

Initial turnover rates of two standard wood substrates following land-use change in subalpine ecosystems in the Swiss Alps

Anita C. Risch, Martin F. Jurgensen, Deborah S. Page-Dumroese, and Martin Schütz

Abstract: Forest cover has increased in mountainous areas of Europe over the past decades because of the abandonment of agricultural areas (land-use change). For this reason, understanding how land-use change affects carbon (C) source–sink strength is of great importance. However, most studies have assessed mountainous systems C stocks, and less is known about C turnover rates, especially of “fresh” organic material (OM). We studied the decomposition of wood stakes of trembling aspen (*Populus tremuloides* Michx.) and loblolly pine (*Pinus taeda* L.) placed on the litter layer and in the mineral soil of five ecosystem types (pastures and forests) — representing the successional development after land abandonment in the eastern Swiss Alps — for 6 years. Wood stake decomposition rates were generally highest in pastures and lowest in early successional forests. Aspen stakes decomposed more rapidly than pine stakes, especially in the mineral soil. Soil temperature (and to a smaller extent soil phosphorus (P) concentration) best explained the differences in decomposition among the ecosystem types. Initial wood decay is temperature-sensitive, and therefore would likely increase under future climate change scenarios.

Résumé : Le couvert forestier a augmenté dans les régions montagneuses de l'Europe au cours des dernières décennies à cause de l'abandon de zones agricoles (changement d'utilisation du sol). Pour cette raison, il est très important de comprendre comment le changement d'utilisation du sol influence la robustesse de la relation source-puits de carbone (C). Cependant, la plupart des études ont évalué les stocks de C dans les systèmes montagneux mais les taux de recyclage du C sont moins connus, particulièrement dans le cas de la matière organique fraîche. Pendant 6 ans nous avons étudié la décomposition de piquets de bois de peuplier faux-tremble (*Populus tremuloides* Michx.) et de pin à encens (*Pinus taeda* L.) placés sur la litière et dans le sol minéral de cinq types d'écosystèmes forestiers (pâturages et forêts) représentatifs des stades de succession après l'abandon des terres dans l'est des Alpes suisses. Le taux de décomposition des piquets de bois était généralement le plus élevé dans les pâturages et le plus faible dans les premiers stades de succession de la forêt. Les piquets de peuplier se sont décomposés plus rapidement que les piquets de pin, particulièrement dans le sol minéral. La température du sol et, dans une moindre mesure, la concentration du P expliquaient le mieux les différences dans la décomposition entre les types d'écosystème. Le stade initial de carie du bois est influencé par la température et, par conséquent, se déroulerait probablement plus rapidement dans le contexte des scénarios de changement climatique futur. [Traduit par la Rédaction]

Introduction

Sink–source dynamics within forested systems are of great importance for the global carbon (C) cycle (e.g., Ryan et al. 2010) — especially in North America and Europe, where the total forested area and amount of woody biomass has greatly increased during the past decades. The main reasons for these increases are farmland and pasture abandonment, climate warming, disturbance suppression (fire, avalanches), nutrient additions, or a combination of these processes (e.g., Liski et al. 2003; Page-Dumroese et al. 2003; Bolliger et al. 2008). In Europe, changes in economic policies caused additional increases in forest cover in remote and mountainous areas (e.g., Gellrich et al. 2007; Tasser et al. 2007; Bolliger et al. 2008; Tappeiner et al. 2008). Consequently, mountain areas are especially important for European C budgets, since they cover >40% of the land base of the continent — as defined by difficult topography and a range of climatic regimes (Nordregio Report of the European Union 2004). The discussion on how land-use change impacts C storage in these mountainous areas has, however, only recently gained increased attention (e.g., Bolliger et al. 2008; Risch et al. 2008; Hagedorn et al. 2010), focusing mostly on how land-use change affects above- and below-ground C stocks

(e.g., Perruchoud et al. 1999; Thuille et al. 2000; Bolliger et al. 2008; Risch et al. 2008; Tappeiner et al. 2008).

In contrast, less attention was given to how changes in land use affect soil C turnover (decomposition) rates. Thuille and Schulze (2005) predicted an increase in soil C stocks following the abandonment of agricultural land within the Alps, whereas Meyer et al. (2011) concluded that such land-use change is likely not a substantial soil C sink. However, with the exception of Gamper et al. (2007), who showed increased C stocks following land abandonment, the focus of these studies has been on turnover rates of different organic material (OM) fractions in mineral soil, ignoring initial turnover rates of “fresh” OM (e.g., woody debris) entering the system. However, understanding turnover rates of “fresh” OM is important when assessing how land-use change affects C source–sink strength of mountainous systems following land abandonment.

Wood decomposition is a function of OM quality (e.g., lignin content or C:N ratio), soil microclimate, and soil physical, chemical, and biological properties (Rayner and Boddy 1988). Using wood from a particular location gives very site-specific information on decomposition rates, but differences in wood quality (lignin content, C:N ratio, etc.) make it difficult to compare these results among sites (Weedon et al. 2009). By using a “standard”

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wood on different sites, wood quality is held constant, and decomposition is a function of soil abiotic (moisture, temperature, O_2 /CO₂ levels, redox potential, etc.) and biotic (microbial biomass, functional diversity, etc.) conditions. Consequently, using standard wood materials as an index to assess biotic and abiotic soil properties affecting OM decomposition rates would give information on ecosystem C cycling across different soil and climatic conditions after land abandonment.

We installed standard wood stakes on two pasture and three forest types representing vegetation development after agricultural abandonment in the Swiss National Park — an area in which successional processes have been studied intensively (Wildi and Schütz 2000, 2007; Risch et al. 2003, 2004, 2008). Wood stakes allow for assessing decomposition processes over longer time frames compared with other standard materials that have been used (e.g., cotton cloth or chopsticks). Also, by using wood stakes, decomposition can be easily measured at different soil depths and very little soil disturbance occurs during installation. Wood is a normal component of forest soils (surface residue, stumps, and large roots) and integrates changes in temperature and moisture conditions over long time periods during decomposition. Further, wood stakes made from different tree species differ in lignin-cellulose ratios, wood density, and chemical properties, and thus are generally decayed by different fungal communities (Lumley et al. 2001; Jurgensen et al. 2006; Weedon et al. 2009).

More specifically, we assessed decomposition rates (mass loss) of wood stakes of two different tree species, trembling aspen (*Populus tremuloides* Michx.) and loblolly pine (*Pinus taeda* L.), at two different soil locations (surface litter layer and mineral soil) to increase our knowledge on how land-use change affects decomposition of fresh material in high-elevation systems. We correlated wood stake decomposition rates with climate variables (air temperature, precipitation, soil temperature, and soil moisture) and soil properties (surface organic layer and mineral C, nitrogen (N) and phosphorus (P) concentrations, and mineral soil pH) over a 6 year period to assess which environmental variables drive decomposition rates within our ecosystems. We expected wood decomposition rates to be highest in the successional “younger” pastures (former land use, no canopy closure of the trees), since soil temperatures and soil nutrient loads would be higher than in forest stands. We also expected higher soil N concentrations and soil temperatures in early successional forests to result in higher wood decomposition rates, as compared with later successional stands (Risch 2004; Risch et al. 2008).

Methods

Study area and experimental design

The Swiss National Park (SNP) is located in the southeastern part of Switzerland and covers an area of 170 km² — 50 km² are forested, 33 km² are grassland, and the rest is rock, scree, and perpetual snow. Elevations range from 1350 to 3170 m a.s.l. The mean annual precipitation and temperature are 871 ± 156 mm and 0.6 ± 0.6 °C (mean ± standard deviation) measured at the SNP weather station in Buffalora (1980 m a.s.l.) between 1960 and 2009 (MeteoSchweiz 2011). Founded in 1914, the Park approaches its 100-year anniversary. No management practices were conducted over these 100 years. However, records of timber harvesting date back to the 14th century, when forests were cut to support the development of a local iron ore industry. Additional harvesting occurred during the 17th, 18th, and 19th centuries to supply charcoal for lime kilns and timber for use in a nearby salt mine. Clear-cutting forest stands for agricultural use (sheep and (or) cattle grazing and hay production) also began as early as the 14th century, and many pastures were used until the Park was established in 1914 (Parolini 2012).

The long-term development of SNP ecosystems has been studied in detail using time series data from permanent plots that date

as far back as 1917 (space-for-time approach; Wildi and Schütz 2000, 2007; Risch et al. 2003, 2004, 2008). Five different ecosystem types representing the successional development of subalpine vegetation in the SNP can be found today: (1) short-grass pastures dominated by *Festuca rubra* L. and *Briza media* L.; (2) tall-grass pastures dominated by *Carex sempervirens* Vill., *Nardus stricta* L., and *Elyna myosuroides* (Vill.) Fritsch; (3) mountain pine (*Pinus montana* Mill.) forests; (4) mixed-conifer stands of mountain pine, Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), larch (*Larix decidua* Mill.), and stone pine (*Pinus cembra* L.); and (5) stone pine – larch stands. For details on the development of these five ecosystem types see Risch et al. (2009). Transitions between these stages have been repeatedly observed on the permanent plots. Short-grass vegetation developed in areas where cattle and sheep rested (high nutrient input) during agricultural land use (from the 14th century to 1914). After the park was established, these sites became preferred grazing sites for red deer (*Cervus elaphus* L.) and are still intensively grazed today (tree encroachment very slow). When red deer grazing pressure of short-grass vegetation ceases, or where cattle and sheep historically grazed but did not rest (Schütz et al. 2003, 2006), tall-grass vegetation is found. These tall-grass pastures are replaced by mountain pine stands, representing the early successional forest stage, in which stem-exclusion processes are predominant today. They further diversify into mixed stands containing larch, Norway spruce, Scots pine, and, to a lesser extent, stone pine. The final successional forest ecosystem is dominated by stone pine and larch (Risch et al. 2003, 2004, 2008). It is difficult to predict the speed of vegetation changes in the area, as it depends on site conditions (e.g., elevation, nutrient availability, and disturbance) and the method used to calculate long-term temporal patterns retrieved from the permanent plots (Wildi and Schütz 2007; Risch et al. 2008). However, it can be assumed that likely over a millennium would pass during succession from short-grass vegetation to stone pine/larch stands (Wildi and Schütz 2007; Risch et al. 2009).

We randomly selected five sites on short-grass vegetation, four sites on tall-grass vegetation, eight sites in mountain pine forest, six sites in mixed forest, and three sites in stone pine – larch stands for a total of 26 study sites. The number of plots per vegetation type was proportional to their abundance in the SNP (Table 1). The sites were found on varying slopes of all cardinal directions, and had soil parent materials of dolomite, limestone, and verrucano-dominated moraines or rubble. All pasture and forest sites were located between 1800 and 2300 m a.s.l. (Table 1), and are part of larger studies on ecosystem productivity or long-term vegetation development (Schütz et al. 2003; Risch et al. 2003, 2004; Thiel-Egenter et al. 2007; Risch et al. 2008; Table 1). A 10 m × 10 m plot was established in the center of each site.

Wood stake decomposition

Loiblolly pine and aspen were used as standard substrates for the study. These species are commonly used as test materials in wood decomposition studies (e.g., Gonzales et al. 2008; Woodward et al. 2011). Our study is also part of a global decomposition project (Jurgensen et al. 2006), in which stakes of these two species are being used as standard “indices” of wood decomposition. Originally, we planned to include wood from local tree species on the forested sites, which would have allowed us to estimate “site-specific” wood decomposition rates. However, this was not possible because of difficulties in obtaining suitable wood stakes from the many tree species present in these stands.

Two “daughter” surface stakes (2.5 cm × 2.5 cm × 15 cm) were cut from a 40 cm long “mother” stake. Similarly, two daughter mineral stakes (2.5 cm × 2.5 cm × 20 cm) were cut from one 50 cm long mother stake. The top of each mineral stake was treated with a wood sealer to reduce wood moisture loss after installation. The 10 cm “control” center section from each mother stake was used to determine the initial mass of the two daughter stakes (time = 0),

Table 1. Ecosystem type, locations (x, y coordinates), elevation (m a.s.l.) of each site, mean annual temperature (Temp. in °C), and mean annual precipitation (Precip. in mm) at each site.

Plot ID	Ecosystem type	x	y	Elevation	Temp.	Precip.
De12	Short-grass	810995	169429	2087	1.1	987
Il Pra	Short-grass	814464	171779	1954	1.8	889
Mi 80	Short-grass	816537	176746	2159	0.8	864
Mu 01	Short-grass	800600	165400	1820	1.1	1242
Mu 21	Short-grass	800590	165450	1830	0.8	1248
Fe 1	Tall-grass	814464	171891	1964	1.8	888
Mi 17	Tall-grass	816627	176897	2121	1.0	855
N 14	Tall-grass	810961	169302	2066	1.2	987
PF 13	Tall-grass	810917	169539	2092	1.1	985
1109	Mountain pine	813877	171983	1990	1.7	891
1110	Mountain pine	813979	171744	1910	2.0	884
1113	Mountain pine	814259	172253	2070	1.3	902
1203	Mountain pine	811024	172422	1970	1.6	893
1307	Mountain pine	810097	171746	2100	1.0	931
1313	Mountain pine	809589	172172	2000	1.4	906
Pin 03	Mountain pine	813696	171757	1897	2.1	883
Pin 04	Mountain pine	814030	171570	1909	2.1	886
807	Mixed	809664	170057	1830	2.4	931
808	Mixed	809848	169828	1850	2.3	940
1316	Mixed	808907	172250	1880	2.1	882
1318	Mixed	809506	171255	2000	2.4	897
1401	Mixed	809058	171393	1730	2.9	877
1508	Mixed	818918	179502	1730	2.9	763
903	Stone pine – larch	811288	170736	1960	1.7	929
905	Stone pine – larch	812045	171407	1910	2.0	898
906	Stone pine – larch	812505	171196	2020	1.4	921

and to calculate wood stake mass loss during the study (for details see [Jurgensen et al. \(2006\)](#)). Kiln-dried loblolly pine wood from North Carolina and aspen wood from the Upper Peninsula of Michigan were used to make the surface and mineral stakes. In late June 2001, five surface stakes of each species were placed 5 cm apart on top of the surface litter layer along three sides of 10 m × 10 m plots (15 surface stakes per wood species per plot), and were secured with a stainless steel ground staple (Forestry Suppliers, Inc., Jackson, Mississippi). In addition, three sets of five aspen and pine wood mineral stakes were inserted vertically 40–50 cm apart in the mineral soil adjacent to the surface stakes on all study plots. To reduce soil compaction and damage to the stakes during installation, the litter layer was removed, stakes were placed level with the mineral soil surface in holes made by a square coring tool, and the litter layer restored. A total of 780 surface and 780 mineral stakes were installed in this study (26 sites × 2 wood species × 15 surface/mineral stakes). In July 2002, 2004, and 2007, five surface and five mineral stakes of each species were removed from all plots. The stakes were air-dried in the field, and then sent to the School of Forest Resources and Environmental Science at Michigan Technological University for processing. In the laboratory, all the surface stakes were dried at 105 °C for 48 h and weighed. To assess wood decomposition changes with soil depth, 2.5 cm × 2.5 cm blocks were cut at 3.8 and 15.2 cm from the top of the stake (depth), dried, weighed, and compared with the respective mother stake control section.

Soil sampling and laboratory analyses

Soil surface organic layer (SOL) samples were collected from random 15 cm radius circular areas located on three sides of each plot. Mineral soil samples were collected immediately below the SOL collection site to a depth of 20 cm with hand trowels. All SOL and mineral samples were oven-dried at 65 °C and weighed. SOL samples were fine-ground to pass a 0.5 mm screen and mineral soil samples were passed through a 2 mm sieve and then fine-ground to pass a 0.5 mm screen. Mineral soil samples from the calcareous moraine and rubble parent material were treated with

a 50% hydrochloric acid solution to remove carbonates, washed with deionized water, and then dried at 60 °C for 1–2 h before analysis ([Loeppert and Suarez 1996](#)). All SOL and soil samples were analyzed for total C and N with a LECO induction furnace at 1000 °C (LECO Corp., St. Joseph, Michigan). Extractable soil P was determined with the Bray I or Olsen method depending on mineral soil pH, and analyzed using the ascorbic acid colorimetric method ([Kuo 1996](#)). For total P in organic samples, the samples were dry-ashed in a muffle furnace at 450° for 6 h, leached with 2 N HNO₃, filtered, and determined by inductively coupled plasma methodology ([Aspila et al. 1976](#)). Soil pH was measured on a 2:1 water to soil paste.

Climate and soil microclimate data

Mean annual precipitation and mean yearly air temperature for each plot were calculated using Swiss climate maps generated by [Zimmermann and Kienast \(1999\)](#). Soil temperature was measured at 4-hour intervals at the 10 cm mineral soil depth in each plot with temperature buttons (TidBiT v2 water temperature data logger, Onset Computer Cooperation, Cape Cod, Massachusetts) for the duration of the study. Soil moisture was determined every hour at a depth of 10 cm on 19 of the 26 plots during the 2005 and the 2006 growing seasons using two permanently installed sensors (Watermark soil moisture sensors, Spectrum Technologies, Inc., Plainfield, Illinois) connected to a data logger (Watchdog 400 series, Spectrum Technologies, Inc., Plainfield, Illinois).

Statistical analyses

No differences in wood decomposition were found for the two mineral soil depths (3.8 and 15.2 cm) for both the aspen and pine stakes, so soil depth decay values were combined to obtain an average mineral wood stake decay. We calculated the decomposition rate constant k for each of three individual incubation periods with eq. (1)

$$(1) \quad k = \ln(Dw_0/Dw_t)/t$$

where Dw_0 is the dry mass prior to insertion and Dw_t is the dry mass at time t . We then assessed how ecosystem type (short-grass, tall-grass, mountain pine, mixed forest, stone pine – larch), time (decomposition rate k calculated after 1 year, after 3 years, and after 6 years), stake location (surface or mineral), and wood type (aspen or pine) affected k using a general linear model (GLM). For this purpose, k was the dependent variable, and ecosystem type, time, location, and wood type and their higher order interactions were the independent variables. Pair-wise differences in k among years and ecosystem types were assessed post hoc using Tukey's HSD test for multiple comparisons. k was box-cox transformed to fulfill the normality criteria. We also assessed how environmental variables (average air temperature, total annual precipitation, soil temperature, soil moisture, SOL N concentration, SOL C:N ratio, SOL P concentration, mineral soil N concentration, mineral soil C:N ratio, mineral soil P concentration, and mineral soil pH) differed among the five ecosystem types using GLMs, where the respective environmental variable was the dependent variable and ecosystem type was the independent factor. In a next step, we assessed how the environmental variables were related to decomposition in the five ecosystems. For this purpose, we averaged all the values available for each environmental variable per ecosystem type and correlated them with the environmental variables using Pearson's correlation coefficient. Data were not transformed for this purpose, as the normality and homogeneity criteria were fulfilled. All statistical analyses were performed with the PASW Statistics 19.0 statistical package (IBM SPSS, Chicago, Illinois).

Results

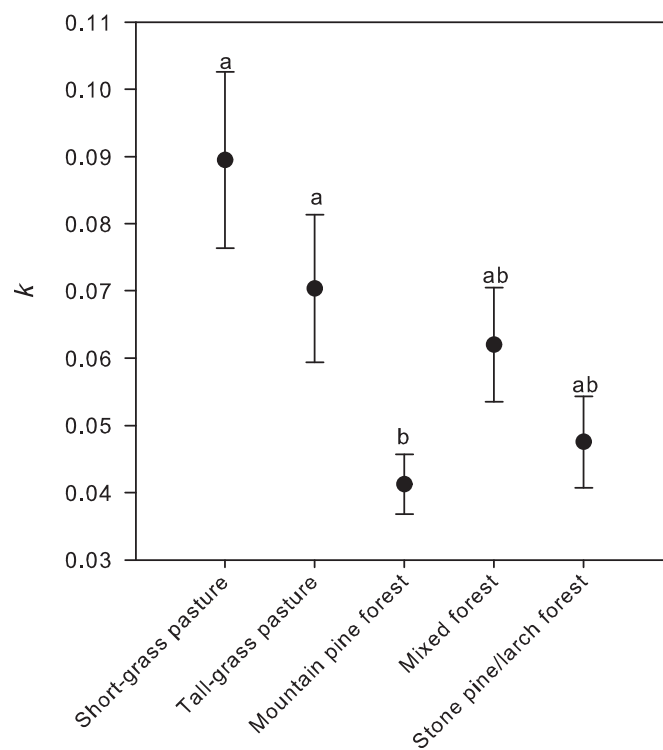
The mass loss of our wood stakes was highly variable among the 26 study sites, the different incubation locations, as well as among wood types (see [Appendix Tables A1–A4](#) for all the data). Our analyses revealed that only the main effects of ecosystem type, time, location, and wood species had explanatory power in the model ([Table 2](#)). All higher order interactions did not further explain decomposition variability found in the data. As we were primarily interested in how mean k (both wood types and both incubation depth) changed among the five ecosystem types that represent secondary succession from pasture to late successional forest in the SNP over the entire period of the study, we conducted pair-wise comparisons over all the data split by ecosystem type. Significantly higher decomposition rates were found in the two pasture types as compared with the mountain pine forest ([Fig. 1](#)). No differences were found among the three forest types or among the pastures and the two later successional forest types (mixed and stone pine – larch forest). Similar patterns were found separately among different ecosystems for stake type and incubation depth ([Figs. 2A–2D](#)). However, because of the high variability of pine stake decomposition on many sites, we only detected significant effects for the aspen stakes regardless of incubation depth. All the environmental variables measured differed significantly among the ecosystem types under study ([Table 3](#)), but only soil temperature followed by mineral soil P concentrations were significantly correlated to mean wood decomposition in the five different ecosystem types ([Table 4](#)).

Wood decomposition rate constant (k) indicated an acceleration in decomposition over time, with annual k rates after 6 years being higher than after 1 and 3 years of incubation ([Fig. 3A](#) and [Table 2](#)). Wood stakes located at the soil surface decomposed much slower than stakes placed in mineral soil ([Fig. 3B](#) and [Table 2](#)), and aspen stakes decomposed significantly faster than pine stakes ([Fig. 3C](#) and [Table 2](#); also see [Fig. 2](#)).

Table 2. Factors, degrees of freedom (df), F , and p values for the general linear model (GLM) model where decomposition rate (k) is the dependent factor and ecosystem, time, wood type, location, and their higher interactions are the independent factors.

Factor	df	F	p
Ecosystem	4	6.278	<0.001
Location	1	26.412	<0.001
Wood type	1	63.567	<0.001
Time	2	20.497	<0.001
Ecosystem × Time	8	1.216	0.290
Ecosystem × Location	4	2.055	0.087
Ecosystem × Wood type	4	1.491	0.206
Time × Location	2	1.917	0.149
Time × Wood type	2	2.127	0.121
Location × Wood type	1	3.129	0.078
Ecosystem × Time × Location	8	0.639	0.745
Ecosystem × Time × Wood type	8	0.872	0.541
Ecosystem × Location × Wood type	4	0.191	0.943
Time × Location × Wood type	2	1.092	0.337
Ecosystem × Time × Location × Wood type	8	0.927	0.494

Fig. 1. Mean decomposition rate (k) for all wood stakes incubated in the five different ecosystems for all sample dates. Different letters indicate significantly different values ($\alpha = 0.05$).



Discussion

Wood decomposition rates in different ecosystem types

As expected, we found significantly higher decomposition rates in the two pasture types, representing the earliest successional stages in the SNP, compared with the mountain pine forest. In contrast with our results, [Gamper et al. \(2007\)](#) detected no statistical difference in the decomposition of surface plant litter (litter bags) and cotton cloths placed on top and within the litter layer of abandoned pastures (30 years before) and young forests in high-elevation spruce forests of northern Italy. However, these results are not directly comparable, as their standard OM materials were placed on or in relatively dry litter layers, whereas our wood

Fig. 2. Decomposition rate (k) among the different ecosystems split by wood type and incubation depth. (A) Surface aspen stakes, (B) surface pine stakes, (C) mineral aspen stakes, and (D) mineral pine stakes.

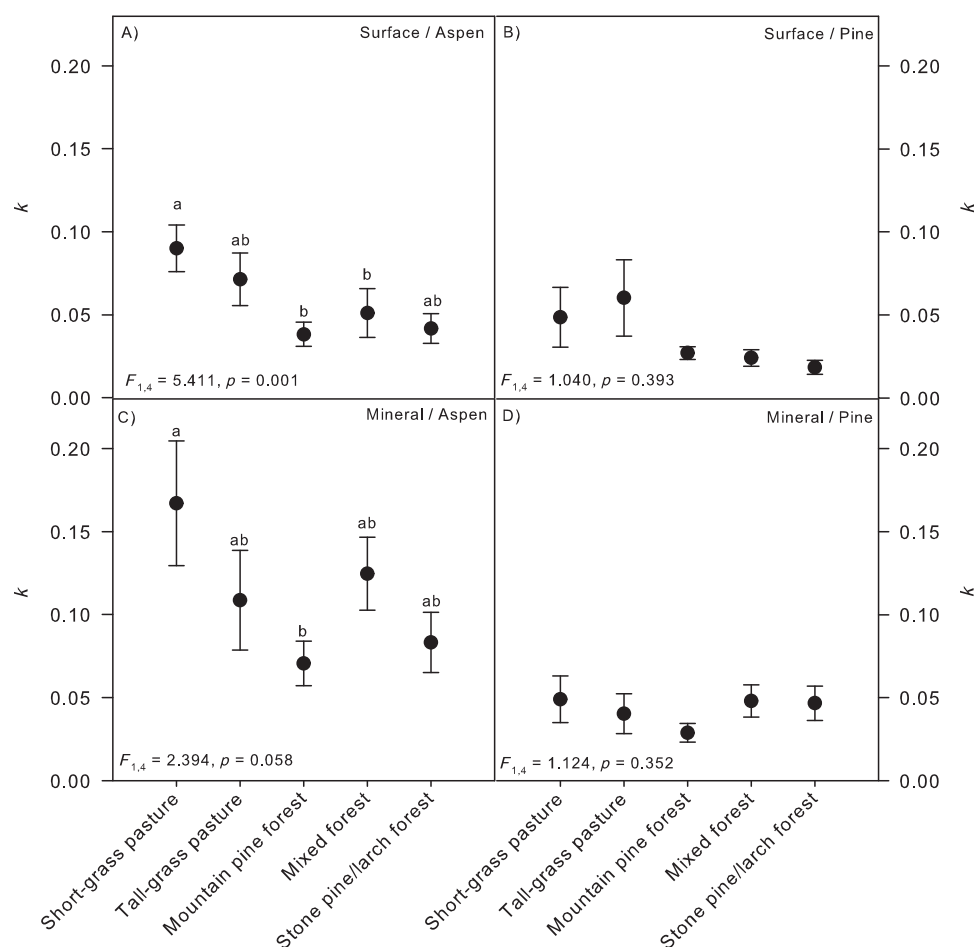


Table 3. Ecosystem type differences of the selected environmental variables.

Variable	Short-grass pasture	Tall-grass pasture	Mountain pine forests	Mixed forests	Stone pine – larch forests	F	p
Air_T	1.1 (0.1)c	1.3 (0.5)c	1.7 (0.05)b	2.5 (0.05)a	1.7 (0.05)b	154.00	<0.001
Precip.	1046.4 (21.8)a	929.3 (8.5)b	897.5 (1.6)bc	882.1 (6.9)c	916.6 (2.2)bc	39.30	<0.001
Soil_T	5.9 (0.05)a	5.0 (0.07)b	4.2 (0.75)c	5.0 (0.21)b	4.2 (0.1)c	24.97	<0.001
Soil_M	53.1 (3.0)a	29.0 (1.2)c	24.5 (1.1)c	39.4 (1.8)b	25.2 (1.2)c	36.46	<0.001
SOL_N	19.4 (4.8)	18.7 (5.9)	8.7 (0.70)	8.2 (0.9)	9.3 (1.2)	194.54	<0.001
SOL_CN	14.6 (0.6)c	17.0 (0.5)c	46.2 (0.7)a	46.2 (1.0)a	38.9 (1.3)b	311.15	<0.001
SOL_P	968.1 (25.9)a	894.7 (34.4)b	374.2 (6.6)d	375.6 (5.7)d	448.0 (7.1)c	318.99	<0.001
ML_N	7.7 (1.8)a	4.2 (0.8)b	2.8 (0.8)c	2.1 (0.7)d	0.7 (0.3)e	351.03	<0.001
ML_CN	14.1 (0.6)c	26.0 (1.4)b	39.2 (2.1)a	27.7 (1.1)b	23.8 (0.5)c	36.65	<0.001
ML_P	20.7 (1.7)a	9.8 (0.2)b	4.3 (0.1)c	3.9 (0.2)c	3.9 (0.2)c	90.69	<0.001
ML_pH	6.7 (0.1)a	5.6 (0.2)b	6.5 (0.1)a	5.9 (0.1)b	3.5 (0.1)c	13.7.34	<0.001

Note: Air_T, mean annual air temperature (°C); Precip., annual precipitation (mm); Soil_T, soil temperature for the top 10 cm of mineral soil (°C); Soil_M, soil moisture for the top 10 cm of mineral soil (%); SOL_N, N concentration of the soil organic layer (g·kg⁻¹); SOL_CN, C:N ratio of the soil organic layer; SOL_P, P concentration of the soil organic layer (mg·kg⁻¹); ML_CN, C:N ratio of the mineral soil (0–20 cm depth); ML_N, N concentration of the mineral soil (g·kg⁻¹; 0–20 cm depth); ML_P, P concentration of the mineral soil (mg·kg⁻¹; 0–20 cm depth); ML_pH, pH of the mineral soil (0–20 cm depth). Numbers represent means and standard error is in parentheses. Different letters indicate significant differences between the ecosystem types ($\alpha = 0.05$).

stakes were incubated on top of the litter layer and in the wetter mineral soil.

Similar to our findings for fresh OM, k values of various mineral soil OM fractions were higher in pastures, as compared with reforested areas in high-elevation ecosystems in Austria with comparable vegetation to our sites (Meyer et al. 2011, 2012). This is particularly interesting, as abandonment and, therefore, reforestation of their sites was much more recent than ours (1988 versus

1914), which could indicate that the first decades after abandonment might be especially important for changes in soil C dynamics (also see Thuille and Schulze 2005). These few studies and our results indicate a general shift from higher decomposition in the pastures towards lower decomposition rates when forests establish.

We were surprised to find the lowest decomposition rates in early successional rather than older forest stands, even though

Table 4. Pearson's correlation coefficient (r) between mean ecosystem decomposition rates (k) and the environmental variables included in our study.

Variable	r	p
Air_T	-0.464	0.431
Precip.	0.814	0.094
Soil_T	0.978	0.004
Soil_M	0.871	0.055
SOL_N	0.844	0.073
SOL_CN	-0.834	0.079
SOL_P	0.864	0.059
ML_N	0.864	0.059
ML_CN	-0.827	0.084
ML_P	0.900	0.037
ML_pH	0.441	0.457

Note: df = 5. Boldface-type values indicate significant correlation. Air_T, average annual air temperature (°C); Precip., annual precipitation (mm); Soil_T, soil temperature for the top 10 cm of mineral soil (°C); Soil_M, soil moisture for the top 10 cm of mineral soil (%); SOL_N, N concentration of the soil organic layer (g·kg⁻¹); SOL_CN, C:N ratio of the soil organic layer; SOL_P, P concentration of the soil organic layer (mg·kg⁻¹); ML_CN, C:N ratio of the mineral soil (0–20 cm depth); ML_N, N concentration of the mineral soil (g·kg⁻¹; 0–20 cm depth); ML_P, P concentration of the mineral soil (mg·kg⁻¹; 0–20 cm depth); ML_pH, pH of the mineral soil (0–20 cm depth).

the differences were not significant statistically. Even though the mountain pine stands had higher mean soil temperatures and N concentrations, the understory in these stands is mainly dominated by ericaceous shrubs that produce litter with high amounts of recalcitrant C (high in phenols and lignin and low in N) that could lead to lower microbial activity and, therefore, decomposition (e.g., Nilsson and Wardle 2005). In contrast, the understory in the later successional forests is more grass- and (or) forb-dominated (cf. Risch et al. 2008), therefore, likely producing less recalcitrant OM. Slower OM decomposition in the mountain pine stands is also indicated by the high C:N ratios in both the litter layer and mineral soil. In addition, these ecosystems had the driest soils.

With the exception of Thuille and Schulze (2005), we are not aware of any study that reported on differences in turnover rates during forest development at high elevations. Even these authors did not directly assess decomposition rates, but used soil data collected from several chronosequence studies (space-for-time approach) to model soil C gains and losses for the 0–20 cm acidic and alkaline mineral soil under spruce forests growing in the German and Italian Alps. The model predictions for the first 50 years of stand development were highly variable, ranging from decreased to increased soil C stocks over a very short time, which makes it difficult to compare their model results with our study. Also, our youngest stands were already 120 years old (see Risch et al. 2008), were dominated by a different tree species (mountain pine), and our space-for-time approach included successional shifts in the dominant tree species composition (mountain pine to stone pine).

Environmental control of decomposition rates across ecosystems

Soil temperature was the best explanatory variable for the differences in mean wood decomposition rates among our ecosystem types. This is similar to many other studies on other soil OM substrates (e.g., leaf litter and mineral soil C fractions), which also found increased decomposition rates with increasing temperature (Ågren and Wetterstedt 2007; Hartley and Ineson 2008; Conant et al. 2011). However, a meta-analysis by Yatskov et al. (2003) showed that wood decomposition was not always sensitive to differences in temperature. Changes in air temperatures affected

the decomposition of wood from decay-susceptible trees, but not the decomposition of wood from decay-resistant trees. Aspen wood responded to changes in temperature, which agrees with our results, and indicates that increased temperature from global climate change would likely accelerate decomposition processes of fresh OM a high-elevation, temperature-limited ecosystems. However, changes in precipitation patterns would also be important, as Gonzales et al. (2008) found that aspen decomposition was strongly influenced by soil moisture conditions across a wide range of climatic conditions.

Differences in wood decomposition rates among our ecosystem types were also related to concentrations of extractable mineral soil P. This was surprising, as we expected the large differences in soil N concentrations among sites would drive decomposition, rather than the less variable soil P concentrations (see Table 3). However, we measured total soil N concentration instead of available mineral N (NH₄ and NO₃), which are the N forms used by most soil microorganisms (e.g., Van der Wal et al. 2007). In contrast, the extractable P concentrations reflect more soluble P forms in the mineral soil, and might be an index of general nutrient availability for wood decomposition in these alpine soils. However, the relationship of P availability and wood decomposition needs additional study in other soils with different climate regimes.

Decomposition rates for different wood species

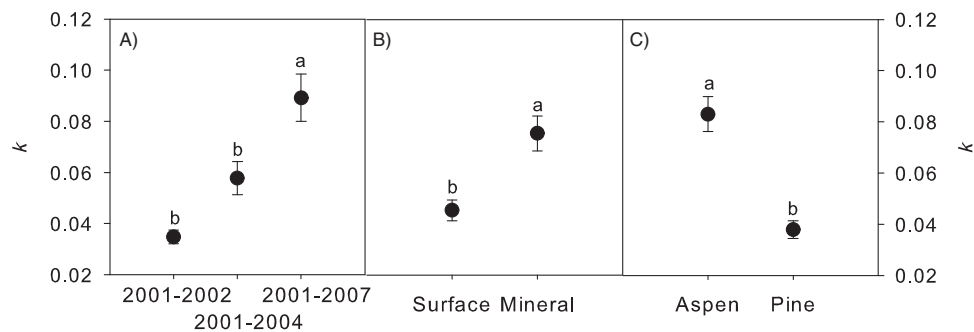
Similar to our study, Freschet et al. (2012) found that logs of European aspen (*Populus tremula* L.) decomposed more rapidly than Scots pine logs, which they attributed to lower aspen wood lignin content and higher pH. The aspen and pine decomposition rates both increased nonlinearly (accelerated decomposition) over time. Angiosperm wood generally decomposes faster than wood from gymnosperms because of differences in wood density, N concentration, lignin concentration, and lignin:N ratio (Rayner and Boddy 1988; Weedon et al. 2009). A meta-analysis of 70 decomposition studies showed that climatic variables and litter quality, especially lignin, total nutrient content, and C:N ratio, were the main drivers of OM decomposition (Zhang et al. 2008; Prescott 2010).

As expected, wood stakes inserted in the wetter mineral soil decomposed much faster than stakes on the surface of the litter layer. Similar results were found by Van der Wal et al. (2007) for birch wood blocks and saw dust placed on the soil surface and in the mineral soil. In a different study format, Smith et al. (2011) did not detect mass-loss differences for wooden dowels among 27 forest ecosystems across North and Central America, in which the dowels were placed vertically so that half was in the air and half in the mineral soil. However, the results from this study are not comparable with ours, as the air-exposed portion of the dowels would act as a “wick” and lower the water content of the dowel in mineral soil. We did not detect any difference in wood decomposition at the 3.8 and 15.2 cm mineral soil depths. In contrast, a north–south European gradient study by Jurgensen et al. (2006) found slower pine stake decomposition at 15 and 25 cm mineral soil depths than at 5 cm depth in the northern Finnish soils, but not in the warmer soils of Poland. They attributed differences in pine stake decomposition rates to mineral soil temperature and moisture gradients, but soil pH and fungal community dynamics could also be factors.

Conclusion

Our results indicate that increased temperatures at higher elevations resulting from alteration of global climatic regimes would likely increase decomposition rates of fresh OM and impact C source–sink relationships in these ecosystems. However, our study should be repeated with other tree species and local wood material across a range of soil conditions in other high-elevation areas to further assess the validity of our conclusions. While the results of our study with pine and aspen wood stakes cannot be

Fig. 3. Mean decomposition rate (k) for all stakes for (A) incubation periods 2001–2002, 2001–2004, and 2001–2007, (B) soil surface and mineral soil incubation, and (C) aspen and pine wood stakes during the entire time of study. Different letters indicate significantly different values ($\alpha = 0.05$).



used to estimate site-specific decomposition rates of coarse roots or woody residue, they did show how standard OM substrates can be used to assess important abiotic factors affecting decomposition across sites with different soils and climatic regimes.

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Appendix

Tables A1–A4 follow.

Table A1. Mass loss of surface aspen stakes (%) after 1 (2002), 3 (2004), and 6 (2007) years of incubation at each of the 26 study sites.

Plot ID	Ecosystem type	Surface aspen stakes		
		2002	2004	2007
De12	Short-grass	4.1 (1.6)	20.6 (8.1)	29.8 (3.3)
Il Pra	Short-grass	3.7 (0.9)	12.4 (2.5)	25.6 (3.3)
Mi 80	Short-grass	3.0 (0.8)	17.3 (1.9)	30.6 (3.0)
Mu 01	Short-grass	7.3 (1.8)	45.6 (4.6)	50.9 (9.5)
Mu 21	Short-grass	7.6 (1.8)	41.5 (6.2)	60.7 (6.6)
Fe 1	Tall-grass	6.8 (2.7)	15.9 (2.3)	36.9 (11.9)
Mi 17	Tall-grass	3.3 (1.2)	14.1 (1.8)	23.4 (1.9)
N 14	Tall-grass	4.5 (2.3)	13.8 (4.3)	68.2 (9.3)
PF 13	Tall-grass	NF	11.7 (2.6)	31.9 (3.6)
1109	Mountain pine	1.1 (1.2)	9.4 (4.2)	11.1 (9.0)
1110	Mountain pine	3.3 (0.6)	22.3 (5.3)	35.6 (2.9)
1113	Mountain pine	3.1 (0.7)	6.2 (1.9)	12.0 (2.0)
1203	Mountain pine	1.6 (0.5)	4.0 (1.9)	14.5 (2.8)
1307	Mountain pine	2.0 (1.4)	6.2 (1.5)	10.9 (4.4)
1313	Mountain pine	3.1 (1.1)	11.3 (3.6)	9.8 (1.5)
Pin 03	Mountain pine	1.0 (1.0)	5.8 (2.5)	17.0 (4.3)
Pin 04	Mountain pine	2.3 (0.8)	7.6 (1.8)	44.4 (12.1)
807	Mixed	2.2 (2.2)	3.9 (2.5)	6.1 (1.7)
808	Mixed	1.4 (1.00)	16.7 (4.4)	71.0 (12.5)
1316	Mixed	1.1 (0.3)	8.2 (1.3)	41.4 (11.2)
1318	Mixed	1.7 (0.9)	7.8 (1.6)	37.9 (8.8)
1401	Mixed	1.7 (0.9)	14.3 (6.0)	29.6 (5.6)
1508	Mixed	0.7 (0.5)	7.3 (1.6)	27.3 (11.3)
903	Stone pine – larch	2.1 (1.6)	7.6 (2.0)	30.3 (9.4)
905	Stone pine – larch	1.5 (0.8)	4.5 (0.5)	18.2 (5.1)
906	Stone pine – larch	4.9 (2.0)	8.6 (2.5)	33.5 (10.4)

Note: Numbers represent means and standard error is in parentheses. NF, no stakes found.

Table A2. Mass loss of surface pine stakes (%) after 1 (2002), 3 (2004), and 6 (2007) years of incubation at each of the 26 study sites.

Plot ID	Ecosystem type	Surface pine stakes		
		2002	2004	2007
De12	Short-grass	0.0 (2.0)	6.4 (—)*	NFA
Il Pra	Short-grass	2.1 (1.0)	3.1 (0.9)	8.9 (2.8)
Mi 80	Short-grass	-1.0 (0.7)	3.1 (0.8)	15.5 (3.8)
Mu 01	Short-grass	3.53 (0.5)	14.9 (2.8)	51.1 (4.2)
Mu 21	Short-grass	1.9 (1.1)	23.4 (6.2)	60.0 (3.3)
Fe 1	Tall-grass	4.4 (2.8)	2.7 (3.3)	12.0 (7.3)
Mi 17	Tall-grass	6.2 (2.0)	1.6 (1.8)	10.0 (2.2)
N 14	Tall-grass	2.3 (1.2)	19.1 (2.4)	65.9 (3.2)
PF 13	Tall-grass	NF	8.2 (2.0)	18.4 (4.5)
1109	Mountain pine	1.3 (0.6)	5.3 (2.9)	17.9 (9.3)
1110	Mountain pine	2.0 (3.0)	3.7 (0.9)	12.5 (1.5)
1113	Mountain pine	0.9 (2.0)	0.9 (2.8)	7.8 (1.5)
1203	Mountain pine	2.3 (1.4)	1.6 (1.3)	15.1 (3.9)
1307	Mountain pine	2.5 (1.5)	0.1 (1.7)	8.5 (2.2)
1313	Mountain pine	3.9 (1.1)	12.2 (8.4)	32.3 (10.8)
Pin 03	Mountain pine	4.6 (2.7)	4.0 (0.9)	9.0 (2.2)
Pin 04	Mountain pine	3.7 (2.1)	6.4 (2.3)	14.8 (3.3)
807	Mixed	3.6 (1.6)	5.1 (1.0)	15.5 (1.4)
808	Mixed	2.8 (1.5)	5.2 (1.2)	19.5 (5.6)
1316	Mixed	4.3 (3.1)	2.4 (2.3)	44.8 (4.5)
1318	Mixed	1.3 (0.9)	2.9 (2.0)	11.3 (3.8)
1401	Mixed	1.3 (2.4)	3.6 (1.7)	18.11 (4.9)
1508	Mixed	-0.2 (0.9)	1.9 (1.7)	1.4 (1.8)
903	Stone pine – larch	0.0 (1.1)	4.4 (2.3)	7.4 (2.7)
905	Stone pine – larch	2.4 (1.2)	2.7 (1.0)	9.9 (1.7)
906	Stone pine – larch	3.2 (1.7)	3.6 (2.3)	13.0 (3.5)

Note: Numbers represent means and standard error is in parentheses. NFA, no stakes found owing to animals (deer) kicking them away; NF, no stakes found.

*Only one stake found.

Table A3. Mass loss of mineral aspen stakes (%) after 1 (2002), 3 (2004), and 6 (2007) years of incubation at each of the 26 study sites.

Plot ID	Ecosystem type	Mineral aspen stakes		
		2002	2004	2007
De12	Short-grass	10.0 (2.0)	16.9 (2.0)	39.3 (1.4)
Il Pra	Short-grass	8.6 (0.5)	37.7 (1.2)	71.4 (3.4)
Mi 80	Short-grass	2.8 (1.1)	12.5 (2.4)	12.2 (2.5)
Mu 01	Short-grass	9.3 (1.5)	58.3 (9.0)	87.8 (1.8)
Mu 21	Short-grass	9.5 (1.2)	35.1 (3.6)	61.3 (8.5)
Fe 1	Tall-grass	5.1 (1.0)	25.4 (7.1)	42.6 (5.9)
Mi 17	Tall-grass	3.2 (1.4)	10.8 (1.3)	21.3 (1.4)
N 14	Tall-grass	7.8 (1.9)	56.6 (8.9)	61.2 (6.9)
PF 13	Tall-grass	8.6 (1.5)	16.5 (1.5)	25.8 (2.1)
1109	Mountain pine	4.6 (1.5)	8.7 (1.7)	31.1 (3.7)
1110	Mountain pine	8.3 (2.8)	7.7 (0.8)	21.8 (4.6)
1113	Mountain pine	3.2 (0.9)	14.3 (5.0)	16.6 (2.0)
1203	Mountain pine	6.1 (1.9)	25.3 (3.1)	74.6 (4.8)
1307	Mountain pine	5.2 (1.8)	20.8 (3.6)	NF
1313	Mountain pine	2.8 (0.9)	24.7 (6.3)	53.4 (6.5)
Pin 03	Mountain pine	2.5 (0.7)	15.2 (3.1)	24.4 (3.3)
Pin 04	Mountain pine	6.9 (1.7)	8.5 (2.0)	17.2 (2.6)
807	Mixed	11.3 (2.0)	45.8 (8.0)	66.7 (9.1)
808	Mixed	4.7 (1.2)	41.7 (8.7)	76.4 (3.8)
1316	Mixed	5.5 (1.5)	23.4 (7.0)	58.1 (9.2)
1318	Mixed	5.6 (1.6)	21.2 (5.7)	44.8 (7.2)
1401	Mixed	4.0 (1.2)	15.0 (4.0)	37.0 (8.1)
1508	Mixed	1.2 (1.0)	11.4 (2.6)	23.4 (8.0)
903	Stone pine – larch	8.0 (0.9)	15.8 (3.7)	51.2 (4.2)
905	Stone pine – larch	3.0 (0.3)	12.9 (4.4)	68.3 (5.5)
906	Stone pine – larch	2.8 (1.0)	15.8 (3.5)	44.8 (10.3)

Note: Numbers represent means and standard error is in parentheses. NF, no stakes found.

Table A4. Mass loss of mineral pine stakes (%) after 1 (2002), 3 (2004), and 6 (2007) years of incubation at each of the 26 study sites.

Plot ID	Ecosystem type	Mineral aspen stakes		
		2002	2004	2007
De12	Short-grass	2.1 (1.1)	5.6 (0.8)	18.3 (3.6)
Il Pra	Short-grass	2.3 (0.4)	5.9 (1.5)	7.3 (1.8)
Mi 80	Short-grass	-0.8 (1.0)	5.4 (1.2)	8.8 (1.6)
Mu 01	Short-grass	4.4 (1.0)	37.9 (4.2)	60.1 (2.6)
Mu 21	Short-grass	0.1 (0.2)	31.8 (4.9)	25.4 (4.9)
Fe 1	Tall-grass	3.8 (1.0)	6.1 (2.1)	25.2 (7.5)
Mi 17	Tall-grass	-0.3 (1.3)	3.1 (1.2)	5.6 (1.2)
N 14	Tall-grass	3.7 (1.2)	21.1 (6.2)	58.9 (5.8)
PF 13	Tall-grass	0.9 (0.9)	5.5 (1.4)	19.5 (2.9)
1109	Mountain pine	-0.5 (1.0)	6.7 (1.0)	17.4 (3.4)
1110	Mountain pine	2.9 (1.1)	7.9 (3.5)	7.4 (1.1)
1113	Mountain pine	1.2 (0.8)	2.3 (1.2)	13.7 (2.0)
1203	Mountain pine	2.0 (0.4)	12.5 (3.0)	46.7 (6.9)
1307	Mountain pine	0.8 (0.7)	14.1 (5.0)	NF
1313	Mountain pine	3.6 (0.9)	10.4 (1.1)	25.6 (3.9)
Pin 03	Mountain pine	1.1 (0.9)	4.4 (1.4)	8.9 (1.8)
Pin 04	Mountain pine	3.8 (0.6)	6.3 (1.7)	10.1 (2.3)
807	Mixed	3.6 (0.7)	16.2 (3.1)	52.2 (8.5)
808	Mixed	0.6 (0.9)	20.8 (3.0)	50.5 (5.0)
1316	Mixed	1.2 (0.8)	9.6 (2.4)	20.0 (6.3)
1318	Mixed	6.1 (1.8)	13.5 (2.3)	20.0 (5.7)
1401	Mixed	3.2 (2.0)	4.9 (2.3)	18.3 (3.9)
1508	Mixed	-0.9 (1.4)	10.7 (2.1)	10.3 (2.5)
903	Stone pine – larch	2.6 (1.29)	12.4 (3.3)	23.8 (5.1)
905	Stone pine – larch	2.0 (0.9)	7.6 (3.3)	48.6 (6.2)
906	Stone pine – larch	2.8 (0.5)	9.3 (1.5)	31.3 (5.8)

Note: Numbers represent means and standard error is in parentheses. NF, no stakes found.