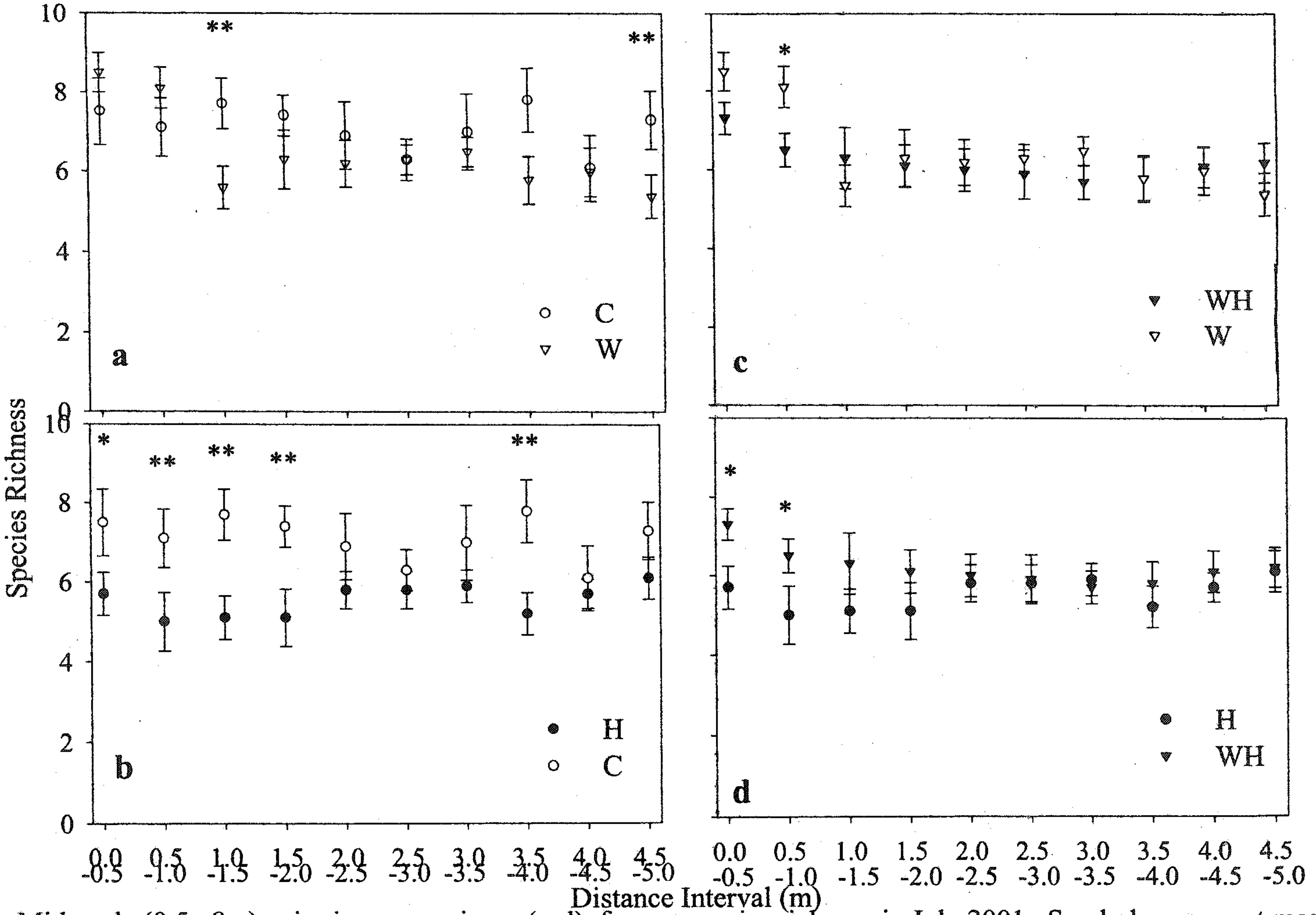


Figure 2.6. Mid-scale (0.5x 8m) pairwise comparisons (a-d)of mean species richness in July 2001. Symbols represent means ±1 SE, and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling. When mean richness is different at a given distance interval, *indicates $p<0.05$, and ** is Bonferroni corrected (p of $0.05/4 = 0.0125$, $p<0.0125$).

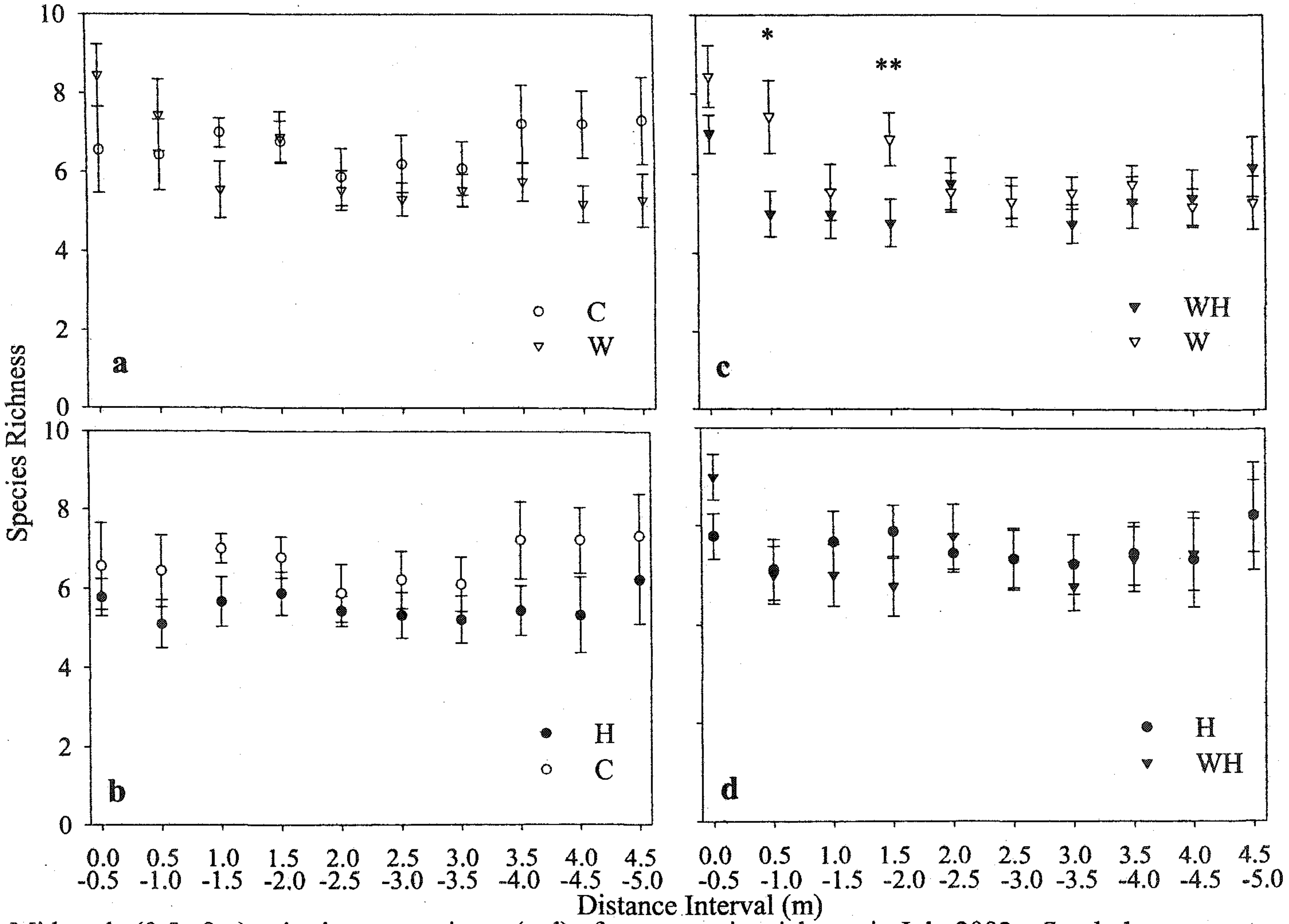


Figure 2.7. Mid-scale (0.5 x8m) pairwise comparisons (a-d) of mean species richness in July 2002 . Symbols represent means ± 1SE and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without weekly human trampling, and **WH**= wildlife trails with weekly human trampling. When mean richness is different at a given distance interval, * indicates $p<0.05$, and ** is Bonferroni corrected (p of $0.05/4 = 0.0125$, $p<0.0125$).

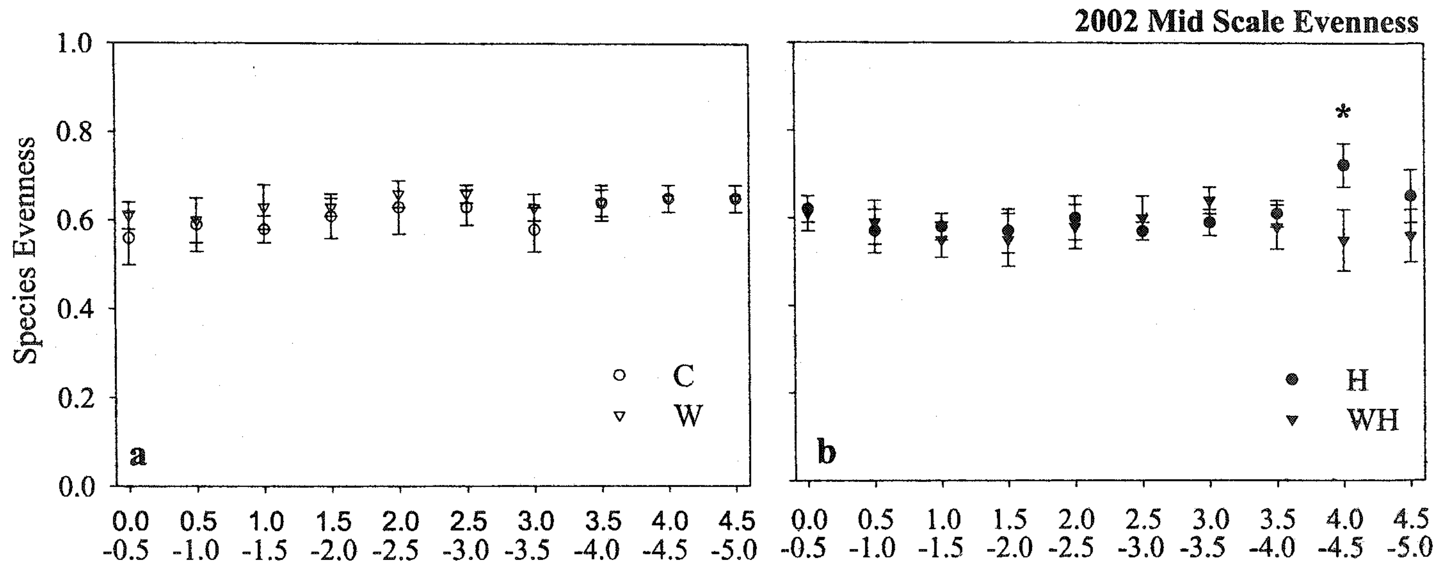


Figure 2.8. Mid-scale pairwise comparisons (a-b) of mean species evenness in July 2002. Symbols represent means +1 SE, and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling. When mean evenness is different at a given distance interval, * indicates $p<0.05$, and ** is Bonferroni corrected (p of 0.05 /4 = 0.0125, $p <0.0125$).

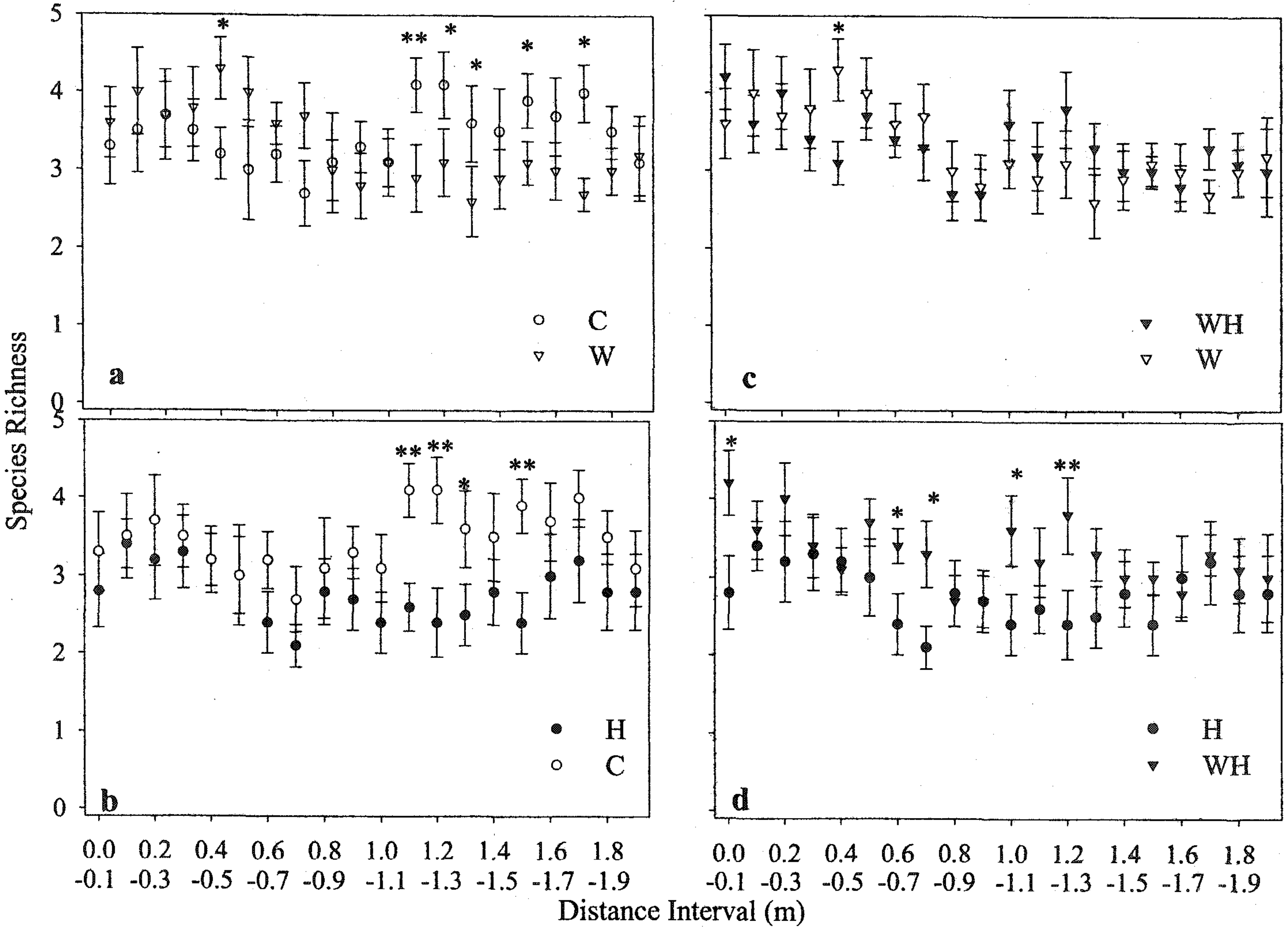


Figure 2.9. Fine-scale (0.1 x8m) pairwise comparisons (a-d) of mean species richness in July 2001. Symbols are means ±1SE and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling. When mean richness is different at a given distance interval, * indicates $p<0.05$, and ** is Bonferroni corrected (p of 0.05 /4 = 0.0125, $p < 0.0125$).

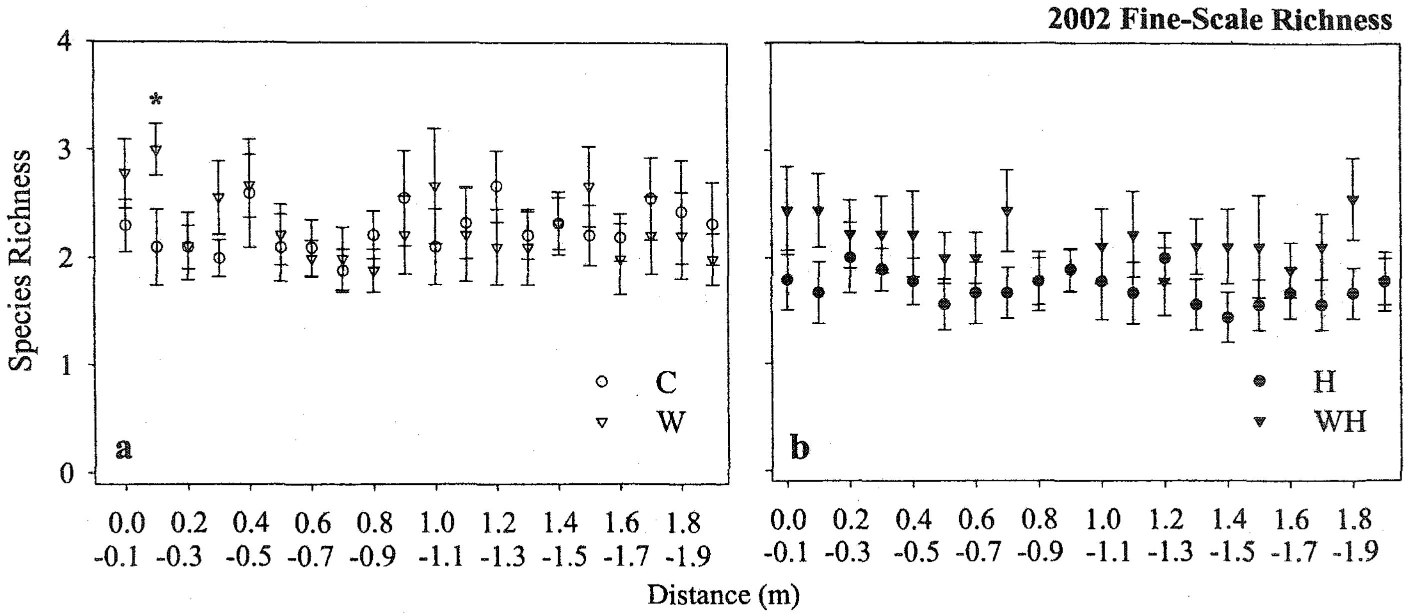


Figure 2.10. Fine-scale (0.1x 8m) pairwise comparisons (a-b) of mean species richness in July 2002. Symbols are means +1SE and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling. When mean richness is different at a given distance interval, * indicates $p<0.05$, and ** is Bonferroni corrected (p of $0.05/4 = 0.0125$, $p<0.0125$).

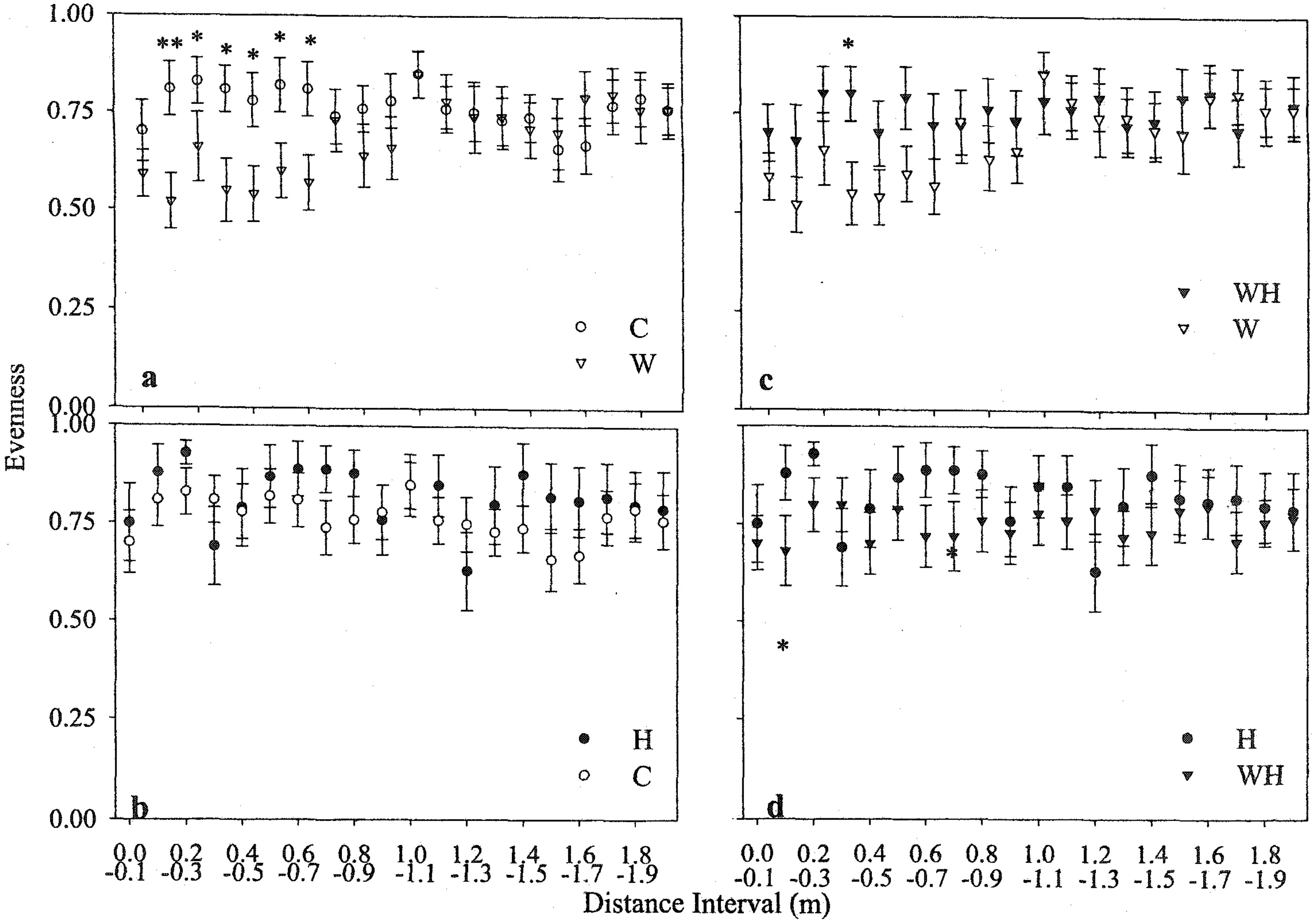


Figure 2.11. Fine-scale (0.1x 8m) pairwise comparisons (a-d) of mean evenness in July 2002. Symbols are means +1 SE, and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling. When mean evenness is different at a given distance interval, * indicates p<0.05, and ** is Bonferroni corrected (p of 0.05 /4 = 0.0125, p <0.0125).

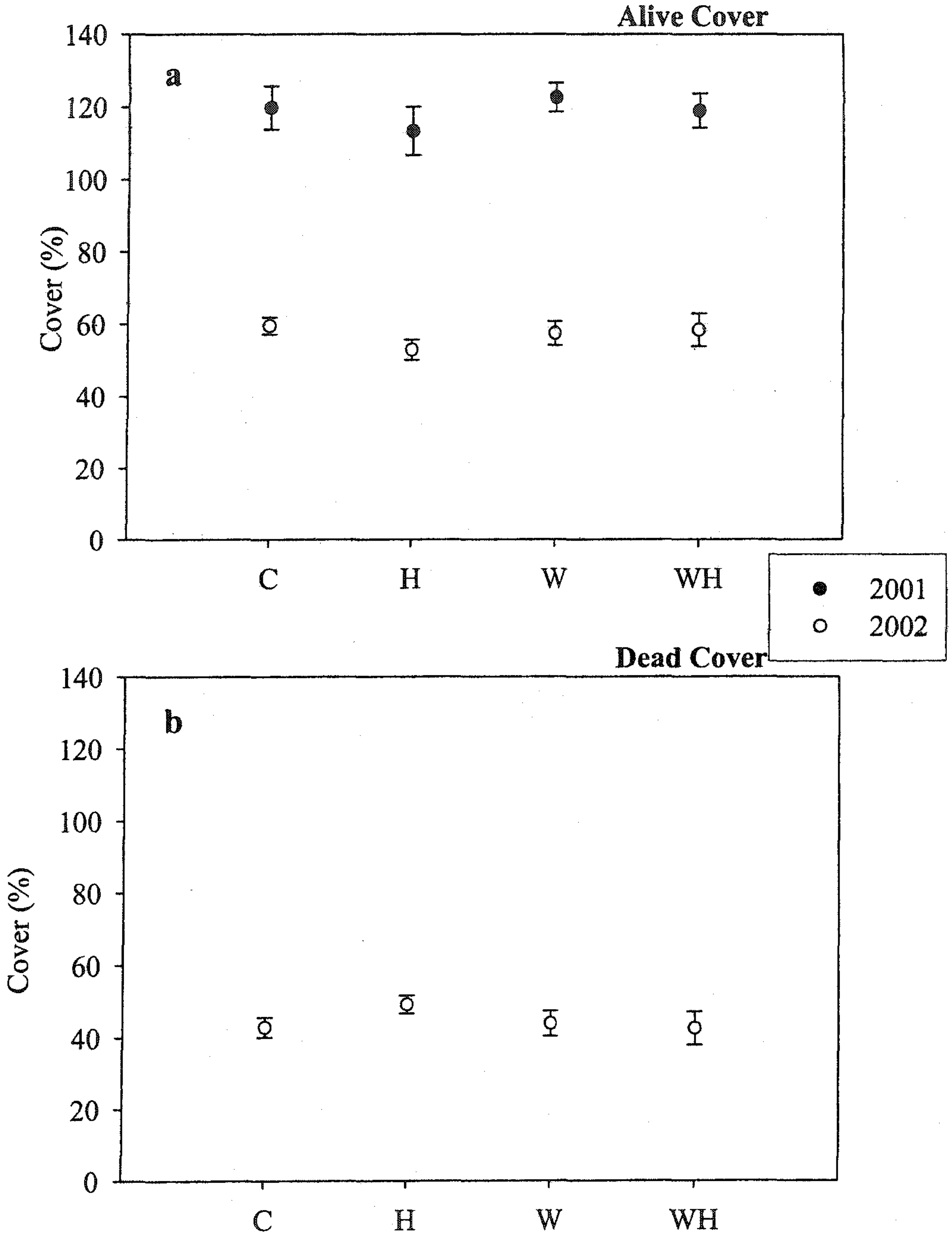


Figure 2.12. Plot- level (5x 8m)means for total cover of a) all living (2001, 2002) and b) dead species (2002). Symbols represent means ± 1 SE, and C= control areas, H= human trails, W= wildlife trails not trampled, and WH= wildlife trails with weekly human trampling.

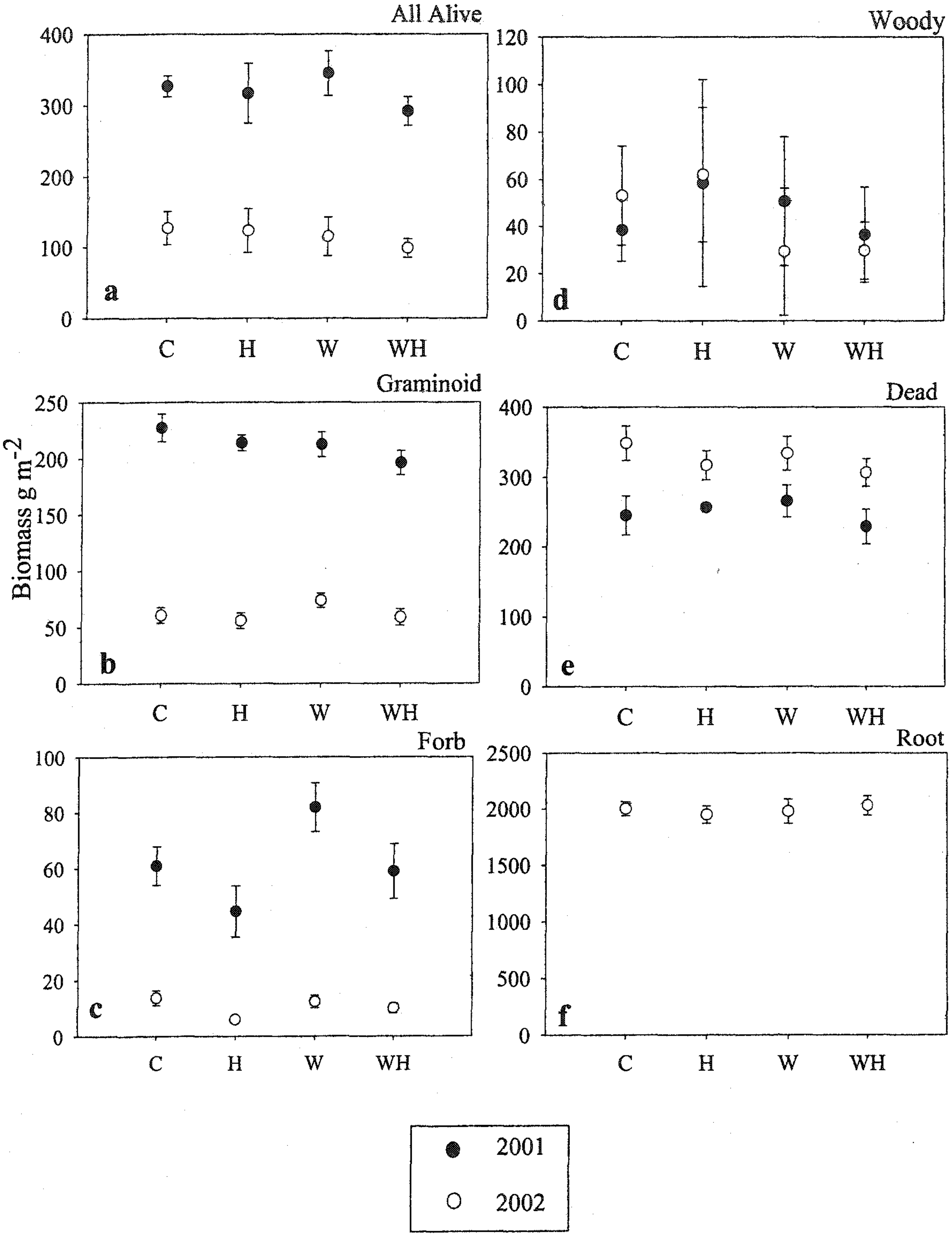


Figure 2.13. Plot-level mean biomass for the aboveground biomass (2001-2002) of **a)** all living species, **b)** living graminoid, **c)** living forb, **d)** living woody species and below-ground (2002) **e)** root biomass. Symbols represent means +1 SE, and C= control areas, H= human trails, W= wildlife trails not trampled,and WH= wildlife trails with human trampling.

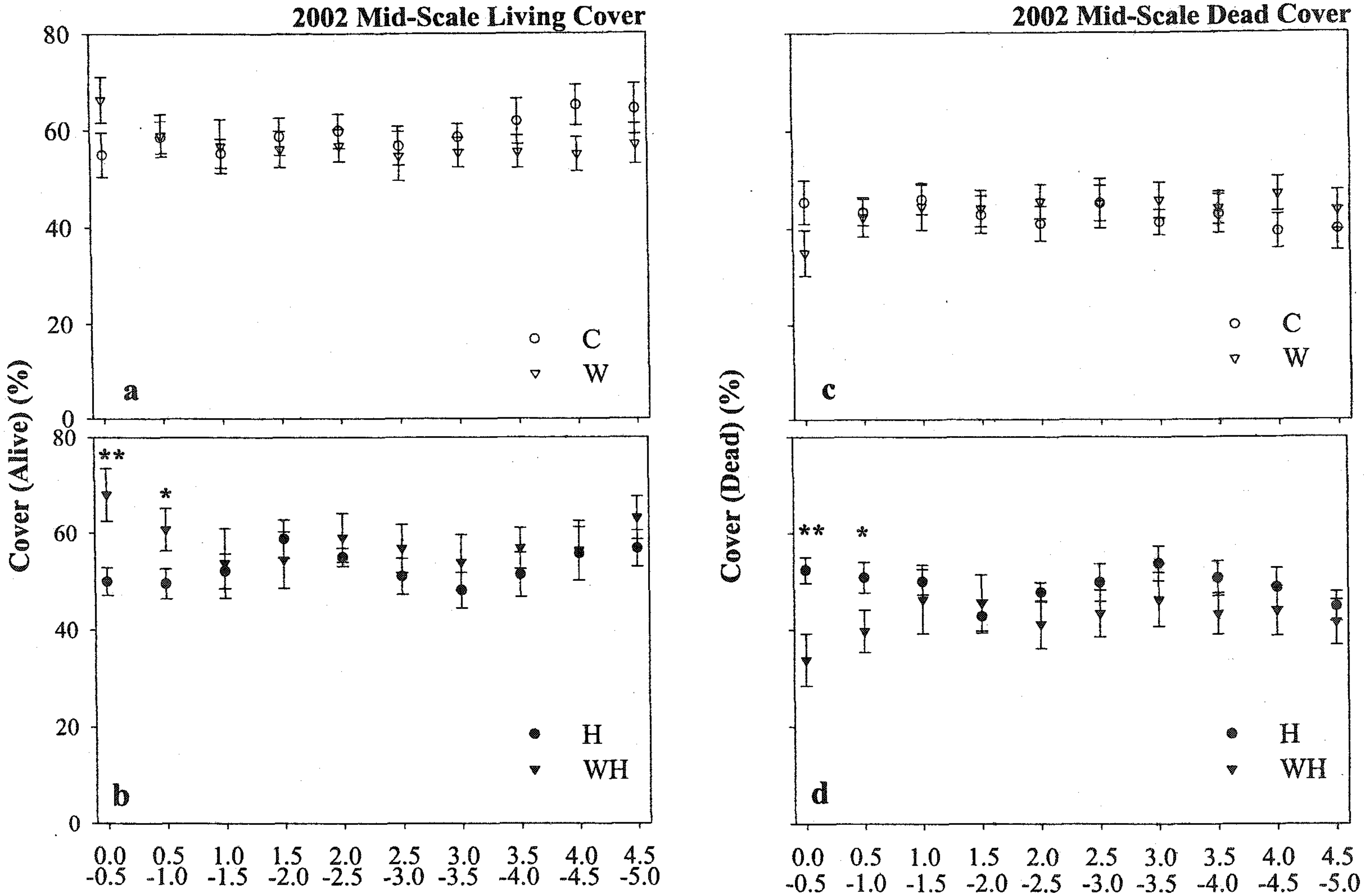


Figure 2.14. Pairwise comparisons of mid-scale (0.5x 8m) mean species cover of living (a-b) and dead (c-d) vegetation in July 2002. Symbols represent means +1 SE, and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling. When mean cover is different at a given distance interval, *indicates $p<0.05$, and ** is Bonferroni corrected (p of 0.05 /4 = 0.0125, $p<0.0125$).

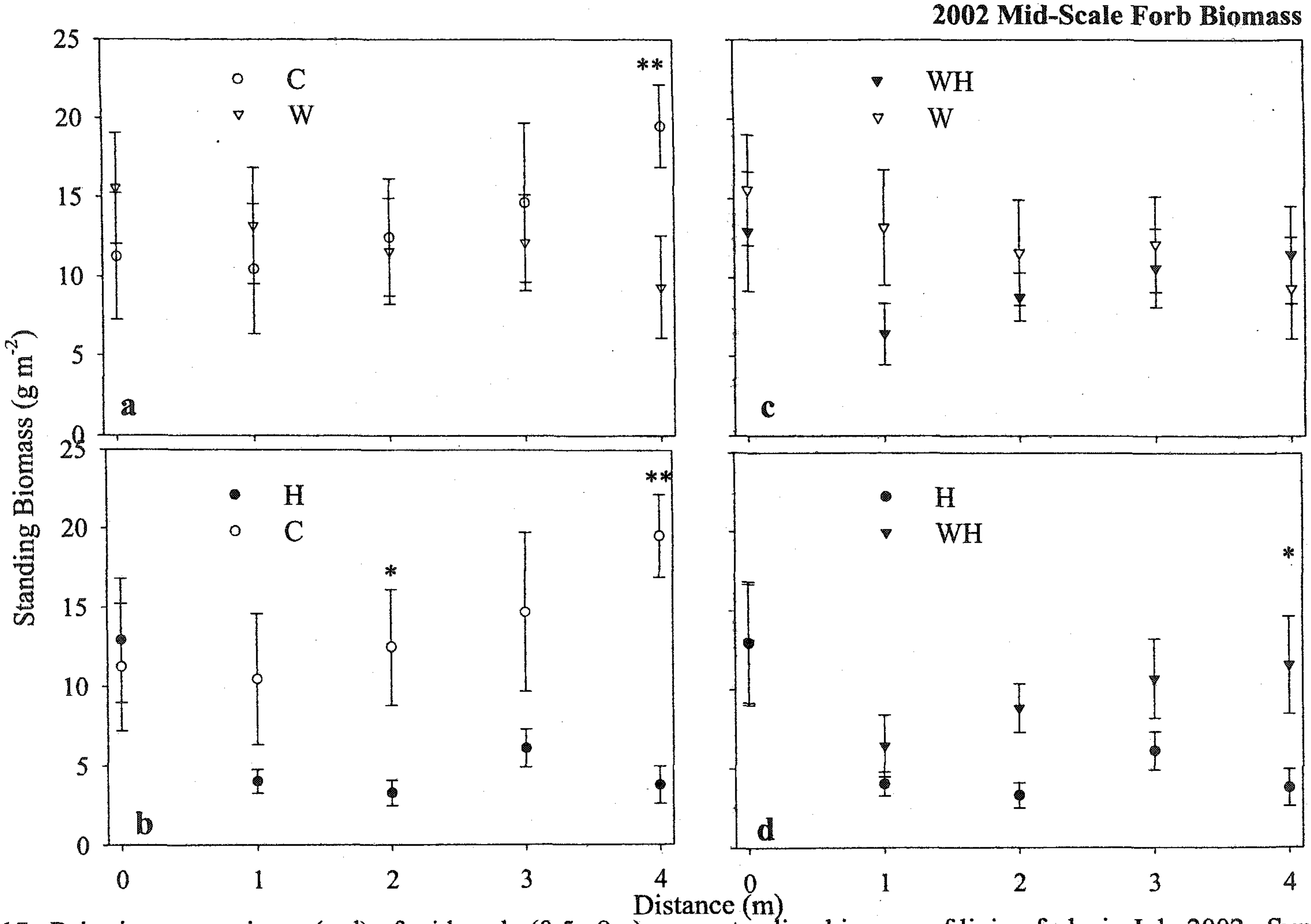


Figure 2.15. Pairwise comparisons (a-d) of mid-scale (0.5x 8m) mean standing biomass of living forbs in July 2002. Symbols represent means +1 SE, and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling. When mean biomass is different at a given distance interval, * indicates p<0.05, and ** is Bonferroni corrected (p of 0.05/4 =0.0125, p <0.0125).

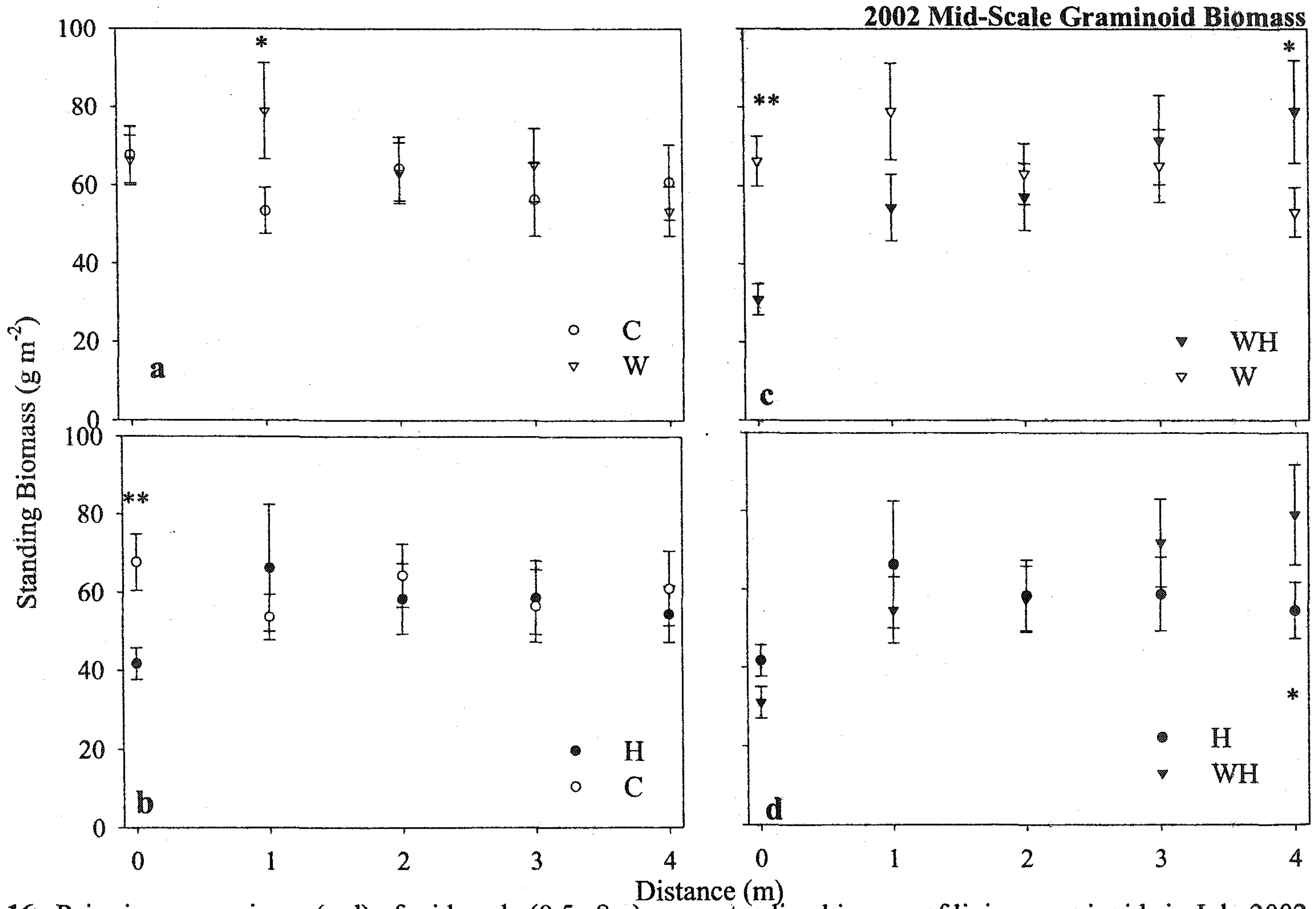


Figure 2.16. Pairwise comparisons (a-d) of mid-scale (0.5x 8m) mean standing biomass of living graminoids in July 2002. Symbols represent means +1 SE, and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling. When mean biomass is different at a given distance interval, * indicates $p<0.05$, and ** is Bonferroni corrected (p of 0.05/4 =0.0125, $p<0.0125$).

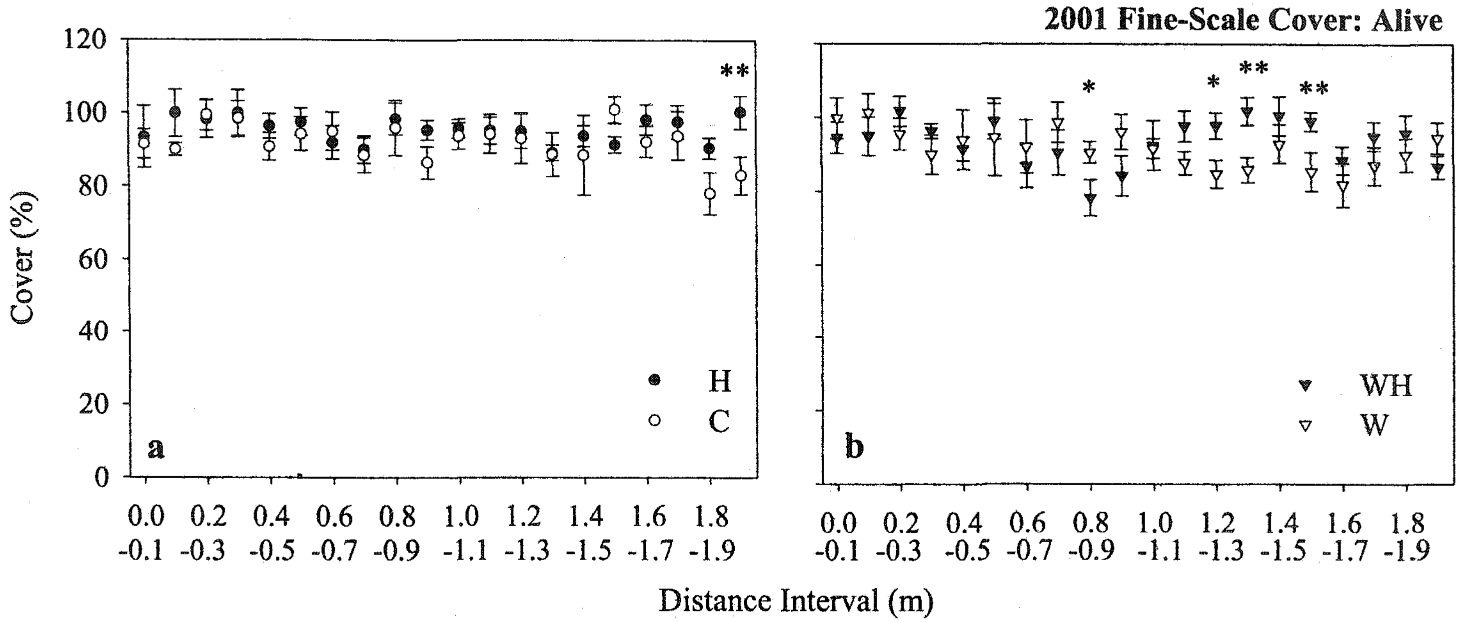


Figure 2.17. Fine-scale (0.1 x8m)) pairwise comparisons (a-b) of mean alive cover in July 2001. Symbols are means +1SE and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling. When mean cover is different at a given distance interval, * indicates $p<0.05$, and ** is Bonferroni corrected (p of $0.05/4 = 0.0125$, $p<0.0125$).

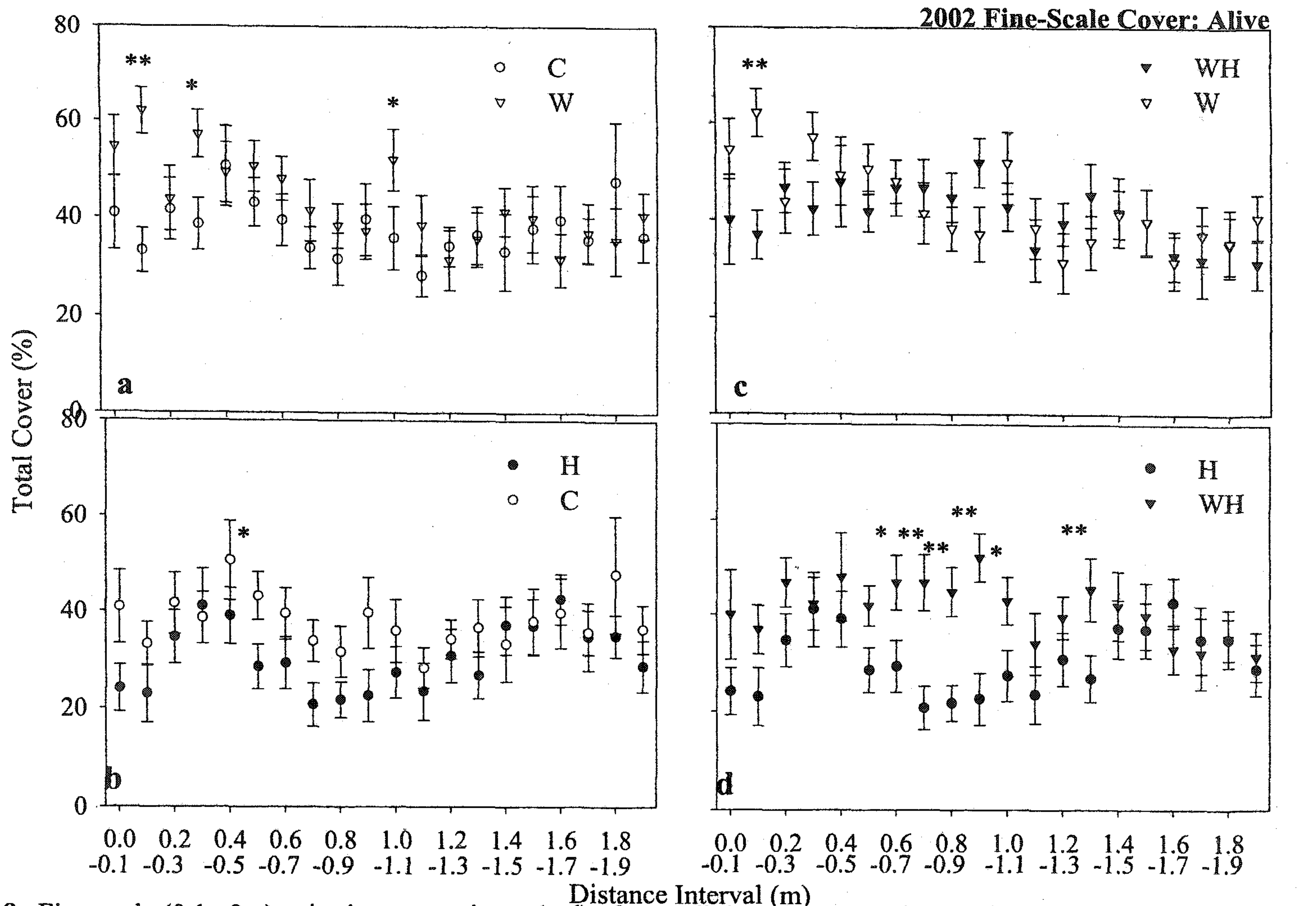


Figure 2.18. Fine-scale (0.1x 8m) pairwise comparisons (a-d) of mean living plant cover in July 2002. Symbols are means + 1 SE, and C= control, H= trail from human trampling, W= wildlife trails without human trampling, and WH= wildlife trails with human trampling. When mean cover is different at a given distance interval, * indicates p<0.05, and ** isBonferroni corrected (p of 0.05 /4 = 0.0125, p <0.0125).

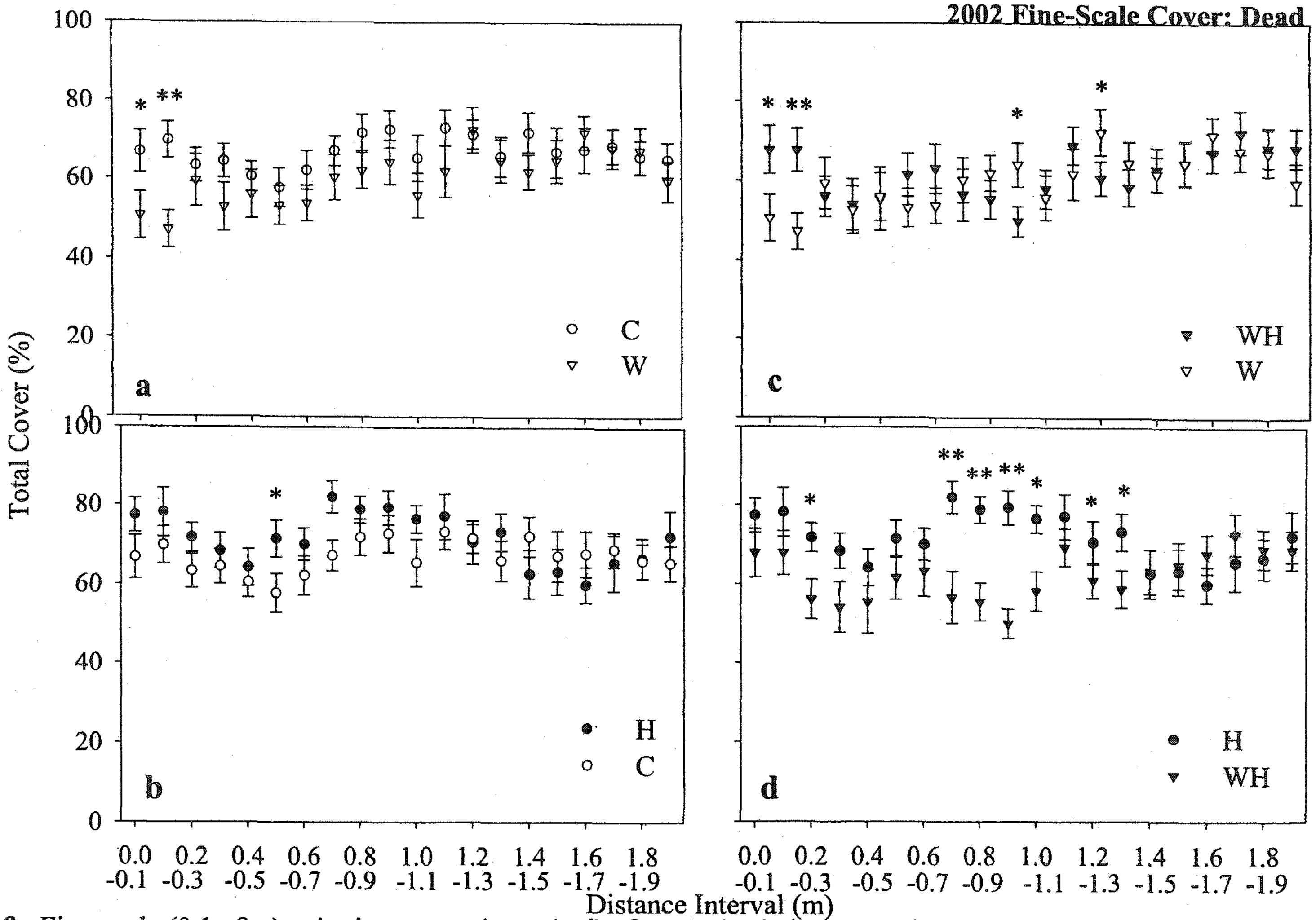


Figure 2.19. Fine-scale (0.1x 8m) pairwise comparisons (a-d) of mean dead plant cover in July 2002. Symbols are means + 1SE, and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling. When mean cover is different at a given distance interval, * indicates p<0.05, and ** is Bonferroni corrected (p of 0.05 /4 = 0.0125, p <0.0125).

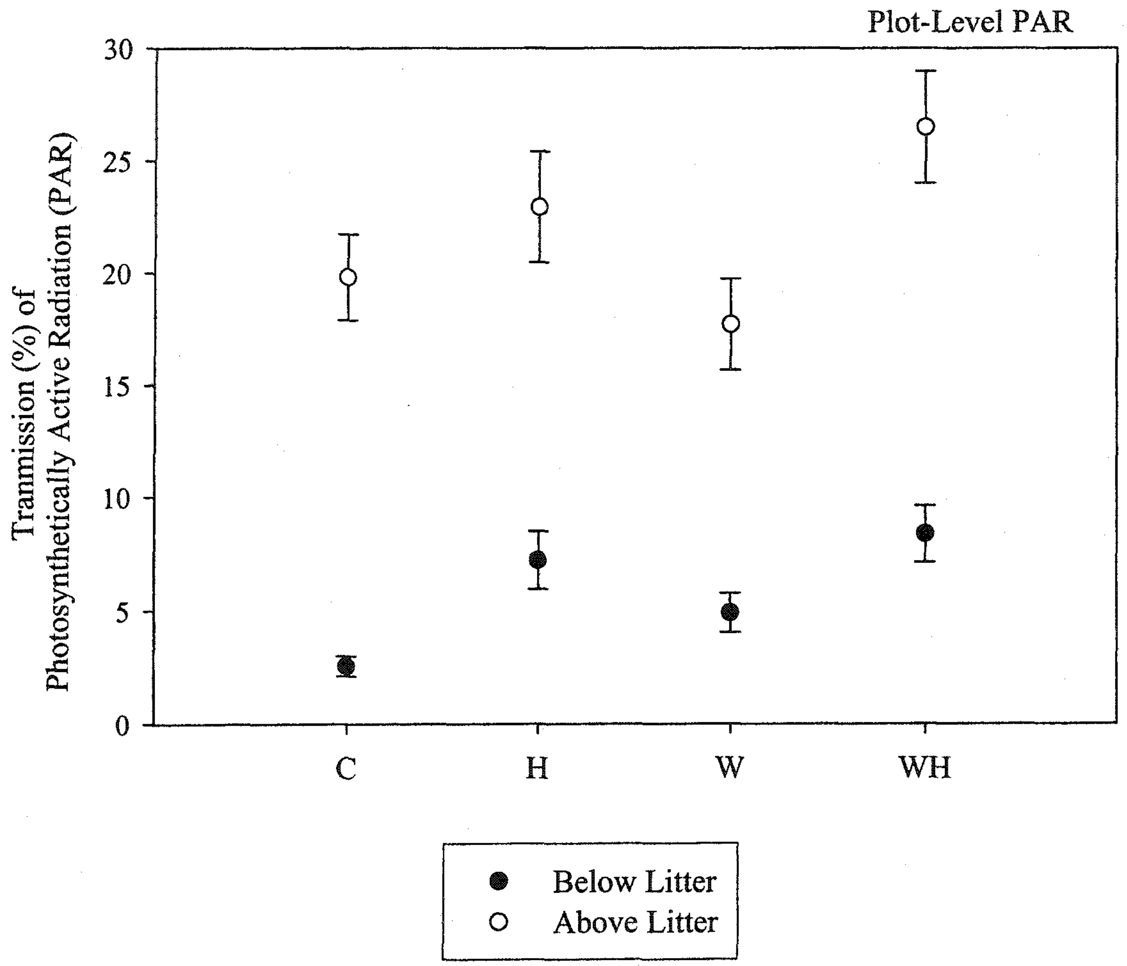


Figure 2.20. Plot-level (5 x 8m) means for PAR above and below litter layers in July 2002. Symbols represent means and error bars are determined by ± standard error of the mean, and C= control areas, H= human trails, W= wildlife trails without human trampling, and WH= wildlife trails with weekly human trampling.

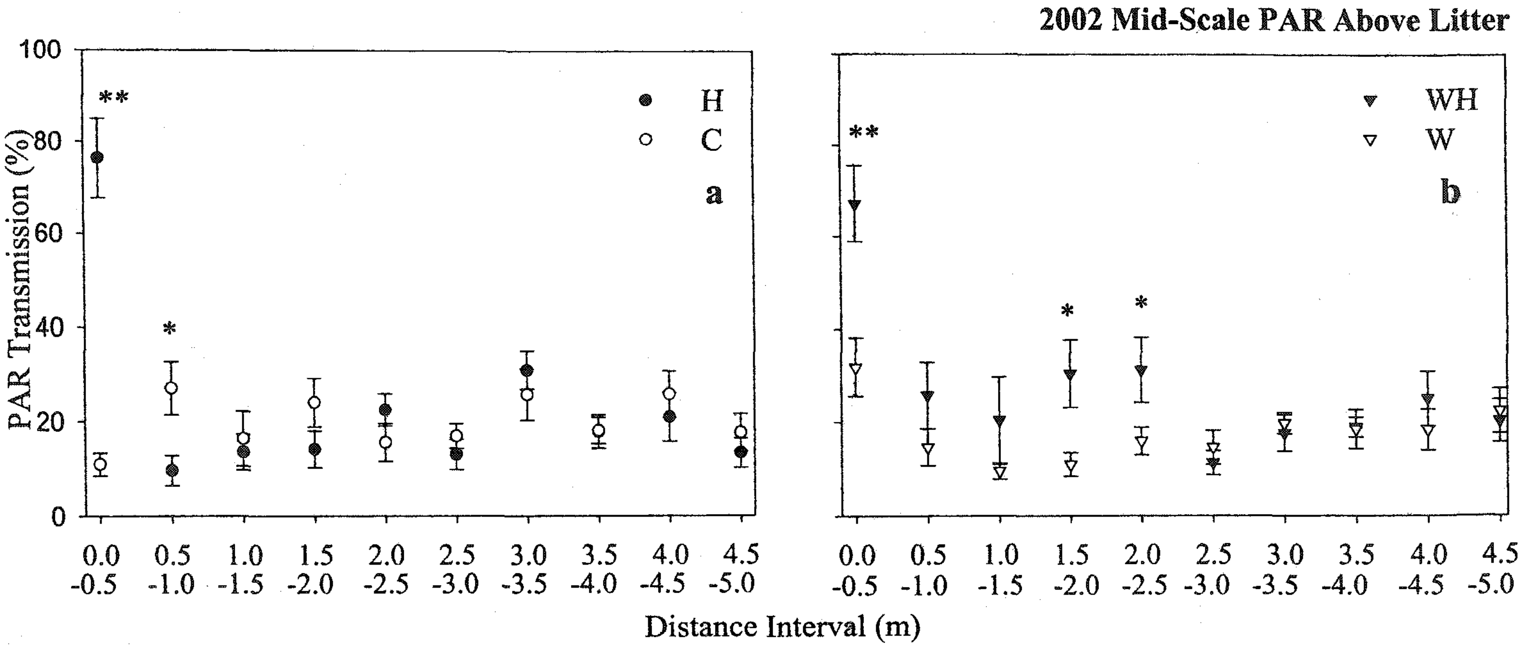


Figure 2.21. Mid-scale (0.5x 8m) pairwise comparisons (a-b) of mean PAR transmission (%) above the litter layer in July 2002. Symbols represent means +1 SE, and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling. When PAR is different at a given distance interval, * indicates $p<0.05$, and ** is Bonferroni corrected (p of 0.05/4 =0.0125, $p <0.0125$).

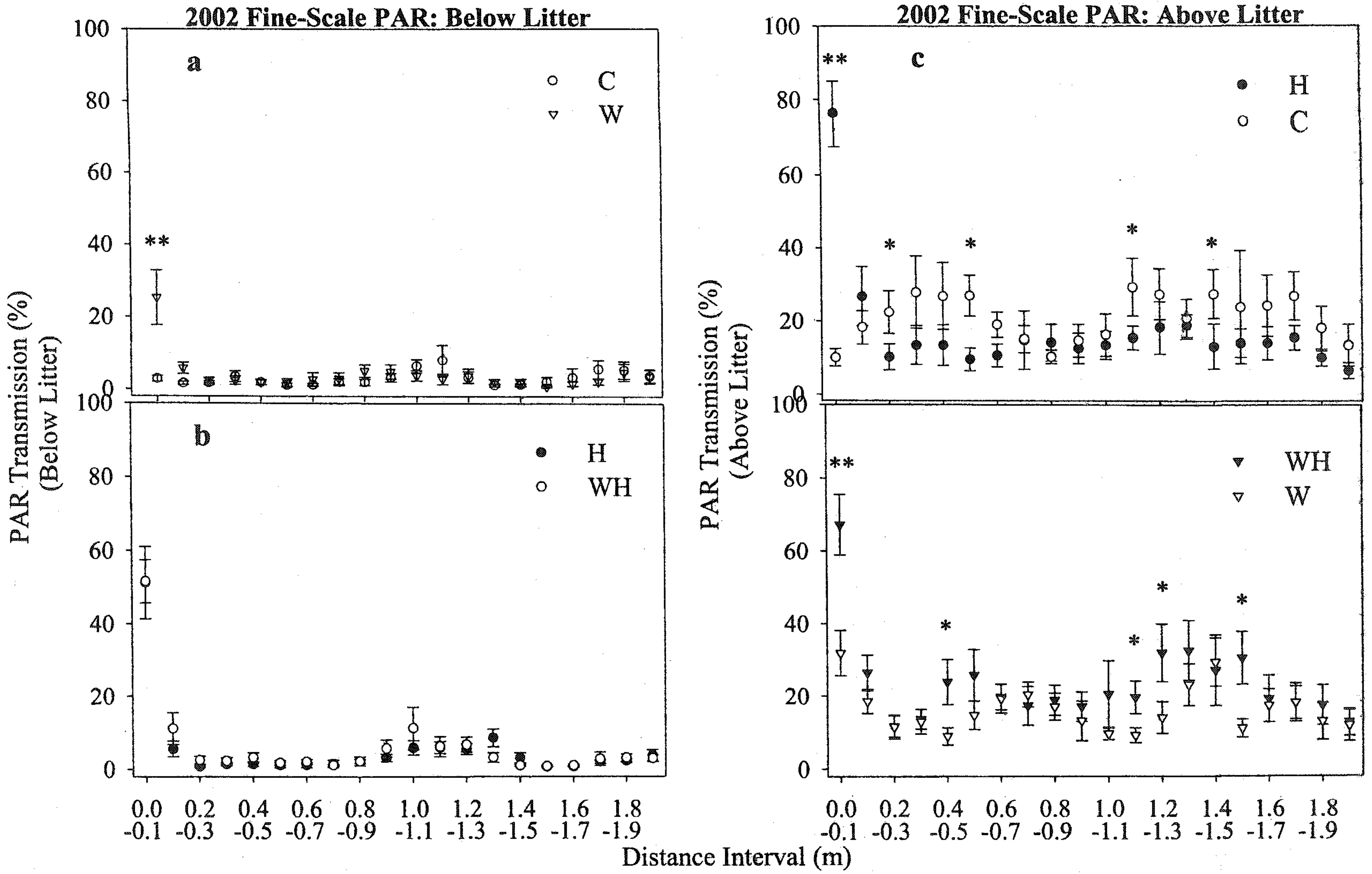


Figure 2.22. Pairwise comparisons of mean transmission of PAR below (a-b) and above (c-d) the litter layer in July 2002 at the fine-scale (0.1 x8m). Symbols represent means +1SE, and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling. When mean PAR is different at a given distance interval, * indicates p<0.05,and ** is Bonferroni corrected (p of 0.05/4 = 0.0125, p<0.0125).

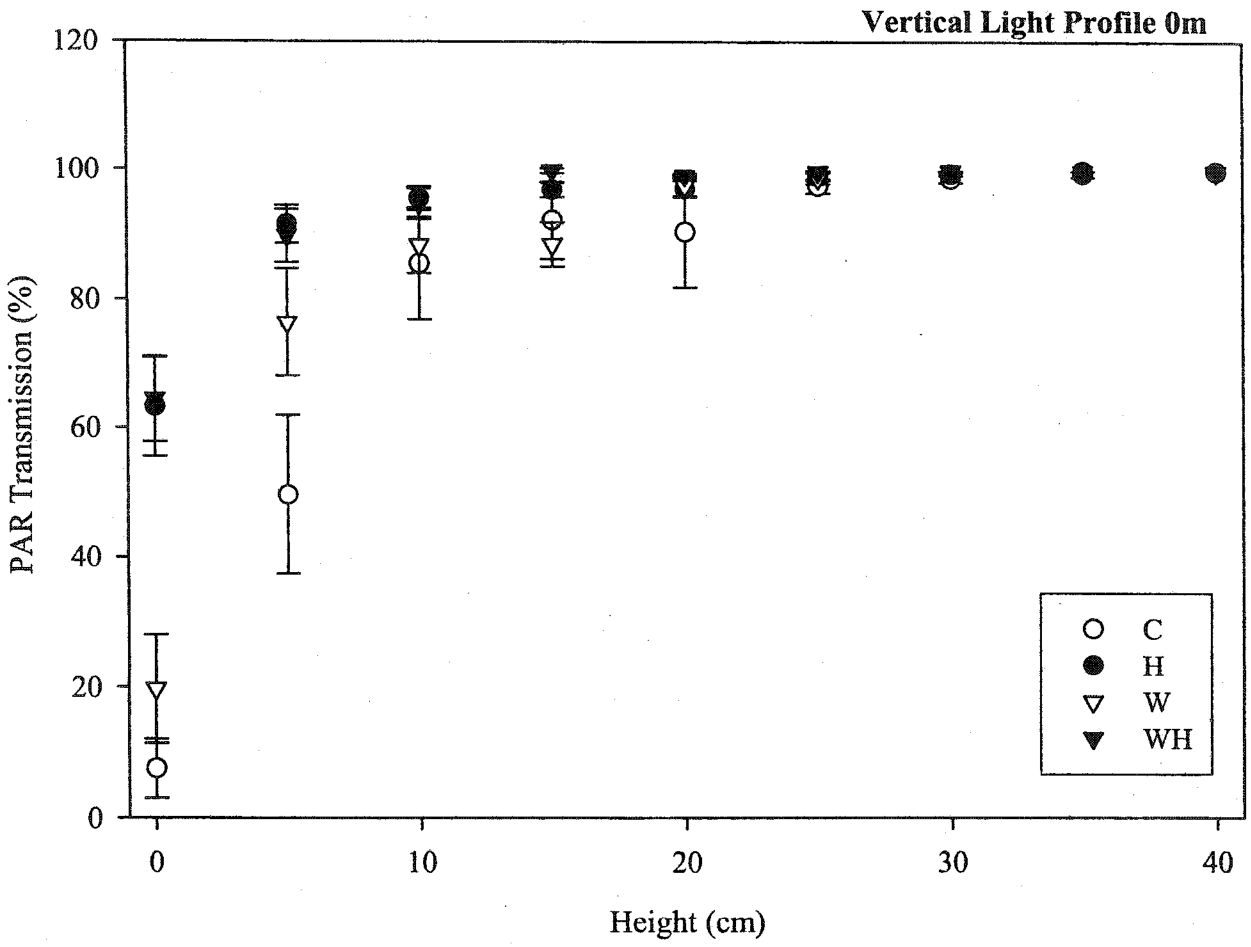


Figure 2.23. Pattern of light available within the vertical profile 0m from human and wildlife trails (and control)(August 2002). Avaulable light reported as Photosynthetically Active Radiation transmitted at 5cm intervals from the ground surface. Symbols represent means +1 SE, and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling.

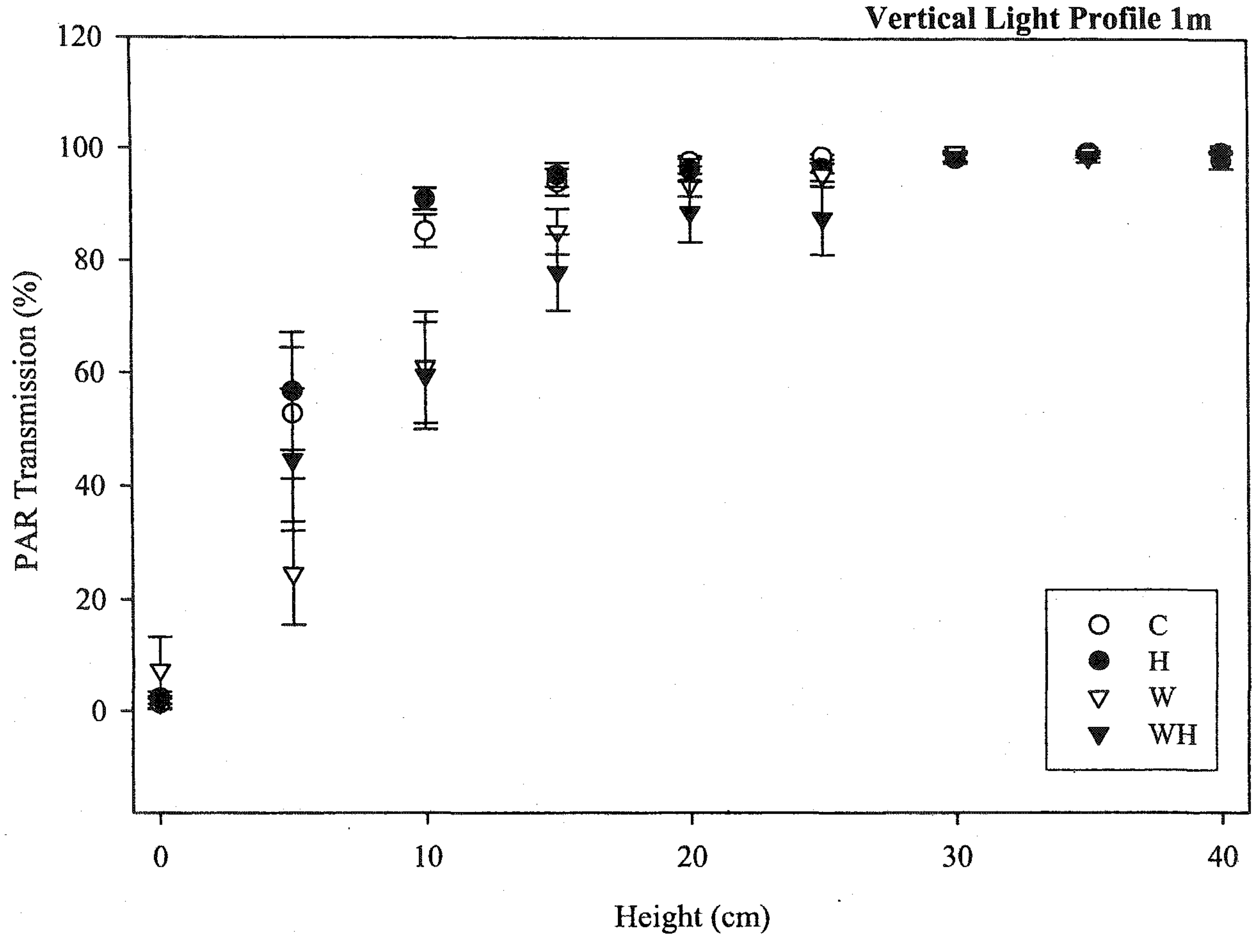


Figure 2.24. Pattern of light available within the vertical profile 1m from human and wildlife trails (and control)(August 2002). Avaulable light reported as Photosynthetically Active Radiation transmitted at 5cm intervals from the ground surface. Symbols represent means+ 1 SE, and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling.

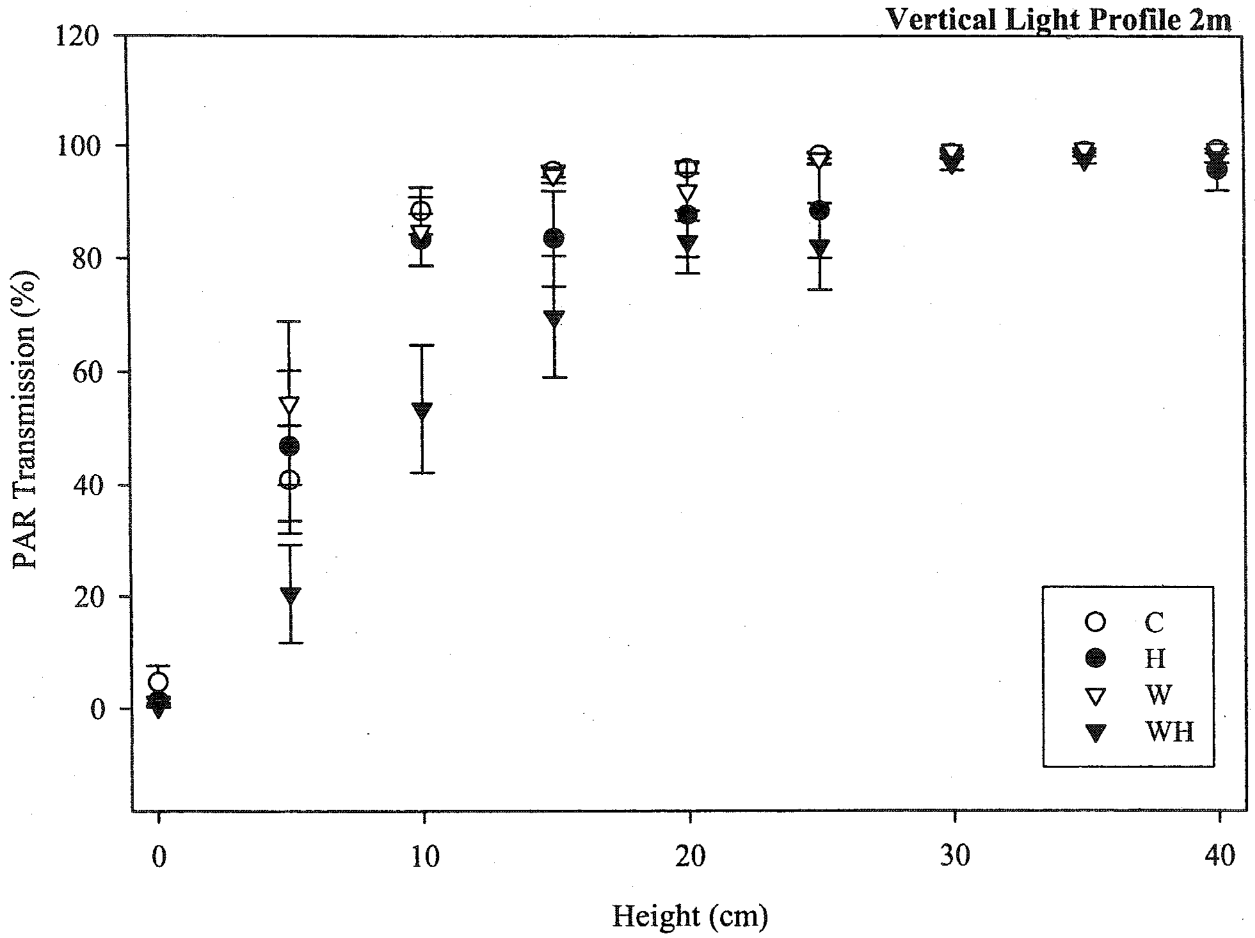
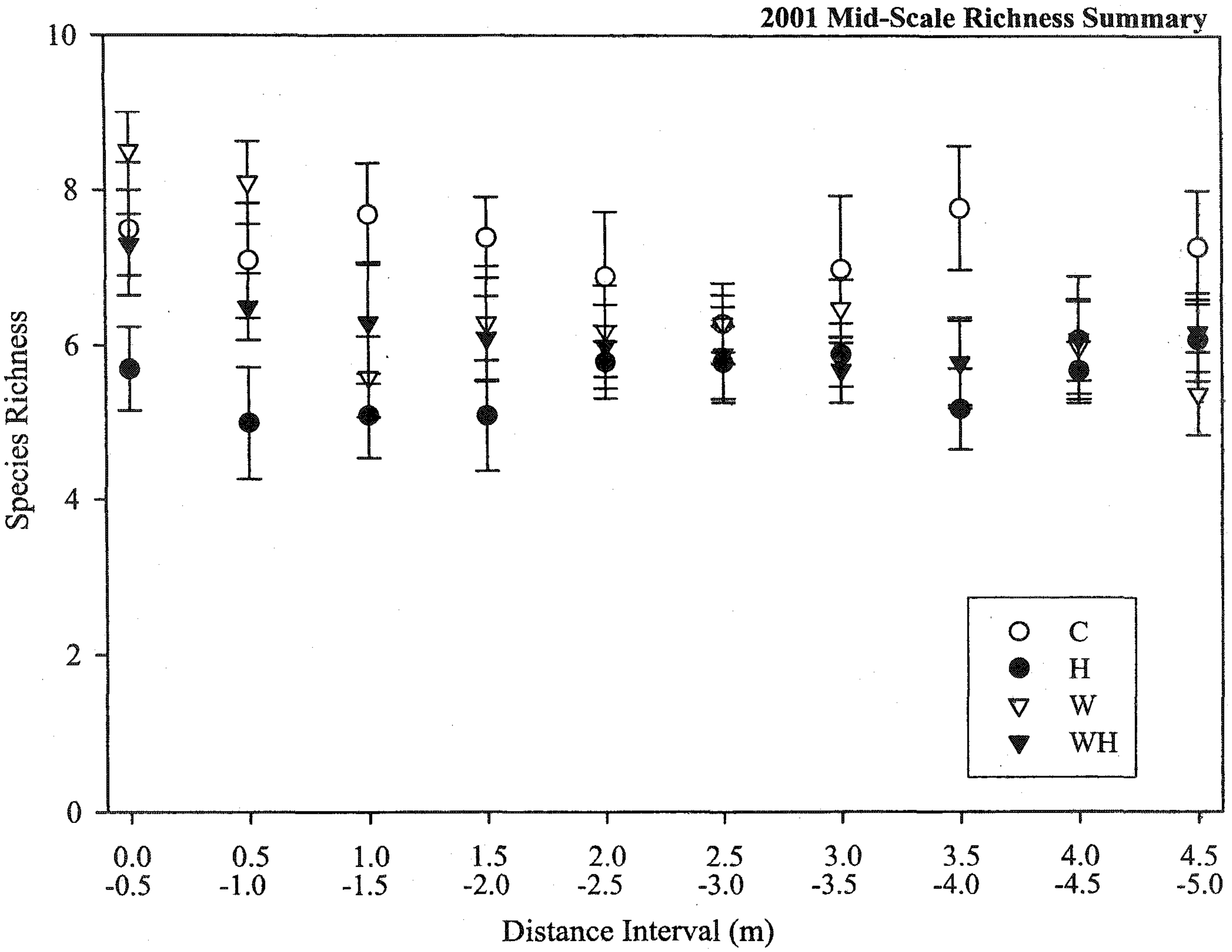
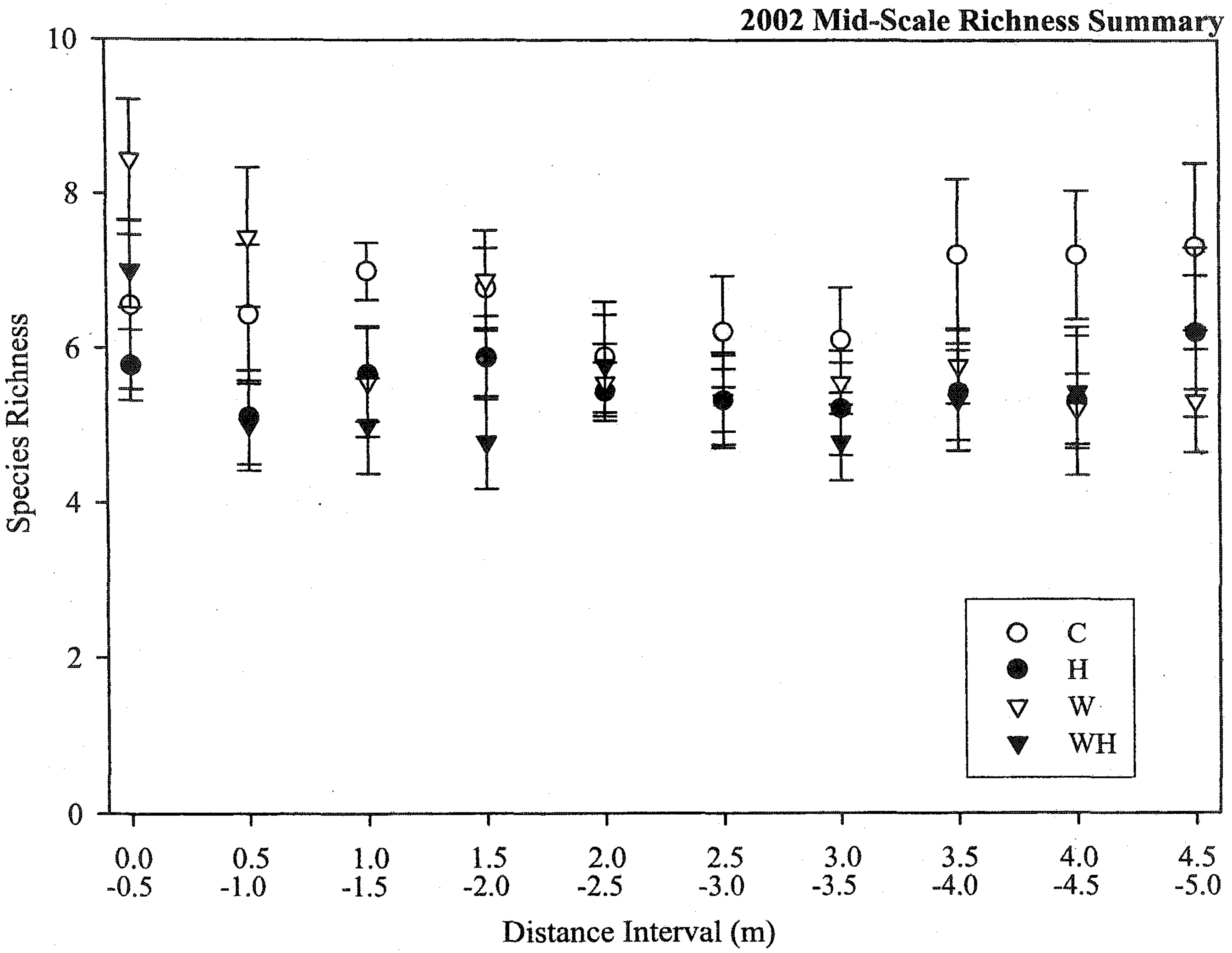


Figure 2.25. Pattern of light available within the vertical profile 2m from human and wildlife trails (and control)(August 2002). Avaulable light reported as Photosynthetically Active Radiation transmitted at 5cm intervals from the ground surface. Symbols represent means + 1 SE, and **C**= control, **H**= trail from human trampling, **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling.



Summary Figure 2.26. Mid-scale (0.5 x8m) pairwise comparisons of mean species richness in July 2001 . Symbols represent means and error bars are determined by ± standard error of the mean, and **C**= control, **H**= trail from weekly human trampling, **W**= wildlife trails without weekly human trampling, and **WH**= wildlife trails with weekly human trampling.



Summary Figure 2.27. Mid-scale (0.5 x8m) pairwise comparisons of mean species richness in July 2002. Symbols represent means and error bars are determined by ± standard error of the mean, and **C**= control, **H**= trail from weekly human trampling, **W**= wildlife trails without weekly human trampling, and **WH**= wildlife trails with weekly human trampling.

Appendix A

Vascular Plant Species found within study plots on the Martin Half (Twp 48m Rg11, 17 SE and SW) in the 2001 and 2002 growing seasons. All nomenclature follows Moss (1983) except [a] Pavlick and Looman (1984) and [b] Little (1942)

ANGIOSPERMAE

MONOCOTYLEDONEAE

- Graminae
  - *Agropyron* Gaertn. species; *dasystachyum*(Hook.)Scribn.
    - *subescodum*
  - *Agrostis scabra* Willd.
  - *Bouteloua gracilis* (HBK) Lag.
  - *Festuca brachyphylla* Schultes
  - *Festuca hallii* (Vasey) Piper [a]
  - *Helictotrichon hookeri* (Schribn.) Henr.
  - *Hierochloe odorata*(L.) Beauv.
  - *Koeleria macrantha* (Ledeb,0 J.A. Schultes f.
  - *Stipa* L. species *curtiseta* (A.S. Hitchec.)
    - *virdula* Trin.
- Iridaceae
  - *Sisyrinchium montanum* Greene

DICOTYLEDONEAE

- Campanulaceae
  - *Campanula rotundifolia* L.
- Caprifoliaceae
  - *Symphoricarpos occidentalis* Hook.
- Caryophyllaceae
  - *Cerastium* L. species
  - *Stellaria* L. species
- Compositae
  - *Achillea millefolium* L.
  - *Antennaria* Gaertn. species
  - *Artemisia frigida* Willd.
  - *Artemisia ludoviciana* Nutt.
  - *Aster falcatus* Lindl.
  - *Aster laevis* L.
  - *Aster* L. species 1
  - Aster species 2
    - *Agoseris glauca* (Pursh) Raf.
    - *Lactuca pulchella* (Pursh) DC
    - *Sonchus arvensis* L.
  - *Cirsium arvense* (L.) Scop.
  - *Cirsium hookerianum* Nutt.
  - *Erigeron* L. species
  - *Solidago* L. species *canadensis*
    - *missouriensis*

Appendix A

Compositae
- *Solidago rigida* L.
- *Taraxacum officinale* Weber

Cruciferae
- Species- mustard

Elaeagnaceae
- *Elaeagnus commutata* L.

Gentiannaceae
- *Gentiana* species

Leguminosae
- *Astragalus* species
- *Astragalus* species 2
- *Astragalus* species 3
- *Thermopsis rhombifolia* (Nutt.) Richards
- *Oxytropis* DC. species
- *Vicia americana* Muhl.

Ranunculaceae
- *Anemone patens* L.
- *Anemone Canadensis* L.

Rosaceae
- *Amelanchier alnifolia* Nutt.
- *Geum triflorum* Pursh
- *Fragaria vesca* L.
- *Potentilla* L. species
- *Rosa arkansana* Porter[b]

Rubiaceae
- *Galium boreale* L.

Santalaceae
- *Comandra umbellata* (L.) Nutt.

Saxifragaceae
- *Heuchera richardsonii* R.Br.

Violaceae
- *Viola* L. species

Appendix B: Survey of Ecologists Conducting Research In Grasslands

The survey was submitted to a non random selection of researchers, selected for email contact from the most recently published papers in databases in which grassland was the key search term; 92 were contacted and 31 individual researchers replied. Of the 31 researchers who replied, 6 resulted from redirection by the initial researcher contacted to either graduate students or colleagues. Two researchers submitted responses for two separate studies bringing the total number of responses to 33.

Text Submitted to Researchers

Hello _________

My name is Melissa Brown, and I am a MSc student working at JC Cahill's lab at the University of Alberta, Canada. My project is centered upon understanding the magnitude of effect of both wildlife (deer, moose, coyote) and human (recreation, research) trails on plant community structure in a local grassland. In an attempt to help put my findings into a broader context, I was hoping that either you, or your project manager/students, may have a few moments to assist me. Specifically, I would like to obtain an estimate of how often you, your lab members, and any other related researchers visit your experimental plots during a single growing season. If you have a few moments, please respond to the following questions. Please note that all responses will remain anonymous, with any reporting of result in thesis or journal publications being done in aggregate.

For one field experiment, in one growing season, please estimate:

1. Number of times per week a treatment plot is visited by any;

(Egs. once a week, 0.25 times a week (for monthly visits))

Visiting may entail taking measures, checking equipment, applying insecticides, etc. Please note that I am looking for total numbers of visits to a plot, and not just the number of visits that you make. For instance, if you are looking at the effects of insecticide application on plant growth in a plot, monitoring growth weekly, and a different researcher is looking at effects of insecticide application and N dynamics, also monitoring weekly, that would be 2 visits per week to the plot.

2. Average number of people present during a single visitation event:
(Eg. principle researcher and assistant = 2)

3. Duration of visitation:
(Eg. 8 weeks)

4. Is this experiment long term research (>1 growing season)?:

Thank you very much for your time and assistance, please feel free to provide estimates for different studies you have underway, or that of a "typical" study if you prefer. Please do not hesitate to contact me if you have any questions.

Your assistance is greatly appreciated,
Melissa Brown

Appendix B Table 1. Responses to the grassland ecology survey, from 33 ecologists conducting research in grasslands. The number of visits per week (#/week) is as given or determined by the actual response. The number of people present at each visit is given as estimated by the researcher. The duration of the visits, or the length of the growing season, as well as the number of growing seasons for which experiments run are reported as given by researchers. GS= growing season and a dashed line indicates no response given.

ID	# Visits /Week	Actual Response	# People / Visit	Duration of visitation	# Growing Seasons
1	1		1	12 weeks	2
2	0.25	1 time per month	2	---	Long Term
3	0.20	10 times per year	2	---	Long Term
4	2		2	52 weeks	3 years
5	1		1	April-Oct	3
6	0.25	1 time per month	2	1-2 days per visit	---
7	7		1	2-3 months	1
8	1		4	4 weeks	---
9	0.5	1 time/month x 9 months 3 time/month x 3 months 2 time/month x 1 month	2	1 year	3
10	0.5	2 times/month x 7 months 3 x every 6 wk x 5 months	1	1 year	2
11	0.17	1 time every 6 weeks	1	GS	2
12	---	---	2	GS	1
13	0.06	3 times per year	2	---	>1
14	0.35	detailed averages	1.5	5 months	>1
15	0.5	1 time every 2 weeks	2	9 months	>1
16	1		1	4 weeks	>1
17	2		1.5	5 weeks	>1
18	1.5	1-2 times/week	2.5	GS	>1
19	1.6		1.5	15 weeks	3
20	2		1	---	---
21	0.02		3	GS- 1 year	>1
22	1		2	48 weeks	>1
23	7		2	4 weeks	10 years+
24	1.05	0.1-2 times/ week	2	March-Oct	7
25	0.19	0.25-.125/ week	3	GS	>1
26	3.5	3-4 times/ week	4.5	GS	---
27	0.5		2.25	All happen in 1-2 days	3
28	0.38	0.25-.5 times/ week	2	2-2.5 months/year	>1
29	2		1	---	---
30	0.5	1 time every 2 weeks	2	GS	>1
31	1		2.5	3 months	>1
32	0.25		2	2 years	>1
33	0.5	1 time every 2 weeks	2	8 weeks	>1

Appendix C: SAS Codes

For the purpose of the following examples;

Library= MJB, data= 2002 and the response variable = richness.

Global Model

In the global model, fixed factors include distance, trail and trampling, while block and treatment plot (=treat) nested within the trail*block* trampling interaction are random factors.

```
proc mixed data= MJB.2002;
class block trail tramp treat;
model richness= distance|trail|tramp/DDFM=SATTERTH;
random block treat(block*trail*tramp);
run;
```

In the global model, distance effects are assumed to be linear ($y=d_x$); therefore candidate models where distance is quadratic or tertiary have the following substitutions at the *model* line:

Quadratic: $y=d_x + d^2_x$

```
model richness= distance|trail|tramp distance2/DDFM=SATTERTH;
```

where distance2= distance squared

Tertiary: $y=d_x + d^2_x + d^3_x$

```
model richness= distance|trail|tramp distance2 distance3/DDFM=SATTERTH;
```

where distance3= distance cubed

Analyses at the plot level do not include the distance term in the model line.

A priori Comparisons

Estimate statements were used with the Global Proc Mixed Model when a response variable varied as a function of a distance interaction (eg. distance* trampling) to compare means of the treatment effects at specified distances.

<u>First the data set was sorted:</u>

```
proc sort data= MJB.2002
        by distance;
```

```
run;
```

Then *A priori* comparisons, by distance

```
proc mixed data= MJB.2002;
        by distance;
        class block trail tramp treat;
        model richness= distance|trail|tramp/DDFM=SATTERTH;
        random block treat(block*trail*tramp);
estimate ‘wildlife trails versus control’ trail –1 1 trail*tramp –1 0 1 0;
estimate ‘human trails versus control’ trampling –1 1 trail*tramp –1 1 0 0;
estimate ‘human trampling on wildlife trails’ trampling –1 1 trail*tramp 0 0 –1 1;
estimate ‘human trampling on wildlife and human trails’ trail –1 1 trail*tramp 0 –1 0 –1;
run;
```

Appendix D. Sub-Study: Damage to Individual Plants

Sub-Study Objective: Does proximity to older wildlife (trampled and not) and new human trails influence damage due to insect herbivores and other factors on individual plants? This sub-study also examined growth and survival of individual plants, but preliminary analyses are not presented or further discussed in this thesis.

Materials and Methods

Study Site and Experimental Design

This sub-study occurred as an extension of the larger community composition and production study (Chapter 2). Therefore, details concerning the study site and general experimental design are found in the Materials and Methods: Study Area (Page 55-58) and Experimental Design and Definition of Treatments (Pages 58-59) in Chapter 2 of this thesis.

Data Collection

To examine the effects of trails and trampling on the damage to individual plants, the damage 1) due to insect herbivory and 2) due to other factors such as pathogens and drought stress, marked individuals were monitored in the 2002 growing season. Species chosen for this study included common native species from different functional groups, including the herbaceous graminoids *Festuca hallii*, the non-graminoid herbaceous perennials *Achillea millefolium, Artemisia ludoviciana, Aster falcatus, Comandra umbellata* and the woody perennials *Rosa arkansana* and *Symphoricarpos occidentalis*. These species were chosen as they were common in the majority of treatment plots and across replicate blocks. While this may introduce a bias of common species, it was necessary in order to obtain sufficient replicates.

Within each treatment plot, individual plants of each chosen species were located along the destructive sampling transect (Appendix Figure D.1). For each chosen species, approximately ten (minimum of three) individuals of each species were selected within the 1.0 x 5m area along the 5m transect. Individuals were selected at a variety of distances from the trail and care was taken to ensure replicates were not clumped in one area. For example, the ten replicates of one species were located at distances of 0.2, 0.6, 1.2, 1.4, 1.7, 2.3, 2.5, 3.0, 3.3, 4.4 m from the trail, instead of all ten located within 0-

2.5m of trails. Any two selected individuals of the same species were at least 15cm apart, and had less than 15% damage at the time of tagging (defined below).

At the time of tagging (3-13 June 2002), height (cm), initial damage (percent of live leaf tissue damaged by insects and observable disease and stress), leaf or tiller number, and perpendicular distance from the trail were recorded. The base of each individual was tagged with coloured telephone wire, with the ends twisted and firmly stuck into the ground. The colour used for each species was randomly chosen at each treatment plot. After tagging and measurements, these plants were not visited individually, but plots were or were not trampled weekly in accordance to assigned trampling treatments. Individual plants were harvested at the end of the growing season (13-17 August 2002), and each tagged plant was recovered and assessed for mortality. Final height and biomass were obtained for all plants, dead and alive. Final damage, however, was only assessed for those plants with live leaf tissue. Final insect herbivory damage was estimated visually as the percent of live leaf area absent due to insect herbivory. All other damage was estimated separately, as the percent of live leaf tissue appeared to suffer from other factors, such as environmental stress or disease.

Data Analysis

Damage due to insect herbivory and other factors were analyzed with a general linear model, using Proc Mixed within the SAS System for Windows V8 (1999). The same global model was used as in Chapter 2 and the model used (Appendix C) and details regarding candidate model selection are as discussed in Chapter 2 (Univariate Analyses, Pages 55-58).

Due to the natural variation and local abundance of individual species between and within replicate blocks, all treatment plots do not always contain enough replicates of each species for analyses. Criteria for inclusion in analyses is as follows: 1) to include the whole treatment plot (eg. W, H, WH or C) in the analyses, 3 (minimum) replicates of the species are alive and recovered in August; 2) each treatment comparison (eg. wildlife trails to control plots) must be present in half the total number of blocks where the species was initially tagged. For example, if *Achillea millefolium* occurs in all ten blocks, then to compare human trails (H) with control area (C), both H and C treatment plots must have at least three *A. millefolium* individuals for comparison within at least five shared blocks.

Preliminary Results

Results from the general linear models are presented in Appendix Table D.1. In this section I focus only on two significant results; the other damage class with *Festuca hallii* and the insect damage class with *Achillea millefolium.*

August insect damage varies with trail and the distance*trail interaction, and trampling influences insect herbivory of *A. millefolium* differently on and near new human trails or older wildlife trails (Appendix Figure D.2). Insect damage is greater near human trails than far from them. Trampling appears to have less of an effect on insect damage directly on wildlife trails than on newer human trails. August damage due to other factors (eg. pathogens and drought stress) varies with distance, trampling and the distance*trampling interaction for individual *F. hallii* plants. Damage is highest on and near both trampled trails (old wildlife and new human) and decreases with distance (Appendix Figure D.2). Damage due to other factors is lower on and near wildlife trails not actively trampled and in control plots, than on near their trampled counterparts.

Discussion of these preliminary findings is found in the Discussion section of Chapter 2 of this thesis .

Appendix Table D.1. Damage to individual plants in 2002, including May damage, August insect and August damage due to other factors. Fixed factors are reported for the general linear model, with corresponding *p* values and with F statistic and degrees of freedom (numerator, denominator): P;$F_{\text{DF num, DF den}}$. All *p* values are in bold font when $p<0.05$. Of all candidate models (where distance is L=linear, Q=quadratic and T=tertiary), only the model(s) with the lowest AIC_C values are presented.

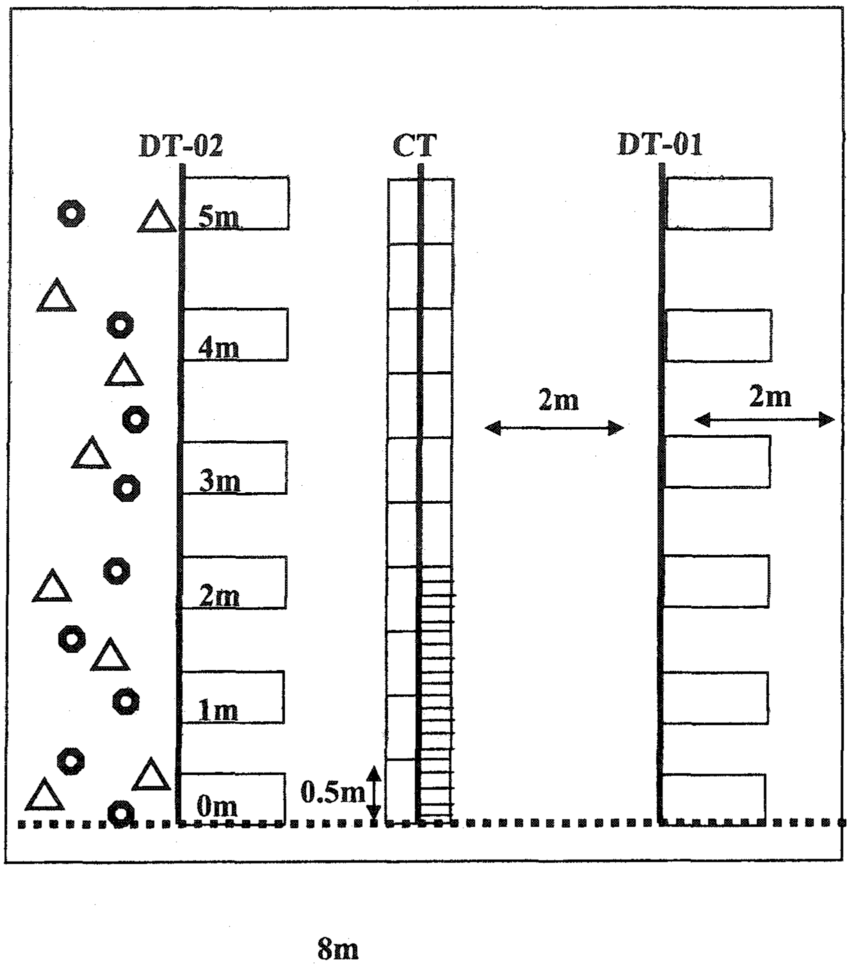
Species	Time	Model	Distance	Trail	Distance * Trail	Trampling	Distance* Trampling	Trail* Trampling	Distance* Trail* Trampling	Distance^2	Distance^3
Festuca hallii All	May	L	0.860 $0.03_{1,274}$	0.997 $0.00_{1,165}$	0.797 $0.07_{1,273}$	0.480 $0.50_{1,163}$	0.061 $3.54_{1,273}$	0.264 $1.25_{1,168}$	0.238 $1.40_{1,273}$	---	---
	Aug Insect	L	0.359 $0.85_{1,230}$	0.850 $0.04_{1,90.3}$	0.528 $0.40_{1,230}$	0.987 $0.00_{1,89.3}$	0.982 $0.00_{1,231}$	0.440 $0.60_{1,90.9}$	0.732 $0.12_{1,230}$	---	---
	Aug Other	L	**0.045** **4.08**$_{1,237}$	0.149 $2.10_{1,154}$	0.622 $0.24_{1,233}$	**<0.000** **20.49**$_{1,148}$	**<0.000** **18.73**$_{1,237}$	0.876 $0.02_{1,153}$	0.694 $0.16_{1,236}$	---	
Achillea millefolium C: W	May	L	0.637 $0.22_{1,75.6}$	0.179 $1.89_{1,33.7}$	0.239 $1.41_{1,70}$	---	---	---	---	---	---
	Aug Insect	L	0.598 $0.28_{1,62.7}$	0.132 $2.31_{1,87}$	0.173 $1.89_{1,86.2}$	---	---	---	---	---	---
	Aug Other	L	0.382 $0.77_{1,85.7}$	0.054 $4.15_{1,21.5}$	0.184 $1.81_{1,56.5}$	---	---	---	---	---	---
Achillea millefolium C:H	May	L	0.330 $0.96_{1,74.2}$	---	---	0.453 $0.57_{1,40.4}$	0.796 $0.07_{1,74.2}$	---	---	---	---
	Aug Insect	L	**0.024** **5.32**$_{1,76}$	---	---	0.528 $0.40_{1,76}$	0.107 $2.66_{1,76}$	---	---	---	---
	Aug Other	L	**0.017** **5.97**$_{1,75.5}$	---	---	0.982 $0.00_{1,18.7}$	0.329 $0.97_{1,75.3}$	---	---	---	---
		Q	0.992 $0.00_{1,74.6}$	---	---	0.932 $0.01_{1,20}$	0.264 $1.27_{1,74.6}$	---	---	0.539 $0.38_{1,74.7}$	---
Achillea millefolium W:WH	May	L	0.876 $0.02_{1,113}$	---	---	0.071 $3.42_{1,44.3}$	0.435 $0.62_{1,113}$	---	---	---	---
	Aug Insect	L	**0.017** **5.85**$_{1,113}$	---	---	0.886 $0.02_{1,112}$	0.631 $0.23_{1,110}$	---	---	---	---
	Aug Other	L	0.814 $0.06_{1,112}$	---	---	0.074 $3.27_{1,110}$	0.272 $1.22_{1,108}$	---	---	---	---
		Q	0.549 $0.36_{1,109}$	---	---	0.058 $3.66_{1,109}$	0.204 $1.63_{1,107}$	---	---	0.476 $0.51_{1,110}$	---

Appendix Table D.1. Continued

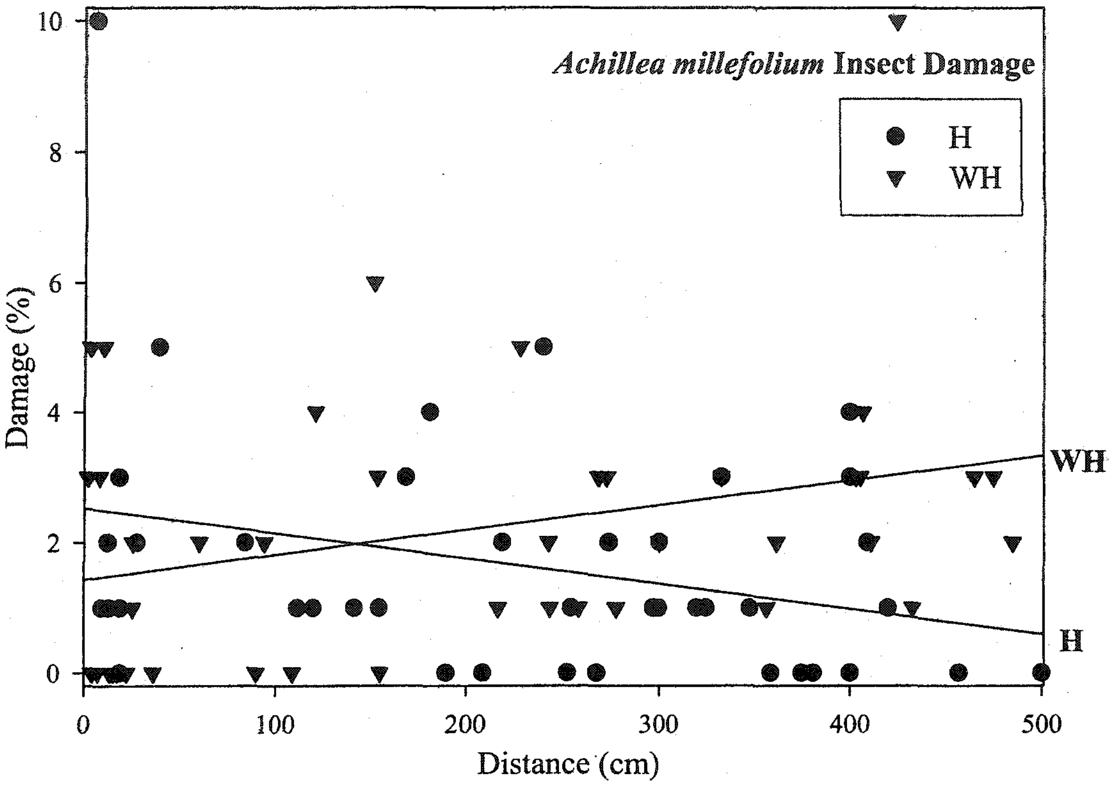
Species	Time Model		Distance	Trail	Distance *Trail	Trampling	Distance* Trampling	Trail* Trampling	Distance* Trail* Trampling	Distance^2	Distance^3
Achillea millefolium	May	L	0.620	0.223	0.901	- - -	- - -	- - -	- - -	- - -	- - -
H:WH			0.25$_{1,99}$	1.50$_{1,101}$	0.02$_{1,102}$						
	Aug	L	0.421	**0.040**	**0.001**	- - -	- - -	- - -	- - -	- - -	- - -
	Insect		0.65$_{1,98}$	**4.68**$_{1,26.2}$	**10.84**$_{1,100}$						
	Aug	L	**0.004**	0.264	0.074	- - -	- - -	- - -	- - -	- - -	- - -
	Other		**8.81**$_{1,95.9}$	1.28$_{1,44.2}$	3.25$_{1,102}$						
		Q	0.986	0.270	0.068	- - -	- - -	- - -	- - -	0.388	- - -
			0.00$_{1,96.1}$	1.23$_{1,100}$	3.39$_{1,101}$					0.75$_{1,96.1}$	
		T	0.282	0.320	0.065	- - -	- - -	- - -	- - -	0.312	0.240
			1.17$_{1,96.8}$	1.00$_{1,99.4}$	3.48$_{1,99.4}$					1.03$_{1,97.7}$	1.40$_{1,97.6}$
Artemesia ludoviciana	May	L	0.746	- - -	- - -	0.844	0.676	- - -	- - -	- - -	- - -
W:WH			0.11$_{1,106}$			0.04$_{1,106}$	0.18$_{1,104}$				
	Aug	L	0.082	- - -	- - -	0.935	0.921	- - -	- - -	- - -	- - -
	Insect		3.09$_{1,102}$			0.01$_{1,27.2}$	0.01$_{1,102}$				
	Aug	L	0.467	- - -	- - -	**0.036**	0.376	- - -	- - -	- - -	- - -
	Other		0.53$_{1,106}$			**4.50**$_{1,106}$	0.79$_{1,106}$				
		Q	0.105	- - -	- - -	**0.032**	0.466	- - -	- - -	0.140	- - -
			2.68$_{1,105}$			**4.74**$_{1,105}$	0.53$_{1,105}$			2.22$_{1,105}$	
		T	**0.023**	- - -	- - -	**0.020**	0.307	- - -	- - -	**0.050**	0.083
			5.34$_{1,104}$			**5.60**$_{1,104}$	1.05$_{1,104}$			**3.96**$_{1,104}$	3.07$_{1,104}$
Aster falcatus	May	L	0.776	0.585	0.611	- - -	- - -	- - -	- - -	- - -	- - -
C: W			0.08$_{1,39.7}$	0.32$_{1,11}$	0.26$_{1,40.2}$						
		Q	0.901	0.608	0.626	- - -	- - -	- - -	- - -	0.834	- - -
			0.02$_{1,38.9}$	0.28$_{1,10.7}$	0.24$_{1,39.2}$					0.04$_{1,39.2}$	
Aster falcatus	May	L	**0.007**	- - -	- - -	**0.049**	**0.003**	- - -	- - -	- - -	- - -
C:H			**7.76**$_{1,60.1}$			**4.86**$_{1,11.4}$	**9.50**$_{1,57.7}$				
		Q	0.082	- - -	- - -	0.071	**0.017**	- - -	- - -	0.330	- - -
			3.14$_{1,57.7}$			3.95$_{1,11.8}$	**6.00**$_{1,57.8}$			0.96$_{1,57.5}$	

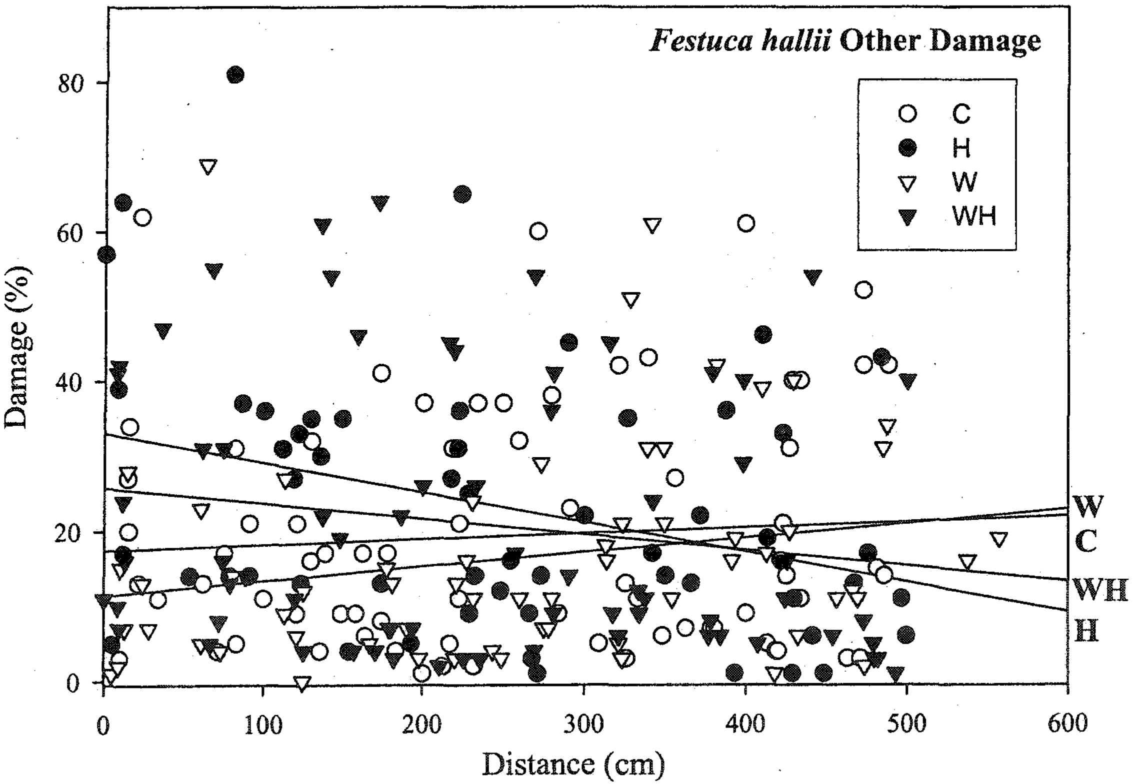
Appendix Table D.1. Continued

Species	Time Model		Distance	Trail	Distance *Trail	Trampling	Distance* Trampling	Trail* Trampling	Distance* Trail* Trampling	Distance^2	Distance^3
Aster falcatus	May	L	0.128	- - -	- - -	0.774	0.405	- - -	- - -	- - -	- - -
W:WH			$2.24_{1,31.8}$			$0.09_{1,13.5}$	$0.71_{1,32.1}$				
		Q	0.921	- - -	- - -	0.854	0.343	- - -	- - -	0.597	- - -
			$0.01_{1,30.2}$			$0.04_{1,14.5}$	$0.93_{1,31.1}$			$0.29_{1,30.6}$	
Aster falcatus	May	L	**0.000**	0.095	0.251	- - -	- - -	- - -	- - -	- - -	- - -
H:WH			**$16.60_{1,51.5}$**	$2.90_{1,53}$	$1.35_{1,52}$						
		Q	**0.018**	0.110	0.456	- - -	- - -	- - -	- - -	0.198	- - -
			$5.94_{1,49.3}$	$2.64_{1,51.6}$	$0.57_{1,49.9}$					$1.70_{1,48.4}$	
Rosa arkansas	May	L	0.326	- - -	- - -	0.500	0.735	- - -	- - -	- - -	- - -
C:H			$0.97_{1,89}$			$0.47_{1,20.6}$	$0.12_{1,78.2}$				
	Aug	L	0.423	- - -	- - -	0.375	0.228	- - -	- - -	- - -	- - -
	Insect		$0.65_{1,72.7}$			$0.80_{1,84.2}$	$1.47_{1,90.5}$				
	Aug	L	0.167	- - -	- - -	0.817	0.618	- - -	- - -	- - -	- - -
	Other		$1.95_{1,73.8}$			$0.05_{1,73.5}$	$0.25_{1,71.7}$				
Symphoricarpos	May	T	0.264	- - -	- - -	0.795	0.604	- - -	- - -	0.121	0.075
occidentalis			$1.27_{1,71.7}$			$0.07_{1,17.2}$	$0.27_{1,72.1}$			$2.47_{1,72.9}$	$3.27_{1,73.3}$
C:H	Aug	L	0.821	- - -	- - -	0.333	0.586	- - -	- - -	- - -	- - -
	Insect		$0.05_{1,75}$			$0.97_{1,31.3}$	$0.30_{1,75}$				
	Aug	L	0.729	- - -	- - -	0.786	0.367	- - -	- - -	- - -	- - -
	Other		$0.12_{1,70.3}$			$0.08_{1,14.2}$	$0.82_{1,71}$				
Symphoricarpos	May	Q	0.799	- - -	- - -	0.918	0.686	- - -	- - -	0.770	- - -
occidentalis			$0.07_{1,88.5}$			$0.01_{1,24.5}$	$0.16_{1,91.3}$			$0.09_{1,91.1}$	
H:WH		T	0.337	- - -	- - -	0.908	0.612	- - -	- - -	0.272	0.240
			$0.93_{1,87}$			$0.01_{1,24.8}$	$0.26_{1,90.3}$			$1.22_{1,87.5}$	$1.40_{1,87.7}$
	Aug	L	0.227	- - -	- - -	0.310	0.849	- - -	- - -	- - -	- - -
	Insect		$1.48_{1,89.9}$			$1.07_{1,26.4}$	$0.04_{1,89.9}$				
	Aug	L	0.192	- - -	- - -	0.603	0.953	- - -	- - -	- - -	- - -
	Other		$1.73_{1,87.2}$			$0.27_{1,88.5}$	$0.00_{1,86.9}$				



Appendix Figure D.1. Experimental Design: One treatment plot with cover transect (CT) and transects for destructive sampling (DT). Position of DT (01 or 02) And side of sampling randomly determined in 2001. Transects start at trail center, represented by the broken line. Cover estimates are taken at two scales; **5m** in 20x 50 cm quadrats and **2m** in 10x 10cm quadrats. Along the destructive transect, standing biomass is sampled in 20 x100cm quadrats. Individual plants were located along DT-02, and each symbol represents a different species.





Appendix Figure D.2. Insect damage for *Achillea millefolium* and damage due to other factors for *Festuca hallii* in 2002. Symbols represent actual data points, and **W**= wildlife trails without human trampling, and **WH**= wildlife trails with human trampling, **H**= trail from weekly human trampling, and **C**= control areas.