

INFLUENCE OF NATIVE BUNCHGRASS AND INVASIVE FORB LITTER
ON PLANT GROWTH IN
A SEMI-ARID BUNCHGRASS PRAIRIE

by

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GLOSSARY

invasive species — (continues to be debated and redefined with research findings) plant species that both spread in space and have negative effects on species already in the space that it enters; in addition, not indigenous to the landscape, non-native, introduced invasive species, new harmful colonizer, aggressive competitor (Lapina et al. 2004; Alpert et al. 2000; Invaders Database System 2003)

invasive or native site — invasive refers to the study site inside the >40-year exclosure fence having dense canopy of *Hypericum perforatum* species versus native reference to the study site outside the fence having species composition consistent with rough fescue and bluebunch wheatgrass *Agropyron spicatum*/*Festuca scabrella* species composition (Mueggler and Stewart 1978)

native plant or species — indigenous to a site, originating at the site

indigenous — originating in and characterizing a particular region or country

plant litter — above-ground senesced (mature) plant material

plant species availability — plants available for colonization because they exist in the landscape at the time of the study

plant litter resource — aboveground plant material and its microclimate

species pool — the nature of plant species and numbers living within the ecosystem, such as propagules available to colonize when a safe site becomes available for the plant part or seed to establish or germinate (Sheley et al. 1996)

species performance — a plant's response potentially to interactions within a plant community such as increase or decrease in the number of plants, amount of space or percent cover the plant fills, and biomass production of new growth in one year

density — measurement of the total number of plants within a given area (can be measured by plant groups or individuals)

annual net primary production NPP — aboveground biomass new growth in one year measured in dried weight (Gurevitch et al. 2002)

ungulates - grazing animals

ABSTRACT

Litter can influence plant species diversity. I investigated plant litter effects for density, cover, and biomass on common St. Johnswort *Hypericum perforatum* L., a non-native-species-group, and a native-species-group. The following hypotheses were tested: litter source would favor species dominant in the litter; the high amount of litter (908 grams) would decrease density more than the moderate amount (454 grams); coarse size litter would decrease density more than fine size; and the effect of litter would depend upon interactions of all three variables. Above-ground plant material was removed from two adjacent sites, one a native bunchgrass prairie (native site), the other infested with St. Johnswort (invasive site). Three-way litter treatments were applied in October 1999 and reapplied in July 2000 in combinations of high- or moderate-amount of litter, native or St. Johnswort species by source, and fine or coarse texture by size. Sampling occurred at peak standing crop July 2000 and 2001. Analysis of variance in 2001 data results follow.

St. Johnswort was decreased by its own litter (all $P < .06$). St. Johnswort and native species were detrimentally influenced more by the high amount of litter than by the moderate amount (all $P < .05$). Although litter size did not influence St. Johnswort, native species biomass was more detrimentally influenced by coarse size litter than by fine ($P < .05$).

When we added more fine size litter, native species were more detrimentally influenced than when we increased the amount of coarse litter ($P < .06$).

In the invasive site, moderate amounts of coarse native litter decreased St. Johnswort. High amounts of coarse St. Johnswort litter decreased it even more (both $P < .05$). The opposite effects were found for native species (both $P < .05$).

In the native site, the only treatment that reduced St. Johnswort more than no litter was the high amount of fine St. Johnswort litter ($P < .05$). The same fine St. Johnswort litter in moderate amounts was the only treatment that did not decrease native species ($P < .05$).

The complexity of litter influence through interactions of amount, source, and size detrimentally and non-detrimentally caused changes to plant species diversity at each site (all $P < .05$).

INTRODUCTION

Objectives and Hypothesis

Invasibility depends more upon the interaction between non-native species and potential new habitat than upon the characteristics of the invading species alone (assessment of studies on invasiveness compiled by Alpert et al 2003; Longsdale 1999; Mantas 2001). Non-native species are not always invasive. Some non-native species can remain non-invasive for long periods of time, even when they spread from human-made habitats into natural ones. Why would it be that in two adjacent sites that *Hypericum perforatum* L. would exhibit invasive characteristics in the site that was fenced for >40 years and not in the other? At some point after introduction to both sites, *H. perforatum* colonized and formed a dense canopy in the fenced site suggesting increased invasiveness not found outside the fenced site in the native bunchgrass prairie. The symptom was an obvious dense canopy of *H. perforatum* in the fenced site that will be referred to as the invasive site. Was it the plant trait, phenology, that prompted *H. perforatum* to shift dominance inside the fenced (invasive) site? The invasive weed scientist community believed, that allowing the litter to accumulate by native bunchgrass species that evolved with large ungulate grazing that can kill perennial grasses is the reason for the abundance of *H. perforatum* in the native bunchgrass prairie. The death of the plants opened sites for new colonizers. *Hypericum perforatum* propagules were available to colonize. As more grass plants died in this manner, more *H. perforatum* plants filled the niches for space and resources. Today near the study site other non-indigenous species are colonizing sites left open by dying grass: *Bromus tectorum* L., *Potentilla recta* L., *Linaria dalmatica* L., *Cynoglossum officinale* L., and *Centaurea maculosa* L.

If litter could indirectly affect resource limiting factors such as the amount of light and moisture required for seed germination; alter microclimate temperature or alter habitat for herbivores; or act as physical, mechanical, or chemical influence on seedling establishment, or by delaying shoot extension and the timing of the leaf unfolding that delays photosynthesis required for plant growth; then litter effect could temporarily shift factors that influence site invasibility. The objective was to look at the causes (litter effect) associated with species density, percent cover, and biomass in *H. perforatum* and native grass and forb species in both the invasive site and the non-invasive (native) site. The non-invasive native site will be referred to in following pages as the native site. Implications of this added knowledge could potentially aid land managers, once non-indigenous species are introduced to a site, to manage litter influence in order to influence temporal or spatial overlap to favor indigenous species.

The first objective was to determine interaction effects of litter source (non-indigenous or indigenous species), amount (454 or 908 grams), and size (fine or coarse texture) on non-indigenous and indigenous species groups' density (number of plants), percent cover, and biomass. The hypothesis is that the effect of litter on the non-indigenous species group (*Hypericum perforatum*, *Bromus tectorum*, and *Potentilla recta*) and indigenous species group (up to fifteen native forb and grass species dependent upon site) density, percent cover, and biomass will depend on some combination of litter source, amount, and size. The next hypothesis is that the effect of litter on the indigenous species group will depend on some combination of litter source, amount, and size.

The second objective was to determine litter source (*Hypericum perforatum* or indigenous species) effect on *H. perforatum* and indigenous species group density, percent cover, and biomass production. The hypothesis is that *Hypericum perforatum* litter will increase *H. perforatum* density, percent cover, and biomass.

The third objective was to determine litter amount (454 grams or 908 grams field weight) effect on *H. perforatum* and native grass and forb species assuming reduced density, percent cover, and biomass. The hypothesis is that increasing the litter amount to the high level (908 grams) will decrease *Hypericum perforatum* or indigenous species group density, percent cover, and biomass.

The fourth objective was to determine litter size (texture), either finely mowed (fine) or coarsely intact (coarse), effect on *Hypericum perforatum* or indigenous species group density, percent cover, and biomass. The hypothesis is that increasing texture to the coarse size will decrease *Hypericum perforatum* and indigenous species group density, percent cover, and biomass.

Literature Review

Hypericum perforatum in Pristine Rangeland

It is well established that *H. perforatum* can and does invade pristine rangeland (Piper G.L. 1992; Powell et al. 1994) and crowd out native and desirable plant species (Invaders Database System 2003; Piper 1999; Coombs 2004). Once *H. perforatum* invades grasslands and pastures it is capable of changing plant community structure by forming dense stands (Powell et al. 1994; Tisdale et al. 1959; White et al. 1994). This dense canopy can reach more than 90 cm (3 feet) in height and may overtop other pasture forb and grass species (Crompton et al. 1988). Native plant community composition is modified when *H. perforatum* displaces indigenous species (Rutledge and McLendon 1996). Dense stands of *H. perforatum* affect ecosystem function by depleting soil moisture (Invaders Database System 2003). *Hypericum perforatum* is known to move water throughout the soil profile and create reserves that allow it to survive long periods of drought.

Hypericum perforatum Reproduction by Seed and Rhizomes

Hypericum perforatum reproduces vegetatively and by seed. *Hypericum perforatum* seeds exhibit both exogenous (characterized by the addition of layers of woody tissue) and endogenous (originating from within an organ or part) dormancy. Seeds require light for germination (Pank et al. 2003). The short root-runners spread horizontally and form new buds (Rutledge and McLendon 1996). *Hypericum perforatum* can sprout from buds on lateral roots. Grazing, mowing, or fire can stimulate the vegetative propagation of *H. perforatum* (Tisdale et al. 1959). The root system of seedlings commonly attains a depth of about 30 cm (one foot) during its first growing season. Mature plants have an extensive root system which extends 120 to 150 cm (4 to

5 feet) in depth and about 90 cm (3 feet) laterally. The deep root system is capable of supporting the plant when soil water has been depleted (Tisdale et al. 1959). *Hypericum perforatum* can delay establishment of indigenous species in disturbed sites (Campbell 1985). A 2-year study in Idaho documented that each plant can average 23,350 seeds. Seeds are spread primarily by water and animals (Rutledge and McLendon 1996) and by wind up to 900 cm (30 feet) from the plant (Tisdale et al. 1959). Seeds have a sticky gelatinous coat that can adhere to wildlife and human clothing (Crompton et al. 1988 cites Sampson and Parker 1930). *Hypericum perforatum* seeds require bare soil, sunlight and/or heavy rain for germination (Tisdale et al. 1959), and high levels of litter can generally inhibit *H. perforatum* seed germination (Rutledge and McLendon 1996).

Hypericum perforatum Compounds

Hypericum perforatum contains the compounds hypericin and pseudohypericin, a broad range of flavonoids including quercetin, amentoflavone, and hyperin, the phloroglucinols hyperforin and adhyperforin, and the essential oil (Upton et al 1997). Plant compounds in *H. perforatum* alter microclimates that can negatively affect animals, fungi, and microbes (Whitson et al. 2000; Powell et al. 1994; Rutledge and McLendon 1996). Light-skinned and haired animals that ingest large quantities of *H. perforatum* can develop severe dermatitis when they are exposed to strong sunlight. Hypericin and pseudohypericin compounds increase in the leaves and flowers with plant growth. Briskin and Gawienowski (2001) (Briskin et al 2000) found that site differences and light differences influenced production of leaf hypericin in *H. perforatum*. Secondary compounds can be initiated by plants as defense (Sirvent and Gibson 2002; Gurevitch et al. 2002) and potentially influence competition between species. Tisdale et al. (1959) suggested that perennial pasture grasses are more competitive plants compared to *H. perforatum*.

Management Studies
on *Hypericum perforatum*
in Native Perennial Grassland

Hypericum perforatum is difficult to control because of its extensive root system and long-lived seeds. Tillage, hand pulling, mowing, or burning appears to be ineffective because vegetative reproduction may be stimulated by mechanical treatment (Tisdale et al. 1959). *Hypericum perforatum* can be controlled by herbicide (Piper 1999). However, wax on the leaves may inhibit herbicide uptake (Invaders Database System 2003). Biological control has been relatively successful using several leaf-feeding beetles (Piper 1992). However, in Canada and at high elevations these insects do not thrive (Rutledge and McLendon 1996; White et al. 1994). Herbicides are often too costly to be of practical value as a management tool for extensive infestations of *H. perforatum* according to Piper (1992 and 2004). Herbicide treatment approaches for small infestations on pasture grasslands follows (Sheley and Petroff 1999 *editors*: Piper 1999 cites William et al. 1996; Crompton et al. 1996): – 2, 4-D at a 908 grams acid equivalent per acre (ae/ac) (2.24 kg ae/ha) rate to kill the plant in the seedling and pre-flowering stages (cites William et al. 1996). Ester formulations of phenoxy herbicides may be more effective than amine or salt formulations (cites Crompton et al. 1988). Spring applications of picloram (0.125 to 1.5 lb acid equivalent per acre [ae/ac] [0.14 to 1.68 kg ae/ha]) or glyphosate (0.187 to 0.375 lb ae/ac [0.21 to 0.42 kg [ae/ha]]) are recommended for the suppression of the weed in pasture, rangeland, and non-cropland sites (Piper 1999).

Jacobs and Sing (unpublished) in a study of *L. dalmatica* found that herbicide use harmed other indigenous forb species when it was applied before the optimum time for its intended target. Pokorny et al. (2005) found that functional group diversity (a set of species that fill all of the niches in a given site), particularly forb diversity, is important

for invasion resistance. Herbicide use can kill non-target species in rangeland settings and decrease diversity, thereby reducing weed-resistance.

Hypericum perforatum L., common St. Johnswort (Upton et al. 1997) is known to invade and form dense canopies in pristine rangeland (Lapina et al. 2004; Invaders Database 2003; Mantas and Jones 2001; Piper GL 2004). Much is known about *H. perforatum* life history and ecophysiology because of its cultivation for use in medicine since its introduction to the U.S. as early as 1793 (Upton et al. 1997). Less is known about *H. perforatum* performance in rangeland settings where it escaped cultivation to infest more than 1.5 million hectares (3.75 million acres) by 1945 in California (first reported about 1900), Idaho (before 1920), Montana (about 1800), Oregon (about 1850), and Washington (since early 1900) (Coombs et al. 2004; Invaders Database System 2003; Piper 1992). *Hypericum perforatum* is listed as a noxious weed in seven states and two provinces in North America (Coombs et al. 2004; Invaders Database System 2003; Piper 2004).

Hypericum perforatum is inventoried on 16,775 hectares (68,065 acres) in Montana (Montana Noxious Weed Summit Advisory Council 2004). Once introduced to pristine and disturbed sites, *H. perforatum* can change plant community structure because it forms dense stands with canopies that reduce resource availability to other plants (Piper 2004; Powell 1994; Tisdale and Hironaka 1959; Whitson 2000).

Common management practices for *H. perforatum* vary in effectiveness at different sites (Clark 1953; Coombs et al. 2004; Cortesero et al. 2000; Crompton et al. 1988; Invaders Database System 2003; Piper 2004; Powell 1994; Sheley and Petroff 1999; Tisdale and Hironaka 1959). Herbicide application is expensive in rangeland systems (Piper 1999; Piper 2004) and release of biological control agents is effective in some ecosystems (Coombs et al. 2004). Although the National Bison Range narrative reports suggest a cyclical effect of biological control on *H. perforatum* near the study

site, in Canada and at high elevations the biological control agent *Chrysolina* sp. does not thrive (Piper 2004; Wedin and Tilman 1990).

Fire (Invaders Database System 2003), grazing, and mechanical control methods (Jacobs et al. 2003) can lead to new growth from buds on its roots (Tisdale and Hironaka 1959; Santarem et al 2003). Concern for management by grazing, and time of grazing (Southwell and Bourke 2001), is because of phytotoxic and cytotoxic properties (Lapina et al. 2004; Couceiro et al. 2006; Invaders Database System 2003) of compounds and flavinoids produced in the *H. perforatum* glands and secretory canals.

These active compounds have been shown to pose a health risk to grazing animals, especially those with light skin. Blistering of the throat and sensitivity to sunlight, including blindness, was reported by the Invaders Database System (2003). Blistering of skin and eyes was reported by the American Botanical Society in 2005 (citing Upton et al 1997) in the case of humans collecting *H. perforatum* for its use in herbal medicine. Essential oils (Schwob et al 2002), hypericin, and other compounds increase in aerial parts as the plant grows (Schwob et al 2004). *Hypericum perforatum* active compounds influence photosensitivity (Cicarelli et al. 2001; Wilhelm et al. 2001) and inhibit growth of some human and animal cancer cells (Martinelli et al. 2004; Pasqua et al. 2003). A 2002 study suggests that *H. perforatum* compounds may inhibit prostate cancer cell growth in humans (Martarelli et al. 2004). Another study showed no evidence of effect in guinea pigs after injection of *H. perforatum* active compounds thought to stimulate excitation (Langosch et al. 2002).

Figure 1 (Page 9) illustrates identifying features of the mature perennial *H. perforatum* plant, Clusiaceae (Lindl.), St. Johnswort Family (Kaul). The plant is many-stemmed and the inflorescence is a flat-topped, open, terminal cyme. The outer perimeter of the perianth (calyx) is broken by five equal sepals housing five yellow petals with numerous (>20) stamens in 3 fascicles. One pistil is compound with 3 to 5 carpels that

Figure 1. Species Identification — St. Johnswort (common) *Hypericum perforatum* L.



bear the ovule and subsequent numerous seeds (top left). Black and translucent glands develop on the leaves, thus the name *perforatum* (top right).

Disturbance and Invasive Species

Educational programs and surveys concerning perceptions about invasive plant species changed public awareness and opinions about soil and water quality, life styles, food resources, fish and wildlife habitat, recreational opportunity, and land use (Sell et al. 1999; Hoopes et al. 2005). Environmental, ecological, and economical concerns (Coombs et al. 2004; Hoopes et al. 2005; Invaders Database System 2003) associated with invasive species movement in semi-arid rangeland in the northwestern United States make it essential that development of management strategies be based upon our understanding of the biology and ecology of these native systems (Sheley et al. 1996; Sheley and Petroff 1999; Tilman and Wedin 1991). Consideration for how we use the land is commonly included in the development of management strategies, both near- and long-term (Jacobs et al. 2003). Recent studies by Sheley et al. (1996) suggested that effective managers of weed-infested-rangeland will be those who incorporate knowledge of site-specific resources and processes with “designed” strategies that influence modifying factors in favor of desired vegetation. Sell et al. (1999) surveyed land managers regarding leafy spurge infestations in rangeland settings and suggested that factors such as cost to control non-indigenous species that exhibit invasive characteristics, perceptions of success and what that means to land use goals, and access to cooperative resources are important considerations when choosing management strategies.

In the United States, federal and state park and range land managers work in partnership with the private sector in the U.S. Bureau of Land Management initiative

known as cooperative weed management areas (CWMA). CWMA (similar to non-profit [NGO] invasive plant control [IPC] organizations in the eastern U.S. and California, according to the National Invasive Species Council [2006]) are common in the western United States because they are designed to initiate shared resources for the purpose of achieving common land use goals (Montana Noxious Weed Summit Advisory Council 2004). Participants in CWMA initiate dialogue in order to develop invasive species management strategies that address common issues of public land use and access, and its impact on public and private resources. Noxious weed roundtables, watershed groups, and CWMA form because management strategies will affect multiple uses of the defined landscape(s) and ecosystem(s). Land use is one example of continuous or duration-based disturbance that can open sites for new colonizers such as non-indigenous species to establish and grow (Sheley et al. 1996). The Sheley et al. (1996) successional rangeland weed management predictive model was designed to address mechanisms that influence how plant communities move toward a climax state because of site availability, species availability, and species performance each associated with contributing processes and modifying factors (modified from Pickett et al. 1987). Tilman (1990) suggested that plant communities will have constraints and tradeoffs with underlying mechanisms based on the actual constraints of each environment and the tradeoffs organisms face. It is important to understand the biology and ecology of the specific site, especially in sites at risk for new non-indigenous colonizers (Mantas et al. 2001), in order to make management decisions that constrain invasive species in favor of desired species composition. Tilman (1990) suggested that competition and mechanism models, such as those that limit resources and disturbance, are easier to test than those dealing with environmental phenomenon.

Invasibility, Species Composition, Disturbance, and Duration

United States National Park Service Director Mainella led the February-March 2006 briefing with delegates from fifty U.S. states and Canada at the National Invasive Weed Awareness Conference in Washington, D.C. concerning invasibility in rangeland and parkland. Invasibility models, such as environmental stress on species performance, allow us to predict potential shift in community vegetation toward or away from dominance by an invading species (Alpert et al. 2000). Plants that are introduced (not indigenous to the ecosystem) are typically referred to as invasive species because they can exhibit highly competitive characteristics and reduce diversity. It is commonly understood that some native species are invasive in some sites, and not all introduced species exhibit invasive characteristics, or invasive characteristics in every site. Director Mainella agreed that species physiology can play a strong role in species response that will vary between sites and disturbance (Woitke and Dietz 2002; Warren et al. 2002).

Warren et al. (2002) investigated dominance by size or complementarity in a series of pot experiments with eight grass species in combinations of pair sets and community levels. They found that larger size species were generally more competitive than smaller ones suggesting that aboveground size would be an important determinant of competition and subsequent regulation of community structure. However, after comparison in biomass between the pairs of species and the difference in relative competitive abilities, they found in some cases smaller and larger species were equally competitive. They also found that similarly sized species sometimes had very different competitive abilities. Absence of one species had a significant effect on the relative biomass of those remaining. In a controlled field study, Woitke and Dietz (2002) tested regenerative processes of two non-indigenous and four indigenous forb species, disturbance modes and duration, and species composition influence on species

performance. Their findings were consistent with different response from non-indigenous species due to type of disturbance (soil perturbation or mowing), and strongly dependent upon species composition because of canopy or regenerative mode that decreased over time, and duration effect that increased over time. Less is known in rangeland systems about litter canopy influence on community weed-resistance.

Weed Resistant Communities and Shift in Invasibility

The implication of weed-resistant rangeland plant communities (Sheley and Carpinelli 2005) is associated with resource availability, species availability, and species performance. Recent studies suggest that functionally diverse plant communities are those that fill the niches for available resources (Pickett et al. 1987; Tilman and Wedin 1991; Sheley et al. 1996; Sheley and Carpinelli 2005; Jacobs et al. 2003; and Krueger-Mangold et al. 2004). If a functionally diverse plant community utilizes all available resources (the definition of functionally diverse), then resources will not be available to invasive plant species. In that scenario, Sheley and Carpinelli (2005) suggested that invasive species may be less likely to establish. In their recent study testing plant species richness, they found that spotted knapweed *Centaurea maculosa* L. density was decreased when species richness, the number of different species on the plant community list, increased. *Centaurea maculosa* L. density was decreased in the presence of three functionally diverse species versus in the presence of a monoculture (single functioning species). Sheley and Carpinelli (2005) findings were consistent with the concept that functionally diverse species composition may utilize the resources that could otherwise become available to invasive species, in this case *C. maculosa*. Weed resistance (Sheley and Carpinelli 2005) and concepts that environmental stress can influence invasibility (Alpert et al. 2000) are associated with functional diversity

(Pokorny et al. 2005). These concepts contrast with theories that the mere presence of a non-indigenous species in the colony will cause shift in vegetation assemblage (Woitke and Dietz 2002) because of aggressive or competitive characteristics. Presumably then, disturbance (such as litter alteration) to influence species performance and availability could potentially influence community-wide diversity (Woitke et al. 2002; Pokorny et al. 2005), weed-resistance (Sheley and Carpinelli 2005), and invasibility (Alpert et al. 2000).

Overall Aboveground Plant Litter Effect on Species Performance

Litter effect on plant community structure was vigorously studied in field experiments and in green house and pot studies suggesting that litter source, litter amount, and litter size may have subtle to strong influence on species performance. Topics range from seedling heights (Olson and Wallander 2000) and germination rates (Bosy and Reader 1995; Crak et al 2004; Faron et al. 2004) to resource availability in restoration (Baer et al. 2004). Litter influenced decomposition rates by soil biota specific to litter source (Ayers et al. 2006). Seedling survival and growth was effected after invasive species removal (Hager 2004). Leaf-litter effected riparian plant diversity (Nilsson et al. 1999). Other topics included germination and seedling growth (Peterson and Facelli 1992), canopy effects (Gurevitch et al. 2002), and soil microbial activity response to temperature, moisture, and litter leaching (Qiu et al. 2005). Herbivory was linked to litter decomposition, litter quality, and vegetation response (Wardle et al. 2002) and nitrogen dynamics (Svejcar and Sheley 2001), carbon transfer of micorrhizae from an indigenous bunchgrass to a non-indigenous invasive species (Carey et al. 2004; Walling and Zabinski 2004), and allelopathic compounds associated with resource availability (Ridenour and Callaway 2001). Litter influenced macrodetritivores (Mayer et al. 2005). Removal of species litter opens pathways for another invsive species (Greiling

and Kichanan 2002). Non-indigenous litter effected soil nutrient cycling processes (Ehrenfeld 2003). A meta-analysis of litter research was conducted in 1999 Xiong and Nilsson (1999).

Xiong and Nilsson (1999) summarized litter studies prior to 1999, most of which were forest related experiments. Their summary included 8 points: 1) species richness, or the number of different species on the plant community list, was more affected by litter than combined species above-ground biomass (annual net primary production [NPP]); 2) litter affected seedling germination more than plant establishment; 3) litter was shown to have more effect over two years than one and in the field more than in the greenhouse; 4) biomass after one year and increased after three years; 5) latitude increase decreased absolute effects of litter on germination; 6) ecosystem type played a role in litter effects; 7) litter source, primarily forb species and tree leaves, had a stronger effect on vegetation than grass litter; and 8) higher amounts of litter generally resulted in decreased overall vegetative biomass. The following literature discussion includes recent findings about litter amount, source, and size effect on species performance through mechanisms defined as physical, chemical, and mechanical.

Litter Source, Amount, and Size Effect on Species Performance

Ehrenfeld (2003) compiled available data that compared pool sizes and flux rates of the major nutrient cycles in invaded and non-invaded systems for invasions of 56 exotic (invasive non-native) species. Ehrenfeld (2003) summarized that exotic plants alter soil nutrient dynamics by differing from indigenous species in biomass and production (frequently but not always increased biomass and net primary production), tissue chemistry, plant morphology, and phenology.

Wedin and Tilman (1990) tested five perennial grass species on a variety of soils for their competition for and utilization of soil nitrogen (N). They found plant litter

feedback (individual species biomass production) and processes that structure vegetation directly related to production of and competition for N. They suggested that annual net primary production and subsequent litter quality were dependent upon species competition for resources, whereas if a species that competes well at low N availability produces litter with high N it could generally be displaced by a species that competes well at high N. The study also suggested that species-specific feedback by litter effects could create localized soil differences that contribute to maintenance of local species diversity.

Olson and Wallander (2002) utilized litter packs as a mechanical barrier in order to influence the amount of irradiation to seeds and seedlings under litter packs. Their finding show that although litter type did not affect seed germination, seedling heights differed by litter type with the tallest seedlings covered by *C. maculosa* and the shortest seedlings were those with no litter. Bosy and Reader (1995) reduced seed germination of four different herb species by using grass litter.

Bosy and Reader (1995) tested grass litter influence on one perennial grass and four forb species (one of which was *H. perforatum*) seedling emergence in a greenhouse or laboratory to better understand the mechanical barrier to shoot extension, physical alteration of the environment by changing light and temperature, and chemical compounds that alter the environment of seeds and inhibit germination. Their litter trays contained more litter than did those of Olson and Wallander (2002) and that could explain the different germination rates. Litter reduced irradiance (light) and air temperature. Litter suppressed seed germination of *H. perforatum* reducing it by 38% of the control (no litter). *Hypericum perforatum* has a small seed, however the other species with the small seed was only reduced by 14%. Litter leachate did not reduce germination of the two small seeded forb species. However, it significantly reduced germination of the two larger seeded species. Grass litter reduced shoot extension for all four species.

Small seeded species and large seeded species seedling emergence was completely (100%) (95 and 96% respectively). When all three mechanisms (physical, chemical, and mechanical) were combined, litter reduced seedling emergence for all four test species; seedling emergence was completely suppressed for two small seeded forb species. Seedling emergence was reduced by 25% and 41% for the two larger seeded forb species. Their findings were consistent with the suggestion that litter removes environmental cues such as light and air temperature that are required for seed germination and subsequent seedling emergence. Their findings were consistent with the suggestions that leachate may influence seed germination and that the mechanical barrier may block shoot extension.

Ayers et al. (2006) tested soil organism response to three tree species litter in a similar environment to see if species encourage soil biota that specialize in the rapid decomposition of their litter. Their findings were consistent with effects on respiration rate by both date and litter type. Litter type was responsible for large differences in respiration rates in the first 70 days. However, the final results at the end of the study showed no difference. They found no support for the concept that tree species mitigate soil biota that favor rapid decomposition and release of nutrients from their own litter.

Ellsworth et al. (2004) tested the physical texture of litter on seedling survival, growth and allocation in a study of Oriental bittersweet, an invasive vine, in a greenhouse. Seeds were placed under deciduous leaf litter in amounts ranging from zero to the equivalent of 16 Mg ha⁻¹. Seedling emergence was not affected by fine size litter, but decreased to <20% as coarse intact litter amount increased to 16 Mg ha⁻¹. As litter amount increased, increased allocation went to hypocotyl and less to cotyledon (above hypocotyl) and radicle, and this effect was greater with intact litter.

Hager (2004) tested the effect of neighboring plants and litter including their removal (four levels) on the non-indigenous invasive species purple loosestrife *Lithrum*

salicaria L. in nine *Typha*-dominated marshes with no standing water. They found no affect on *L. salicaria* seedling survival in the presence of *Typha* plants and litter in the relatively dry wetland site. However, removal of both plants and litter in drier wetlands allowed increased growth of *L. salicaria* seedlings. They recommended no disturbance in wetlands at risk to invasion by *L. salicaria*, or small scale strategic disturbance for control. In dry sites, the presence of both plant and litter effect on the growth of *L. salicaria* suggests that plants and litter affect the same limiting resource. In combination, plants and litter reduced that resource to lower levels than when either was removed.

Nilsson et al. (1999) tested leaf-litter levels on riparian vegetation along gradients ranging from complete litter removal to addition of up to 6000 g/m² (35-40 cm deep). Nilsson et al. (1999) took into consideration external factors such as disturbance by river deposition of leaf litter and climate such as precipitation and light. Plant biomass decreased with increasing litter mass but did not vary with site-dependent variables such as climate and soil. Species density for various plant life traits varied with litter mass, summer air temperature, and summer precipitation. Litter biomass was found to be the most important variable for all life traits except for rhizomatous and stoloniferous species, which were more dependent upon summer precipitation. The implications for riparian sites along riverways where flooding deposits litter mass is that litter mass will be the primary predictor variable of relative changes to species density and plant biomass (climate second).

Peterson and Facelli (1992) tested litter influence on seedling establishment of two woody species having differing seed sizes. Leaf litter, needle litter, or their mix were applied in thin or deep layers over fifty seeds in standard greenhouse potting mix and watered to field capacity. Emerged seedlings and date of first leaf unfolding and seedling mortality were counted every 2-3 days for the first two months. The complete plant biomass was measured, dried and weighed. Litter cover significantly delayed

development of *Betula* seedlings with litter amount having effect (no effect for litter type on emergence of *Betula*). They found that the amount of litter is more important to seedling emergence than litter type when present in naturally occurring amounts. Size of seed and time of fall (whether above or below the litter layer), extension through litter layer (height of cotyledon) and delayed leaf mass for photosynthesis surface, and subsequent plant species robustness (decreased biomass), together, may leave the plant a poor competitor.

Implications of Litter Source

Litter accumulation may effect primary production and fragmentation (Liston et al. 2003). Liston et al. (2003) tested sexual reproduction versus clonal spread in a semi-arid bunchgrass community and presumed that litter accumulation in the center of the plant reduced tiller development and subsequent primary production. Litter source is important because plants can have primary metabolites for basic processes such as photosynthesis and secondary compounds that are initiated for defense or attraction of pollinators (Gurevitch et al. 2002). Leachate of these chemicals were shown to influence microbial activity (Qiu et al. 2005; Wardle et al. 2002).

Some biological control agents reduced and/or prevented the establishment of other more effective agents (Coombs et al. 2004). Coombs et al (2004) found that the leaf beetle *Chrysolina quadrigemina* may have inhibited the establishment of *Agrilus hyperici* on *Hypericum perforatum* in Australia by causing boom-bust oscillations of the weed (Coombs cites Briese 1977). The source of litter such as *H. perforatum* will contain secondary compounds (Moore 1979; Mosaleeyanon et al. 2005) that through leachate may influence herbivory, biological control agents and ungulates, and subsequent interactions with other plants and herbivores in a community (Coombs et al. 2004; Bosy and Reader 1995; Olson and Wallander 2002).

Materials and Methods

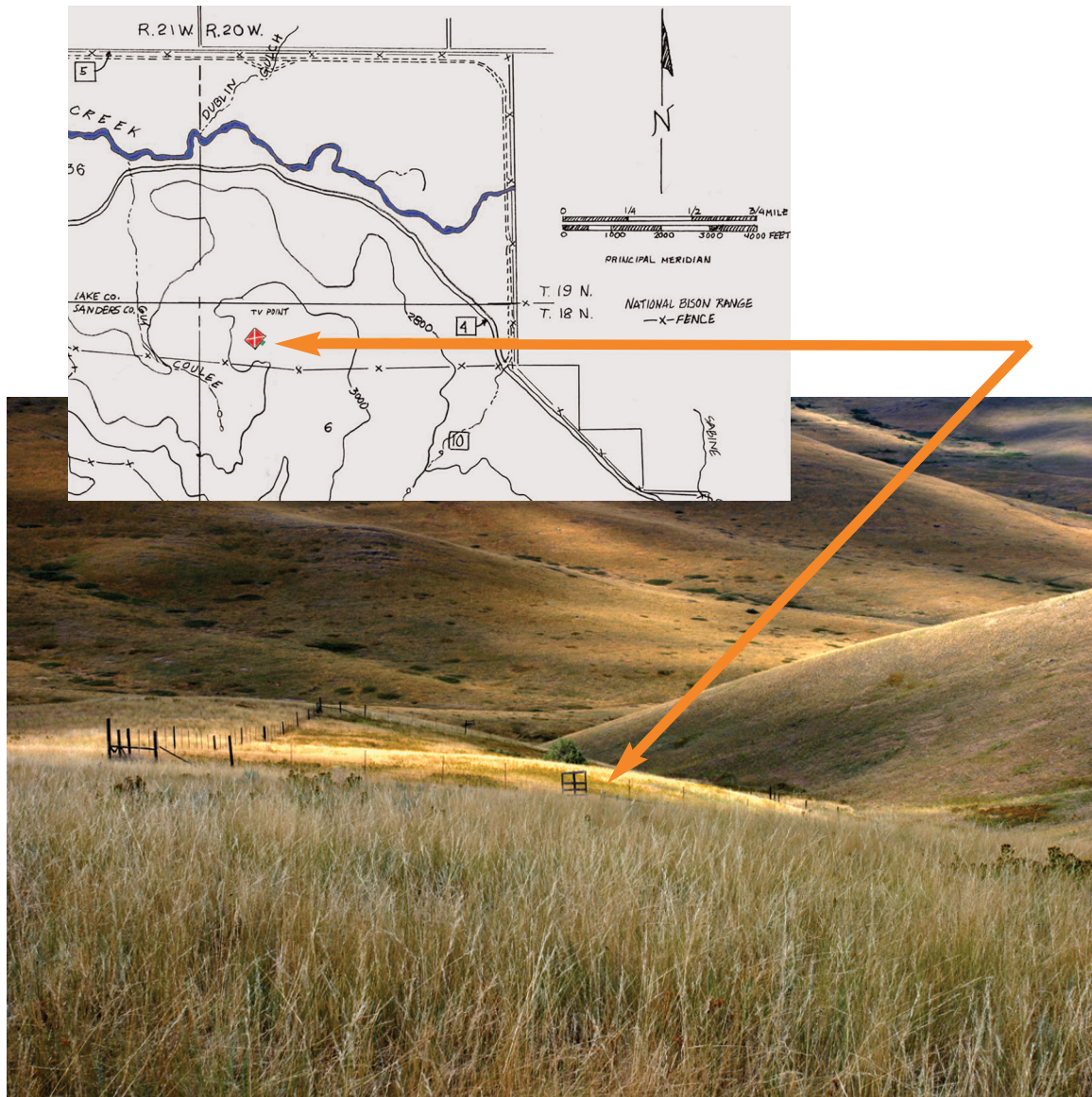
Study Site Description and Plant Material Collection

Two adjacent sites, one outside and one inside a >40-year exclosure fence, were used for the experiment. The vegetation diversity and structure appeared to be different at each site (Figure 3 Page 21). Historically, the site vegetation was the native *Festuca scabrella*/*Agropyron spicatum* plant association that is widespread in the northwestern U.S. and considered a late seral plant community (Mueggler and Stewart 1978). Generally in the surrounding area in protected low pockets where moisture appeared to collect, we observed the indigenous *Symphoricarpos occidentalis* Hook. (western snowberry) in association with *Hypericum perforatum*. National Bison Range narrative reports indicate that herbicide control of *H. perforatum* was discontinued in 1959 and the biological control agent *Chrysolina* sp. was released. More recent narratives (1999) document release of additional biological control agents (Figure 2) on non-indigenous species infestations near the site: *Centaurea maculosa* L., *Bromus tectorum* L., *Potentilla recta* L., *Linaria dalmatica* L., and *Cynoglossum officinale* L. The distance between the two distinct functional groups separated by a fence was approximately 3.6 meters (4 yards). Either side of the exclosure fence was selected to test two seemingly different plant communities in close proximity. The invasive site will mean the site inside the exclosure fence, and native site will mean outside the exclosure fence.

Figure 2. Biological Control Agents — *Anaitis piagiato*, *Zeuxidiplosis giardi*, *Chrysolina hyperici*, *Agrilus hyperici*, *Anaitis piagiata*, *Agrilus hyperici*, and *C. quadrogemina*.



Figure 3. Topographic Map and Site Photograph — The red highlighted box indicates the invasive site inside the enclosure fence adjacent to the native site. Orange arrows point to the location on both the topographic map and the photograph.



The study was conducted on a north-west facing hillslope of former Glacial Lake Missoula near Moiese, Montana (Figure 3), 64 km (40 miles) north of Missoula on the North Side Unit of the National Bison Range refuge located at T.18 N. 47° 21', R. 20 W. 114° 11'. Elevation is 960 meters (3,200 feet) with 38 to 48 cm (~15 to 19 inches)

annual precipitation. Confounding influence of climate and soil parent material was eliminated by using two adjacent study sites (Wedin and Tilman 1996 and 1990). The soil parent material is an argillite glacial till consistent with the description in the U.S. Geological Soil Survey (NRCS 1999). The major and minor landforms are foothill and hillslope. Both sites are located on a northwest aspect hillslope (29%) in a foothill environment. Two soil pits were excavated at the same hour of the day (Figure 4), one in the invasive site and one in the native site. Samples were collected from each horizon and field soil profile descriptions were noted. Soil samples were analyzed by the Montana State University Soil Analytical Lab, Department of Land Resources and Environmental Sciences. Soil moisture content and weather changes occur throughout the day. In order to eliminate confounding weather and moisture distribution influence the pits were excavated and sampled simultaneously. Sampling included moisture, clay, rock fragments, pH (Table 2), and distribution of clay and moisture in the profile (Figure 4). Rock fragments were measured and counted on-site.

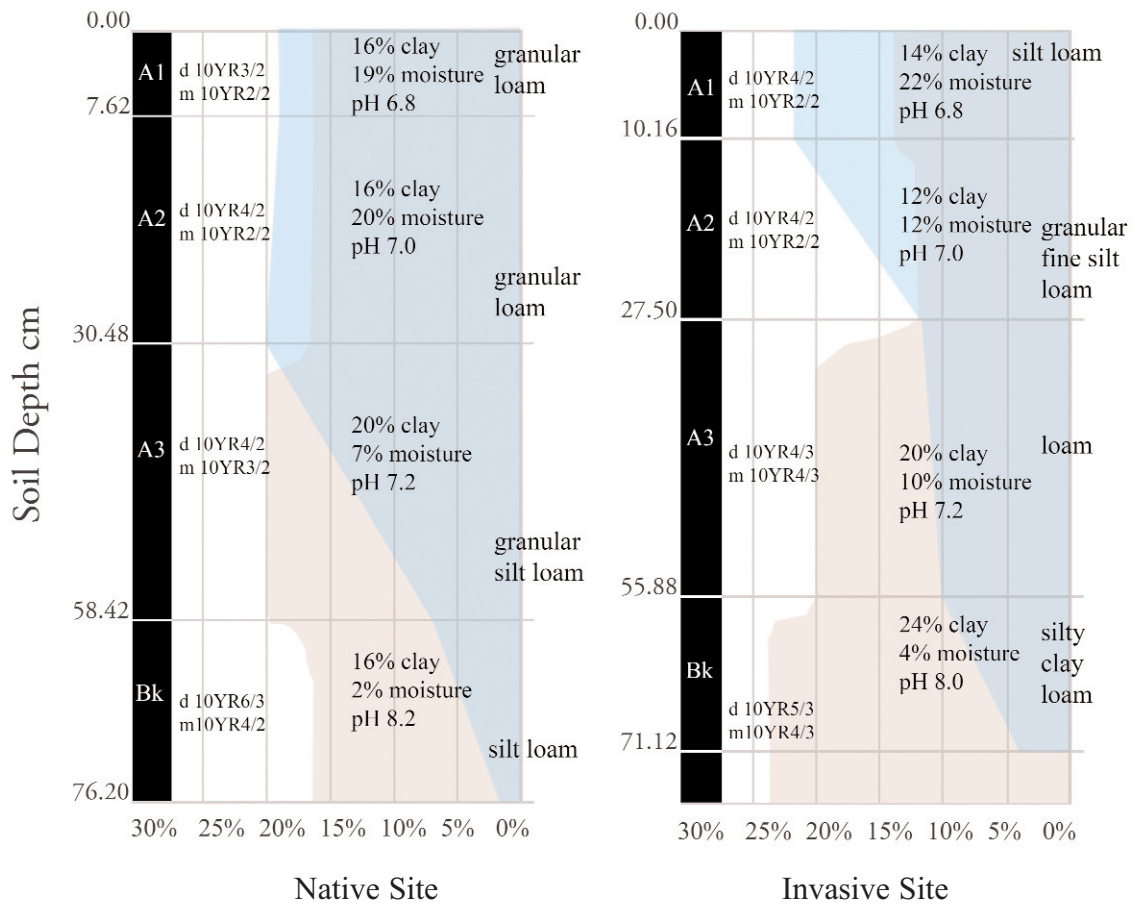
Table 1. Soil Organic Matter.

Site	Diagnostic horizon			
	A1	A2	A3	Bk
Invasive	5.60%	4.55%	2.25%	0.63%
Native	5.84%	3.55%	2.81%	0.48%

Table 2. Soil Moisture, Clay Content, Rock Fragments, and pH.

Site	Diagnostic horizon	Soil Weight in grams		% Moisture	% Clay	Rock Fragments		pH
		wet	oven dry			Volume	Weight	
Invasive	A1	825g	540g	22%	14%	2%	52%	6.8
Invasive	A2	1272g	1119g	12%	12%	25%	40%	7.0
Invasive	A3	3170g	2855g	10%	20%	20%	22%	7.2
Invasive	Bk	1568g	1510g	4%	24%	50%	74%	8.2
Native	A1	930g	756g	19%	16%	2%	41%	6.8
Native	A2	730g	587g	20%	16%	20%	31%	7.0
Native	A3	2955g	2739g	7%	20%	10%	84%	7.2
Native	Bk	1587g	1558g	2%	16%	5%	70%	8.2

Figure 4. Diagnostic Horizon Soil Pits.



The A diagnostic horizons had distinct color delineation separating A1, A2, and A3 (Figure 4). The Bk diagnostic horizon reflects Calcic soils determined by moderately thick lime crusts on the underside of larger rock fragments in the A3 and Bk horizons in both pits. The Bk horizon reflects the degree of calcium (CaCO_3) and magnesium carbonate (MgCO_3) in the soil. The rise in pH from A1 to Bk also indicated an increase in calcium and magnesium carbonate with depth. Soil color was matched both wet (moist) and dry to the Munsell Color Guide and is represented by d = dry soil and m = wet (moist) soil. The soil surface is represented as 0.00 soil depth. Sites will not be compared for the purpose of this study.

Experimental Design

In October 1999 we used a mulching mower with a collection back to remove and collect above-ground plant material to ~2.54 cm above the soil surface and applied eight combinations of non-indigenous or indigenous litter to 1.0 m² plots. Litter was collected and weighed in bulk in the field and applied within six hours. Litter collected from the native site and from the invasive site was applied in the following combination levels: 1) litter source (non-indigenous or indigenous), litter amount (454 or 908 grams), and litter size (finely mowed or intact coarse). No litter was applied to the control plot. The complete factorial was arranged in a randomized block design and replicated four times at each site (Figure 5). The aboveground plant material was clipped and removed during sampling in mid-July 2000 and litter was reapplied in the same manner (one treatment of two litter removals and applications - October 1999 and July 2000).

Figure 5. Field Study Site with Plot Stakes



Vegetation Collection and Preparation for Litter Treatment

Indigenous litter was collected from the indigenous grass and forb species “source” in the native site and kept separate from the non-indigenous litter that was collected from the non-indigenous species “source” inside the exclosure fence in the invasive site. Half of the litter was collected in a bag attached to a lawn mower creating “fine” size litter <7.62 cm length and kept separate from the other half of the litter that was clipped at ~2.54 cm above the soil surface and left intact to create “coarse” size litter. Litter was weighed in the field in brown paper bags with either 454 grams or 908 grams. Treatment combinations of amount, source, and size were individually and loosely spread horizontally with approximate equal distribution across 1.0 m² plots.

Sampling

At peak standing crop in July 2001 we counted and averaged species density (number of plants) within three sub-samples by random placement of a 0.2 x 0.5 meter (0.1 m) frame. Percent cover was estimated in each frame fashioned after Daubenmire (1970). Annual new plant growth (biomass production) was clipped at ~2.54 cm above the soil surface in each entire 1 m² plot and separated by species. Samples were placed in labeled brown bags and transported (five hours) to Montana State University Plant Growth Center where the bags were opened and placed in the oven at 60° C for 48 hours and weighed to obtain dry weight.

Statistical Analysis

Data were analyzed using a linear model analysis of variance (ANOVA) © 2002-2003 by SAS Institute, Cary NC, USA ® 9.1 (TS1M3) to determine the main effects and interactions from litter source, litter amount, and litter size. Some biomass and *Festuca*

idahoensis data were transformed to normalize and homogenize variances. Means were reported without the transformation applied. The ANOVA model allowed us to individually or jointly analyze species density, percent cover, and biomass for each treatment and the no litter control. The following species and species groups were identified: non-indigenous species; *H. perforatum* L. juvenile and/or adult; *Potentilla recta* L.; *Bromus tectorum* L.; indigenous grass; *Festuca idahoensis* (Elmer); *Poa sandbergii* (Vasey); bunchgrass (not *P. sandbergii* and not *F. idahoensis*); indigenous forb; *Lupinus sericeus* (Nutt.); *Chrysopsis villosa* (Pursh); *Dianthus armeria* L.; *Artemisia frigida* (Willd.); *Tragopogon dubius* (Scop.); *Clarkia pulchella* (Pursh); *Antennaria umbrinella* (Nutt.); *Taraxacum officinale* (Weber); *Achillea millefolium* L.; *Microseris lindleyi* (A. Gray); and “other” forb; and moss. Moss was collected at the soil surface and the biomass dried and weighed.

Treatments were labeled with 3 integers as follows (Table 3): if wt=0 and spp=0 and text=0 then trt = '000'; if wt=1 and spp=1 and text=1 then trt = '111'; if wt=1 and spp=1 and text=2 then trt = '112'; if wt=1 and spp=2 and text=1 then trt = '121'; if wt=1 and spp=2 and text=2 then trt = '122'; if wt=2 and spp=1 and text=1 then trt = '211'; if wt=2 and spp=1 and text=2 then trt = '212'; if wt=2 and spp=2 and text=1 then trt = '221'; if wt=2 and spp=2 and text=2 then trt = '222'.

Table 3. Litter Treatments

Weight (Amount)	Species (Source)	Texture (Size)
0 Counted	0 Counted	0 Counted
1 454 grams	1 Indigenous (Native)	1 Finely Mowed
2 908 grams	2 Non-Indigenous	2 Coarse Intact

Subsamples were averaged per plot replicate for analysis of variance. Outliers that skewed distribution were removed because they were explained in the data collection documentation. The general linear regression model included source; amount; size; two-way interactions of source, amount and size; and three-way interactions of amount, source, and size.

RESULTS

Invasive SiteLitter Interactions Effect on
Non-Indigenous Species Group

ANOVA results (Table 4) (all $P < .05$) show that only the treatment of 908 grams (the high weight) *Hypericum perforatum* coarse size litter (highlighted in green) (Treatment 222) decreased non-indigenous species group density compared to no litter (000 highlighted in pink) and the moderate weight (454 grams) indigenous coarse litter (112 highlighted in pink) treatments. The only treatments that did not decrease non-indigenous species group percent cover were the moderate weight (454 grams) indigenous coarse (112) and fine size (111) litter. Non-indigenous species group biomass was decreased by the high weight (908 grams) indigenous coarse size (222) litter and the high weight of non-indigenous coarse (222) and fine size (221) litter.

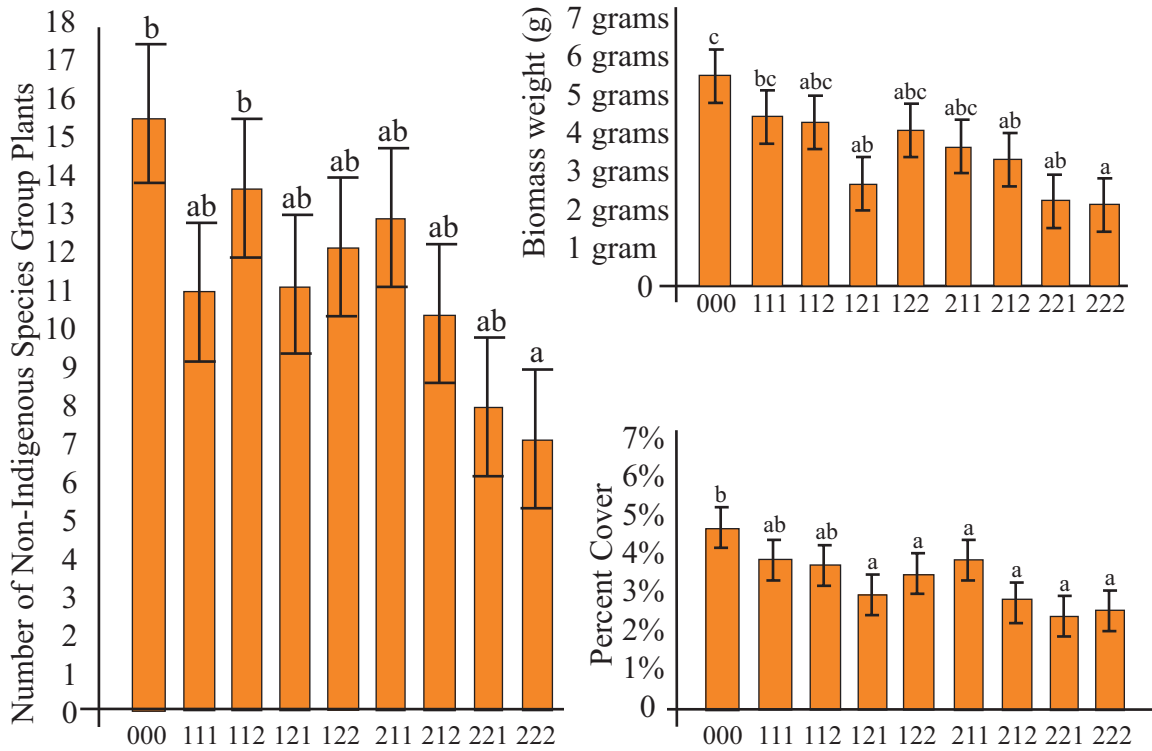
The least square means ($LSM \pm SE$) from 4 no litter samples and 32 treatment samples of density, percent cover, and biomass are listed in Table 4. The alphabet character next to the LSM indicates significant difference determined at $P < .05$. For example, alphabet character a is statistically different from b. However, neither a nor b is statistically different from ab.

Table 4. Non-Indigenous Species Group Density ($LSM \pm 2.1 SE$) per 0.1 m², Percent Cover ($LSM \pm 0.6 SE$), and Biomass dried weight in grams per 1.0 m² ($LSM \pm 0.7 SE$).

Trt	000	111	112	121	122	211	212	221	222
Density	15.83 ^b	11.08 ^{ab}	14.25 ^b	11.33 ^{ab}	12.58 ^{ab}	13.50 ^{ab}	10.50 ^{ab}	8.58 ^{ab}	7.58 ^a
% Cov	4.58 ^b	3.92 ^{ab}	3.75 ^{ab}	3.00 ^a	3.58 ^a	3.92 ^a	2.92 ^a	2.42 ^a	2.67 ^a
Bio(g)	5.70 ^c	4.49 ^{bc}	4.29 ^{abc}	2.78 ^{ab}	4.10 ^{abc}	3.69 ^{bc}	3.43 ^a	2.41 ^a	2.20 ^a

Litter treatment: 000 = No Litter; 111 = 454g indigenous fine; 112 = 454g indigenous coarse; 121 = 454g non-indigenous fine; 122 = 454g non-indigenous coarse; 211 = 908g indigenous fine; 212 = 908g indigenous coarse; 221 = 908g non-indigenous fine; and 222 = 908g non-indigenous coarse.

Figure 6. LSM±SE Non-Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass weight in grams per 1.0 m².



Litter treatment: 000 = No Litter;
 111 = 454g indigenous fine; 112 = 454g indigenous coarse;
 121 = 454g non-indigenous fine; 122 = 454g non-indigenous coarse;
 211 = 908g indigenous fine; 212 = 908g indigenous coarse;
 221 = 908g non-indigenous fine; and 222 = 908g non-indigenous coarse.

Figure 6 graphically duplicates the results from Table 3. The alphabet letter above the SE bar indicates means difference determined at $P < .05$. Non-indigenous species group density was strongly positively correlated (all $r P < .01$) with percent cover and biomass (Table 5).

Table 5. Pearson Correlation Correlation and Regression Estimates.

Density/biomass per 0.1 m ²	$r = 0.43$ ($P < .01$)	intercept 9.11	slope 0.59
Density per 0.1 m ² /percent cover	$r = 0.84$ ($P < .01$)	intercept 0.69	slope 3.22
Percent cover/biomass per 1.0 m ²	$r = 0.67$ ($P < .01$)	intercept 1.28	slope 0.58

Litter Interactions Effect on Indigenous Species Group

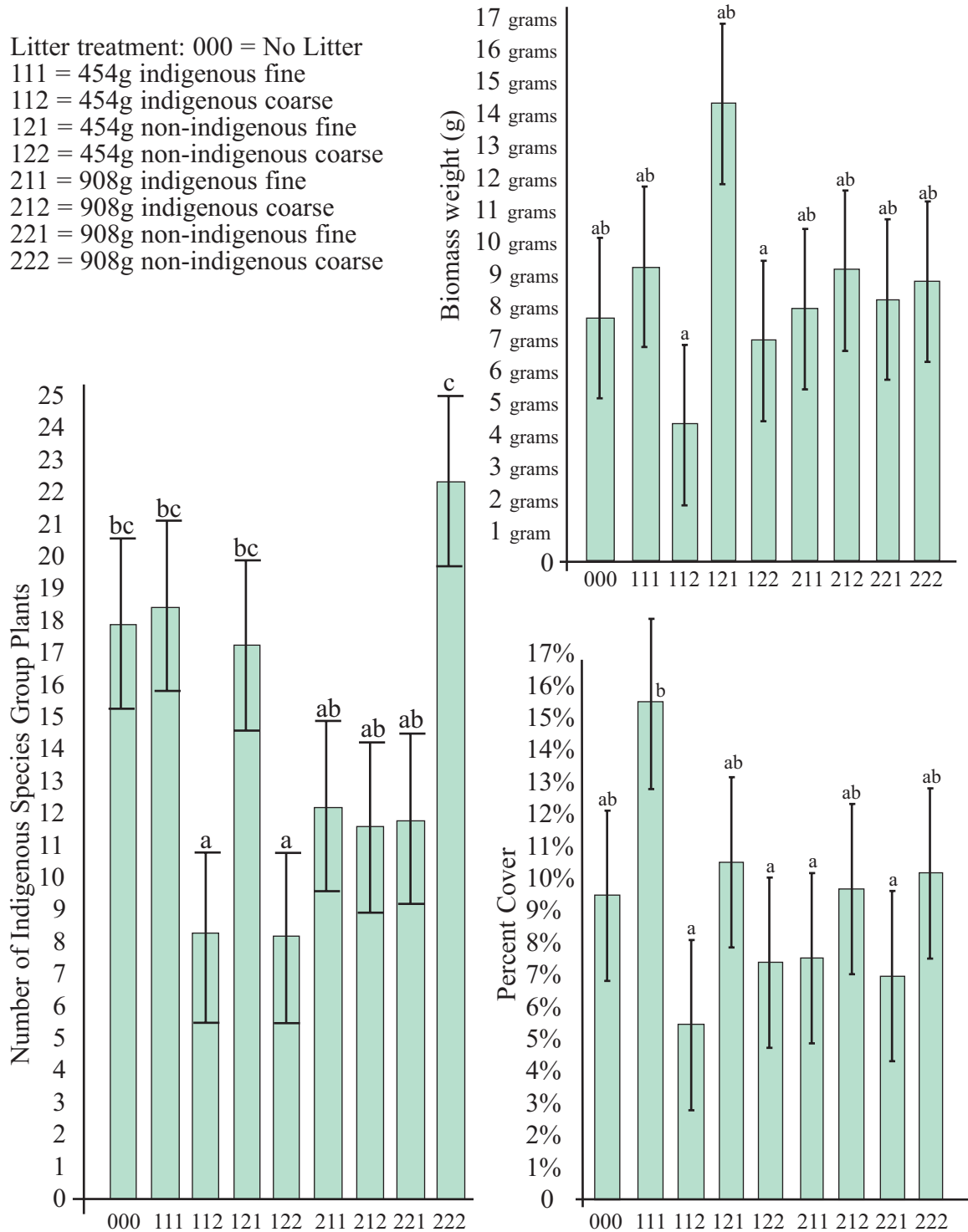
ANOVA results in Table 6 show that only treatments (highlighted pink) of the moderate weight (454 grams) coarse size indigenous (112) and non-indigenous (122) litter decreased indigenous species group density compared to the high weight (908 grams) non-indigenous coarse (222) litter (highlighted green). The only treatments that did not decrease percent cover were the moderate amount of weight (454 grams) indigenous fine (111) and coarse (112) litter treatments. The moderate amount (454 grams) coarse size indigenous (112) and non-indigenous (122) treatments, and the high amount (908 grams) fine size indigenous (211) and non-indigenous (221) litter treatments decreased percent cover compared to the moderate amount (454 grams) indigenous fine size (111) litter treatment. Only treatments of the moderate amount (454 grams) coarse size indigenous (112) and non-indigenous (122) litter decreased biomass compared to the moderate amount (454 grams) non-indigenous fine size (121) litter. The least square means (LSM $\pm$ SE) from 4 no litter samples and 32 treatment samples of density, percent cover, and biomass are listed in Table 6. The alphabet character next to the LSM indicates significant difference determined at $P < .05$. For example, alphabet character a is different from b. However, neither a nor b is different from ab.

Table 6. Indigenous Species Group Density (LSM $\pm$ 2.8 SE) per 0.1 m², Percent Cover (LSM $\pm$ 2.6 SE), and Biomass dried weight in grams per 1.0 m² (LSM $\pm$ 2.4 SE).

	000	111	112	121	122	211	212	221	222
Density	17.83 ^{bc}	18.33 ^{bc}	8.17 ^a	17.17 ^{bc}	8.09 ^a	12.09 ^{ab}	11.58 ^{ab}	11.75 ^{ab}	22.25 ^c
% Cov	9.50 ^{ab}	15.50 ^b	5.50 ^a	10.50 ^{ab}	7.42 ^a	7.59 ^a	9.75 ^{ab}	7.00 ^a	10.25 ^{ab}
Bio(g)	7.57 ^{ab}	9.12 ^{ab}	4.49 ^a	14.12 ^b	6.91 ^a	7.92 ^{ab}	9.12 ^{ab}	8.09 ^{ab}	8.70 ^{ab}

Litter treatment: 000 = No Litter; 111 = 454g indigenous fine; 112 = 454g indigenous coarse; 121 = 454g non-indigenous fine; 122 = 454g non-indigenous coarse; 211 = 908g indigenous fine; 212 = 908g indigenous coarse; 221 = 908g non-indigenous fine; and 222 = 908g non-indigenous coarse.

Figure 7. LSM $\pm$ SE Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass per 1.0 m².



Litter Two-Way Interaction Effect on Indigenous Species Group

The two-way interaction effect (Table 7) of amount and size is figured by taking the difference between the least square means (LSM) for 454 grams and subtracting the LSM for 908 grams from it. Then multiply the difference by the LSM average of fine size litter treatments. Do the same for the LSM average of coarse size litter treatments and subtract it from the value for fine size. The result is the effect of fine size litter. To figure other two-way comparisons refer back to the treatment table (000 = no litter; 111 = 454 grams native fine, etc.). Take the first value 1 = 454 grams, or 1 = native; or 1 = fine as the first value in the equation. The equation for finding amount and size interaction effect on indigenous species group (I) density (D) would be formulated:

$$I = \frac{D(454 \text{ grams}) - D(908 \text{ grams})}{\text{fine size texture}} \text{ minus } \frac{D(454 \text{ grams}) - D(908 \text{ grams})}{\text{coarsely intact texture}}$$

Adding more fine size litter (Table 7) decreased indigenous species density 15 per 0.1 m², cover (9%), and biomass 7 grams per 1.0 m² (all $P < .06$) more than coarse litter. Increasing indigenous litter texture from fine to coarse (Table 7) decreased indigenous species density 6 per 0.1 m² ($P < .15$) more than non-indigenous litter. However, no interaction effect was found on cover or biomass (both $P > .27$).

Table 7. LSM $\pm$ SE Differences between Two-Way Interaction Effect on Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass per 1.0 m².

Interaction	Density	Percent Cover	Biomass
Amount and Size	14.62 $\pm$ 4.0 $P < .04$	9.25 $\pm$ 3.7 $P < .02$	6.82 $\pm$ 3.4 $P < .06$
Source and Size	6.04 $\pm$ 4.0 $P < .15$	4.00 $\pm$ 3.7 $P < .28$	-1.58 $\pm$ 3.4 $P < .66$

Litter Source Effect
on *Hypericum perforatum*

ANOVA results (Table 8) show that non-indigenous species litter, but not the indigenous species litter, decreased *Hypericum perforatum* density compared to no litter ($P < .02$). Non-indigenous species litter decreased *H. perforatum* percent cover compared to indigenous species litter and no litter ($P < .04$). Indigenous species litter decreased *H. perforatum* biomass compared to no litter and non-indigenous species litter decreased *H. perforatum* biomass even more ($P < .05$). Non-indigenous species litter caused greater decrease in *H. perforatum* performance than no litter and indigenous species litter treatments (all $P < .05$). The least square means (LSM $\pm$ SE) from 4 no litter samples, and 16 indigenous species litter and 16 non-indigenous species samples of density, percent cover, and biomass are listed in Table 8. The alphabet character next to the LSM indicates significant difference determined by $P < .05$. For example, alphabet character a is different from b. However, neither a nor b is different from ab.

Table 8. LSM $\pm$ SE *Hypericum perforatum* Density per 0.1 m², Percent Cover, and Biomass dried weight in grams per 1.0 m².

	No Litter	Indigenous Litter	Non-Indigenous Litter
Density	15.67 $\pm$ 2.0 ^b	11.81 $\pm$ 1.0 ^{ab}	9.81 $\pm$ 1.0 ^a
Percent Cover	4.50 $\pm$ 0.5 ^b	3.50 $\pm$ 0.2 ^b	2.73 $\pm$ 0.2 ^a
Biomass (grams)	5.63 $\pm$ 0.7 ^c	3.80 $\pm$ 0.3 ^b	2.79 $\pm$ 0.3 ^a

Hypericum perforatum density, percent cover, and biomass were strongly positively correlated (Table 9) to non-indigenous species group density ($r = 0.98$), percent cover ($r = 0.96$), and biomass ($r = 0.98$) (all $P < .01$).

Table 9. Pearson Correlation Coefficient and Regression Estimates.

<i>Hypericum perforatum</i> L. / Non-Indigenous Species Group Correlation				
Density	$r = 0.98$ ($P < .01$)	intercept	-0.24	slope 1.00
Percent Cover	$r = 0.96$ ($P < .01$)	intercept	0.20	slope 0.05
Biomass	$r = 0.98$ ($P < .01$)	intercept	0.10	slope 0.94

Hypericum perforatum percent cover, and biomass was higher (Table 10) in plots treated with indigenous species litter versus non-indigenous species litter (all $P < .05$).

Table 10. LSM $\pm$ SE Differences between Litter Source Effect on *Hypericum perforatum* Density per 0.1 m², Percent Cover, and Biomass per 1.0 m².

Litter Treatment Comparison	Density	Percent Cover	Biomass
Indigenous vs Non-Indigenous	2.00 $\pm$ 1.4 $P < .17$	0.77 $\pm$ 0.3 $P < .03$	1.01 $\pm$ 0.5 $P < .05$

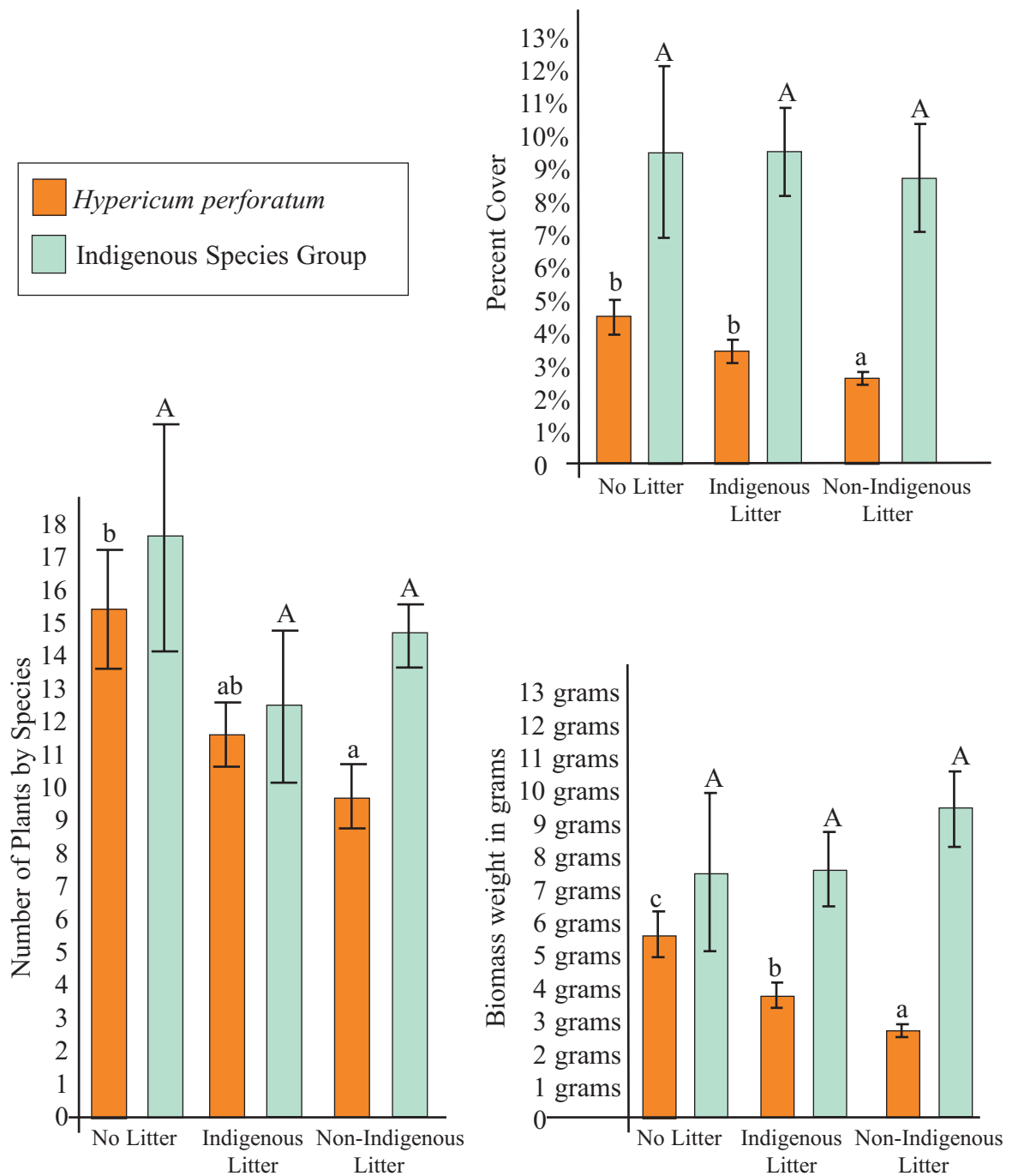
Litter Source Effect on Indigenous Species Group

No litter source effect (Table 11) was found for indigenous species group density, percent cover, and biomass (Figure 8) was found for indigenous species group density, percent cover, and biomass.

Table 11. LSM $\pm$ SE Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass dried weight in grams per 1.0 m².

	No Litter	Indigenous Litter	Non-Indigenous Litter
Density	17.83 $\pm$ 3.5 ^a	12.54 $\pm$ 2.4 ^a	14.81 $\pm$ 1.7 ^a
Percent Cover	9.50 $\pm$ 2.7 ^a	9.58 $\pm$ 1.4 ^a	8.79 $\pm$ 1.4 ^a
Biomass (grams)	7.57 $\pm$ 2.5 ^a	7.66 $\pm$ 1.2 ^a	9.45 $\pm$ 1.2 ^a

Figure 8. LSM $\pm$ SE Litter Source Effect on *Hypericum perforatum* and Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass per 1.0 m².



Litter treatment: 000 = no litter; 111 = 454g indigenous fine; 112 = 454g indigenous coarse; 121 = 454g non-indigenous fine; 122 = 454g non-indigenous coarse; 211 = 908g indigenous fine; 212 = 908g indigenous coarse; 221 = 908g non-indigenous fine; 222 = 908g non-indigenous coarse

Indigenous species group density was strongly positively correlated (Table 12) to percent cover and biomass (all $P < .01$).

Table 12. Pearson Correlation Coefficient and Regression Estimates.

Indigenous Species Group				
Density/biomass	$r = 0.46$ ($P < .01$)	intercept	9.11	slope 0.59
Density/percent cover	$r = 0.62$ ($P < .01$)	intercept	6.70	slope 0.81
Percent cover/biomass	$r = 0.58$ ($P < .01$)	intercept	4.32	slope 0.58

Litter Amount Effect
on *Hypericum perforatum*

ANOVA results (Table 13) show that the high amount (908 grams), but not the moderate amount (454 grams), decreased *Hypericum perforatum* density and percent cover compared to no litter ($P < .02$). The moderate amount (454 grams) decreased biomass, and the high amount (908 grams) decreased it even more ($P < .01$). LSM $\pm$ SE from 4 no litter, 16 moderate and 16 high litter amount samples are listed in Table 13.

Table 13. LSM $\pm$ SE *Hypericum perforatum* Density per 0.1 m², Percent Cover, and Biomass dried weight in grams per 1.0 m².

	No Litter	454 grams Litter	908 grams Litter
Density	15.67 $\pm$ 2.0 ^b	11.81 $\pm$ 1.0 ^{ab}	9.80 $\pm$ 1.0 ^a
Percent Cover	4.50 $\pm$ 0.5 ^b	3.46 $\pm$ 0.3 ^{ab}	2.77 $\pm$ 0.3 ^a
Biomass (grams)	5.63 $\pm$ 0.7 ^b	3.76 $\pm$ 0.4 ^a	2.84 $\pm$ 0.4 ^a

NOTE: alphabet character represents significance determined at $P < .05$

Hypericum perforatum LSM $\pm$ SE were higher (Table 14) in plots treated with the moderate amount (454 grams) litter (percent cover 0.69% $P < .05$) (biomass 0.92 grams $P < .08$) than in plots treated with the high amount (908 grams). Both the moderate and high amount of litter decreased density, percent cover, and biomass compared to no litter (all $P < .10$).

Table 14. LSM $\pm$ SE Differences between Litter Amount Effect on *Hypericum perforatum* Density per 0.1 m², Percent Cover and Biomass per 1.0 m².

Litter Treatment Comparison	Density	Percent Cover	Biomass
454 vs 908 grams	2.04 $\pm$ 1.4 $P < .16$	0.69 $\pm$ 0.3 $P < .05$	0.92 $\pm$ 0.5 $P < .08$
Amount and Source Combination	-4.50 $\pm$ 2.8 $P < .13$	-0.88 $\pm$ 0.7 $P < .20$	-0.75 $\pm$ 1.0 $P < .45$
Amount and Size Combination	-4.58 $\pm$ 2.8 $P < .12$	-0.95 $\pm$ 0.7 $P < .17$	-0.84 $\pm$ 1.0 $P < .40$
Control vs 454 grams	3.83 $\pm$ 2.2 $P < .10$	1.04 $\pm$ 0.5 $P < .06$	1.87 $\pm$ 0.8 $P < .03$
Control vs 908 grams	5.88 $\pm$ 2.2 $P < .02$	1.73 $\pm$ 0.5 $P < .01$	2.79 $\pm$ 0.8 $P < .01$

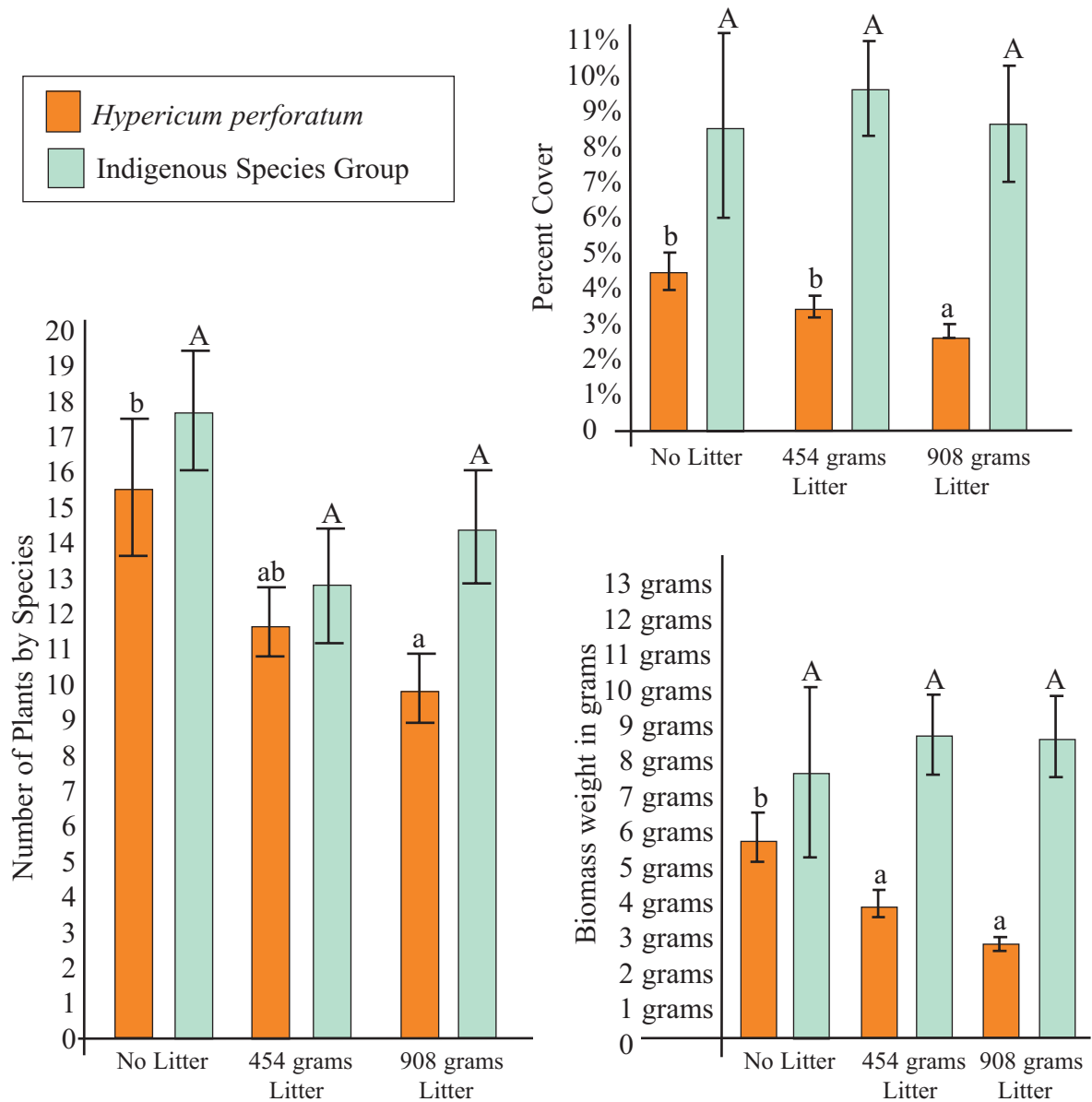
Litter Amount Effect on Indigenous Species Group

ANOVA results show no litter amount effect on indigenous species group density, percent cover, or biomass. LSM $\pm$ SE from 4 no litter, 16 moderate and 16 high litter amount samples are listed in Table 15. The alphabet character represents difference in means determined at $P < .05$.

Table 15. LSM $\pm$ SE Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass dried weight in grams per 1.0 m².

	No Litter	454 grams Litter	908 grams Litter
Density	17.83 $\pm$ 3.5 ^a	12.94 $\pm$ 1.7 ^a	14.42 $\pm$ 1.7 ^a
Percent Cover	8.65 $\pm$ 1.4 ^a	9.73 $\pm$ 1.4 ^a	8.65 $\pm$ 1.4 ^a
Biomass (grams)	7.57 $\pm$ 2.5 ^a	8.66 $\pm$ 1.3 ^a	8.46 $\pm$ 1.3 ^a

Figure 9. LSM $\pm$ SE Litter Amount Effect on *Hypericum perforatum* and Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass per 1.0 m².



Litter treatment: 000 = No Litter;
 111 = 454g indigenous fine; 112 = 454g indigenous coarse;
 121 = 454g non-indigenous fine; 122 = 454g non-indigenous coarse;
 211 = 908g indigenous fine; 212 = 908g indigenous coarse;
 221 = 908g non-indigenous fine; 222 = 908g non-indigenous coarse.

Litter Size Effect on
Hypericum perforatum Density

ANOVA results (Table 16) show that *Hypericum perforatum* density, percent cover, and biomass were lower in both fine and coarse size treatments versus no litter (all $P < .05$). LSM $\pm$ SE from 4 no litter, 16 fine size and 16 coarse litter size samples are listed in Table 16. The alphabet character represents difference in means determined at $P < .05$.

Table 16. LSM $\pm$ SE *Hypericum perforatum* Density per 0.1 m², Percent Cover, and Biomass dried weight in grams per 1.0 m².

	No Litter	Finely Mowed Litter	Coarsely Intact Litter
Density	15.67 $\pm$ 2.1 ^b	10.83 $\pm$ 1.1 ^a	10.79 $\pm$ 1.0 ^a
Percent Cover	4.50 $\pm$ 0.5 ^b	3.23 $\pm$ 0.3 ^a	3.00 $\pm$ 0.3 ^a
Biomass (grams)	5.63 $\pm$ 0.7 ^b	3.28 $\pm$ 0.4 ^a	3.32 $\pm$ 0.4 ^a

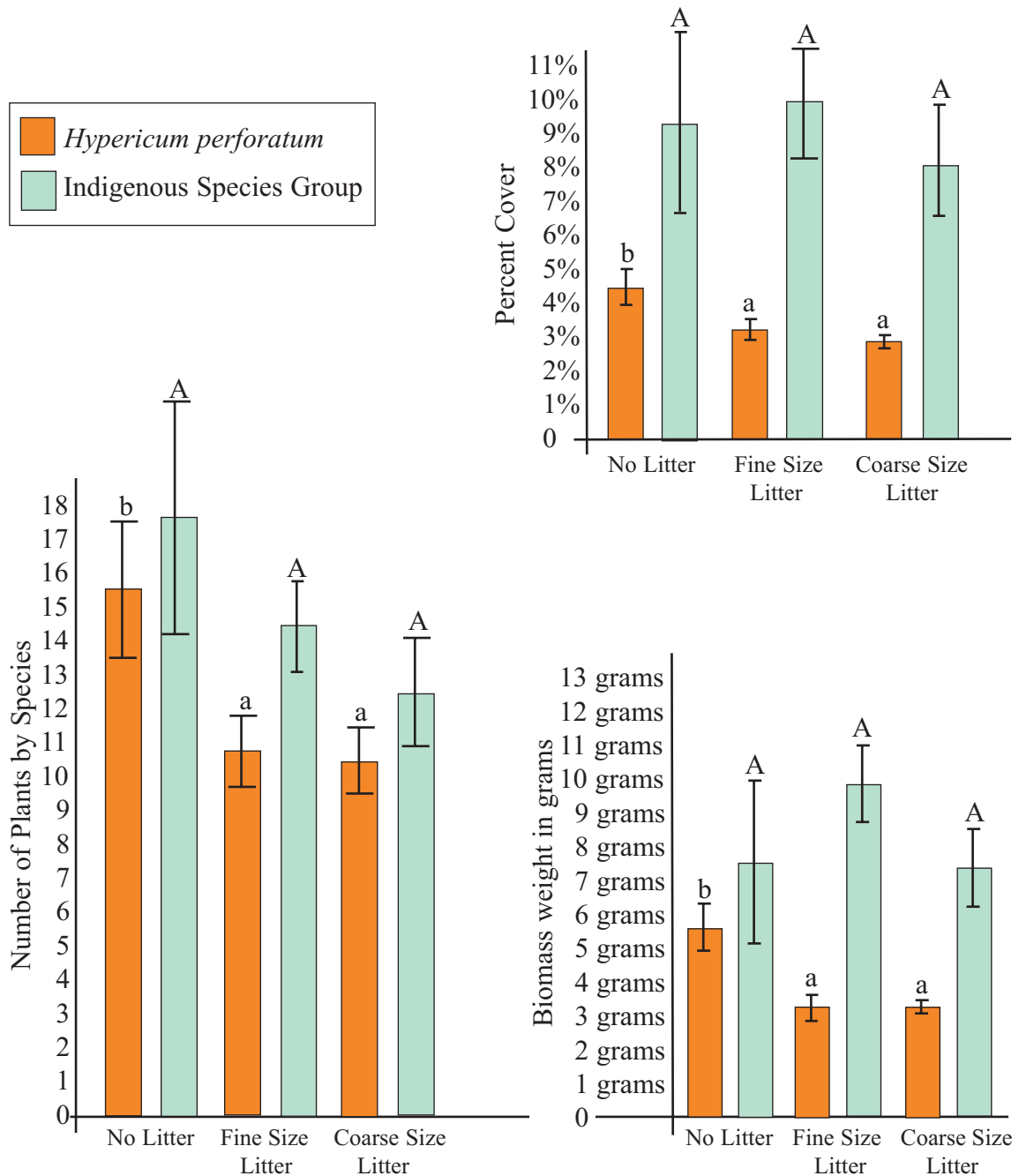
Litter Size Effect
on Indigenous Species Group

ANOVA results (Table 17) show no litter size effect on indigenous species group density, percent cover, and biomass. The bar chart (Figure10) is on Page 40.

Table 17. LSM $\pm$ SE Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass dried weight in grams per 1.0 m².

	No Litter	Finely Mowed Litter	Coarsely Intact Litter
Density	17.83 $\pm$ 3.5 ^a	14.83 $\pm$ 1.7 ^a	12.52 $\pm$ 1.6 ^a
Percent Cover	9.50 $\pm$ 2.7 ^a	10.15 $\pm$ 1.4 ^a	8.23 $\pm$ 1.4 ^a
Biomass (grams)	7.57 $\pm$ 2.5 ^a	9.81 $\pm$ 1.2 ^a	7.31 $\pm$ 1.2 ^a

Figure 10. LSM $\pm$ SE Litter Size Effect on *Hypericum perforatum* and Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass per 1.0 m².



Litter treatment: 000 = No Litter; 111 = 454g indigenous fine; 112 = 454g indigenous coarse; 121 = 454g non-indigenous fine; 122 = 454g non-indigenous coarse; 211 = 908g indigenous fine; 212 = 908g indigenous coarse; 221 = 908g non-indigenous fine; and 222 = 908g non-indigenous coarse.

Native Site Litter Effect

Litter Interactions Effect on Non-Indigenous Species Group

ANOVA results (Table 18) show that only the high amount (908 grams) non-indigenous fine size (221 highlighted in green) litter decreased non-indigenous species group density compared to no litter (000 highlighted in pink). The only treatments that decreased non-indigenous species percent cover were the high amount of fine size indigenous (211) and non-indigenous (212) source litter. No effect was found on biomass.

The least square means ($LSM \pm SE$) from 4 no litter samples and 32 treatment samples of density, percent cover, and biomass are listed in Table 18. The alphabet character next to the LSM indicates significant difference determined at $P < .05$. For example, alphabet character a is different from b. However, neither a nor b is different from ab.

Table 18 Non-Indigenous Species Density ($LSM \pm 1.0$ SE) per 0.1 m², Percent Cover ($LSM \pm 0.6$ SE), and Biomass dried weight in grams per 1.0 m² ($LSM \pm 0.3$ SE).

	000	111	112	121	122	211	212	221	222
Density	4.33 ^b	1.92 ^{ab}	3.75 ^{ab}	2.67 ^{ab}	2.50 ^{ab}	1.75 ^{ab}	2.50 ^{ab}	1.00 ^a	1.50 ^{ab}
% Cov	1.09 ^{ab}	1.08 ^{ab}	2.50 ^b	0.92 ^{ab}	1.42 ^{ab}	0.67 ^a	0.92 ^{ab}	0.50 ^a	0.83 ^{ab}
Bio (g)	0.40 ^a	0.61 ^a	0.54 ^a	0.18 ^a	0.36 ^a	0.79 ^a	0.42 ^a	0.62 ^a	0.42 ^a

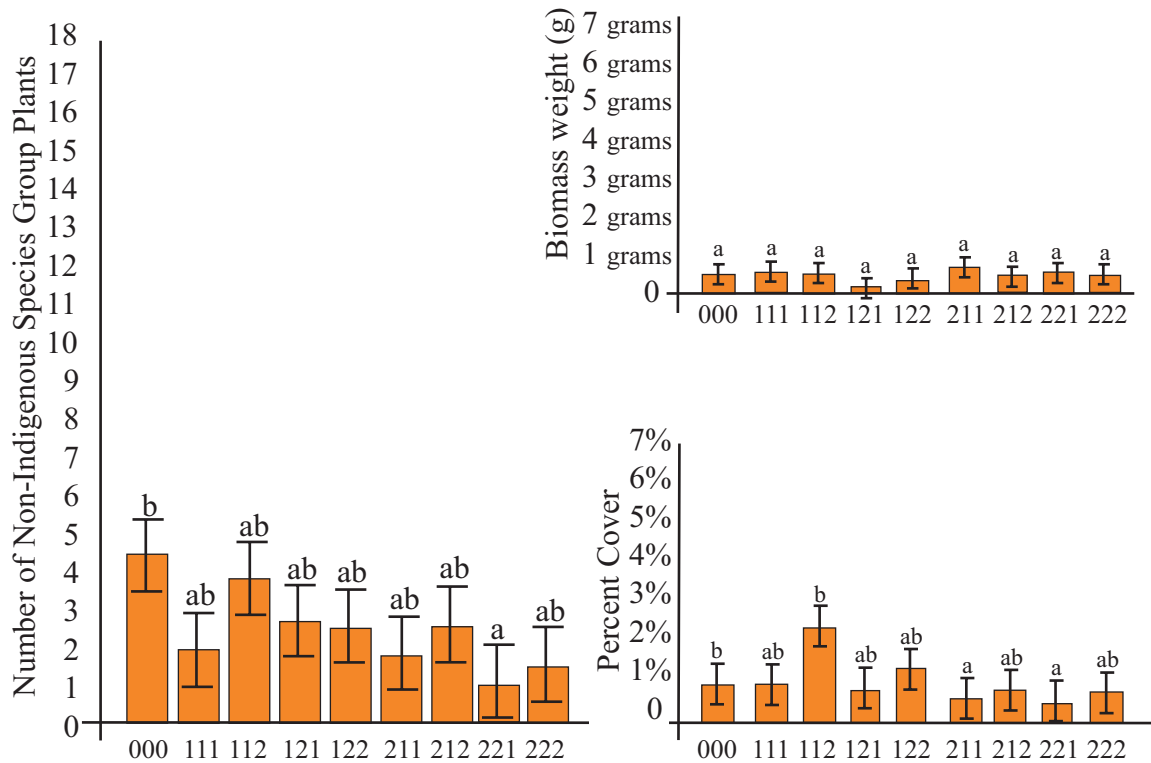
Non-indigenous species density was strongly positively correlated with percent cover ($P < .01$) and percent cover moderately positively correlated with biomass ($P < .04$) (Table 19). Non-indigenous species density strongly positively correlated with all species combined density ($P < .01$).

Table 19. Pearson Correlation Correlation and Regression Estimates.

Density/biomass	$r = 0.21$ ($P < .22$)	intercept 1.98	slope 0.95
Density/percent cover	$r = 0.71$ ($P < .01$)	intercept 0.90	slope 1.40
Percent cover/biomass	$r = 0.36$ ($P < .04$)	intercept 0.71	slope 0.82

Density:

Non-Indigenous Group/All Species	$r = 0.73$ ($P < .01$)	intercept -0.97	slope 0.16
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Figure 11. LSM $\pm$ SE Non-Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass per 1.0 m².

Litter treatment: 000 = No Litter; 111 = 454g indigenous fine; 112 = 454g indigenous coarse; 121 = 454g non-indigenous fine; 122 = 454g non-indigenous coarse; 211 = 908g indigenous fine; 212 = 908g indigenous coarse; 221 = 908g non-indigenous fine; and 222 = 908g non-indigenous coarse.

Litter Interactions Effect on Indigenous Species Group

ANOVA results (Table 20) show that all of the treatments except the moderate amount (454 grams) of non-indigenous fine size (121 highlighted in green) decreased indigenous species group density ($P < .05$) compared to the no litter (000 highlighted in green). Only the high amount (908 grams) of indigenous fine (211) and non-indigenous fine (221) decreased percent cover compared to no litter (000). Only the high amount (908 grams) non-indigenous fine (221) and coarse (222) litter decreased biomass.

The least square means (LSM $\pm$ SE) from 4 no litter samples and 32 treatment samples of density, percent cover, and biomass are listed in Table 20. The alphabet character next to the LSM indicates significant difference determined at $P < .05$. For example, alphabet character a is statistically different from b. However, neither a nor b is statistically different from ab. Indigenous species group density was strongly positively correlated (Table 21) with percent cover and biomass (all $P < .02$).

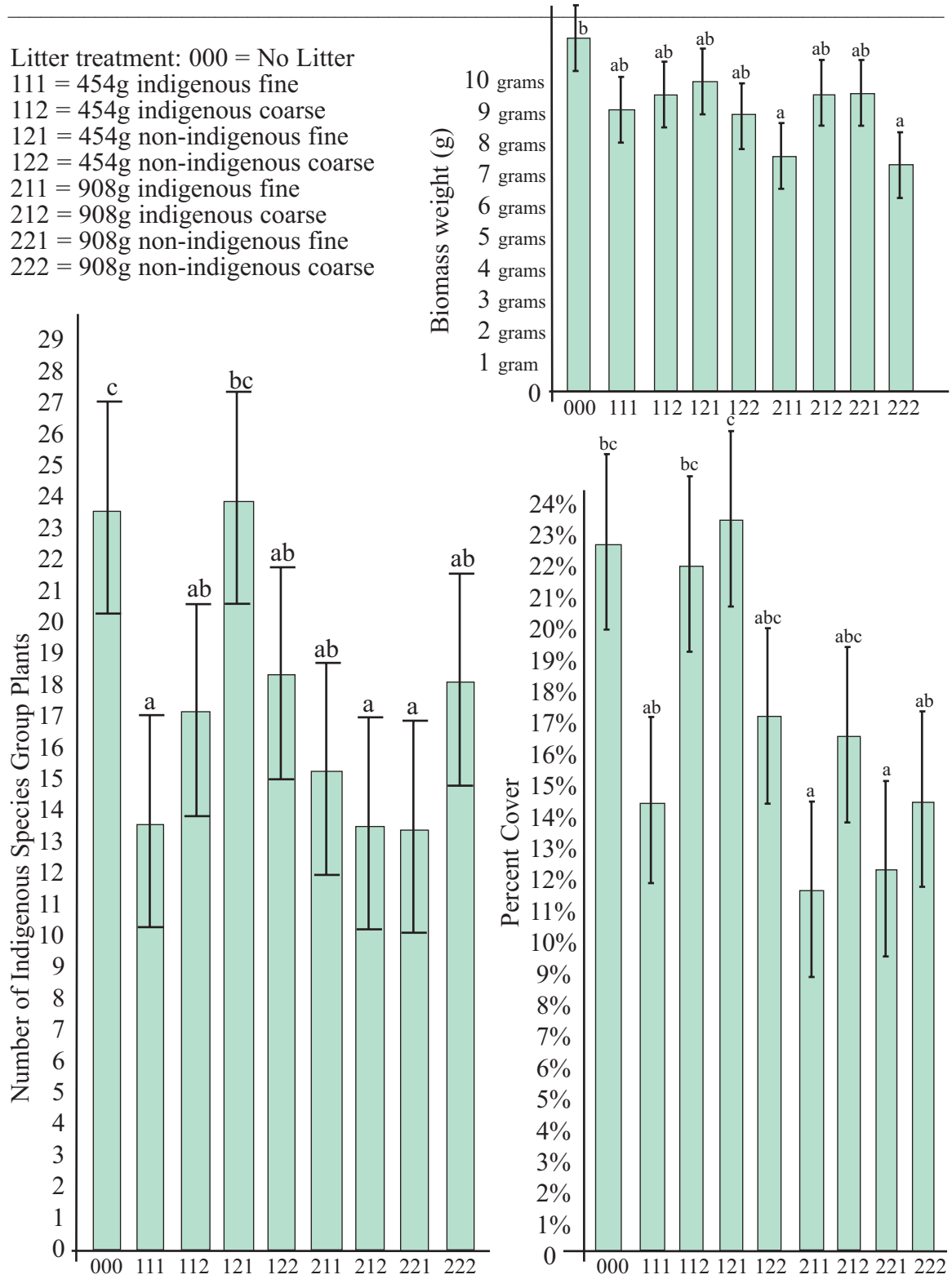
Table 20. Indigenous Species Group Density (LSM $\pm$ 3.4 SE) per 0.1 m², Percent Cover (LSM $\pm$ 2.9 SE), and Biomass dried weight in grams per 1.0 m² ($\pm$ 1.2 SE).

	000	111	112	121	122	211	212	221	222
LSM	23.58 ^c	13.58 ^a	17.17 ^{ab}	23.92 ^{bc}	18.33 ^{ab}	15.25 ^{ab}	13.66 ^a	13.42 ^a	18.17 ^{ab}
% Cov	22.67 ^{bc}	14.33 ^{ab}	21.92 ^{bc}	23.42 ^c	17.17 ^{abc}	11.50 ^a	16.42 ^{abc}	12.25 ^a	14.50 ^{ab}
Bio (g)	11.30 ^b	9.07 ^{ab}	9.56 ^{ab}	9.98 ^{ab}	8.94 ^{ab}	7.63 ^a	9.52 ^{ab}	9.68 ^{ab}	7.35 ^a

Table 21. Pearson Correlation Correlation and Regression Estimates.

Density/biomass per 0.1 m ²	r = 0.40 ($P < .02$)	intercept 3.44	slope 1.58
Density/percent cover per 0.1 m ²	r = 0.60 ($P < .01$)	intercept 4.94	slope 0.76
Percent cover/biomass per 1.0 m ²	r = 0.59 ($P < .01$)	intercept 0.42	slope 1.81

Figure 12. LSM $\pm$ SE Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass per 1.0 m².



Litter Source Effect
on *Hypericum perforatum*

ANOVA results (Table 22) show that non-indigenous litter, but not indigenous litter, decreased *Hypericum perforatum* density compared to no litter ($P < .05$). Litter source effect was not found for percent cover. Indigenous litter decreased *H. perforatum* biomass and non-indigenous litter decreased it even more ($P < .05$). The least square means (LSM $\pm$ SE) from 4 no litter samples, and 16 indigenous species litter and 16 non-indigenous species samples of density, percent cover, and biomass are listed in Table 22. The alphabet character next to the LSM indicates significant difference determined by $P < .05$. For example, alphabet character a is statistically different from b. However, neither a nor b is statistically different from ab. *Hypericum perforatum* density and biomass were not correlated (Table 23) with non-indigenous species density ($P < .55$). However, percent cover was strongly correlated ($P < .01$).

Table 22. LSM $\pm$ SE *Hypericum perforatum* Density per 0.1 m², Percent Cover, and Biomass dried weight in grams per 1.0 m².

	No Litter	Indigenous Litter	Non-Indigenous Litter
Density	4.33 $\pm$ 0.9 ^b	2.25 $\pm$ 0.5 ^{ab}	1.65 $\pm$ 0.5 ^a
Percent Cover	1.09 $\pm$ 0.6 ^a	1.12 $\pm$ 0.3 ^a	1.12 $\pm$ 0.3 ^a
Biomass (grams)	0.40 $\pm$ 0.1 ^b	0.36 $\pm$ 0.1 ^b	0.14 $\pm$ 0.5 ^a

Table 23. Pearson Correlation Correlation and Regression Estimates.

<i>Hypericum perforatum</i> L. / Non-Indigenous Species Group Correlation				
Density	r = 0.10 ($P < .55$)	intercept	1.98	slope 0.48
Percent Cover	r = 0.68 ($P < .01$)	intercept	0.72	slope 1.36
Biomass	r = 0.22 ($P < .22$)	intercept	0.22	slope 0.09
<i>Hypericum perforatum</i> L.				
Density/biomass	r = 0.72 ($P < .01$)	intercept	0.23	slope 7.51
Density/percent cover	r = 0.73 ($P < .01$)	intercept	0.86	slope 1.47
Percent cover/biomass	r = 0.68 ($P < .01$)	intercept	-0.02	slope 0.65

Although no effect (Table 24) was found on density and percent cover, *Hypericum perforatum* biomass was decreased by indigenous species litter compared to non-indigenous litter ($P < .01$). *Hypericum perforatum* density was higher in the no litter treatment than in plots treated with indigenous species litter ($P < .06$) and even higher than in plot treated with non-indigenous litter ($P < .02$).

Table 24. LSM $\pm$ SE Differences between Litter Source Effect on *Hypericum perforatum* Density per 0.1 m², Percent Cover, and Biomass per 1.0 m².

Litter Treatment Comparison	Density	Percent Cover	Biomass
<i>Hypericum perforatum</i> L.			
Indigenous vs Non-Indigenous Species	0.60+0.7 <.37	0.46+0.4 <.24	0.22+0.7 <.01
Control vs Indigenous Species	2.08+1.1 <.06	-0.04+0.6 <.95	0.04+0.1 <.68
Control vs Non-indigenous Species	2.69+1.1 <.02	0.42+0.6 <.49	0.26+0.1 <.02

Litter Source Effect on Indigenous Species Group

ANOVA results (Table 25) show that indigenous species group density was lower in both indigenous litter and non-indigenous litter compared to no litter ($P < .05$). No litter source effect was found for percent cover and biomass. LSM $\pm$ SE from 4 no litter, 16 fine size and 16 coarse size samples are listed in Table 25. The alphabet character represents difference in means determined at $P < .05$.

Table 25. LSM $\pm$ SE Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass dried weight in grams per 1.0 m².

	No Litter	Indigenous Litter	Non-Indigenous Litter
Density	28.58 $\pm$ 3.4 ^b	14.92 $\pm$ 1.7 ^a	18.46 $\pm$ 1.7 ^a
Percent Cover	22.67 $\pm$ 3.3 ^a	16.04 $\pm$ 1.6 ^a	16.83 $\pm$ 1.6 ^a
Biomass (grams)	1.30 $\pm$ 1.1 ^a	8.94 $\pm$ 0.6 ^a	9.00 $\pm$ 0.6 ^a

Litter Amount Effect
on *Hypericum perforatum*

ANOVA results (Table 26) show that the high amount (908 grams), but not the moderate amount (454 grams), decreased *Hypericum perforatum* density and biomass compared to no litter ($P < .05$). Although amount effect was not found to be statistically different from no litter, the high amount (908 grams) decreased percent cover ($P < .03$) compared to the moderate amount (454 grams). LSM $\pm$ SE from 4 no litter, 16 fine size and 16 coarse litter size samples are listed in Table 26. The alphabet character represents difference in means determined at $P < .05$.

Table 26. LSM $\pm$ SE *Hypericum perforatum* Density per 0.1 m², Percent Cover, and Biomass dried weight in grams per 1.0 m².

	No Litter	454 grams Litter	908 grams Litter
Density	4.33 $\pm$ 0.9 ^b	2.58 $\pm$ 0.5 ^{ab}	1.31 $\pm$ 0.5 ^a
Percent Cover	1.09 $\pm$ 0.5 ^{ab}	1.35 $\pm$ 0.3 ^b	0.44 $\pm$ 0.3 ^a
Biomass (grams)	0.40 $\pm$ 0.1 ^a	0.31 $\pm$ 0.1 ^a	0.18 $\pm$ 0.1 ^a

Hypericum perforatum density ($P < .07$) was 1.27 higher, percent cover ($P < .03$) was 0.92 higher, and biomass ($P < .06$) was 1.33 higher (Table 27) in the moderate amount (454 grams) of litter compared to the high amount (908 grams). Density ($P < .01$) was 3.02 higher and biomass ($P < .05$) was 0.09 grams higher in no litter compared to the high litter amount (908 grams).

Table 27. LSM $\pm$ SE Differences between Litter Amount Effect on *Hypericum perforatum* Density per 0.1 m², Percent Cover, and Biomass per 1.0 m².

Litter Treatment Comparison	Density	Percent Cover	Biomass
454 vs 908 grams	1.27 $\pm$ 0.7 $P < .07$	0.92 $\pm$ 0.4 $P < .03$	1.33 $\pm$ 0.6 $P < .06$
Control vs 454 grams	1.75 $\pm$ 1.0 $P < .11$	-0.27 $\pm$ 0.6 $P < .66$	0.09 $\pm$ 0.1 $P < .42$
Control vs 908 grams	3.02 $\pm$ 1.0 $P < .01$	0.65 $\pm$ 0.6 $P < .29$	0.09 $\pm$ 0.1 $P < .05$

Litter Amount Effect on Indigenous Species Group

ANOVA results (Table 28) show that indigenous species density was decreased by both the moderate amount (454 grams) and the high amount (908 grams) of litter compared to no litter ($P < .05$). The high amount (908 grams) decreased percent cover ($P < .02$) compared to the moderate amount (454 grams). The high amount (908 grams), but not the moderate amount (454 grams) decreased indigenous species group biomass compared to no litter ($P < .05$). LSM $\pm$ SE from 4 no litter, 16 fine size and 16 coarse litter size samples are listed in Table 28. The alphabet character represents difference in means determined at $P < .05$.

Table 28. LSM $\pm$ SE Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass dried weight in grams per 1.0 m².

	No Litter	454 grams Litter	908 grams Litter
Density	28.58 $\pm$ 3.4 ^b	18.25 $\pm$ 1.71 ^a	15.12 $\pm$ 1.71 ^a
Percent Cover	22.67 $\pm$ 3.0 ^b	19.21 $\pm$ 1.5 ^b	13.67 $\pm$ 1.5 ^a
Biomass (grams)	11.30 $\pm$ 1.1 ^b	9.39 $\pm$ 0.6 ^{ab}	8.54 $\pm$ 0.6 ^a

Indigenous Species percent cover was 5.54% higher ($P < .02$) in the moderate amount (454 grams) compared to the high amount (908 grams) of litter (Table 29).

Density was higher in no litter than in the moderate amount ($P < .02$) and even higher than in the high amount ($P < .01$).

Table 29. LSM $\pm$ SE Differences between Litter Amount Effect on Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass per 1.0 m².

Litter Treatment Comparison	Density	Percent Cover	Biomass
454 vs 908 grams	3.13 $\pm$ 2.4 $P < .22$	5.54 $\pm$ 2.0 $P < .02$	0.84 $\pm$ 0.8 $P < .32$
Control vs 454 grams	10.33 $\pm$ 3.8 $P < .02$	3.46 $\pm$ 3.2 $P < .30$	2.31 $\pm$ 1.3 $P < .11$
Control vs 908 grams	13.46 $\pm$ 3.8 $P < .01$	9.00 $\pm$ 3.2 $P < .01$	2.46 $\pm$ 1.3 $P < .08$

Litter Size Effect
on *Hypericum perforatum*

ANOVA results (Table 30) show that fine size, but not coarse size, decreased *Hypericum perforatum* density compared to no litter ($P < .05$). Both fine and coarse size litter decreased *H. perforatum* percent cover compared to no litter ($P < .05$). No effect was found on biomass. LSM $\pm$ SE from 4 no litter, 16 fine size and 16 coarse litter size samples are listed in Table 30. The alphabet character represents difference in means determined at $P < .05$.

Table 30. LSM $\pm$ SE *Hypericum perforatum* Density per 0.1 m², Percent Cover, and Biomass dried weight in grams per 1.0 m².

	No Litter	Finely Mowed Litter	Coarsely Intact Litter
Density	4.33 $\pm$ 0.9 ^b	1.60 $\pm$ 0.5 ^a	2.29 $\pm$ 0.5 ^{ab}
Percent Cover	1.09 $\pm$ 0.6 ^a	0.58 $\pm$ 0.3 ^a	1.21 $\pm$ 0.3 ^a
Biomass (grams)	0.40 $\pm$ 0.1 ^a	0.18 $\pm$ 0.6 ^a	0.31 $\pm$ 0.6 ^a

Litter Size Effect
on Indigenous Species Group

ANOVA results (Table 31) show that fine and coarse size litter decreased indigenous species group density and percent cover compared to no litter ($P < .05$). Coarse size, but not fine size, decreased biomass compared to no litter ($P < .05$). No effect was found between fine and coarse size litter.

Table 31. LSM $\pm$ SE Indigenous Species Group Density per 0.1 m², Percent Cover, and Biomass dried weight in grams per 1.0 m².

	No Litter	Finely Mowed Litter	Coarsely Intact Litter
Density	28.58 $\pm$ 3.5 ^b	16.54 $\pm$ 1.8 ^a	16.83 $\pm$ 1.8 ^a
Percent Cover	22.67 $\pm$ 3.3 ^b	15.38 $\pm$ 1.6 ^a	17.50 $\pm$ 1.6 ^a
Biomass (grams)	11.30 $\pm$ 1.1 ^b	9.39 $\pm$ 0.6 ^{ab}	8.54 $\pm$ 0.6 ^a

DISCUSSION

Hypericum perforatum was decreased by its own litter. *Hypericum perforatum* and indigenous species as a group were detrimentally influenced more by the high amount of litter than by the moderate amount. Although litter size did not influence *H. perforatum*, indigenous species biomass was more detrimentally influenced by coarse size litter than by fine. When we added more fine size litter, indigenous species were more detrimentally influenced than when we increased the amount of coarse litter. In the invasive site, moderate amounts of coarse indigenous litter decreased *H. perforatum*. High amounts of coarse *H. perforatum* litter decreased it even more. The opposite effects of the same treatments were found on indigenous species. In the native site, the only treatment that reduced *H. perforatum* more than no litter was the high amount of fine *H. perforatum* litter. The same fine *H. perforatum* litter in moderate amounts was the only treatment that did not decrease indigenous species.

The complexity of litter influence through interactions of amount, source, and size detrimentally and non-detrimentally caused changes to plant species diversity at each site (all $P < .05$).

Results Unique to the Invasive Site

Indigenous Species Group Response. It is commonly understood that community interaction is dependent upon plant species present at the site. In the invasive site, the *Hypericum perforatum* canopy that formed during the >40-year enclosure was removed as part of site preparation. Adding more fine size litter (Table 7) decreased indigenous species density, cover, and biomass (all $P < .06$) more than coarse litter (Figure 13). It might be that the increased amount of fine litter effect, but not as much with coarse,

Figure 13. LSM Litter Amount and Size Interaction Effect on Indigenous Species Group in the Invasive Site.

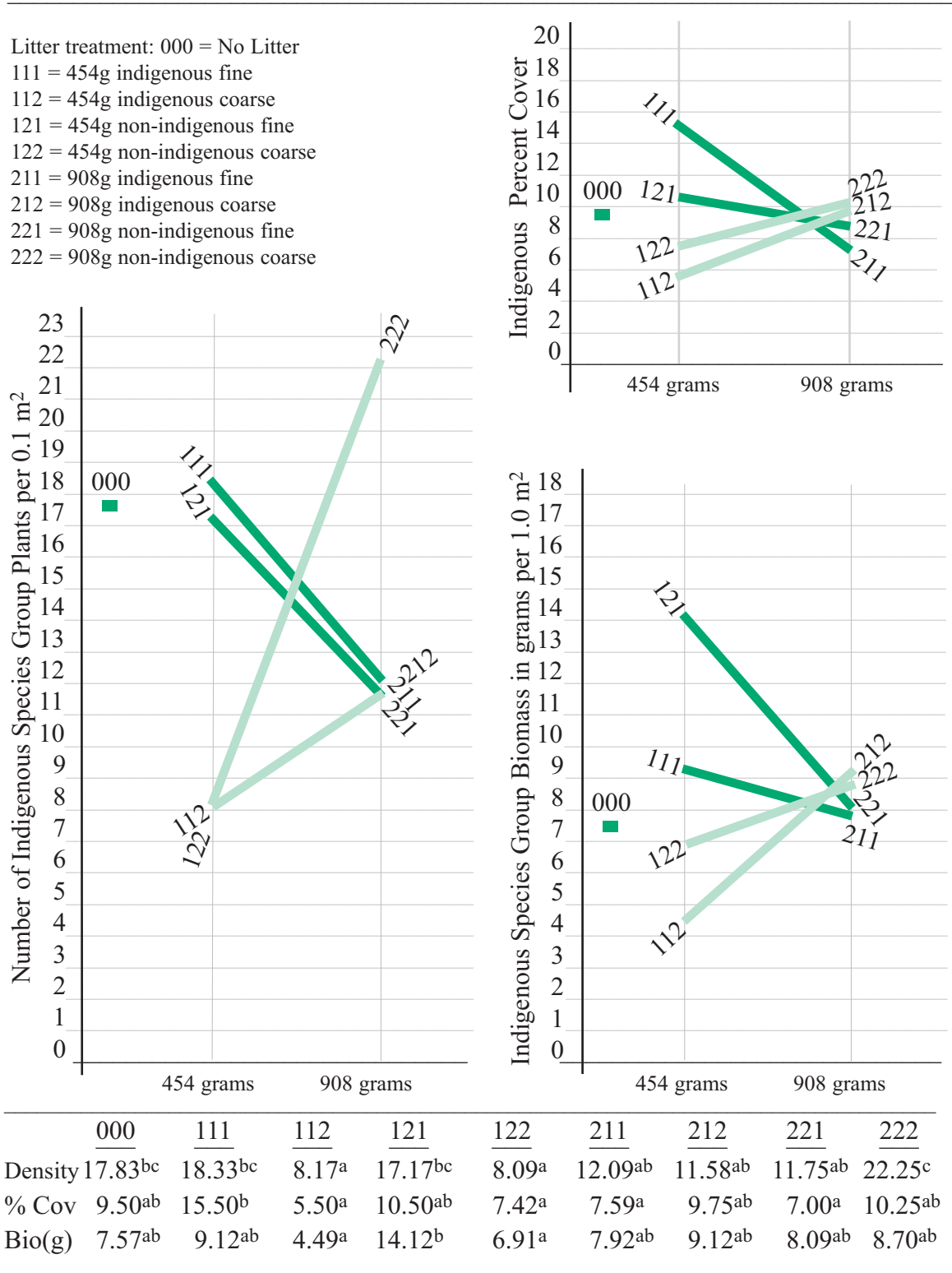
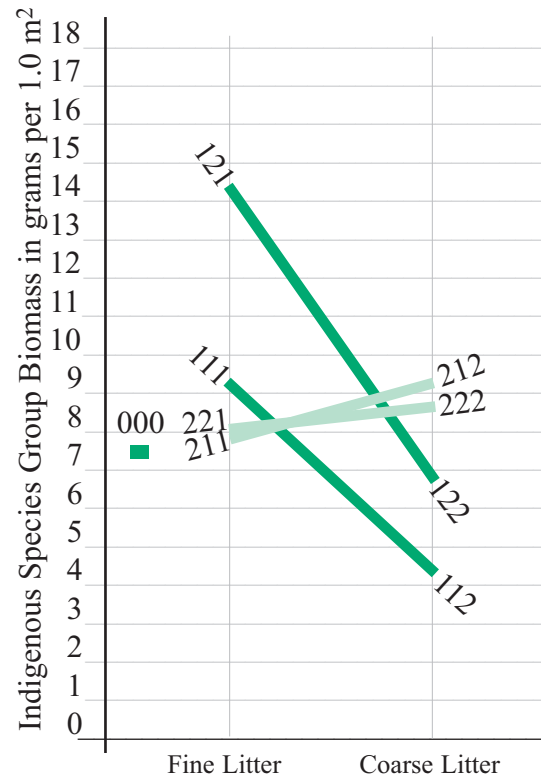
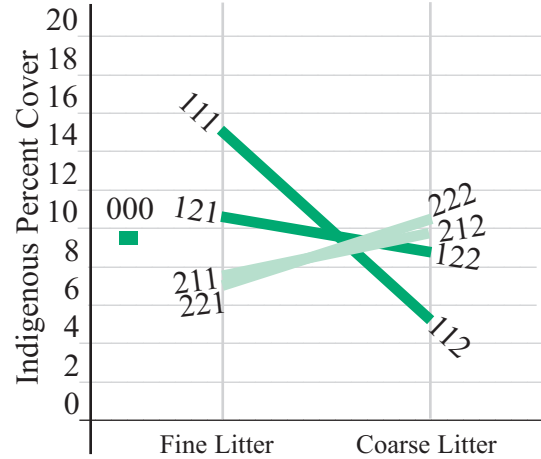
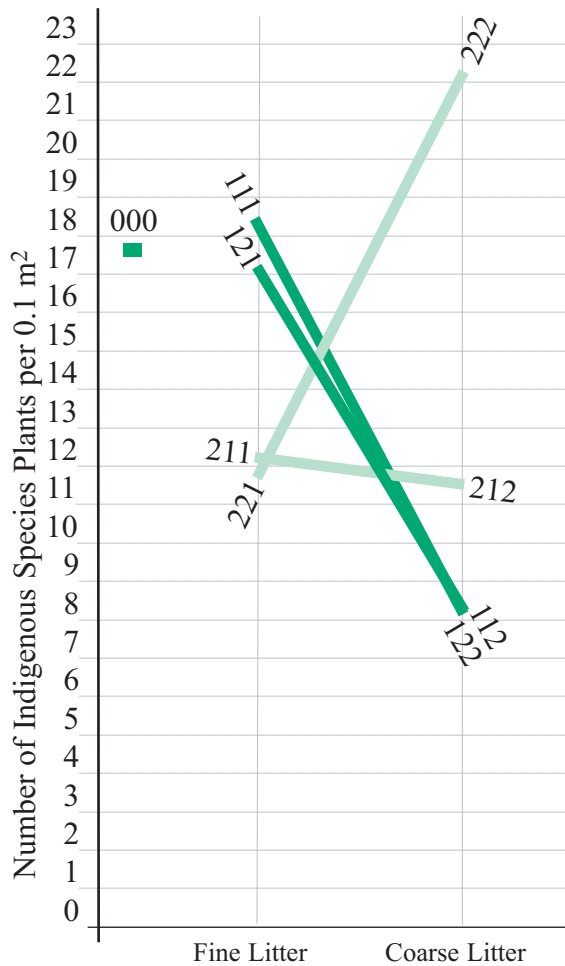


Figure 14. LSM Litter Source and Size Interaction Effect on Indigenous Species Group in the Invasive Site.

Litter treatment: 000 = No Litter
 111 = 454g indigenous fine
 112 = 454g indigenous coarse
 121 = 454g non-indigenous fine
 122 = 454g non-indigenous coarse
 211 = 908g indigenous fine
 212 = 908g indigenous coarse
 221 = 908g non-indigenous fine
 222 = 908g non-indigenous coarse



	000	111	112	121	122	211	212	221	222
Density	17.83 ^{bc}	18.33 ^{bc}	8.17 ^a	17.17 ^{bc}	8.09 ^a	12.09 ^{ab}	11.58 ^{ab}	11.75 ^{ab}	22.25 ^c
% Cov	9.50 ^{ab}	15.50 ^b	5.50 ^a	10.50 ^{ab}	7.42 ^a	7.59 ^a	9.75 ^{ab}	7.00 ^a	10.25 ^{ab}
Bio(g)	7.57 ^{ab}	9.12 ^{ab}	4.49 ^a	14.12 ^b	6.91 ^a	7.92 ^{ab}	9.12 ^{ab}	8.09 ^{ab}	8.70 ^{ab}

influenced energy processes and allocation (Ellsworth et al. 2004). Ellsworth found with increased amount of litter that energy was allocated to the Oriental bittersweet hypocotyl and less so to the cotyledon and radicle, and the effect was greater with intact (coarse) litter.

When indigenous litter fine texture was increased to coarse size (Table 7) indigenous species group density decreased more ($P < .15$) than by non-indigenous litter (Figure 14). No source by size interaction effect was found on cover or biomass. Bosy and Reader (1995) showed that dense grass litter in trays completely reduced irradiation below the litter layer. It is possible that intact (coarse) native grass and forb species litter allowed less light to pass through than finely mulched litter (Olson and Wallander 2002). It might be that the larger size (coarse) *H. perforatum* (non-indigenous) litter source acted as a mechanical barrier to shoot extension preventing plant growth. It might be that coarse litter directly or indirectly influenced moisture, air movement, or soil temperature because of textural canopy effects (Aber and Melillo 2001; Bartholomew and Norman 1946; Briggs and Knapp 1995). Moisture and air temperature are known to influence pathogens, insects, and other microbes that feed on seedlings. The larger size (coarse) litter may have delayed native grass and forb species seedling emergence through the litter layer. The delay could put the timing of the opening of forb species leaf surface later than other competing species (Peterson and Facelli 1992).

Only the moderate-amount coarse indigenous and non-indigenous litter decreased indigenous species group density (Table 4 Page 30) compared to the high amount non-indigenous coarse (all $P < .05$). Invasive non-indigenous plant species (Ehrenfeld 2003) tend to have higher standing crop (biomass), more rapid decomposition rates than co-occurring native plants, and more extractable inorganic nitrogen (N) underneath. It is possible that the increased amount of coarse *H. perforatum* litter (non-indigenous) through increased decomposition rates released more extractable inorganic N into the

soil subsequently increasing N mineralization rates more than the moderate amount of litter (Bowman et al. 2004). More nutrients may be available to plants. However, it would not explain the decrease of *H. perforatum* and non-indigenous species group density response to the high amount of its own coarse litter.

Non-Indigenous Species Group Response. Only the high amount of St. Johnswort coarse litter (source, amount, and size interaction) decreased non-indigenous species group density in the invasive site compared to the moderate amount of native coarse and no litter (all $P < .05$).

Results Unique to the Native Site

Hypericum perforatum Response. Only the high amount non-indigenous fine litter (three-way source, amount, and size interaction) decreased non-indigenous species group density compared to no litter ($P < .05$). Fine litter, but not coarse, decreased *H. perforatum* density compared to no litter ($P < .05$). Fine litter may act as a mechanical barrier to light to a greater degree than coarse litter (Bosy and Reader 1995; Olson and Wallander 2002). *Hypericum perforatum* grows in direct sunlight. Compounds produced in the leaves and flowers increase as the plant grows (Briskin and Gawienowski 2000; Briskin et al. 2000). Light is a requirement for *H. perforatum* seed germination (Pank et al. 2003). It may be that the finely mulched litter eliminated the light required by *H. perforatum* seeds to germinate or for seedlings to emerge. Fine litter, more than coarse litter, may limit air movement and moderate air temperature and moisture regimes that subsequently might increase seedling disease by pathogens. Finely mulched litter may decompose more rapidly than coarse litter subsequently facilitating earlier nutrient availability to plants compared to coarse litter. However, if that were true it would not explain the decrease in *H. perforatum* caused by fine versus coarse litter, nor the decrease in indigenous species caused by coarse versus fine litter.

Indigenous Species Group Response. Annual net primary production (biomass) and species performance can be associated with plant species interaction in competing for available resources (Stohlgren et al. 1999; Tilman and Wedin 1991; Wardle et al. 2002; Krueger-Mangold et al. 2004). Coarse litter and the high litter amount caused the greatest reduction in indigenous species group cover and biomass. All treatments decreased indigenous species group density except for the the no litter and 454 grams *H. perforatum* fine litter (all $P < .05$). No difference was found between the treatment of 454 grams *H. perforatum* fine litter and no litter. Although not measured, it may be that the treatment effect on shade, air movement and temperature, and moisture, associated with the 454 grams *H. perforatum* fine litter replicated the effect of no litter.

Results

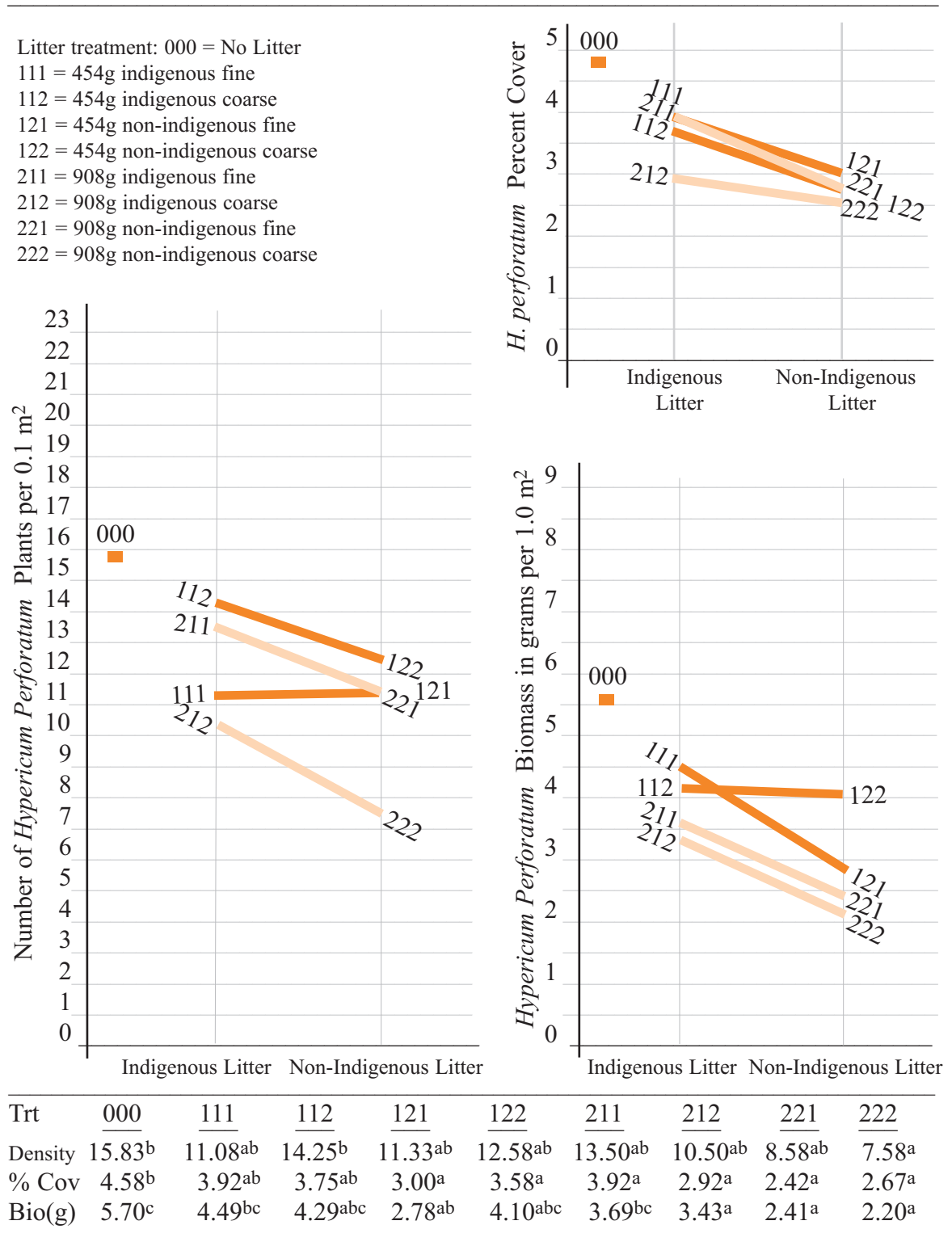
Common to Both Sites

Litter effect depended on interactions of source, size, and amount (all $P < .05$). *Hypericum perforatum* litter caused greater decrease in *H. perforatum* density and biomass than indigenous litter (both $P < .05$). Litter source effect on cover varied. The high amount of litter caused greater decrease in *H. perforatum* density, cover, and biomass than the moderate amount (all $P < .05$).

Interactions of Litter Source, Amount, and Size Effect

Hypericum perforatum litter caused greater decrease in *H. perforatum* that was decreased even more by the high amount ($P < .05$). Non-indigenous (Figure 15) species group density in the invasive site was highest in plots (Figure 15 Page 56) treated with the moderate amount of coarse intact indigenous litter. Density was lowest in the high amount of its own coarse intact litter. Qiu et al (2005) investigated microbial activity and

Figure 15. LSM Litter Source, Amount, and Size Interaction Effect on Non-Indigenous Species Group in the Invasive Site



found higher CO₂ efflux with higher temperatures. The CO₂ efflux was higher at the initiation of higher temperature than after. The efflux remained stable when the temperature was controlled. This suggests that the temperature differences below grass litter (Bosy and Reader 1995) influence on microbial activity (Qiu et al 2005) and subsequent release of CO₂ may play a role in the higher *H. perforatum* density in plots treated with native grass and forb species litter compared to *H. perforatum* litter.

Because air movement and fluctuating temperature can have an effect on seed germination (Rice 1985 cited by Bosy and Reader) and soil water and temperature fluctuate throughout the day (Blicker et al. 2003), perhaps plant species perform at higher levels of density, cover, and biomass at specific zones of temperature and moisture. In the invasive site where *H. perforatum* litter decomposition influenced soils (Olson and Wallander 2002), it may be possible that the temperature of the soil was moderated more by grass litter than by invasive forb litter (Bosy and Reader 1995). Temperature moderation by litter source may explain the higher *H. perforatum* density in moderate amounts of grass litter versus high amounts of its own litter

In the native site, non-indigenous species density and percent cover were lowest in the high amount of non-indigenous fine size litter ($P < .05$). All other treatments were not different from no litter. Indigenous species group density was highest in no litter and the moderate amount of non-indigenous fine size litter. There may be an issue with leachate in the soil in the invasive site below the *H. perforatum* dense canopy. Olson and Wallander (2002) used soil cores to integrate the effects of invasive forbs on soil properties. They found that of the species tested that germination was greatest on non-infested soils except for the non-indigenous *Euphorbia* species germination on infested soils from the *Euphorbia* site. They found reduced seed germination to be higher in *Centaurea* infested soils than in *Euphorbia* infested soils. They suggested it could have been from the effect of different secondary chemistry or root structure of the two species

on soil chemical and physical properties. Bosy and Reader (1995) used leachate to investigate germination of *H. perforatum* and found that the leachate solution did not reduce germination statistically for two species (*H. perforatum* 1% and *Verbascum* 0%) with relatively small seeds. Germination was reduced by the leachate solution for two larger seeded species (*Centaurea* 10% and *Dipsacus* 34%).

Hypericum perforatum litter caused the greatest decrease in *H. perforatum* density ($P < .05$) possibly due to compounds accumulating from leachate from increased amounts of its own litter coupled with those produced in its own new growth. Hypericin compounds in *H. perforatum* are associated with inducible plant defense mechanisms (Sirvent and Gibson 2002).

Bosy and Reader (1995) investigated grass litter packs used to remove environmental effect and suppress seed germination and seedling emergence by limiting irradiance and air temperature as a physical effect. They used more litter in their packs than did Olson and Wallander (2002) whose study showed that seedling height but not germination was affected by litter packs limiting environmental cues of light and air temperature. Bosy and Reader cited Grime et al (1981) study on shading and air temperature showing little effect on *Hypericum* germination. Bosy and Reader also cited Rice (1985) findings that showed reduced fluctuation in air temperature beneath litter can explain lower forb germination.

Field weight of native grass and forb litter compared to *H. perforatum* forb dominated litter (difference in size and density) collected for treatments could have differentially influenced the blockage of light and movement of air.

Litter Source Effect

Hypericum perforatum percent cover and biomass were higher in the invasive site and biomass was higher in the native site in plots treated with indigenous versus

non-indigenous species litter. No litter source effect was found on indigenous species group density, cover, or biomass. Again, this could be from the air or soil temperature influenced by grass litter. It could also be plant traits and induced hypericins and hyperforin in *H. perforatum* in response to conditions created by the presence of grass and forb litter versus its own litter (Sirvent and Gibson 2002). Sirvent and Gibson (2002) investigated *H. perforatum* secondary metabolites to determine if there were plant defense systems mediated by chemical elicitors. Levels of hypericin doubled compared to the control when inoculated with 1×10^4 spores per ml. Higher doses overwhelmed the plant defenses. Perhaps the biotic interaction with indigenous grass and forb litter induced *H. perforatum* plant defense responses that influenced not the number of plants but increased vigor and annual net primary production. Perhaps the biotic interaction of non-indigenous forb litter induced native indigenous grass and forb species plant defense responses again influencing not the number of plants but increased vigor and production.

Litter Amount Effect

The inducible plant defense may have also played a role in litter amount effect on *Hypericum perforatum*. The high amount of litter had greater influence on decreased *H. perforatum* density, percent cover, and biomass than the moderate amount (all $P < .05$). In the invasive site the high amount of litter decreased indigenous species group density more than the moderate amount ($P < .05$). That could be because large amounts of litter mechanically restrict seed soil contact. No amount effect was found on indigenous species group cover or biomass. The high amount of litter may have created the physical barrier blocking sunlight and air movement (Bosy and Reader 1995). The high amount may have influenced the microclimate below the air soil boundary where interaction with arbuscular mycorrhizae could be transferring carbon (Carey et al 2004) or influencing allelopathic interference (Ridenour and Callaway).

Litter Size Effect

No size effect was found on *H. perforatum* or indigenous species group density, cover, or biomass (all $P > .05$). Although it had no independent effect, in combination with litter source and litter amount, it may still play a role in abiotic factors such as air movement and moisture cover. Litter size, or its physical shape and texture, make up the location where nutrients and water are deposited and stored for insects and pathogens that feed on plant parts. Alpert et al. (2000) compiled a model of measuring invasibility that included minimum to maximum levels of altered disturbance regimes and low levels of environmental stress. If litter size (texture) provides a physical location for microclimate, then altering the microclimate by changing size (texture) could become the environmental stress (Alpert et al. 2000) level that influences the mossy layer at the soil surface (Kimmerer 2003). Kimmerer (2003) suggests that the mossy layer influences moisture movement through the soil that moderates temperatures that affect nutrient availability to plants.

The complexity of litter interactions was unique at each site. Some effects were common to both sites such as *H. perforatum* litter decreasing *H. perforatum* density more than indigenous species litter. Litter application in all combinations decreased indigenous and non-indigenous plant species density compared to no litter. Litter effect on indigenous and non-indigenous species was strongly dependent upon the interaction of the amount of litter, the source of litter, and the size of litter.

CONCLUSION

Implications of Litter Management and Invasive Species

The focus on the canopy inside the fence and the adjacent native community at the National Bison Range was for the purpose of better understanding litter influence on *Hypericum perforatum* capacity to colonize and establish. Heightened concern at the Range as early as 1926 prompted use of herbicide that was temporarily discontinued in 1959 when biological control agents were released.

Grazing practices also changed and the exclosure fence was constructed for the purpose of studying the effect of rest. Allowing the perennial grass litter to accumulate can cause an abundance of dead plant litter in the center of the plant trapping nutrients and shading the growing parts at the plant's base. Lack of sunlight required for the plant to carry on photosynthesis can hinder perennial grass ability to grow and will eventually kill the plant.

Drought combined with accumulated litter can cause perennial grasses to die leaving standing litter that could otherwise provide mulch on the soil surface versus dry and bare conditions that over time can lead to desertification (Keppel 2003). Hard bare soil can restrict water and air, and compromise other conditions required for seeds to germinate. It is possible that returning the land to grazing by large ungulates similar to its evolution could mitigate *Hypericum perforatum* presence by reducing loss from over-rest of perennial grasses. Plants do not evolve in isolation. They evolve interacting with abiotic and biotic factors in communities (functional groups) unique to their ecosystem.

Litter had a strong influence on *Hypericum perforatum* species density, cover, and biomass. The effect was dependent upon the interaction of the source, amount, and size of litter. Figure 16 shows the study site four years after the conclusion of the study.

The grass canopy on the left is the location of the study site inside the exclosure fence. The *Hypericum perforatum* canopy on the right is where litter was not removed and no litter treatment was administered. *Hypericum perforatum* was decreased the greatest in its own litter. Two combinations of litter interactions decreased *H. perforatum* and increased indigenous species density. Invasion biology research should include a better understanding of defense mechanisms such as compounds induced in *H. perforatum* possibly by its own canopy and chemistry. More precise knowledge is needed about litter influence on microclimates in systems dominated by invasive non-indigenous species. If litter effect over time can change community dynamics in invaded systems toward desired, diverse, or functional vegetation groups that fill all of the niches creating a weed-resistant state, then more litter research is warranted.

Figure 16. Study Site Photograph July 2005



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APPENDIX

Analysis of Variance Tables

Table 38. ANOVA TABLE 1. Invasive Site - Non-Indigenous Species

Dependent Variable: Non-Indigenous Species				
Source	DF	Sum of Squares	Mean Square	F Value
Model	11	845.762847	76.887532	4.36
Error	24	423.432428	17.643018	
Corrected Total	35	1269.195275		
Source	Pr > F			
Model	0.0013			
R-Square	Coeff Var	Root MSE	Non-Indigenous Mean	
0.666377	35.91841	4.200359	11.69417	
Source	DF	Type III SS	Mean Square	F Value
rep	3	620.8016972	206.9338991	11.73
trt	8	224.9611500	28.1201437	1.59
Source	Pr > F			
rep	<.0001			
trt	0.1790			

TABLE 39. ANOVA TABLE 2. Invasive Site - Indigenous Species

Dependent Variable: Indigenous Species				
Source	DF	Sum of Squares	Mean Square	F Value
Model	11	954.864331	86.805848	2.75
Error	24	758.341344	31.597556	
Corrected Total	35	1713.205675		
Source	Pr > F			
Model	0.0186			
R-Square	Coeff Var	Root MSE	Indigenous Mean	
0.557355	39.75602	5.621170	14.13917	
Source	DF	Type III SS	Mean Square	F Value
rep	3	175.1492306	58.3830769	1.85
trt	8	779.7151000	97.4643875	3.08
Source	Pr > F			
rep	0.1655			
trt	0.0154			

Table 40. ANOVA TABLE 3. Native Site - Non-Indigenous Species

Dependent Variable: Non-Indigenous Species				
Source	DF	Sum of Squares	Mean Square	F Value
Model	11	105.4560639	9.5869149	2.46
Error	24	93.4874333	3.8953097	
Corrected Total	35	198.9434972		
Source	Pr > F			
Model	0.0315			
Error				
Corrected Total				
R-Square	Coeff Var	Root MSE	Non-Indigenous Mean	
0.530080	81.06280	1.973654	2.434722	
Source	DF	Type III SS	Mean Square	F Value
rep	3	69.20774167	23.06924722	5.92
trt	8	36.24832222	4.53104028	1.16
Source	Pr > F			
rep	0.0036			
trt	0.3603			

Table 41. ANOVA TABLE 4. Native Site - Indigenous Species

Dependent Variable: Indigenous				
Source	DF	Sum of Squares	Mean Square	F Value
Model	11	954.864331	86.805848	2.75
Error	24	758.341344	31.597556	
Corrected Total	35	1713.205675		
Source	Pr > F			
Model	0.0186			
Error				
Corrected Total				
R-Square	Coeff Var	Root MSE	Indigenous Mean	
0.557355	39.75602	5.621170	14.13917	
Source	DF	Type III SS	Mean Square	F Value
rep	3	175.1492306	58.3830769	1.85
trt	8	779.7151000	97.4643875	3.08
Source	Pr > F			
rep	0.1655			
trt	0.0154			

Table 42. ANOVA TABLE 5. Invasive Site - *Hypericum perforatum*

Dependent Variable: <i>Hypericum perforatum</i>				
Source	DF	Sum of Squares	Mean Square	F Value
Model	11	899.123306	81.738482	5.17
Error	24	379.749594	15.822900	
Corrected Total	35	1278.872900		
Source	Pr > F			
Model	0.0004			
R-Square	Coeff Var	Root MSE	<i>Hypericum perforatum</i> Mean	
0.703059	35.04156	3.977801	11.35167	
Source	DF	Type III SS	Mean Square	F Value
rep	3	662.5696556	220.8565519	13.96
trt	8	236.5536500	29.5692062	1.87
Source	Pr > F			
rep	<.0001			
trt	0.1129			

Table 43. ANOVA TABLE 6. Native Site - *Hypericum perforatum*

Dependent Variable: <i>Hypericum perforatum</i>				
Source	DF	Sum of Squares	Mean Square	F Value
Model	11	122.4622778	11.1329343	3.14
Error	24	84.9899444	3.5412477	
Corrected Total	35	207.4522222		
Source	Pr > F			
Model	0.0092			
R-Square	Coeff Var	Root MSE	<i>Hypericum perforatum</i> Mean	
0.590316	85.06471	1.881820	2.212222	
Source	DF	Type III SS	Mean Square	F Value
rep	3	76.32855556	25.44285185	7.18
trt	8	46.13372222	5.76671528	1.63
Source	Pr > F			
rep	0.0013			
trt	0.1690			
