Available online at www.sciencedirect.com
SCIENCE DIRECT®
Forest Ecology and Management 208 (2005) 347–358
Forest Ecology and Management
www.elsevier.com/locate/foreco

Conifer invasion of forest meadows transforms soil characteristics in the Pacific Northwest

Robert Griffiths *, Michael Madritch [1], Alan Swanson [2]

Department of Forest Science, Richardson Hall, Oregon State University, Corvallis, OR 97331, USA

Received 16 May 2004; received in revised form 14 January 2005; accepted 14 January 2005

Abstract

In many areas, chemical and biological characteristics of soils change when trees colonize meadows. To determine if the invasion of high meadows by forests in the central Cascade Mountains of Oregon altered soil properties, we measured soil properties along transects from mountain meadows through transition zones, where trees were becoming established, into mature forest. The differences observed in this study support the view that N is more available in meadow soils than in forest soils and that N pools and cycling change markedly when trees invade mountain meadows. β-Glucosidase activity in the transition zone soil was close to that in the forest soil and much lower than that in the meadow soil, suggesting qualitative changes in microbial populations as microorganisms adjusted to changes in litter quality. High correlations between litter depth and most variables in meadow soil, which were not observed in transition zone soil or mature forest soil, suggest that litter may control other aspects of biogeochemical cycling in meadows. With the exception of laboratory respiration, the values observed in the transition zone soil lay between those in meadow soil and those in forest soil; in most cases, they were closer to those in forest soil. This suggests that soil properties shift rapidly toward those found in forests as trees invade meadows. These rapid changes may alter soils so that they are more likely to support trees than grass.

Keywords: Forest meadow; Oregon Cascade Mountains; Soil biogeochemistry; Tree invasion

1. Introduction

Although forest meadows make up a relatively small fraction of the total area of the central Cascade Mountains of Oregon, their flora includes a large variety of plant species that greatly enrich biodiversity over the landscape (Hickman, 1976). Under present climatic conditions and forest management, surrounding forests are invading many high-dry mountain meadows of the Pacific Northwest, providing an

* Corresponding author. Tel.: +1 541 737 6559; fax: +1 541 737 1393.
E-mail address: griffithsr@fsl.orst.edu (R. Griffiths).
[1] Present address: Department of Entomology, University of Wisconsin, Madison, WI 53706, USA.
[2] Present address: Yellowstone Ecological Research Center, 2048 Analysis Drive Suite B, Bozeman, MT 59718, USA.

0378-1127/$ – see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2005.01.015

opportunity to study changes in soil properties in response to vegetative succession (Franklin et al., 1971; Magee and Antos, 1992; Yakimenko, 1997; Miller and Halpern, 1998).

Although the origin of these meadows is not known with certainty, it is likely they have been maintained by aboriginal burning (Popenoe et al., 1992; Miller and Halpern, 1998). Factors responsible for the current invasion also are not known with certainty, but climate change, fire suppression, and termination of sheep grazing may have all contributed (Popenoe et al., 1992; Miller and Halpern, 1998). In a comprehensive study of tree invasion in the central Cascade Mountains of Oregon, Miller and Halpern (1998) noted that autogenic factors (e.g., trees influencing the establishment of seedlings by altering microclimate) may also control this process. In addition to controlling moisture, the pioneer trees could alter soil properties, thereby increasing seedling establishment.

Forest managers are looking for techniques to reverse invasion of high elevation mountain meadows by nearby forests while maintaining biological and habitat diversity (Popenoe et al., 1992). One objective of this study was to provide basic information about biogeochemical transformations associated with tree invasion that could be used to monitor the effectiveness of different treatments.

Grasslands and forests differ greatly in soil chemistry (Göceoğlu, 1988; Popenoe et al., 1992; Hart et al., 1993; Ross et al., 1996; Yakimenko, 1997), rates of litter decomposition (Hunt et al., 1988; Köchy and Wilson, 1997), and food web composition (Hunt et al., 1987; Ingham et al., 1989). Our study was designed to measure changes in both chemical and biological characteristics of high-elevation mountain meadows as they are invaded by adjacent forests. We included analysis of the transition zone in order to obtain a rough idea of which soil properties change most rapidly after tree invasion.

2. Materials and methods

2.1. Site descriptions and sampling

All five research sites were on ridge-tops on or near the H.J. Andrews Experimental Forest (Blue River, OR) in the central Cascade Mountains. Because of forest fire control and lack of grazing since the 1930s, surrounding forest vegetation has been encroaching on these meadows. The mature forests are dominated by *Abies grandis* (Dougl. ex D. Don) Lindl. (grand fir), *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), and *Pinus contorta* Dougl. ex Loud. (lodgepole pine) (Charles Halpern, University of Washington, Seattle, WA, personal communication). Most of the invading trees were *A. grandis* and *P. contorta*. The vegetation in the meadows was dominated by grasses (35%), forbs (38%), and sedges and rushes (18%). *Festuca rubra* L. and *Bromus carinatus* Hook. & Arn. were the most common grasses; *Fragaria vesca* L. and *F. virginiana* Duchesne, *Achillea millefolium* L., *Eurybia radulina* (Gray) Nesom, *Lupinus latifolius* Lindl. ex J.G. Agardh, *Hieracium gracile* Hook. and *Pteridium aquilinum* (L.) Kuhn, the most common forbs; *Carex pensylvanica* Lam., the most common sedge; and *Phlox diffusa* Benth., the most common shrub (Charles Halpern, personal communication).

Meadow soils were Pachic Haplocryolls, fine-loamy, mixed mineralogy, deep loams with very well-developed mollic epipedons ranging from 63 to 90 cm. The top mineral soil had a dark layer 63–90 cm deep. Soils in the transition zone were Typic Haplocryolls with much shallower and less well developed mollic epipedons. In general, these soils had lighter colors than meadow soils and a top mineral soil horizon approximately 5–15 cm deep. In the forests, the soils were Dystric Cryochrepts and were generally reddish or yellowish with a top mineral soil horizon approximately <3 cm deep. The mollic epipedons in these soils were very shallow, only a few cm deep (John Phillips, USDA Forest Service, Blue River, OR, personal communication).

Five contiguous transects were sampled in five separate meadow-forest transition zones from late July to early August 1998. All five sites were selected to have essentially the same aspect, slope, elevation, and parent material. Four of the meadows were located along the same ridgeline separated by forested areas. The distance between the meadows was approximately 0.5 km; they should be considered distinct sites for purposes of statistical analysis. The fifth site was located on another ridge-top approximately 30 km to the west. Each 225-m transect comprised three 75-m segments (1 segment/zone): forest meadows; transition

zones, where conifers were becoming established in forest meadows; and forests with relatively little understory vegetation and no grass. The leading edge of the transition zone was well defined by a distinct line of conifers at the meadow interface. The end of the transition zone on the forest side was defined by the lack of grass on the forest floor. Although we did not conduct tree-ring analyses on the trees within the transition zone, we judged trees at the meadow edge to be about 10–15 years old (seedlings excluded). The trees at the other end of the transition zone were much older, possibly approaching the age of the trees in the mature forest zone. On the basis of fire history and other factors, we estimated the age of the trees at the other end of the transition zone to be about 100 years.

A 4.7 cm × 10 cm soil core was taken and field observations were made every 5 m along each transect. The samples were transported to the laboratory in an ice chest and stored at 15 °C until analysis, usually within 16 h of their receipt.

2.2. Field measurements

Litter depth, mineral soil respiration, soil temperature, and ectomycorrhizal mat percentages were measured in the field. Mineral soil respiration was measured with a nondispersive infrared CO_2 analyzer (LI-6200, LI-COR Inc., Lincoln, NE). Measurements were made for 1 min after the chamber gas had reached ambient CO_2 concentration. The instrument was calibrated at each location against a known standard. A Q_{10} adjustment was made for ambient soil temperature. Soil temperature was measured at a depth of 10 cm by electronic thermometers calibrated at 0 °C with ice water.

The spatial distribution of ectomycorrhizal mats was determined visually by inspecting the relative abundance of mats in 4.7 cm × 10 cm cores. The aerial extent of mats within five cores was reported as a percent. This approach has been used successfully in the past to document ectomycorrhizal mat distribution patterns in coniferous forests of the Pacific Northwest (Griffiths et al., 1996).

2.3. Laboratory analyses

In preparation for laboratory analyses, all soils were sieved through a 2-mm sieve. Soil pH was measured in 1:10 (soil:distilled water) slurries of oven-dried (100 °C) soil. These slurries were shaken for 1 h before pH values were read with a Sigma model E4753 electrode (Sigma Chemical, St. Louis, MO). Soil organic matter (SOM) of oven-dried soil was measured by loss-on-ignition at 550 °C for 6 h. Percent soil moisture was calculated as the difference in weight between field-moist soil and oven-dried soil (100 °C for 8 h) divided by dried soil mass.

Denitrification potential was measured by the method of Groffman and Tiedje (1989) as modified by Griffiths et al. (1998). Each reaction vessel (25-ml Erlenmeyer flask) contained 5 g of field-moist soil, particles <2 mm. Flasks were sealed with rubber serum-bottle stoppers and purged with Ar to displace O_2 in the headspace gas. After purging, 2 ml of a 1 mM solution of glucose and NO_3^- was added to each flask. Flasks were preincubated at 25 °C for 1 h. This preincubation period was used because previous time-series experiments showed a lag in N_2O production during this period, followed by linear N_2O production rates during the following 2–4 h (unpublished data). After preincubation, 0.5 ml of headspace gas was removed from the reaction vessel and injected into a gas chromatograph (GC) fitted with an electron capture detector (Hewlett-Packard model 5890 GC, connected to a Hewlett-Packard model 3396 integrator; Hewlett-Packard, Palo Alto, CA). The integrator was calibrated by the external calibration method with known gas standards. The stainless steel column (2 m × 3 mm) was packed with Poropak-N. The carrier was oxygen-free N. Oven temperature was 55 °C; injection temperature was 125 °C. A second headspace N_2O analysis was made after an additional 2-h incubation at 25 °C. The net N_2O released over these 2 h was used to estimate N_2O production rates.

Laboratory respiration, which represents the basal respiration rate for soil microorganisms, was measured on field-moist, sieved soils. Soils (4 g dry weight) were brought to 75% moisture content by adding enough sterile deionized water to equal 3 g water per 25-ml Erlenmeyer flask. The flasks were sealed with serum-bottle stoppers and incubated at 24 °C for 1 h before the first headspace CO_2 measurement was made. The flasks were incubated for another 2 h and headspace CO_2 concentration was again measured. The same GC, integrator, and temperatures were used for this assay as were used

to measure N_2O, but in this case the GC was equipped with a flame ionization detector and a methanizer in series, and the column was packed with Poropak-R (50/80 or 80–100 mesh). Long-term respiration rates, a measure of labile soil C, were measured from the same flasks, incubated at 24 °C for another 14 days before the headspace CO_2 assay was repeated.

Substrate-induced respiration (SIR) was also measured in these soils. The reaction vessels were prepared as before, except that 0.1 ml of 1 M glucose solution (0.1 ml H_2O in the controls) was added to the reaction vessel. The assay for CO_2 evolution was the same as that for laboratory respiration. SIR was calculated by subtracting CO_2 evolution rates without glucose from those with glucose.

Extractable NH_4^+ was determined by shaking 10 g of field-moist soil with 50 ml of 2 M KCl for 1 h (Keeney and Nelson, 1982), adding 0.3 ml of 10 M NaOH to the slurry, and measuring NH_4^+ concentration with an Orion model 95–12 NH_4^+ electrode (Orion Research Inc., Boston, MA). Potential mineralizable N (PMN) was measured by the water-logged technique of Keeney and Bremner (1966). For each analysis, 10 g of field-moist soil was added to 53 ml of distilled water in a 20 mm × 125 mm screw-cap test tube and incubated at 40 °C for 7 days. Then 53 ml of 4 M KCl was added to the slurry, and NH_4^+ concentration was determined with the NH_4^+ electrode. PMN was calculated as the difference between initial and final NH_4^+ concentrations.

β-Glucosidase is an enzyme that hydrolyzes cellobiose. Its activity was determined by the spectrophotometric assay of Tabatabai and Bremner (1969), as modified by Caldwell et al. (1999). One milliliter of 10 mM *p*-nitrophenyl β-D-glucopyranoside substrate was added to duplicate 1-ml subsamples containing a soil slurry (1 g dry weight in 1 ml deionized H_2O); controls had no substrate. The tubes were shaken and then placed in a 30 °C water bath for 2 h. After incubating, 1 ml of substrate solution was added to the controls, and all reactions were stopped immediately by addition of 2 ml of 0.1 M tris[hydroxymethyl]aminomethane at pH 12.0. The mixtures were centrifuged for 5 min at 500 × *g* and 0.2 ml of the supernatant was diluted with 2.0 ml deionized water. The optical density was measured at 410 nm. The standard curve was prepared from 0.02 to 1.0 μmol ml^{-1} *p*-nitrophenol (pNP).

2.4. Statistical analyses

Mean values for the three zones were compared by multifactor ANOVA for each of the five transects, as were mean values for all the meadow, transitional, and forest segments. All data that were not normally distributed were log transformed before ANOVA analyses were performed. Significant differences among means were determined with Fisher's protected least significant difference ($P \leq 0.05$). Correlations among variables were made with Spearman rank analysis. A discriminant analysis was made on all data points; the variables were pH, litter depth, fungal mat percentages, and β-glucosidase activity.

In addition to the ANOVA analysis to determine the significance of treatment differences, change-point analyses were made to determine when there was a statistically significant pattern shift along the transect moving from meadows into the transition zone and from forests into the transition zone. Using mean values from all transects, an overall mean for each zone was calculated along with the standard error (Wales, 1972). Smoothed data were generated, using a five-point average. The point along the transect at which the smooth value exceeded the mean ± 1 S.E. was the change point for that transition. Change points going from meadow to the forest on one end of the transect (MCP) and from the forest into the transition zone on the other end (FCP) were calculated.

All statistical analyses were conducted with Statgraphics® Plus for Windows® (Statistical Graphics Corporation, Rockville, MD).

3. Results

3.1. Contrasts between meadow and forest soils

Soils in meadows differed significantly from those in mature forests on the basis of the mean values for all five transects for half of the variables: pH, soil temperature, denitrification potential, litter depth, field respiration, β-glucosidase activity, and ectomycorrhizal mats (Table 1). When individual samples along each transect segment of the individual transects were used in analysis, meadow and forest segments were significantly different in soil moisture and labile C concentrations along all five transects. Fungal mat

Table 1
Mean values for all three segments of five transects

Variable	Meadow	Transition	Mature
Soil			
Moisture (%)[a]	23.6	30.1	30.3
pH	5.35a	5.25b	5.14c
Temperature (°C)	14.2a	13.4ab	12.0b
Extractable NH_4^+ (nmol gdw^{-1})	0.42	0.29	0.19
Potential mineralizable N (nmol gdw^{-1})	9.4	9.2	8.7
Denitrification potential (ng N gdw h^{-1})	23.9a	9.7b	4.8b
Litter depth (cm^2)	0.50b	3.15a	4.32a
Soil organic matter (%)	25.2	24.3	24.0
Labile C (μg C gdw day^{-1})[a]	10.3	13.6	14.0
Respiration			
Field (g m^2 h^{-1})	9.9b	15.0a	16.1a
Laboratory (μg C gdw h^{-1})	3.0	3.4	3.4
Substrate-induced (μg C gdw h^{-1})	2.96	2.98	3.06
β-Glucosidase (μmol gdw h^{-1})	0.21a	0.14b	0.12b
Total fungal mats (%)	0.11b	13.8a	33.6a

Within a row, values followed by different letters are significantly different at $P < 0.05$ by ANOVA on the mean values for each segment of each transect.

[a] Variables that showed significant differences between grass and forest soils within each of the five transects. In these analyses, values for all samples collected along each transect were treated as separate observations. An autocorrelation analysis showed no consistent autocorrelations at the 5-m sampling interval used in this study.

percentages, litter depth, denitrification potential, field respiration, and β-glucosidase levels showed the greatest percent difference between meadow and forest zones (Table 2).

In meadow soils, litter depth was tightly coupled with denitrification, β-glucosidase activity, SOM, and PMN concentration in the Spearman rank correlations (Table 3). In forest soils, on the other hand, litter depth covaried positively with extractable NH_4^+ and negatively with β-glucosidase activity and substrate respiration, a trend that was also observed in the transition zone (Table 3).

3.2. Changes in the transition zone

Three variables (pH, β-glucosidase, and fungal mats) showed linear responses throughout the transition zone. Three variables (denitrification potential, litter depth, soil moisture) reached forest levels well within the transition zone (Fig. 1a–i).

Table 2
Percent change between meadow and forest zones for the variables that showed a statistically significant difference in the ANOVA for the means of all sites or that showed significant differences by transect for all five transects

Variable	Change (%)[a]
Soil	
Moisture	28.4
pH	39.7
Temperature	(15.5)
Denitrification potential	(79.9)
Litter depth	764
Labile carbon	35.9
Field respiration	62.6
β-Glucosidase	(42.9)
Total fungal mats	30,455

[a] Values in parentheses are negative values.

With the exception of laboratory respiration rates, values in transitional zones were intermediate between those in the meadow and mature forest segments (Table 1). In most cases, values in the transition zone soils were closer to those in forests than to those in meadows. The unique qualities of meadow and forest soils were also seen in our discriminant analyses (Fig. 2). The centroids for the transition zone fell between those for the meadow and forest clusters, further supporting the view that the transition zone is moving meadow soils towards those typical of forests ($P = 0.0000$ for Function 1 and 0.010 for Function 2).

Table 3
Spearman rank correlations (r values) between litter depth and other variables in grass, transition, and mature transect segments

Variable	Meadow	Transition	Mature
Extractable NH_4^+	−0.07	0.46*	0.30*
Potential mineralizable N	0.52*	−0.06	0.02
Denitrification potential	0.25*	−0.25*	0.00
Soil organic matter	0.36*	−0.13	0.16
Respiration			
Field	0.23*	0.26	0.11*
Substrate-induced	0.31*	−0.20	−0.15
β-Glucosidase	0.44*	−0.33*	−0.19*

* $P < 0.05$.

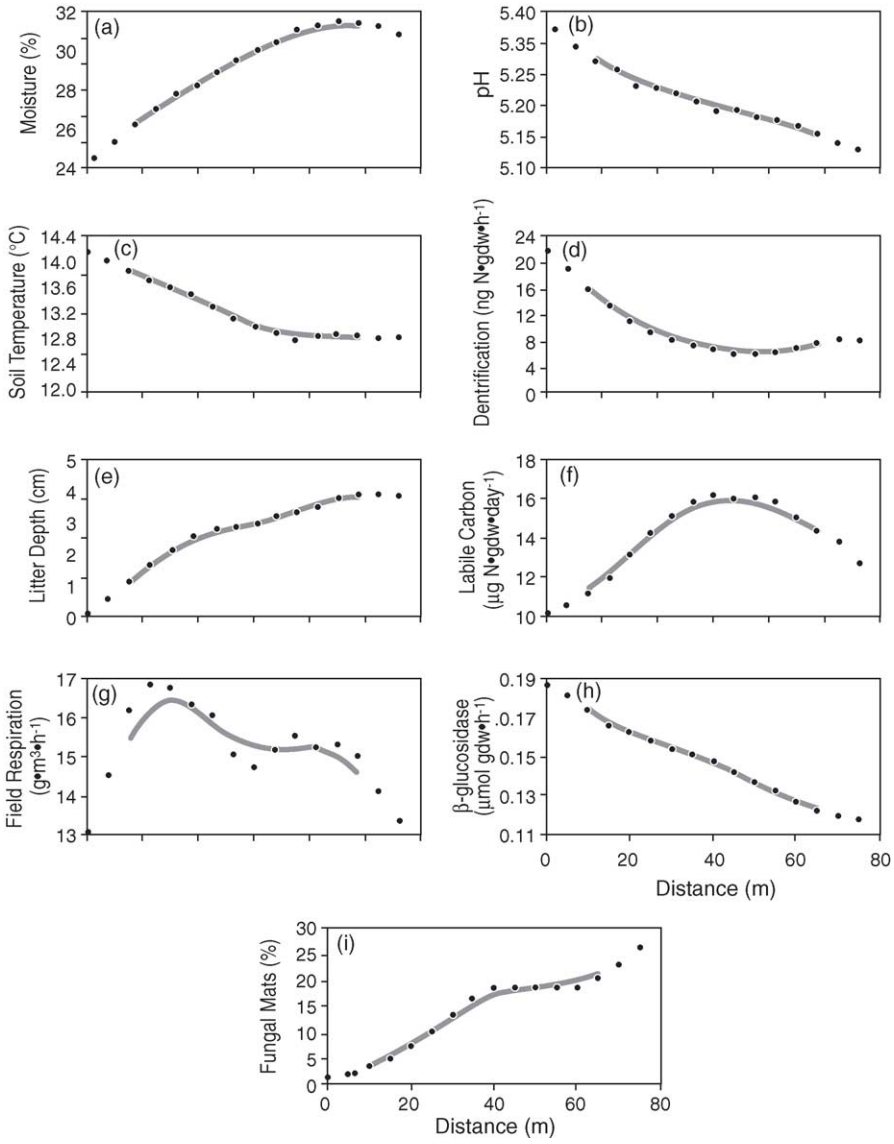

Fig. 1. Scatter plots of smoothed data within the transition zone. The smoothed data were generated using a period of 5 and the smoothing function of Statgraphics® Plus for Windows®.

3.3. Change points

Change-point analysis showed significant changes in most variables from mean meadow values at or near the meadow-transition zone edge. These are demonstrated in plots for soil moisture and temperature, denitrification potential, litter depth, β-glucosidase, and fungal mats (Fig. 3a–f). Plots of transition zones using smoothed data show an initial linear response in the transition zone for all of these variables (Fig. 1a–i). Linear correlations were tight for all but one variable in the same segments (Table 4). In most cases, the absolute values of slopes along the first half of transition zones were higher than those along the second half.

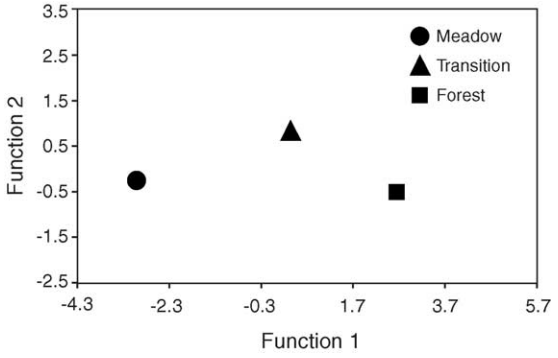

Fig. 2. Centroids for meadow, transition and forest zones generated by discriminant function analysis using pH, litter depth, fungal mat percentages, and β-glucosidase activity. The *P*-values for Functions 1 and 2 are 0.0000 and 0.010, respectively.

Table 4
The results of linear regression analyses using smoothed data for variables along the first (0–30 m) and second (35–75 m) half of the transition zone

Variable	First half			Second half		
	Slope	R^2	*P*-value	Slope	R^2	*P*-value
Soil						
Moisture	0.147	99.0	0.0000	0.037	58.2	0.017
pH	−0.004	95.4	0.0002	−0.002	97.3	0.0000
Temperature	−0.028	99.4	0.0000	−0.006	55.4	0.025
Denitrification potential	−0.46	97.5	0.0000	0.046	46.5	0.043
Litter depth	0.075	99.0	0.0000	0.024	92.3	0.0000
Labile carbon	0.173	97.5	0.0000	−0.082	81.5	0.0008
Field respiration	0.095	53.4	0.061	−0.031	37.5	0.080
β-Glucosidase	−0.001	98.5	0.0000	−0.0009	98.9	0.0000
Fungal mats	0.403	94.9	0.0002	0.189	76.1	0.0022

4. Discussion

Our working hypothesis before we started this study was that different variables would start changing at different points along the transition zone as trees invade mountain meadows, and the variables would show different lags. This did not occur in the variables that showed significant responses. In essentially every

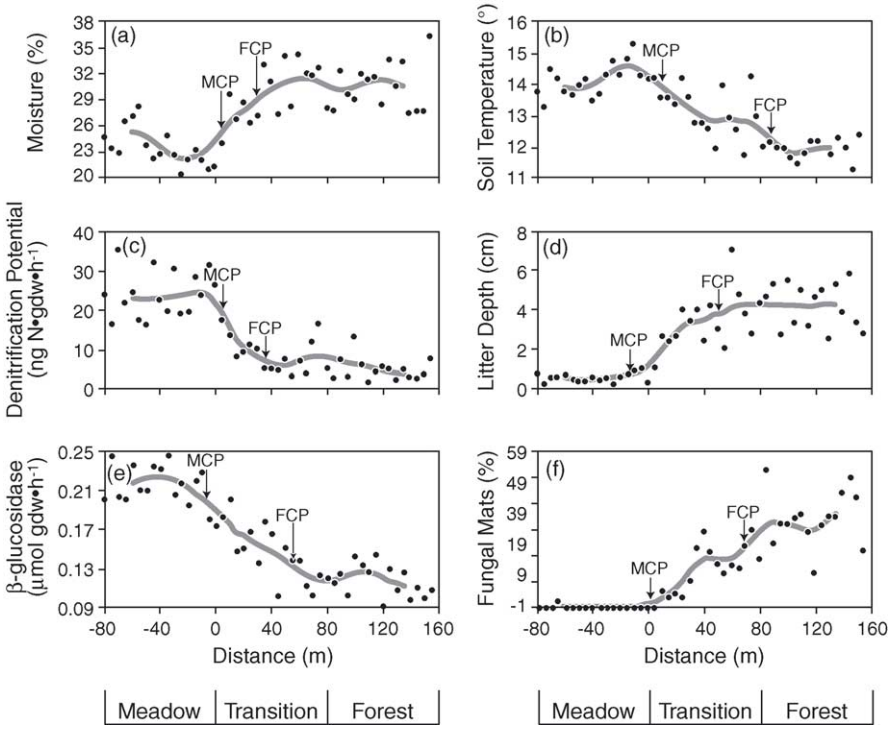

Fig. 3. Scatter plots of distances from the meadow-forest edge against the mean values at each sample location for all five transects. MCP, the location of the meadow-to-forest change point; FCP, location of the forest-to-meadow change point.

case, change occurred either at the meadow-forest edge or even within the meadow adjacent to the edge. Even though grass was found throughout the transition zone, the shift to forest values was essentially complete for all variables at some point within the transition zone.

4.1. Contrasts between meadow and forest soils

4.1.1. Carbon

Even though litter depth in meadows was only 12% of that in forests, this variable apparently was pivotal in cycling organic matter in meadows, as shown by high positive correlations between litter depth and other variables. These correlations may, however, be driven by more than surface litter. Since a large portion of fixed C is transported into the rhizosphere in grasses (Parton et al., 1978; Oades, 1988), rhizosphere C in meadows may have covaried with surface litter.

The transport of fixed C belowground may result in qualitative differences in soil chemistry and organic matter between meadow and forest soils. In Russia, humic material accumulated within the grass rooting zone, accompanied by lower bulk densities and changes in pH and exchangeable Ca^{2+} and Mg^{2+}, during the first 50 years of meadow formation (Yakimenko, 1997). According to Oades (1988), the high percentage of organic matter allocated belowground in grasslands explains the occurrence of deep, dark organic surface layers, such as those we observed (unpublished field observations). This dark band of soil was greatly reduced by the invasion of trees and further reduced in mature forest soils.

The relatively large allocation of fixed C to the rhizosphere by grasses may account for the elevated SOM often found in grassland A horizon soils (Göceoğlu, 1988; Hixson et al., 1990; Jenkinson, 1991; Popenoe et al., 1992; Feige et al., 1995; Ross et al., 1996; Yakimenko, 1997). In the Popenoe et al. (1992) study, however, no significant differences were found between meadows and forest soil SOM concentrations in the top 10 cm of mineral soil. This result is essentially the same as ours.

Field respiration rates of meadow soil were only 49% of those in forest soil. Since soil respiration rates may reflect relative indexes of productivity in different vegetative assemblages (Ellis, 1969; Williams et al., 1997; Law et al., 1999, 2000), reduced field respiration rates in meadow soil may reflect lower primary productivity. This is what we would expect from published data comparing grassland and forest net primary productivity (NPP). NPP in grasslands typically is roughly half those in forests (Schlesinger, 1991; McGuire et al., 1992; Chapin, 1993). The lower NPP may also explain the lower (but not statistically different) labile C concentrations and laboratory respiration rates we found in meadow soils.

4.1.2. Nitrogen

In general, grassland organic matter tends to be enriched in N relative to C (Hixson et al., 1990; Popenoe et al., 1992; Köchy and Wilson, 1997), and, on a mass basis, N in grass litter is roughly twice that found in forest litter (Daubenmire and Prusso, 1963; Henzell, 1973; Aber and Melillo, 1980). This, along with faster decomposition in grasses, may explain why N mineralization rates in grasslands are typically higher than those in forests (Göceoğlu, 1988; Hixson et al., 1990; Ross et al., 1996). Both direct measures of N in our study (PMN and extractable NH_4^+) were higher in meadow than in forest mineral soil, but these differences were not statistically significant.

Denitrification potentials in meadow mineral soils were 5 times greater than those in forest soils. Since these assays are conducted under standardized conditions with excess NO_3^- and glucose and essentially no O_2, this assay measures denitrifying enzyme activity (DEA) (Groffman and Tiedje, 1989). DEA is correlated with mineralized N and N mineralization in soils (Melillo et al., 1983; Schipper et al., 1993; Griffiths et al., 1998; Stenberg, 1998).

The higher denitrification rates in meadow soils most probably reflect a higher availability of mineralized N to denitrifiers than is the case in forests (Griffiths and Swanson, 2001). This suggests a system that does not efficiently retain N, an observation made earlier by Dickinson (1983). Several studies indicate that N cycling may be accelerated in meadows. In New Zealand, net N mineralization rates (14-day incubations) in forest soils were only 61.5% of those in adjacent grassland soils in the top 10 cm of mineral soils (Ross et al., 1996). Total and microbial N were also significantly greater in the top 10 cm of grassland soils and to depths up to 50 cm. When litter N was added to the soil totals for the top 50 cm, N in the grass system was twice that in forests. A study by Wedin and

Pastor (1993) suggests that grassland systems that have higher net mineralization also have greater N availability. In a study comparing two forest meadows with adjacent forest soils in the same general location as the sites used in our study, Heichen (2002) found nitrogen mineralization rates in forest soils to be 41% of that in adjacent meadows. She also found that C:N ratios were significantly greater (by 25%) in forest than in meadow soils.

The lower denitrification rates in forest soils may reflect, not only lower N cycling rates, but also better retention of mineralized N (Johnson, 1992). In a study of N mineralization in forest soils, Stark and Hart (1997) observed that net mineralization rates were low, even though gross rates were very high, suggesting that the microbial community sequesters mineralized N very efficiently. Ectomycorrhizal mats can decompose litter directly and move the released N directly to the host tree (Aquilera and Griffiths, 1993; Read, 1993). Such mats occurred frequently in the mature forest segments of our transects but were essentially absent in meadows.

4.1.3. Differences in soil biota

The significantly lower concentrations of ectomycorrhizal mats and elevated β-glucosidase levels that we found in grasslands support earlier observations (Hunt et al., 1987; Ingham et al., 1989; Heichen, 2002) that microbial assemblages differ in grassland and forest soils. These differences also appear in the next higher trophic level, microbial consumers (Cromack et al., 1988; Ingham et al., 1989).

The hosts for ectomycorrhizae are trees; no meadow vegetation is known to support them. Reestablishment of these mats after stand harvest may take decades (Griffiths et al., 1996). The large and significant difference in the occurrence of mycorrhizal mats was thus as expected from the distribution of hosts and the time required to produce ectomycorrhizal mats after seedling establishment.

The phenomenon of microorganisms adjusting their enzymatic production to reflect the relative abundance of specific types of compounds in litter and detritus has long been observed in various ecosystems (Ladd, 1978; Griffiths et al., 1982; Sinsabaugh and Linkins, 1990; Sinsabaugh, 1994; Wagner and Wolf, 1998). If more readily accessible cellulose and N enhance the ability of a microbial population to decompose cellulose and cellobiose (a disaccharide product of cellulose decomposition), SIR and β-glucosidase should covary in meadows but not in forests, as in fact, we observed. This suggests a qualitative functional difference in microbial populations in meadow and forest soils, caused either by increased enzyme production by similar microbial populations or by actual shifts in the types of organisms present.

Both bacteria and fungi can produce β-glucosidase, which cleaves cellobiose (Eivazi and Tabatabai, 1988; Wagner and Wolf, 1998) and is induced by this substrate (Chróst, 1991). SIR is tightly correlated with microbial biomass (Horwath and Paul, 1994; Beck et al., 1997). Meadow and forest soils did not differ significantly in SIR; however, β-glucosidase activities were 66% higher in meadow soils. If β-glucosidase activities also were directly correlated with microbial biomass, we would expect no significant differences between meadow and forest. The microbial population thus may have shifted qualitatively toward one adapted to the higher cellulose availability in grass litter.

The relative abundance of cellulose in grass and tree litter is similar, but the concentration and types of lignin differ (Bailey, 1973; Berg and Staaf, 1980; Edmonds, 1987). Lignin in tree litter tends to protect cellulose from microbial attack. This, along with the higher N levels (Daubenmire and Prusso, 1963; Henzell, 1973; Aber and Melillo, 1980), may explain why grass litter decomposes faster than tree litter (Göceoğlu, 1988; Hixson et al., 1990; Ross et al., 1996).

4.2. Changes in the transition zone and change points

Smooth plots of the transition zone showed that the initial response in the first half of the transition zone was essentially linear; values approached those in forests in the second half. This is also reflected in the linear regression analyses. With one exception, the linear response in the first half of transition zone was tight and highly significant. These results all suggest that soil changes caused by trees as they invade meadows take place soon after trees get established in the meadow. This response tapers off the further one goes into the transition zone, as reflected by the lower

slopes and generally poorer fit to linear responses in the second half of the transition zone. The locations of forest change points (FCP), where values indistinguishable from forest values were attained, in the second half of the transition zone occurred at different locations for different variables. This suggests that, even though grass was present throughout the transition zone, the trees were clearly dominating soil biogeochemical cycling. This does not imply, however, that the soils in the transition zone were indistinguishable from those of forests. The discriminate analysis clearly shows that the soils in each of these zones were significantly different from one another.

4.3. Forest management implications

This study has shown that, as hypothesized, meadow and forest soils have different properties and that meadow soil rapidly assumes forest soil characteristics as forests invade meadows. Although the meadow soils were somewhat drier and warmer in the summer, when these studies were conducted, than those in the forest, these differences probably did not persist during most of the year. The observed differences likely were driven by qualitative differences in grass and tree litter, resulting in differences in the biogeochemical properties of microbial decomposers, more than by differences in microclimate generated by the vegetation.

Forests were invading all of the meadows studied. In isolated areas on similar sites where individual trees had become established within the meadow, islands of conifer seedlings soon followed (Miller and Halpern, 1998). Where these pioneer trees were cut, new seedlings rapidly reestablished, suggesting that the trees had altered the soils so as to enhance seedling survival. From a management perspective, cutting trees in and adjacent to mountain meadows clearly is unlikely to be the best strategy for expanding or maintaining mountain meadows under current climatic and disturbance regimes. Fire may well be the best management tool for reestablishing grasses on these sites, since this mechanism probably maintained them before 1900 (Popenoe et al., 1992).

Managers faced with different options for reversing the invasion of mountain meadows by surrounding forests would find it useful to be able to evaluate the effectiveness of various treatments by monitoring treated sites. Of the variables studied, fungal mat percentages, litter depth, denitrification potential, field respiration, and β-glucosidase activities showed the most dramatic shift from meadow to forest zones. Although we did not document it formally, we observed that the depth of the dark organic layer associated with grass roots decreased dramatically as grassy areas were converted to forest.

Our study was not designed to determine which of these variables would revert most rapidly when trees are removed and grasses reintroduced. It does provide some clues, however, as to which variables might be useful in assessing the effectiveness of meadow restoration. If soils in the treated area are compared with those of neighboring meadows and forests, elevated denitrification potentials and β-glucosidase and depressed soil respiration and fungal mat percentages relative to forest soils would indicate that conditions associated with meadow soils prevail. On longer time scales, the development of a deep dark organic soil layer and the absence of tree seedling establishment would also be obvious indicators of a successful manipulation.

Acknowledgements

We thank Amy Holcomb for her assistance with the soil analyses, Brian Mitchell, Edwin Price, Ronald Slangen, and Cedar Johnson for their assistance in conducting observations and soil analyses in the field, Alison F. Moldenke for editing the manuscript, John Phillips of the USDA Forest Service for the soil classification, and Charles Halpern of the University of Washington for the vegetation survey. We thank the National Science Foundation for financial support from the Long-Term Ecological Research program. This contribution is from the Andrews Experimental Research Group and the Forest Research Laboratory (Paper 3411), Oregon State University, Corvallis.

References

Aber, J.D., Melillo, J.M., 1980. Litter decomposition: measuring relative contributions of organic matter and nitrogen to forest soils. Can. J. Bot. 58, 416–421.

Aquilera, L., Griffiths, R.P., 1993. Nitrogen in ectomycorrhizal mat and non-mat soils of different-age Douglas-fir forests. Soil Biol. Biochem. 25, 1015–1019.

Bailey, R.W., 1973. Structural carbohydrates. In: Butler, G.W., Bailey, R.W. (Eds.), Chemistry and Biochemistry of Herbage, vol. 1. Academic Press, London, pp. 157–211.

Beck, T., Joergensen, R.G., Kandeler, E., Makeschin, F., Nuss, E., Oberholzer, H.R., Scheu, S., 1997. An interlaboratory comparison of ten different ways of measuring soil microbial biomass. Soil Biol. Biochem. 29, 1023–1032.

Berg, B., Staaf, H., 1980. Decomposition rate and chemical changes of Scots pine needle litter: II. Influence of chemical composition. In: Persson, T. (Ed.), Structure and Function of Northern Coniferous Forests: An Ecosystem Study. Swedish Natural Science Research Council, Stockholm, pp. 373–390.

Caldwell, B.A., Griffiths, R.P., Sollins, P., 1999. Soil enzyme response to vegetation disturbance in two lowland Costa Rican soils. Soil Biol. Biochem. 31, 1603–1608.

Chapin III, F.S., 1993. Functional role of growth forms in ecosystem and global processes. In: Ehleringer, J.R., Field, C.B. (Eds.), Scaling Physiological Processes: Leaf to Globe. Academic Press, San Diego, pp. 287–312.

Chróst, R.J., 1991. Environmental control of the synthesis and activity of aquaticmicrobial ectoenzymes. In: Chróst, R.J. (Ed.), Microbial Enzymes in Aquatic Environments. Springer-Verlag, New York, pp. 29–59.

Cromack Jr., K., Fichter, B.L., Moldenke, A.M., Entry, J.A., Ingham, E.R., 1988. Interactions between soil animals and ectomycorrhizal fungal mats. Agric. Ecosyst. Environ. 24, 161–168.

Daubenmire, R., Prusso, D.C., 1963. Studies of the decomposition rates of tree litter. Ecology 44, 589–592.

Dickinson, N.M., 1983. Decomposition of grass litter in a successional grassland. Pedobiologia 25, 117–126.

Edmonds, R.L., 1987. Decomposition rates and nutrient dynamics in small-diameter woody litter in four forest ecosystems in Washington, USA. Can. J. For. Res. 17, 499–509.

Eivazi, R., Tabatabai, M.A., 1988. Glucosidases and galactosidases in soils. Soil Biol. Biochem. 20, 601–606.

Ellis, R.C., 1969. The respiration of soil beneath some Eucalyptus forest stands as related to the productivity of the stands. Aust. J. Soil Res. 7, 349–357.

Feige, B.J., Melillo, J., Cerri, C.C., 1995. Change in the origin of soil organic matter; pasture introduction in Rondania (Brazil). Plant Soil 175, 21–29.

Franklin, J.F., Moir, W.H., Douglas, G.W., Wiberg, C., 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arct. Alp. Res. 3, 215–224.

Göceoğlu, M., 1988. Nitrogen mineralization in volcanic soil under grassland, shrub and forest vegetation in the Aegean region of Turkey. Oecologia 77, 242–249.

Griffiths, R.P., Swanson, A.K., 2001. Forest soil characteristics in a chronosequence of harvested Douglas-fir forests. Can. J. For. Res. 31, 1871–1879.

Griffiths, R.P., Caldwell, B.A., Morita, R.Y., 1982. Seasonal changes in microbial heterotrophic activity in subarctic marine waters as related to phytoplankton primary productivity. Mar. Biol. 71, 121–127.

Griffiths, R.P., Bradshaw, G.A., Marks, B., Lienkaemper, G.W., 1996. Spatial distribution of ectomycorrhizal mats in coniferous forests of the Pacific Northwest USA. Plant Soil 180, 147–158.

Griffiths, R.P., Homann, P.S., Riley, R., 1998. Denitrification enzyme activity of Douglas-fir and red alder forest soils of the Pacific Northwest. Soil Biol. Biochem. 30, 1147–1157.

Groffman, P.M., Tiedje, J.M., 1989. Denitrification in north temperate forest soils: relationships between denitrification and environmental factors at the landscape scale. Soil Biol. Biochem. 21, 621–626.

Hart, S.C., Firestone, M.K., Paul, E.A., Smith, J.L., 1993. Flow and fate of soil nitrogen in annual grassland and a young mixed-conifer forest. Soil Biol. Biochem. 25, 431–442.

Heichen, R.S., 2002. Biology and chemistry of a meadow-to-forest transition in the Central Oregon Cascades. M.S. thesis, Oregon State University, Corvallis, 85 pp.

Henzell, R.F., 1973. The nitrogen cycle of pasture ecosystems. In: Butler, G.W., Bailey, R.W. (Eds.), Chemistry and Biochemistry of Herbage, vol. 2. Academic Press, London, pp. 227–246.

Hickman, J.C., 1976. Non-forest vegetation of the central western Cascade Mountains of Oregon. Northwest Sci. 50, 145–155.

Hixson, S.E., Walker, R.F., Skau, C.M., 1990. Soil denitrification rates in four subalpine plant communities of the Sierra Nevada. J. Environ. Qual. 19, 617–620.

Horwath, W.R., Paul, E.A., 1994. Microbial biomass. In: Weaver, R.W., Angle, S., Bottomley, P., Smith, S., Tabatabai, A., Wollum, A. (Eds.), Methods of Soil Analysis: Part 2. Microbial and Biochemical Properties. Soil Science Society of America, Madison, WI, pp. 753–773.

Hunt, H.W., Coleman, D.C., Ingham, E.R., Ingham, R.E., Elliott, E.T., Moore, J.C., Rose, S.L., Reid, C.P.P., Morley, C.R., 1987. The detrital food web in a shortgrass prairie. Biol. Fertil. Soils 3, 57–68.

Hunt, H.W., Ingham, E.R., Coleman, D.C., Elliott, E.T., Reid, C.P.P., 1988. Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. Ecology 69, 1009–1016.

Ingham, E.R., Coleman, D.C., Moore, J.C., 1989. An analysis of food-web structure and function in a shortgrass prairie, a mountain meadow, and a lodgepole pine forest. Biol. Fertil. Soils 8, 29–37.

Jenkinson, D.S., 1991. The Rothamsted long-term experiments: are they still useful? Agron. J. 83, 2–10.

Johnson, D.W., 1992. Nitrogen retention in forest soils. J. Environ. Qual. 21, 1–12.

Keeney, D.R., Bremner, J.M., 1966. Comparison and evaluation of laboratory methods of obtaining an index of soil nitrogen availability. Agron. J. 58, 498–503.

Keeney, D.R., Nelson, D.W., 1982. Nitrogen—inorganic forms. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis. American Society of Agronomy, Madison, WI, pp. 643–698.

Köchy, M., Wilson, S.D., 1997. Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. Ecology 78, 732–739.

Ladd, J.N., 1978. Origin and range of enzymes in soil. In: Burns, R.G. (Ed.), Soil Enzymes. Academic Press, New York, pp. 51–96.

Law, B.E., Baldocchi, D.D., Anthony, P.M., 1999. Below-canopy and soil CO_2 fluxes in a ponderosa pine forest. Agric. For. Meteorol. 94, 171–188.

Law, B.E., Waring, R.H., Anthony, P.M., Aber, J.D., 2000. Measurements of gross and net ecosystem productivity and water vapor exchange of a Pinus ponderosa ecosystem and an evaluation of two general models. Global Change Biol. 5, 1–15.

Magee, T.K., Antos, J.A., 1992. Tree invasion into a mountain-top meadow in the Oregon coast range, USA. J. Vegetative Sci. 3, 485–494.

McGuire, A.D., Melillo, J.M., Joyce, L.A., Kicklighter, D.W., Grace, A.L., Moore III, B., Vorosmarty, C.J., 1992. Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. Global Biogeochem. Cycles 6, 101–124.

Melillo, J.M., Aber, J.D., Steudler, P.A., Shimel, J.P., 1983. Denitrification potentials in a successional sequence of northern hardwood forest stands. Environ. Biogeochem. 35, 217–228.

Miller, E.A., Halpern, C.B., 1998. Effects of environment and grazing disturbance on tree establishment in meadows of the western Cascade range, Oregon, USA. J. Vegetative Sci. 9, 265–282.

Oades, J.M., 1988. The retention of organic matter in soils. Biogeochemistry 5, 35–70.

Parton, W.J., Singh, J.S., Coleman, D.C., 1978. A model of production and turnover of roots in shortgrass prairie. J. Appl. Ecol. 47, 109–131.

Popenoe, J.H., Bevis, K.A., Gordon, B.R., Sturhan, N.K., Hauxwell, D.L., 1992. Soil–vegetation relationships in Franciscan terrain of northwestern California. Soil Sci. 56, 1951–1952.

Read, D.J., 1993. Plant-microbe mutualisms and community structure. In: Schulze, E.-D., Mooney, H.A. (Eds.), Biodiversity and Ecosystems Function. Springer-Verlag, New York, pp. 181–209.

Ross, D.J., Tate, K.R., Feltham, C.W., 1996. Microbial biomass, and C and N mineralization, in litter and mineral soils of adjacent montane ecosystems in a southern beech (Nothofagus) forest and a tussock grassland. Soil Biol. Biochem. 28, 1613–1620.

Schipper, L.A., Cooper, A.B., Harfoot, C.G., Dyck, W.J., 1993. Regulators of denitrification in an organic riparian soil. Soil Biol. Biochem. 25, 925–933.

Schlesinger, W.H., 1991. Biogeochemistry: An Analysis of Global Change. Academic Press, San Diego, CA, p. 443.

Sinsabaugh, R.L., 1994. Enzymatic analysis of microbial pattern and process. Biol. Fertil. Soils 17, 69–74.

Sinsabaugh, R.L., Linkins, A.E., 1990. Enzymatic and chemical analysis of particulate organic matter from a boreal river. Freshwater Biol. 23, 301–309.

Stark, J.M., Hart, S.C., 1997. High rates of nitrification and nitrate turnover in undisturbed coniferous forests. Nature 385, 61–64.

Stenberg, B., 1998. Soil attributes as predictors of crop production under standardized conditions. Biol. Fertil. Soils 27, 104–112.

Tabatabai, M.A., Bremner, J.A., 1969. Use of *p*-nitrophenyl phosphate for assay of soil phosphatase activity. Soil Biol. Biochem. 1, 301–307.

Wagner, G.H., Wolf, D.C., 1998. Carbon transformations and soil organic matter formation. In: Sylvia, D.M., Fuhrmann, J.J., Hartel, P.G., Zuberer, D.A. (Eds.), Principles and Applications of Soil Microbiology. Prentice Hall, Upper Saddle River, NJ, pp. 218–258.

Wales, B.A., 1972. Vegetation analysis of north and south edges in a mature oak-hickory forest. Ecol. Monogr. 42, 451–471.

Wedin, D.A., Pastor, J., 1993. Nitrogen mineralization dynamics in grass monoculture. Oecologia 96, 186–192.

Williams, M., Rastetter, E.B., Fernandes, D.N., Goulden, M.L., Shaver, G.R., Johnson, L.C., 1997. Predicting gross primary productivity in terrestrial ecosystems. Ecol. Appl. 7, 882–894.

Yakimenko, E.Y., 1997. Soil comparative evolution under grasslands and woodlands in the forest zone of Russia. In: Lal, R., Kimble, J.K., Stewart, B.A. (Eds.), Management of Carbon Sequestration in Soil. CRC Press, New York, pp. 391–404.