Norwegian University
of Life Sciences

Master's Thesis 2016 60 ECTS
Department for Ecology and Natural Resource Management

Small-scale spatial variation in soil properties within an old-growth European beech forest and two Norway spruce forests.

Eivind Bølum Thomassen
Master in Biology

Abstract

The aim of this study was to investigate species related differences in soil carbon and nitrogen concentration, pH and condensed tannin content in topsoil's in Norway spruce (*Picea abies*) European beech (*Fagus sylvatica*) forests. Samples were collected in two Norway spruce sites and one old-growth European beech forest in South-Eastern Norway. Research on spatial distribution and differences in soil properties in beech and spruce has been studied in the temperate zone. However, no comparative studies have investigated differences in secondary compounds in topsoil's between European beech and Norway spruce forests. This might be of importance as larger tannin structures decompose slower, and are believed to be able to remain in the soil over time and potentially add to the stable carbon pool found in boreal forest soils. Also, in the literary studies done in conjunction with this thesis, no research showing differences in topsoil content of condensed tannins between spruce and beech where to be found. Topsoil samples were collected in old-growth beech forest, a Norway spruce forest growing in an area previously dominated by beech, and in a younger primary Norway spruce forest. The samples were analysed for carbon and nitrogen concentration, C/N ratio, pH and total condensed tannin content. Topsoil samples were collected at spatial intervals of 2 meters, with samples being taken up to 10 meters in all cardinal directions from a centre point. The results suggest that a change from spruce to beech forest will not induce significant changes to the concentrations and distribution of the measured soil properties. Few significant differences in the measured variables were found between the forest sites, and the highest variation was found within forest sites. This indicates that other factors than dominating tree species are more influential for small-scale spatial variations in soil properties. However, the results for spatial distribution of the measured variables does not constitute evidence that the parameters for soil properties would not show temporal variation with a shift towards more beech forest. To conclude further on this, more sampling sites and a larger number of samples would have to be included in the model.

Acknowledgements

First, I would like to thank my supervisors, Mikael Ohlson, Line Nybakken and Johan Asplund for all the help they have provided regarding my thesis. I would also like to thank Annie Aasen for all the help with laboratory analyses, and for sharing her knowledge about how to avoid mistakes when doing measurements in the lab.

I wish to give a thank you to Yngvild for the good days of fieldwork, and all the help with sample collection. I wish to thank my parents, Grethe and Frank, not only for initially sparking my interest for biology, but also for your help trying to make it easier for me to find time for writing this thesis. I send a special thank you to my girlfriend Sanna for being awesome, and for the help with proofreading my thesis. Finally, I would like to thank my dog, Hera, for always making me smile all those times I came home late after a long day, either in the field, at the lab or behind the computer screen.

17th May 2016

Ås

Eivind Bølum Thomassen

Contents

Introduction

The topsoil layer represents an important link in the biogeochemical cycle between the forest floor and deeper soil layers. Topsoil's are dynamic environments and are largely affected by several external abiotic factors, such as annual precipitation, topography and seasonal and regional variations in climate (Matějka & Starý 2009). Biotic factors of importance include input of organic material and litter, interaction by macro and microorganisms and cat-ion exchange from plants. These factors manifest their impact at different spatial scales. Topographic features may create different patches within a seemingly homogenous forest stand (Thompson & Grime 1979). Soil texture, moisture and chemical composition shows great heterogeneity within one single forest, especially along topographic gradients (Benayas et al. 2004). However, the relative importance of the different environmental and biological factors at different spatial scales remains poorly understood (Grüneberg et al. 2014). Bringmark (1989) stated that within a seemingly homogenous forest stand, soil properties can show great heterogeneity.

Amongst the most obvious biotic factors that influence soil parameters in a forest, are the tree species composition. Norwegian forests are dominated by Norway spruce (*Picea abies*, hereafter referred to as spruce), but the latitudinal range of broadleaves species are estimated to expand following the rise in global temperatures predicted in this century (Hickler et al. 2012). A warmer climate is predicted to negatively affect species like spruce that are adapted to colder environments in the higher latitude areas in Northern–Europe(Meier et al. 2012). Meanwhile, species adapted to milder winters and longer growing seasons are predicted to be favoured by a warmer climate, and expand their latitudinal range northwards.

Because temperature and precipitation are key-factors regulating the distribution of European beech (Fagus sylvatica, hereafter referred to as beech) (Benayas et al. 2004; Bolte et al. 2009) the species is expected to expand its distribution range northward with rising temperatures (Falk & Hempelmann 2013). Currently, continuous beech forests are found in Denmark and in southern Sweden, while a few isolated populations can be found along the coast of southern Norway (Bolte et al. 2009). These populations are considered the northernmost populations of beech in Europe (Jalas et al. 1972). Warmer climates and less precipitation could give European beech a competitive advantage towards Norway spruce. Therefore, over time, a shift in

vegetation regime from forest dominated by spruce, to forests dominated by beech can be expected (Bolte et al. 2009).

A regime shift in domination tree species might influence soil properties in several ways, of which only a few can be hypothesized. Change in canopy structure is one factor that might influence parameters in the topsoil. Solar influx to the forest floor influences soil temperatures and therefore decomposition rates of litter and organic material (OM) in the upper soil layers (Rozenbergar et al. 2011). Both Norway spruce and European beech create dense canopies allowing little influx of light to the forest floor. Ground vegetation within both forest types are dominated by shade tolerant species, along with scattered populations of grasses and bushes mostly found in canopy gaps. Although there is little research on what effect said regime shift will have on solar flux to forest floor, together with rising air temperatures this might prove to be an important influencing factor on decomposition rates, as well as creating different conditions for ground vegetation and soil organisms. Canopy structure further affects the amount and distribution of precipitation reaches the forest floor. Since both high and low moisture content effects degradation negatively, a change in canopy structure is likely to affect processes in the soil related to moisture content, especially in the topsoil layer (Tanaka & Hashimoto 2006).

Trees are chemical engineers that modify the soil environment within the proximity of the stand (Miles 1981). Fine-scale variation in soil properties is suggested to arise mainly from tree influence (Häkkinen et al. 2010). Regarding fine-scale spatial variation of carbon, supply and distribution of litter is one of the key factors (Liski & Westman 1995). Trees alter the soil environment through the quality, quantity and concentration of inhibitory secondary compounds in their litter. Conifers, like spruce, are known to grow on acidic soils that are low on nutrients. Meanwhile, European beech has been shown to increases base cat-ions in the soil (Cremer et al. 2016). Secondary compounds in tree litter, like polyphenols, vary between species both in quantity and quality. Little is known about the rate of degradation of different polyphenols in soil or how polyphenols interact with soil particles, soil C and OM (Kanerva et al. 2008; Schmidt 2012). Although precise data on the dynamics of polyphenols in soils are scarce, it is believed that they constitute a large fraction of total organic C found in soils (Kraus et al. 2003)

One class of polyphenols found in both beech and spruce are tannins. Tannins are a diverse group of compounds, and the fourth most abundant plant derived compound found in soil (Kraus et al. 2003). Tannins can constitute 10-25% of dry weight of foliar biomass in woody species. Tannins enter the soil through dead plant material, like leaves, branches and dead trunks, or through exudation from roots (Kraus et al. 2003). As the broadleaves shed their leaves and the spruce loose needles, tannins are released into the litter layer and eventually into the topsoil layer. Both European beech and Norway spruce produce condensed tannins (CT), and are found in the leaves and needles (Albers et al. 2004). According to Quideau et al. (2011) tannins can affect soil biochemistry and degradation of soil organic matter (SOM) through three chemical activities: protein binding, metal complexation and antioxidant activity. Protein binding by tannins inhibits microbial enzymes and immobilize nitrogen (Joanisse et al. 2007). Because of the variety in the chemical structure of tannins, some decompose faster, while other form resilient complexes with other soil particles and organic compounds in the organic layer. Larger tannin structures decompose slower, and is believed to be able to remain in the soil over time and potentially add to the stable carbon pool found in boreal forest soils (Kraus et al. 2003).

Temporal and spatial variability of soil properties are hard to measure and estimate due to the need of extensive soil sampling (Conant et al. 2003). Carbon concentrations within forest soils have been studied extensively because soils represent the largest terrestrial stock of carbon (Jandl et al. 2007b)However, temporal changes in soil carbon (soil C) have been hard to detect following repeated measurements. Further Vesterdal et al. (2013) stated that species-specific effects on C stocks are difficult to pinpoint, because soil C is regulated both by direct and indirect factors. Tree species are not randomly distributed within a landscape, and their presence is affected by some of the same abiotic and biotic factors that alter soil C pools. Nutrients like nitrogen (N) are known to show heterogenic distribution within plant communities, and the distribution relates to species dominance and composition (Tateno & Takeda 2003). According to Tamm (1991)nitrogen is the main limiting nutrient of primary productivity in boreal forests. Therefore, availability of N affects plant community dynamics, species interactions and succession. Studies have emphasized the need of repeated inventories to understand how concentrations of C and N change both spatially and temporally in Europe (Grüneberg et al. 2014; Sabatini et al. 2015; Schulp et al. 2008).

The aim of this study is to assess differences in topsoil properties in beech and spruce forest ecosystems. Knowledge about the differences between topsoil properties in beech and spruce forest ecosystems is a crucial to understanding how a regime shift in dominating tree species will influence the large areas of soil affected, and even hint on how this again affects carbon storage. The topsoil properties that were measured in this study are carbon and nitrogen (hereafter referred to as C and N) concentrations, C/N ratios, pH and condensed tannins (hereafter referred to as CT). Samples were collected in an old-growth beech forest, a Norway spruce forest growing in an area previously dominated by beech, and in a younger primary spruce forest.

The following hypotheses are tested:

1. Because of the heterogeneous nature of the forest floors soils properties will too show great heterogeneity. Variation in soil carbon and nitrogen concentrations will be greater within the different forests stands, compared to differences between stands.

2. Soil CT content is higher in the spruce forests than in the beech forests.

3. Soil pH is lower within the spruce stands.

4. C/N ratios are higher in both Norway spruce forests.

Materials and methods

Study area and species

Soil samples were collected within and surrounding Brånakollene nature reserve (59°11' N, 10°02' E; 200 m.a.s.l) and south of Lake Allumtjerna (59°10' N, 10°02' E, 68.9 m.a.s.l) in the municipality of Hedrum, Vestfold, SE Norway (see Tab.1; Fig.1). Two sites were situated in Brånakollene nature reserve, were samples were collected in a European beech (*Fagus sylvatica*) forest and in a spruce forest. The third site was a Norway spruce (*Picea abies*) forest located south of the Lake Allumtjerna.

The beech forest in Brånakollene nature reserve is primarily dominated by old-growth forest, and has only experienced minor logging activity since 1910 (Korsmo 1975). The reserve covers 19.2 ha and was protected by law in 1980 (Miljøverndepartementet. 1980). The reserve is considered a genetic resource reserve for European beech. The second area in Brånakollene was a managed spruce forest surrounding Brånakollene nature reserve. This spruce forest is growing in an area previously dominated by beech (Asplund 2016). The trees within this forest belonged to different age groups ranging from 40 to 55 years (Lie 2016). The third study area south of Lake Allumtjerna consisted of younger spruce stands, with trees ranging from 40 to 45 years old. This area had previously been covered by spruce.

Table 1. Coordinates for study sites in Brånakollene and Allumtjerna

Study site	Plot	Coordinates
Brånakollene (Beech)	1	59°11'665'N, 010°03'025'E
Brånakollene (Spruce)	2	59°11'566'N, 010°02'840'E
Allumtjerna (Spruce)	3	59°10'556'N, 010°02'646'E

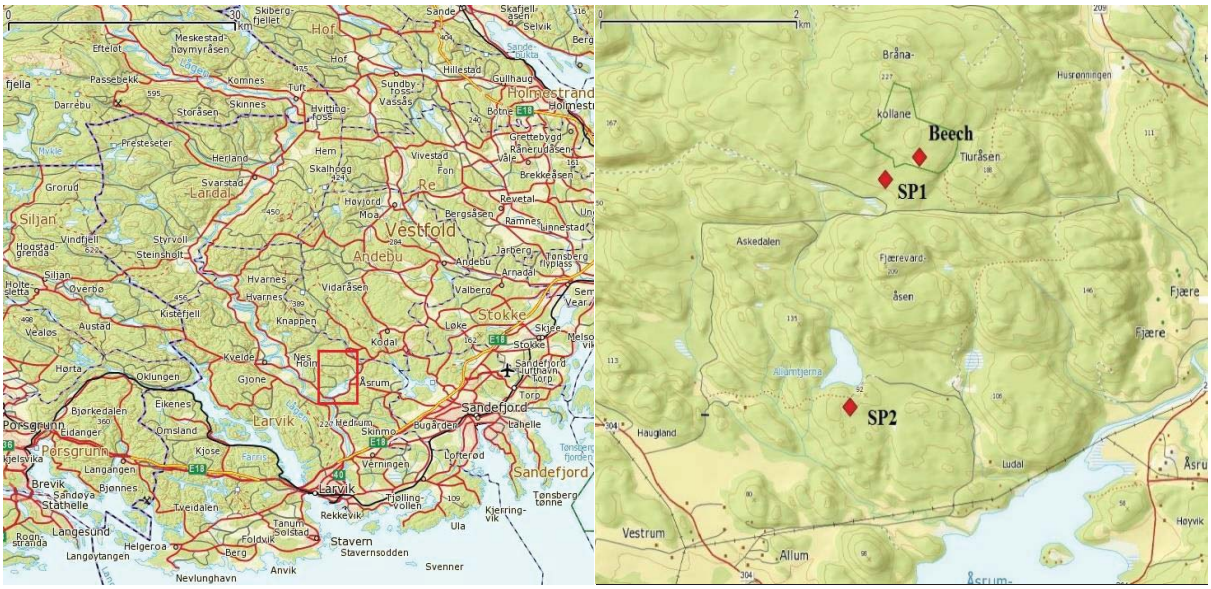


Figure 1. Study sites in Brånakollene and Allumtjerna. Brånakollene nature reserve is outlined with green lines. SP1= spruce forest in Brånakollene, SP2 = Spruce forest south of lake Allumtjerna.

Soil sampling

At each site, soil samples were collected from four plots. Soil depth was measured using a soil auger. Features in the landscape like outcropping rocks, trees and dead logs could affect the spatial soil sampling. Therefore, sampling plots were selected in sites where the samples could be collected 10 meters in all cardinal directions from a center point. Four plots were selected in each site, with 21 samples collected from each plot. In total 84 top soil samples were collected in each site.

Topsoil samples were collected after a prefixed pattern to measure spatial distribution in soil tannins, pH, carbon and nitrogen (Fig.2). A center hole was selected, and a sample was cored. Then 5 samples were taken in each cardinal direction with an interval of 2 meters between each plot. Cardinal directions were determined by using a GPS and a compass.

Extraction of topsoil samples was conducted using a soil core sampler. Topsoil samples were cored to a depth of approximately 6 cm. However, soil depth, rocks and roots did not enable a sample depth of 6 cm for all soil samples. After sample collection, the mean depth of the hole was measured by measuring the depth on four opposing sides of the hole. Samples were stored in labeled paper bags.

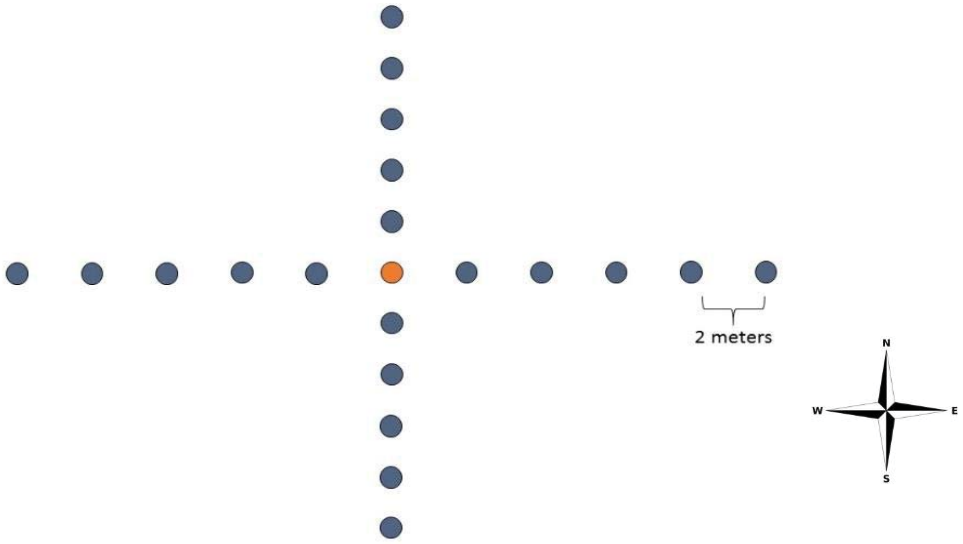


Figure 2. Soil sampling design.

Soil sample preparation

Soil samples where dried, where dried, weighed and sieved in preparation for analysis. Drying was done within 12 hours of collection, and done at 30 ºC to prevent degradation of polyphenols in the soil. Dry samples were sorted, removing sticks, stones, roots and large pieces of plant material before weighing.

Samples were weighed and then sieved through a soil sifter (2mm). Every sample was thoroughly sieved and then weighted again. The sieved sample was then homogenized to powder using a Retsch MM400 ball mill (Retsch, Haag, Germany). Every sample was milled for 30 seconds. Milled samples were transferred to plastic zip bags and then weighed. Homogenized samples were then stored at room temperature (approx. 20 °C) in a dark room to prevent photo degradation.

Carbon, Nitrogen and C/N ratio measurement

10 mg of homogenized soil from each sample was used for C and N concentration measurements. An Elementar Vario MICRO cube (Elementar Analysensysteme GmbH, Hanau, Germany) was used to determine C and N concentration and C/N ratios for all 252 samples.

pH-analysis

A sample of 3 ml of homogenized soil from each sample were placed in a 15ml tube with 8 ml purified water, and mixed using a Vortex. Samples were left overnight, before being mixed a second time. pH-values were measured after the second mixing using inoLab pH 720 precision pH meter (WTW GmbH, Weilheim, Germany).

Tannin extraction

The extraction method for condensed tannins follows the procedure as described by Kanerva et al. (2008). In total 156 soil samples were used for tannin analysis. Samples were selected from all sampling sites, and from the distances; 0 (center point), 2 meters, 6 meters and 10 meters, which resulted in 13 samples from each sampling site.

Approximately 200 mg soil from each sample was suspended in 4 ml 70% acetone, and then put on a planar shaker (200 rpm) for 1 hour. Samples were then centrifuged at 1500 rpm X 10 minutes, and the supernatant was then collected in a 15ml glass tube. Extraction from the solid residue was repeated twice. Collected supernatants were evaporated at 30 °C in a vacuum centrifuge (Eppendorf concentrator plus).

The condensed tannins was analyzed from the extracts by the butanol-HCL-iron assay described by (Hagerman 2002). 0.5 ml of MeOH were added to dry extractions, and shaken on a Vortex. 3 ml of Acid butanol (950 ml butanol and 50 ml HCL) and 0.1 ml of iron reagent (2% Ferric ammonium sulfate in 2N HCL) were added before the samples were put in boiling water for 1 hour. After cooling, absorbance was measured using a UV-spectrophotometer (Shimadzu, Kyoto, Japan). Absorbance was then used to calculate CT content per gram soil (mg/g^{-1}).

Data analysis

All statistical analyses were performed with R studio (RStudio 2015). Figures were made using Graphpad prism 6 (Prism 2014).Tables were made with the stargazer package for R (Hlavac 2013) and compiled using TexStudio (van der Zander et al. 2009). A linear mixed-effects model (lme-model) was used to analyze the differences between and within the study sites (Pinheiro et al. 2014). Sampling plots was used as a random factor when comparing the three main sites. Distance from the center hole was applied as a random factor when analyzing for differences between plots within each site. Analysis of variance was done on the lme-model. Multiple comparisons of soil properties was conducted with the Tukey-HSD function from the multcomp package (Hothorn et al. 2008). The CV function of the raster-package was used to calculate

coefficients of variation (Hijmans & Van Etten 2013). Differences in spatial variation of C and N concentration and CT content analyzed by calculating CVs for each variable for each sampling distance. This was done for variables within all study sites. Spatial variation in C and N concentrations were analyzed for distances between 2 and 10 meters from the center hole (Fig.2). Spatial variation in CT was analyzed for distances 2, 6 and 10 meters from the center hole (Fig.2). CVs for the different distances were then used as response variables and analyzed using the same lme-model that was used to detect between and within site differences.

The Shapiro-Wilk-test and qqnorm function was used to test for normality of variables. In cases where the assumptions of normal distribution were not met, data transformations were done using log-transformation. However, some variables could not be transformed to show a normal distribution. Although not all variables were normally distributed, residual plots indicated no violations of the assumptions of homoscedasticity and normal distribution of residuals. Statistically significant differences were set to $P < 0.05$.

Maps were created with QGis 2.8 (Team 2013). Latitude and longitude measurements were only noted for the center hole in each plot. All coordinates plotted in the maps were calculated using a excel-spreadsheet made by Dutch (2015) with formulas developed by Karney (2011), to enable conversion of latitude and longitude to UTM (Dutch 2015). Latitude and longitude measurements for center holes were converted to UTM. Coordinates for all the other sampling plots were then calculated based on the coordinates from the center hole. An open source map of Norway was used for all maps (Kartverket).

Results

The results for N, C and pH did not indicate any significant differences in-between the forest stands. C/N ratios were highest in the spruce forest in Brånakollene, and significantly higher than in the beech forest. Meanwhile, the average C/N content in site SP2 was not significantly different from either the other spruce or beech forest. The Spruce forest in Brånakollene also showed the highest average CT content, but the only significant difference was to the other spruce forest, which had the lowest CT content. (Fig.3, Tab.5). All three sites had relatively low pH.

The results for mean values are showed in table 2, including standard deviation (SD) and coefficient of variation (CV) for nitrogen, carbon, condensed tannin (CT mg/g^{-1}) content. The mean values for the measured variables on each site, is presented in tables 3 to 5. Table 6 presents the result from the analysis of variances (ANOVA) conducted on the linear mixed-effect model. P-values from the for ANOVA on spatial differences in coefficients of variances (CV) are presented in table 7. The staple graph in table in figure 3 shows mean values for each site and measured variable, with different letters above the stable indicating significant differences. Standard errors (SE) and statistical differences at a 0,05 significance level are included here .

Table 2. Mean values ± SD and coefficient of variation (CV*100) for nitrogen (N), carbon (C), condensed tannin (CT mg/g^{-1}) content, C-to-N ratio and pH. The table shows averages for all three sites. Number of samples (n).

Parameter	n	Mean	SD	Min	Max	CV
N (%)	252	1.38	0.53	0.31	2.97	40.22
C (%)	252	29.65	12.55	5.84	70.60	40.94
C/N	252	22.39	5.13	15.93	33.65	
CT	156	94.67	58.98	8.45	300.73	62.29
pH	156	4.25	0.37	3.67	5.85	

Table 3. Mean values ± SD and coefficient of variation (CV*100)for Nitrogen (N), carbon (C), Condensed tannin (CT mg/g^{-1}) content, C-to-N ratio and pH for plots in the beech forest in Brånakollene nature reserve. Number of samples (n).

Parameter	n	Mean	SD	Min	Max	CV
N (%)	84	1.49	0.64	0.368	2.973	43.04
C (%)	84	31.54	13.65	8.00	70.60	43.27
CN	84	21.16	2.40	15.93	29.72	
CT	52	102.41	62.71	11.82	300.73	61.24
pH	52	4.20	0.29	3.67	4.94	

Table 4. Mean values ± SD and coefficient of variation (CV*100) for Nitrogen (N), carbon (C), Condensed tannin (CT mg/g^{-1}) content, C-to-N ratio and pH for plots in the spruce forest surrounding Brånakollene nature reserve. Number of samples (n).

Parameter	n	Mean	SD	Min	Max	CV
N (%)	84	1.30	0.423	0.352	2.08	32.16
C (%)	84	31.71	11.20	5.85	47.10	34.57
CN	84	23.95	3.09	16.50	33.65	
CT	52	119.24	58.73	18.11	291.48	49.25
pH	52	4.22	0.35	3.67	4.98	

Table 5. Mean values ± SD and coefficient of variation (CV*100) for Nitrogen (N), carbon (C), Condensed tannin (CT mg/g^{-1}) content, C-to-N ratio and pH for plots in the spruce forest south of Lake Allumtjerna. Number of samples (n).

Parameter	n	Mean	SD	Min	Max	CV
N (%)	84	1.14	0.43	0.31	2.92	38.56
C (%)	84	25.80	10.69	5.84	61.59	41.72
CN	84	22.18	2.27	17.99	29.98	
CT	52	62.36	38.05	8.45	171.38	61.01
pH	52	4.32	0.45	3.68	5.85	

Table 6. Results from the ANOVA conducted on the results from the linear mixed-effects model. The table show results of analysis of variance between the three sites (Sites) and within each study site. SP1 = Norway spruce forest in Brånakollene. SP2 = Norway spruce forest south of Lake Allumtjerna. Bold numbers indicate a P-value < 0.05.

Site	Carbon			Nitrogen			C/N ratio			Condensed tannins			pH		
	Df	*F*	*P*	*Df*	*F*	*P*	*Df*	*F*	*P*	*Df*	*F*	*P*	*Df*	*F*	*P*
All Sites	9	1.76	0.307	9	2.60	0.127	9	3.38	0.08	9	12.52	**0.002**	9	0.30	0.745
Beech	3	4.21	**.0082**	3	2.62	0.056	3	14.88	**< .001**	3	1.44	0.242	3	2.11	0.111
SP1	3	3.29	**0.025**	3	3.41	**0.021**	3	13.54	**< .001**	3	0.71	0.549	3	9.07	**<.001**
SP2	3	7.70	**< .001**	3	9.85	**< .001**	3	14.96	**<.001**	3	1.75	0.169	3	8.29	**<.001**

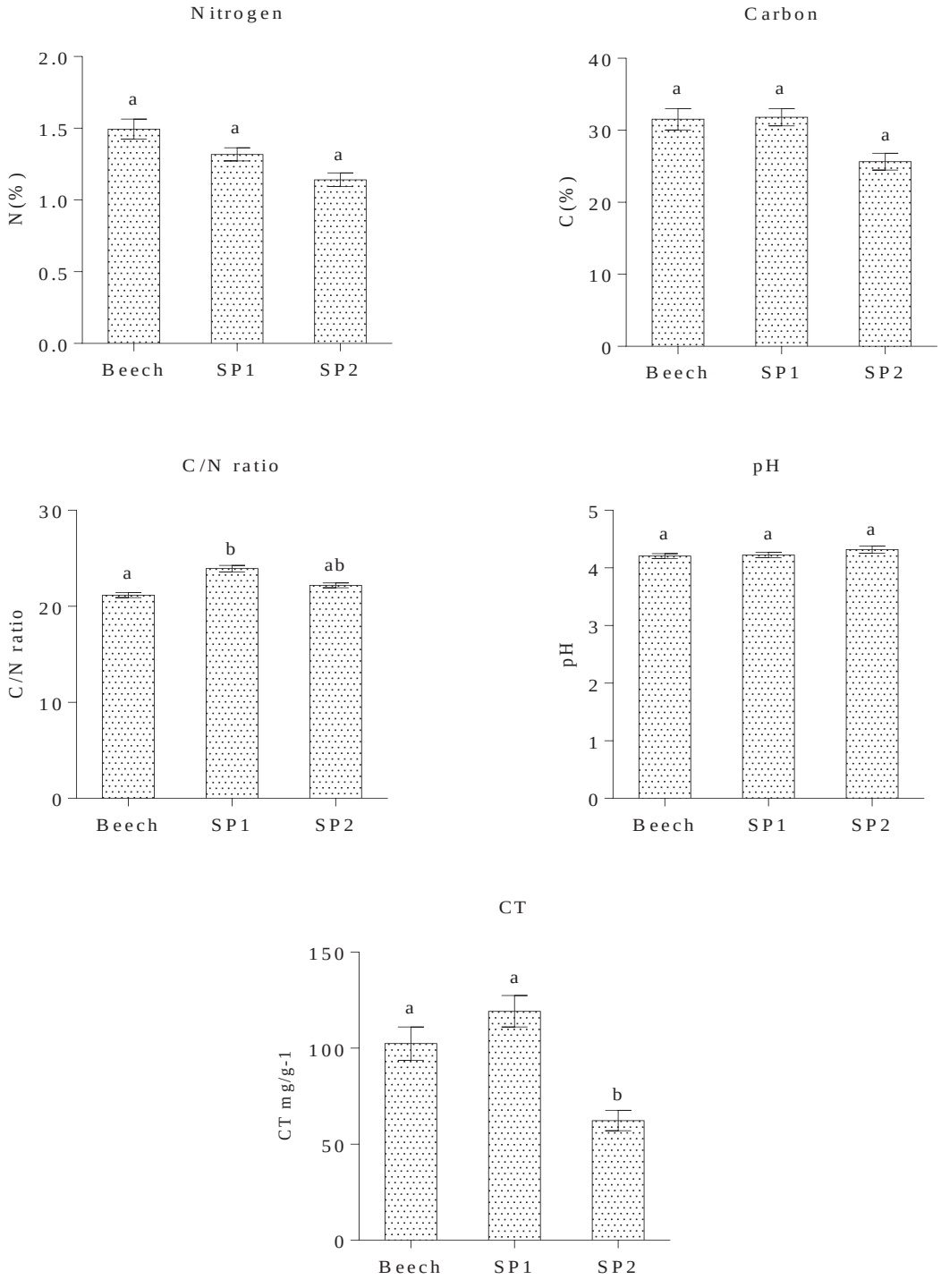


Figure 3. Mean values ± SE. Letters above the SD-bars indicate significant differences between sites detected by Tukeys HSD test. $P < 0.05$. SP1 = Spruce forest in Brånakollene; SP2 = Spruce forest south of Lake Allumtjerna

Table 7. P-values for ANOVA on differences in CV between different distances between sampling plots. Results for N (%), C (%) and CT (CT mg/g-1) are shown. Significant differences between different distances were only detected for CT in the beech forest. Results from Tukey contrasts are given. Bold numbers indicate a P-value < 0.05.

Parameter		Beech	SP1	SP2
N		0.201	0.098	0.652
C		0.404	0.207	0.815
CT		**0.0089**	0.961	0.675
Tukey				
	2-6m	0.059		
	2-10m	**0.032**		
	6-10m	**<.001**		

Nitrogen

There was no significant difference in N concentration between sites (Tab.6). Coefficients of variation (CV) were higher in the beech forest, followed by SP2 and then SP1 (Tab.3 to 5). Although, CVs indicated a higher dispersion of N concentration values in the beech forest, ANOVA found no significant difference in N concentration within the beech forest (Tab.6). However, the post-hoc test revealed a significant difference between plot 2 and 3 (Appendix 2). On the other hand, significant differences among plots were found within both spruce sites (Tab.6). Differences in N concentration were larger in the SP2 site than in the SP1 (Tab.6, Appendix.7 and 12). ANOVA of indicated no variation in N concentration with greater distances between sampling plots (Tab.7).

Carbon

Carbon concentration did not show any significant difference between the three sites (Tab.6). CVs were similar in the beech and SP2 site, while it was considerably lower in the SP1 site (Tab.3 to 5). C concentration was significantly different between plots within all forest sites (Tab.6). The greatest differences were found in the SP2, followed by SP1 and the beech forest. The Tukey test revealed significant differences between plot 2 and 3 in the beech forest.

C concentration was significantly different between plot 4 and plot 1 in the SP1 forest. Within the SP2 site, plot 3-2 and 2-1 differed significantly in C concentration. Similar to the results from N, the variation in C concentration did not increase significantly with greater distance between sampling plots within any of the three sites (Tab.7).

C/N ratio

The ANOVA showed no significant difference in C/N ratio between sites (Tab.6). However, the p-value is low, so the sites are close to be significantly different. The Tukey test yielded no significant differences between the spruce sites, while a significant difference was detected between the SP1 and the beech forest (Fig.3). C/N ratios showed significant differences within all forest sites (Tab.6, Appendix.3, 8 and 13). The SP1 forest had the highest mean C/N ratio, and the beech had the lowest mean C/N ratio (Tab.3 and 4).

Soil pH

The ANOVA found no significant difference in pH between the sites (Tab.6). ANOVAs indicated no significant differences in pH within the beech forest, but detected significant differences within both spruce sites (Tab.6, Appendix.4, 9 and 14).

Condensed tannins

CT content was the only measured variable that was significantly different between sites (Tab.6). However, CT content was not different between the two sites in Brånakollene. CT content was significantly different between SP2 and both of the sites in Brånakollene. However, CT content was not different between the two sites in Brånakollene (Fig.3).

CVs were higher for CT than for any of the other measured variables (Tab.3 to 5). The CV of CT in SP1 was lower compared to the beech and SP2 site.

ANOVAs detected no significant differences in CT content within sites (Tab.6, Appendix.5, 10 and 15). Variation in CT content was significantly different with increasing distance within the beech site (Tab.7). Interestingly, CT variation was greater between samples collected at 6 meters and 10 meters, than samples collected at 2 and 10 meters (Tab.7). Variation in CT content was not significantly different at different spatial scales in both spruce sites (Tab.7).

Discussion

Carbon

Total C concentration was not different between the sites, indicating no species-specific effects on this parameter. The ANOVA supported the hypothesis of greater differences within than between sites. Differences in C concentration were only significant within spruce sites. The beech forest showed no significant difference in C concentration. Downslope areas of the forest floor showed higher C concentrations than inclined sampling plots (Plot 1 and 2, Appendix.1). This is most likely caused by the accumulation of litter in such terrain. Both plot 1 and 2 were situated in flatter parts of the forest floor, receiving more influx of particulate organic matter (POM) and litter transported from surrounding slopes.

C concentration was significantly different between plots within the SP1 site, confirming hypothesis x (Tab.6, Appendix.6). Stand density can yield an explanation of the greater differences between plots in the SP1 site. Stand density was not measured, but was observed to be higher within plot 3 and 4 in the SP1 site (Appendix.6). Higher stand density around these plots might results in a greater and more even accumulation of litter along the forest floor. Although, C concentration was significantly different among several plots within SP1, CVs for C concentration did not differ significantly with increasing distance between sampling plots. Thus, indicating an even variation of C concentration along the forest floor.

Differences in C concentration between plots were highest within the SP2 site. No significant difference in CVs was found with increasing distance between sampling plots. Therefore, the gap in CT content between the sites in Brånakollene and Allumtjerna might stem from increased degradation of SOM in the organic layer following logging disturbance. Logging may influence the SC in several ways. Forest harvesting alter the topsoil layer, both by mixing

topsoil into the mineral layer, and by increasing exposure to weather, potentially increasing soil erosion and nutrient leaching (Kreutzweiser et al. 2008). Logging machinery disturb the soil including both compression of the soil, and effects similar to that of tilling in other places, meaning it can both aerate the soil and hinder oxygen to get into the soil in other places (Frey et al. 2009). Disturbances to the forest floor following the logging may also have increased soil biological activity, increasing degradation of plant residue. Disturbances to forest soils might happen over a short period, but can alter soil properties for a considerable time. According to the Covington-curve, SOC concentrations may decrease as much as 50% within 20 years after forest harvest disturbance (Covington 1981). If both the beech and SP1 forest have experienced fewer disturbances compared to SP2, it may explain the lower carbon concentration. However, sampling site selection may have affected the result, since sampling sites in spruce 2 may not have been as spatially distributed as in the beech and SP1 forest.

Topography and thickness of soil might explain the greater variety of C within the beech forest. Cremer et al. (2016) found that Norway spruce stands were associated with significantly higher C concentrations in the forest floor compared to European beech plots. Interestingly, common garden experiments have shown that the quantity of litter input from beech and spruce are similar. Therefore, differences in C stocks beneath different tree species must be attributed to other soil forming factors (Vesterdal et al. 2008).

Nitrogen

N concentration was not significantly different among sites. Overall, the SP1 site showed the lowest relative variation of N concentration (Tab.4). The reason can be that plot 3 and 4 were situated in close proximity. Therefore, N content in plot 3 and 4 may be auto correlated, thus lowering the overall variation. The same can be said about the CV value for the SP2 site. In this site as well, plots were located relatively close, and if the plots had been located further away, maybe the CV value of N might have been similar to the value observed for beech.

Troedsson (1969) found that total N content did not correlate, when sampling distance exceeded 1 m in conifer forests in Sweden. Semivariograms were not calculated, and therefore auto-correlated effects must be interpreted from the maps (Appendix.7).

It is likely that the topographic distribution of sampling plots in the terrain have affected the result. N content showed a significant spatial variation only within spruce plots, which also can be related to the low degree of autocorrelation found by Troedsson (1969). However, the

variation within the beech site was close to significant (P = .056). Analysing the topographical lines in the map of N content in the beech site (Appendix.2), shows that all plots, except plot 3, were situated in downslope areas. The N distribution in these areas is more uniform, which could correlate to the plots being located in similar terrains. Sloping terrains could mean all these plots are exposed to leaching of N from the surrounding slopes. In addition, the map of C content distribution in the beech forest is almost identical to the map of N distribution, illustrating the accumulation of organic material in these plots (Appendix.1).

C/N ratio

Mean C/N ratios were higher in the spruce sites compared to the beech site, in accordance with hypothesis 3. Although SP2 was not significantly different from the beach site (Fig.3). C/N ratios tend to be higher beneath conifers compared to broadleaves, because of the high lignin/N ratios in conifer litter. The low nitrogen input slows down decomposition, and allows organic matter to accumulate (Schulp et al. 2008). The results were in accordance with Cremer et al. (2016) who found higher C/N ratios beneath Norway spruce stands compared to European beech stands.

Within the beech forest, C/N ratios were higher in downslope areas. More water is percolating through the soil in sloping terrain than in flat, as the surrounding slopes drain into the downslope area. This allows for more organic matter to accumulate, especially troughs and where the terrain flattens out again.

Mixed stands of Norway spruce and European beech is one of the most researched stand mixtures in Europe. Research has been done on the productivity of the two species is affected by mixing, and variation in soil properties and chemical composition of topsoil and deeper soil horizons (Cremer et al. 2016; Pretzsch et al. 2010). C/N ratios decrease when broadleaves are incorporated into conifer stands (Berger et al. 2002). C/N ratios decrease following the increase in more degradable litter from broadleaves (Augusto et al. 2002).

pH

The data shows no significant difference in pH between sites dominated by beech or by spruce. Therefore there is no support for the hypothesis that pH would be lower in spruce dominated sites. Further, analysis of variance detected significant variation in pH within both spruce sites (Tab.6). pH may be affected by several factors like distance to trees and decaying plant material like logs (Krueger et al. 2016). While some studies in spruce forest found no autocorrelation

of pH at distances down to 20 cm (James & Riha 1986). Spatial variation and autocorrelation in pH are determined by several factors within the soil and aboveground environment, and direct cause-effect relationships are hard to detect. Although pH values did not show the same relative variation within the study sites, the maps (Appendix.4, 9 and 14) visualize how areas of the forest floor consequently are correlated, and where distinct differences in pH are present. Although spruce is thought to acidify soils, this effect could not be specifically shown in this study. The study only analyses pH, and do not cover the development of pH over time, neither the effect of the soil buffer capacity or soil acidity. It is possible that soil acidity increased in the younger spruce forest, without the pH being significantly effected compared to the beech forest.

Condensed Tannins

CT concentration was significantly different between the sites, but the variation was not related to tree species (Tab.6; Fig.3). CT content was similar in SP1 and the beech forest, while mean CT content was significantly lower in SP2. Although, ANOVAs of CT showed no significant within forest sites, CV values for CT was higher than CV values for any of the other soil properties.

The high CV value for CT is visualized in the maps showing CT content within each site (Appendix.5, 10 and 15). The high variability in CT within each plot seemed to be attributed to topography. Sampling plots situated in steeper slopes seemed to contain less CT compared with downslope plots. CT, along with other phenolic compounds is water-soluble, and are released from living foliage and litter by rainwater (Kuiters 1990). The highest CT levels in the beech forest were observed in plot 1 (Appendix.5), were the forest floor received water flow from the surrounding areas. Likely, the high CT content arises from more influx of organic matter from the nearby vegetation. Another factor was the presence of Norway spruce and birch (*Betula pubescens*) trees within the beech forest. Higher CT content in the northern row of samples in plot 4 (Appendix.5) in the beech site may partly be attributed to litter from birch trees, which normally contains high levels of tannins (Suominen et al. 2003).

Condensed tannins may enter the soil through degradation of roots. Roots constitutes a major part of biomass found within a forest ecosystem, and are therefore likely contributing significant amounts of tannins to the soil (Kraus et al. 2003). Because spruce have shallow root systems, root exudation of tannin may explain the higher CT content within SP1 (Jandl et al. 2007a).

Soil type and clay content is suggested to be major factors affecting sorption of CT and other polyphenols in soils (Schmidt 2012). Neither soil type nor clay content was estimated in this study, but both factors might explain some of the variation found within study sites.

Conclusion

As for the first hypothesis, carbon and nitrogen concentration shows greater variation within than between sites. Variations in carbon content were only significant within the spruce sites, but the study further indicates that the topographic terrain influences both C and N content more than the dominating tree species of the site. Any causation can not be established from this study, but likely explanations include the topography's influence on accumulation of litter, and hydrological patterns influencing transports of organic material with soil water. This leads us to reject the hypothesis but does not automatically mean that the dominating species in the forest stand has no influence C and N content of the top soil. Rather that here, other factors where of larger importance. To further determine the effect of dominating tree species on these variables, larger sampling sizes and more sites would be required.

As for the second hypothesis, significant differences in variations in CT content between forests were found between the spruce sites but could not be shown between beech and spruce sites. There were also significant differences within sites. This leads us to reject the second hypothesis and again indicates that here, other factors than domination tree species in the stand where of larger importance.

As for the third hypothesis, soil pH was showed no significant difference in between stands and only significant difference within the spruce forests. On this basis, the third hypothesis is rejected. Here, other factors than dominating tree species in the forest stands are of more importance to the soil pH. These are likely related to the geology in the area as well as the and the quality of the quality of the participation.

As for the forth hypothesis, the C/N ratio was highest for SP1, the spruce forest that had former been a beech forest, and for this site a significant difference from the beech forest was detected. However, a significant difference for the forest stands dominated by different species, was not detected. Meanwhile, the C/N ratios within all the forest stands showed significant differences. On this basis, the forth hypothesis is rejected. If the dominating tree species in the stand influences the C/N ratio, other factors are of larger importance here. Such factors may include

which the plants, patterns for accumulation of litter on the forest floor and hydrological patterns are using inorganic N-compounds.

Its important to note that the rejection of the hypothesises does not necessary mean that the transition from spruce to beech would not influence the soil property parameters that are studied. It is likely that the great number of factors that influence soil properties means the models require more sites and samples to show correlation. In other words; to show correlation for the given parameters in the populations, the models might require a larger number of sites and total samples to estimate the variables. Further, the results for spatial variations in variables are not conclusive enough to indicate any evidence that the parameters for soil properties would not show temporal variation with a shift towards more beech forest.

References

Albers, D., Migge, S., Schaefer, M. & Scheu, S. (2004). Decomposition of beech leaves (Fagus sylvatica) and spruce needles (Picea abies) in pure and mixed stands of beech and spruce. *Soil Biology and Biochemistry*, 36 (1): 155-164.

Asplund, J. (2016). Vegetation history of the spruce forest in Brånakollene and the spruce forest south of Lake Allumtjerna. *Personal communication.* .

Augusto, L., Ranger, J., Binkley, D. & Rothe, A. (2002). Impact of several common tree species of European temperate forests on soil fertility. *Annals of Forest Science*, 59 (3): 233-253.

Benayas, J. M. R., Sánchez-Colomer, M. G. & Escudero, A. (2004). Landscape-and field-scale control of spatial variation of soil properties in Mediterranean montane meadows. *Biogeochemistry*, 69 (2): 207-225.

Berger, T. W., Neubauer, C. & Glatzel, G. (2002). Factors controlling soil carbon and nitrogen stores in pure stands of Norway spruce (Picea abies) and mixed species stands in Austria. *Forest Ecology and Management*, 159 (1): 3-14.

Bolte, A., Hilbrig, L., Grundmann, B., Kampf, F., Brunet, J. & Roloff, A. (2009). Climate change impacts on stand structure and competitive interactions in a southern Swedish spruce–beech forest. *European Journal of Forest Research*, 129 (3): 261-276.

Bringmark, E. (1989). Spatial variation in soil pH of beech forests in relation to buffering properties and soil depths. *Oikos*: 165-177.

Conant, R. T., Smith, G. R. & Paustian, K. (2003). Spatial Variability of Soil Carbon in Forested and Cultivated Sites. *Journal of Environmental Quality*, 32 (1).

Covington, W. W. (1981). Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology*, 62 (1): 41-48.

Cremer, M., Kern, N. V. & Prietzel, J. (2016). Soil organic carbon and nitrogen stocks under pure and mixed stands of European beech, Douglas fir and Norway spruce. *Forest Ecology and Management*, 367: 30-40.

Dutch, S. (2015). Spreadsheet for Converting UTM to Latitude and Longitude (Or Vice Versa). *University of Wisconsin - Green Bay*.

Falk, W. & Hempelmann, N. (2013). Species Favourability Shift in Europe due to Climate Change: A Case Study for Fagus sylvatica L. and Picea abies (L.) Karst. Based on an Ensemble of Climate Models. *Journal of Climatology*, 2013: 18.

Frey, B., Kremer, J., Rüdt, A., Sciacca, S., Matthies, D. & Lüscher, P. (2009). Compaction of forest soils with heavy logging machinery affects soil bacterial community structure. *European Journal of Soil Biology*, 45 (4): 312-320.

Grüneberg, E., Ziche, D. & Wellbrock, N. (2014). Organic carbon stocks and sequestration rates of forest soils in Germany. *Global change biology*, 20 (8): 2644-2662.

Hagerman, A. E. (2002). *The tannin handbook*: Oxford.

Hickler, T., Vohland, K., Feehan, J., Miller, P. A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T. R., Cramer, W., et al. (2012). Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. *Global Ecology and Biogeography*, 21 (1): 50-63.

Hijmans, R. J. & Van Etten, J. (2013). *Raster: geographic data analysis and modeling. R package version 2.1-49*: See http://CRAN. R-project. org/package= raster.
Hlavac, M. (2013). stargazer: Well-Formatted Regression and Summary Statistics Tables. *R package version 5.2. http://CRAN. R-project. org/package= stargazer*.
Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, 50 (3): 346--363.
Häkkinen, M., Heikkinen, J. & Mäkipää, R. (2010). Tree influence on carbon stock and C:N ratio of soil organic layer in boreal Scots pine forests. *Canadian Journal of Soil Science*, 90 (4): 559-566.
Jalas, J., Suominen, J., Kurtto, A., Lampinen, R., Junikka, L. & Fröhner, S. E. (1972). *Atlas Florae Europaeae: Distribution of Vascular Plants in Europe: Pteridophyta (Psilotaceae to Azollaceae)*.
James, B. R. & Riha, S. J. (1986). pH buffering in forest soil organic horizons: relevance to acid precipitation. *Journal of Environmental Quality*, 15 (3): 229-234.
Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D. W., Minkkinen, K. & Byrne, K. A. (2007a). How strongly can forest management influence soil carbon sequestration? *Geoderma*, 137 (3): 253-268.
Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D. W., Minkkinen, K. & Byrne, K. A. (2007b). How strongly can forest management influence soil carbon sequestration? *Geoderma*, 137 (3–4): 253-268.
Joanisse, G., Bradley, R., Preston, C. & Munson, A. (2007). Soil enzyme inhibition by condensed litter tannins may drive ecosystem structure and processes: the case of Kalmia angustifolia. *New Phytologist*, 175 (3): 535-546.
Kanerva, S., Kitunen, V., Loponen, J. & Smolander, A. (2008). Phenolic compounds and terpenes in soil organic horizon layers under silver birch, Norway spruce and Scots pine. *Biology and Fertility of Soils*, 44 (4): 547-556.
Karney, C. F. (2011). Transverse Mercator with an accuracy of a few nanometers. *Journal of Geodesy*, 85 (8): 475-485.
Kartverket. Topografisk Norgeskart 2: . *Statens Kartverk*.
Korsmo, H. (1975). Naturvernrådets landsplan for edellauvskogsreservater i Norge. IV. Hordaland, Sogn og Fjordane og Møre og Romsdal. *Botanisk institutt, Ås-NLH*.
Kraus, T. E., Dahlgren, R. A. & Zasoski, R. J. (2003). Tannins in nutrient dynamics of forest ecosystems-a review. *Plant and Soil*, 256 (1): 41-66.
Kreutzweiser, D. P., Hazlett, P. W. & Gunn, J. M. (2008). Logging impacts on the biogeochemistry of boreal forest soils and nutrient export to aquatic systems: a review. *Environmental Reviews*, 16 (NA): 157-179.
Krueger, J., Böttcher, J., Schmunk, C. & Bachmann, J. (2016). Soil water repellency and chemical soil properties in a beech forest soil—Spatial variability and interrelations. *Geoderma*, 271: 50-62.
Kuiters, A. (1990). Role of phenolic substances from decomposing forest litter in plant–soil interactions. *Acta botanica neerlandica*, 39 (4): 329-348.
Lie, M. H. (2016). Approximate age of the spruce forest in Brånakollene and of the spruce forest south of Lake Allumtjerna. . *Personal communication.*

Liski, J. & Westman, C. J. (1995). Density of organic carbon in soil at coniferous forest sites in southern Finland. *Biogeochemistry*, 29 (3): 183-197.
Matějka, K. & Starý, J. (2009). Differences in top-soil features between beech-mixture and Norway spruce forests of the Šumava Mts. *Journal of Forest Science*, 55 (12): 540-555.
Meier, E. S., Lischke, H., Schmatz, D. R. & Zimmermann, N. E. (2012). Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography*, 21 (2): 164-178.
Miles, J. (1981). Effects of trees on soils. *Forest and woodland ecology: an account of research being done in ITE. Cambridge, NERC/Institute of Terrestrial Ecology*: 85-88.
Miljøverndepartementet. (1980). Forskrift om fredning for Brånakollene naturreservat, Hedrum kommune, Vestfold. *Norwegian Ministry of Environment.* .
Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2014). R Core Team (2014) nlme: linear and nonlinear mixed effects models. R package version 3.1-117. *Available at h ttp://CRAN. R-project. org/package= nlme*.
Pretzsch, H., Block, J., Dieler, J., Dong, P. H., Kohnle, U., Nagel, J., Spellmann, H. & Zingg, A. (2010). Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Annals of Forest Science*, 67 (7): 712.
Prism, G. (2014). Version 6.0 Demo. *GraphPad Software*.
Quideau, S., Deffieux, D., Douat-Casassus, C. & Pouységu, L. (2011). Plant polyphenols: chemical properties, biological activities, and synthesis. *Angewandte Chemie International Edition*, 50 (3): 586-621.
Rozenbergar, D., Kolar, U., Cater, M. & Diaci, J. (2011). Comparison of four methods for estimating relative solar radiation in managed and old-growth silver fir-beech forest. *Dendrobiology*, 65.
RStudio, T. (2015). RStudio. *RStudio: Integrated Development for R. RStudio, Inc., Boston, MA*
Sabatini, F. M., Zanini, M., Dowgiallo, G. & Burrascano, S. (2015). Multiscale heterogeneity of topsoil properties in southern European old-growth forests. *European Journal of Forest Research*, 134 (5): 911-925.
Schmidt, M. A. (2012). *Tannins in Natural Soil Systems*: Miami University.
Schulp, C. J., Nabuurs, G.-J., Verburg, P. H. & de Waal, R. W. (2008). Effect of tree species on carbon stocks in forest floor and mineral soil and implications for soil carbon inventories. *Forest Ecology and Management*, 256 (3): 482-490.
Suominen, K., Kitunen, V. & Smolander, A. (2003). Characteristics of dissolved organic matter and phenolic compounds in forest soils under silver birch (Betula pendula), Norway spruce (Picea abies) and Scots pine (Pinus sylvestris). *European journal of soil science*, 54 (2): 287-293.
Tamm, C. O. (1991). *Introduction: Geochemical Occurrence of Nitrogen. Natural Nitrogen Cycling and Anthropogenic Nitrogen Emissions*: Springer.
Tanaka, K. & Hashimoto, S. (2006). Plant canopy effects on soil thermal and hydrological properties and soil respiration. *Ecological Modelling*, 196 (1): 32-44.
Tateno, R. & Takeda, H. (2003). Forest structure and tree species distribution in relation to topography-mediated heterogeneity of soil nitrogen and light at the forest floor. *Ecological Research*, 18 (5): 559-571.

Team, Q. D. (2013). QGIS geographic information system. *Open Source Geospatial Foundation Project*.
Thompson, K. & Grime, J. P. (1979). Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *The Journal of Ecology*: 893-921.
Troedsson, T. (1969). Small-scale spatial variation in forest soil properties and its implications for sampling procedures.
van der Zander, B., Sundermeyer, J., Braun, D. & Hoffmann, T. (2009). TeXstudio 2.10.8 - A LaTeX Editor; An integrated writing environment for creating LaTeX documents.
Vesterdal, L., Schmidt, I. K., Callesen, I., Nilsson, L. O. & Gundersen, P. (2008). Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *Forest Ecology and Management*, 255 (1): 35-48.
Vesterdal, L., Clarke, N., Sigurdsson, B. D. & Gundersen, P. (2013). Do tree species influence soil carbon stocks in temperate and boreal forests? *Forest Ecology and Management*, 309: 4-18.

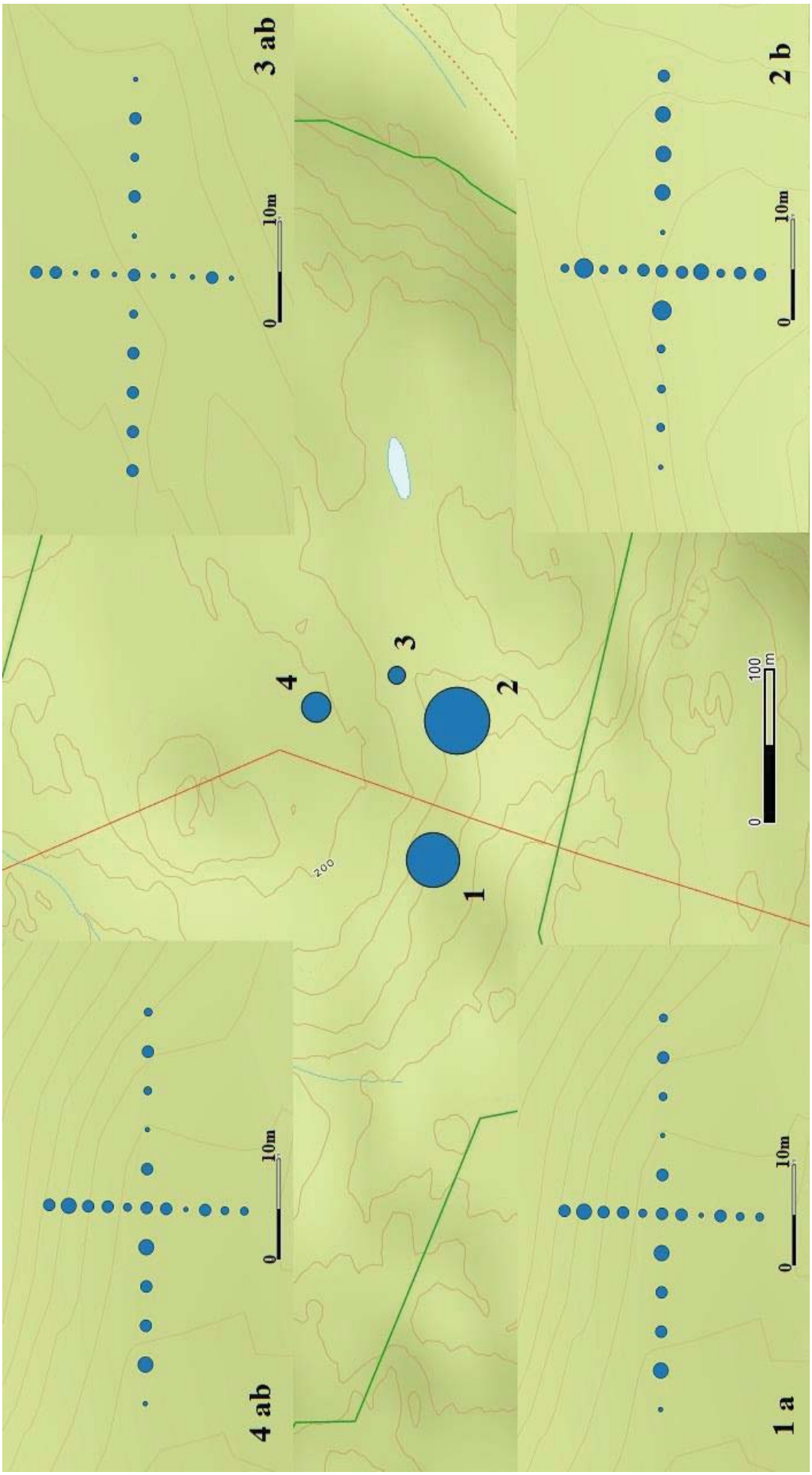


Figure 1. Mean C content in the beech site, and actual C concentrations (%) of all top soil samples from each plot in the beech site. Letters indicate results from the Tukey HSD test, with a significant value of, P <.05. Plots that share a letter are not significantly different in mean C concentration (%).

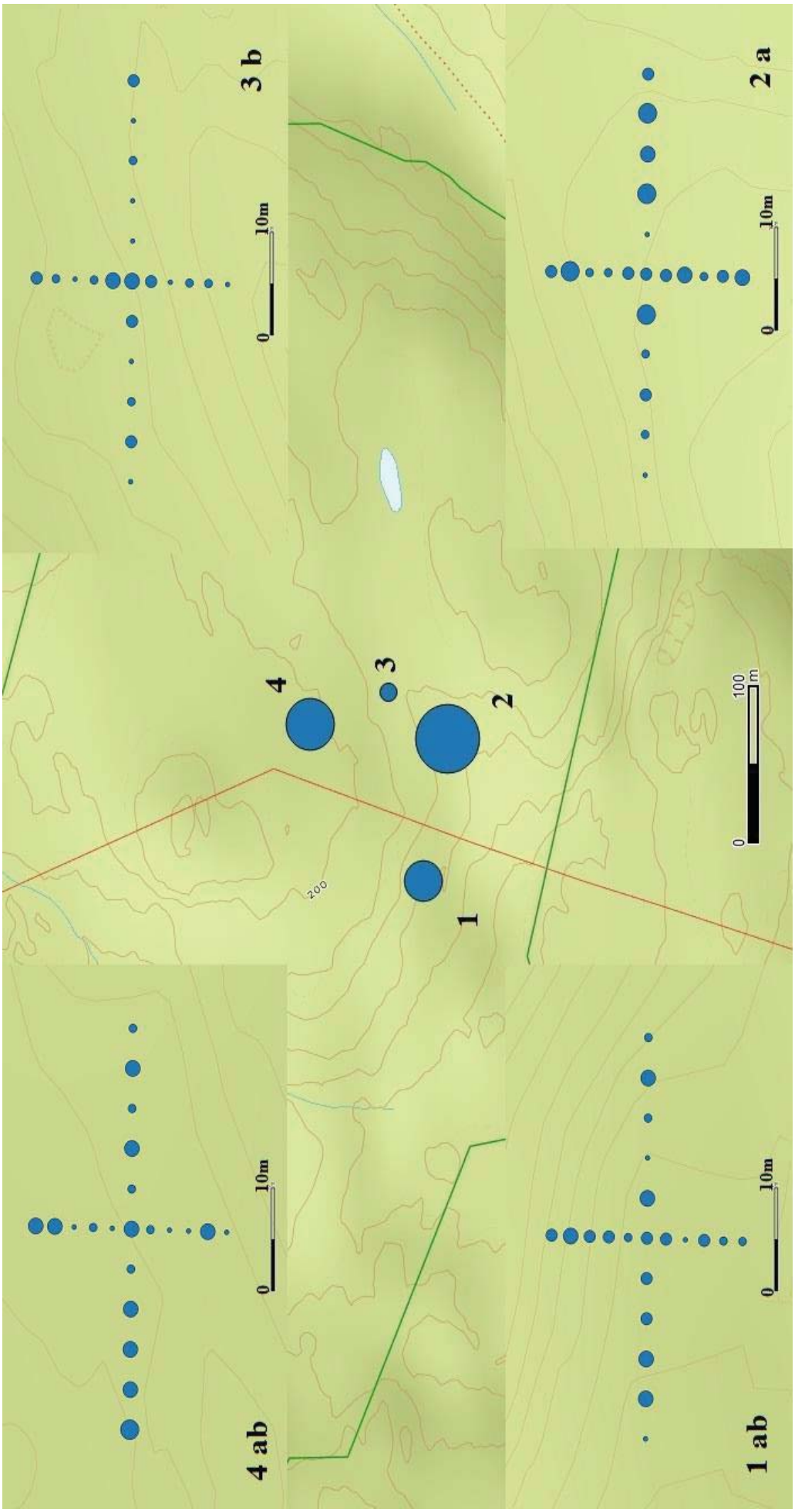


Figure 2. Mean N content in the Brånakollene site, and actual N concentrations (%) of all top soil samples from each plot in the beech site. Letters indicate results from the Tukey HSD test, with a significant value of; P <.05. Plots that share a letter are not significantly different in mean N concentration (%).

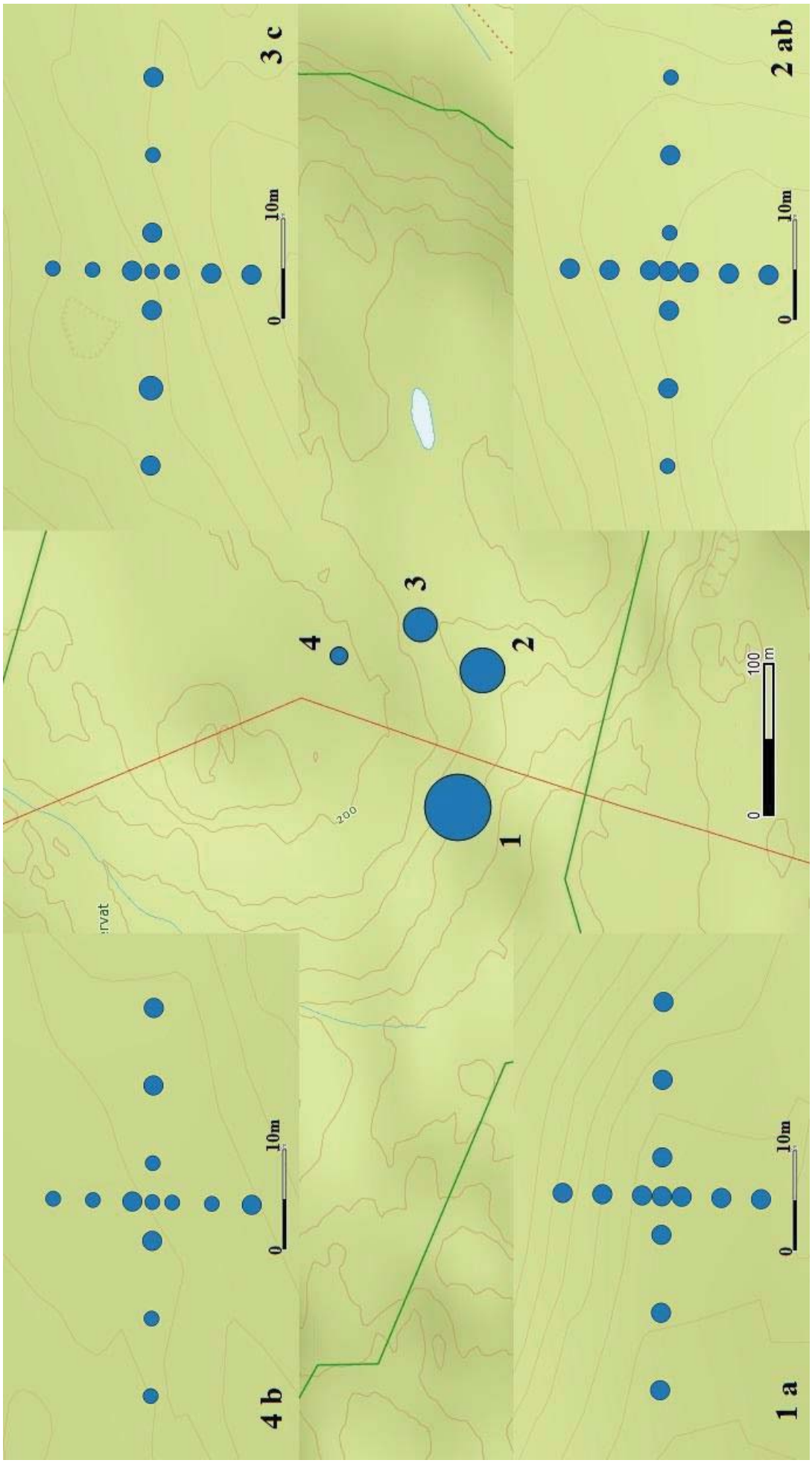


Figure 3. Mean CN ratio for each plot in the Beech site, and actual CN ratios of all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of; P <.05. Plots that share a letter are not significantly different in mean C/N ratio.

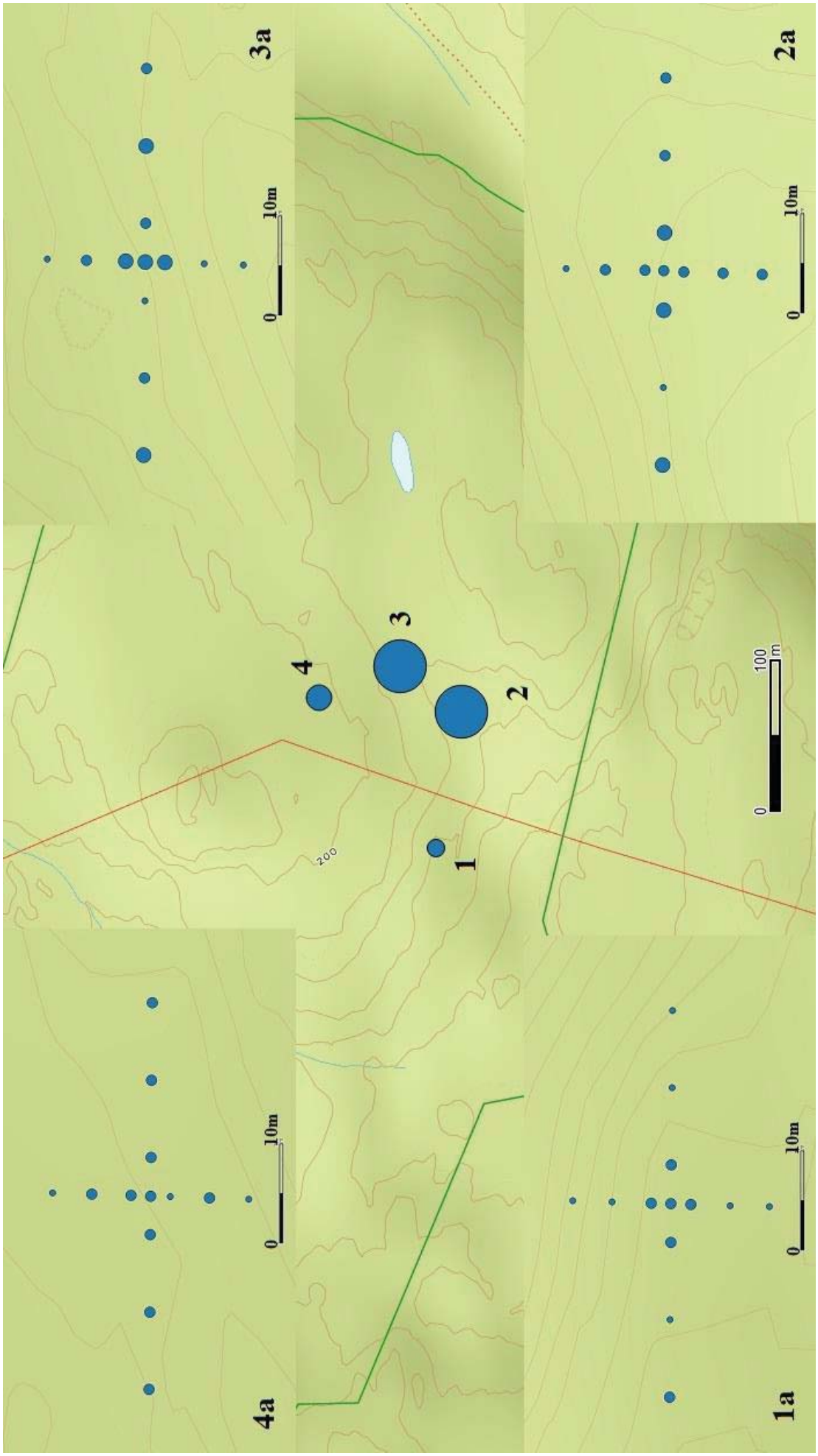


Figure 4. Mean pH for each plot in the Beech site, and actual pH of all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of; P <.05. Plots that share a letter are not significantly different.

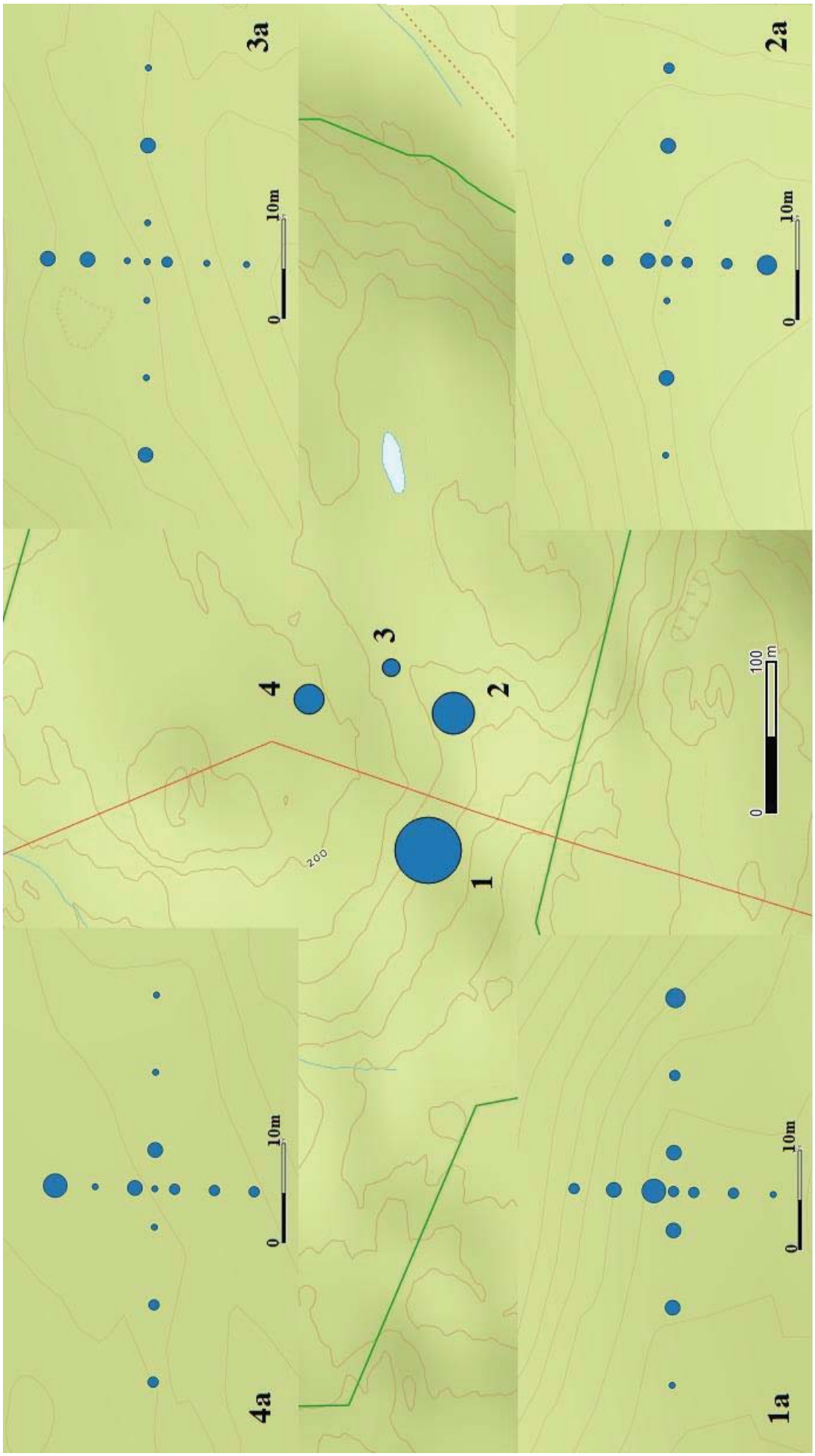


Figure 5. Mean content of condensed tannins (CT mg/g-1) for each plot in the Beech site, and actual CT content of all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of; P <.05. Plots that share a letter are not significantly different in mean CT content (mg/g-1).

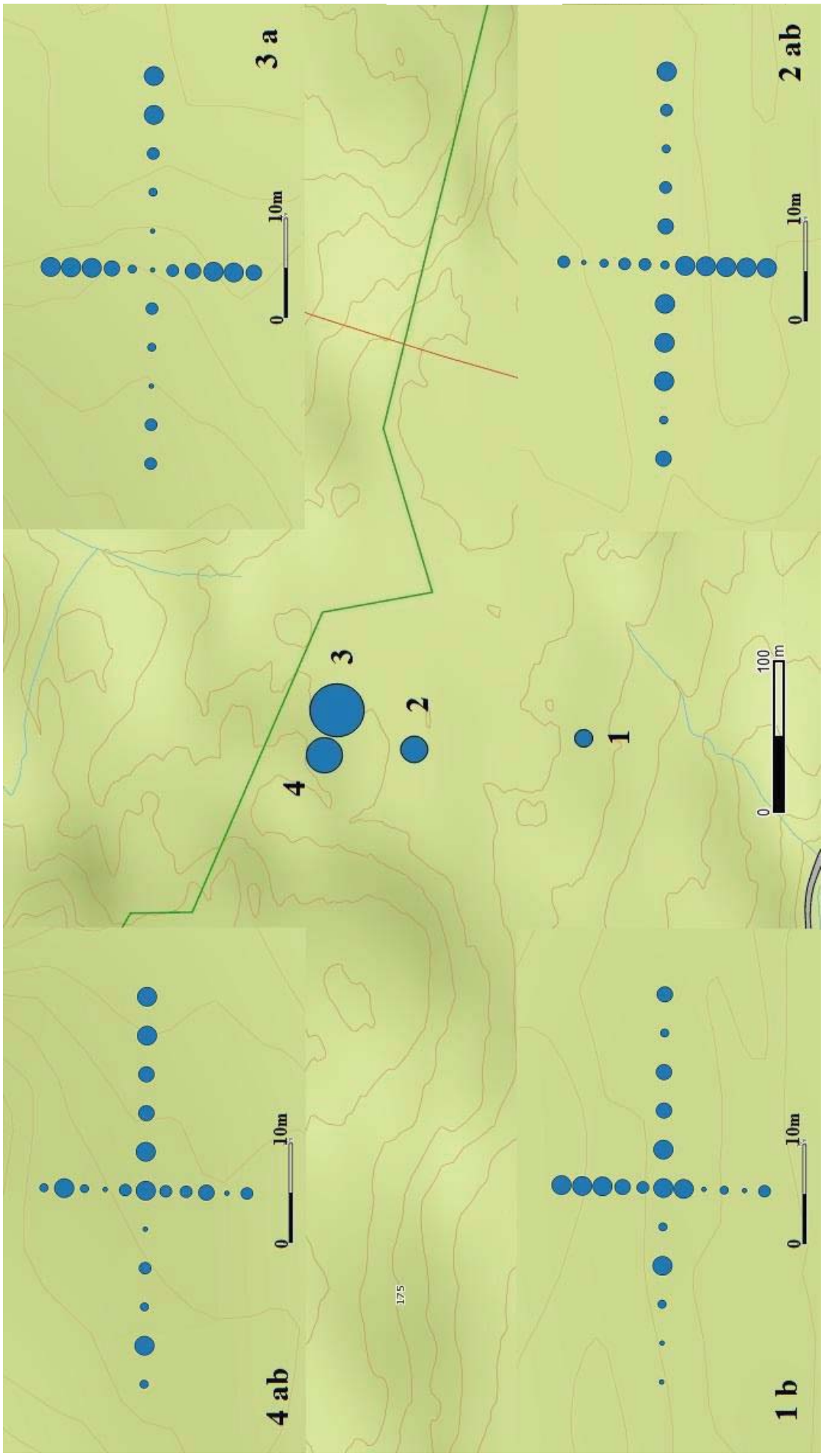


Figure 6. Mean C content for each plot in the SP1 site, and actual C concentration (%) of all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of, P <.05. Plots that share a letter are not significantly different in mean c concentration (%).

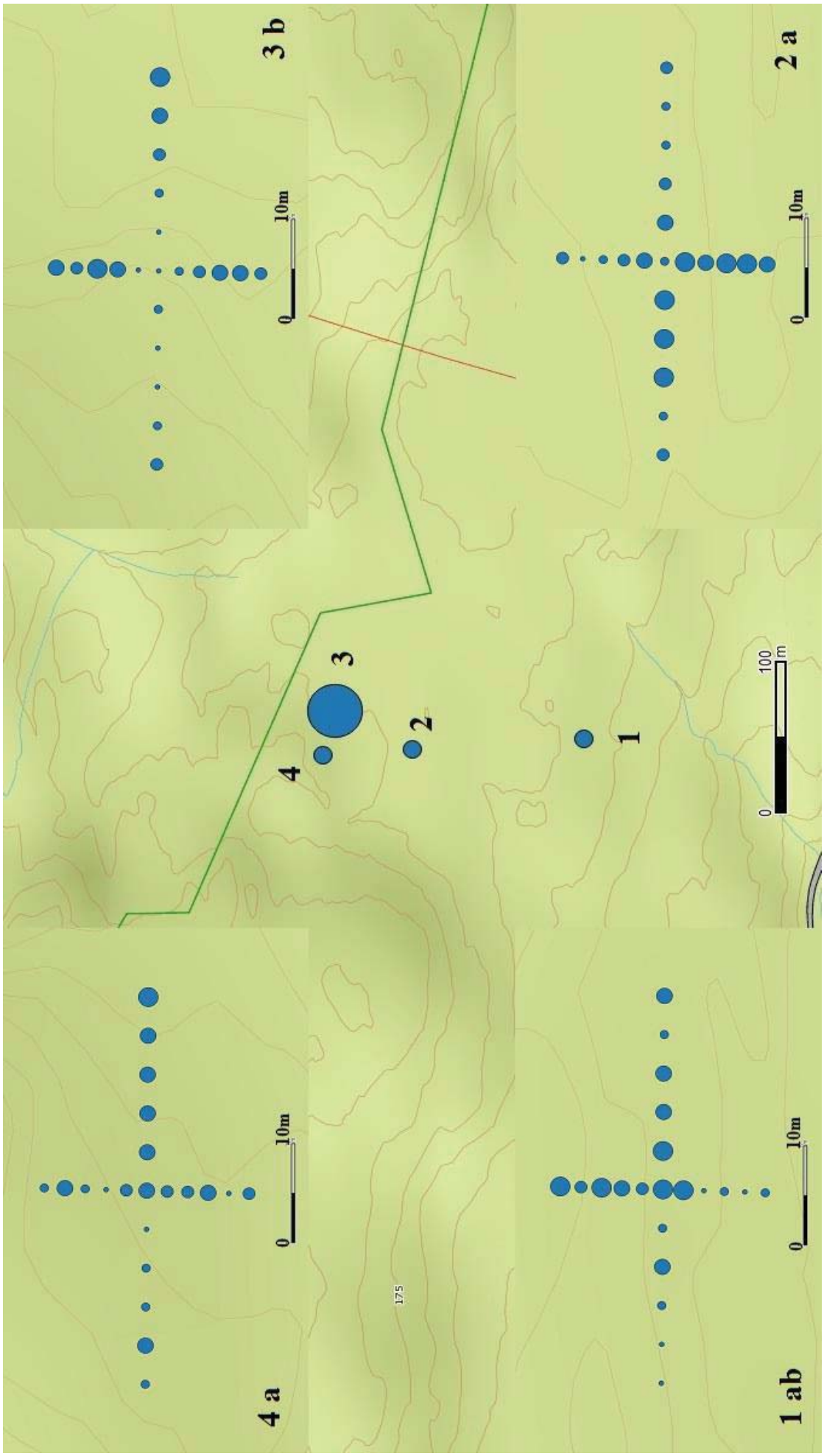


Figure 7. Mean N content for each plot in the SP1 site, and actual N concentration (%) of all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of, P <.05. Plots that share a letter are not significantly different in mean N concentration (%).

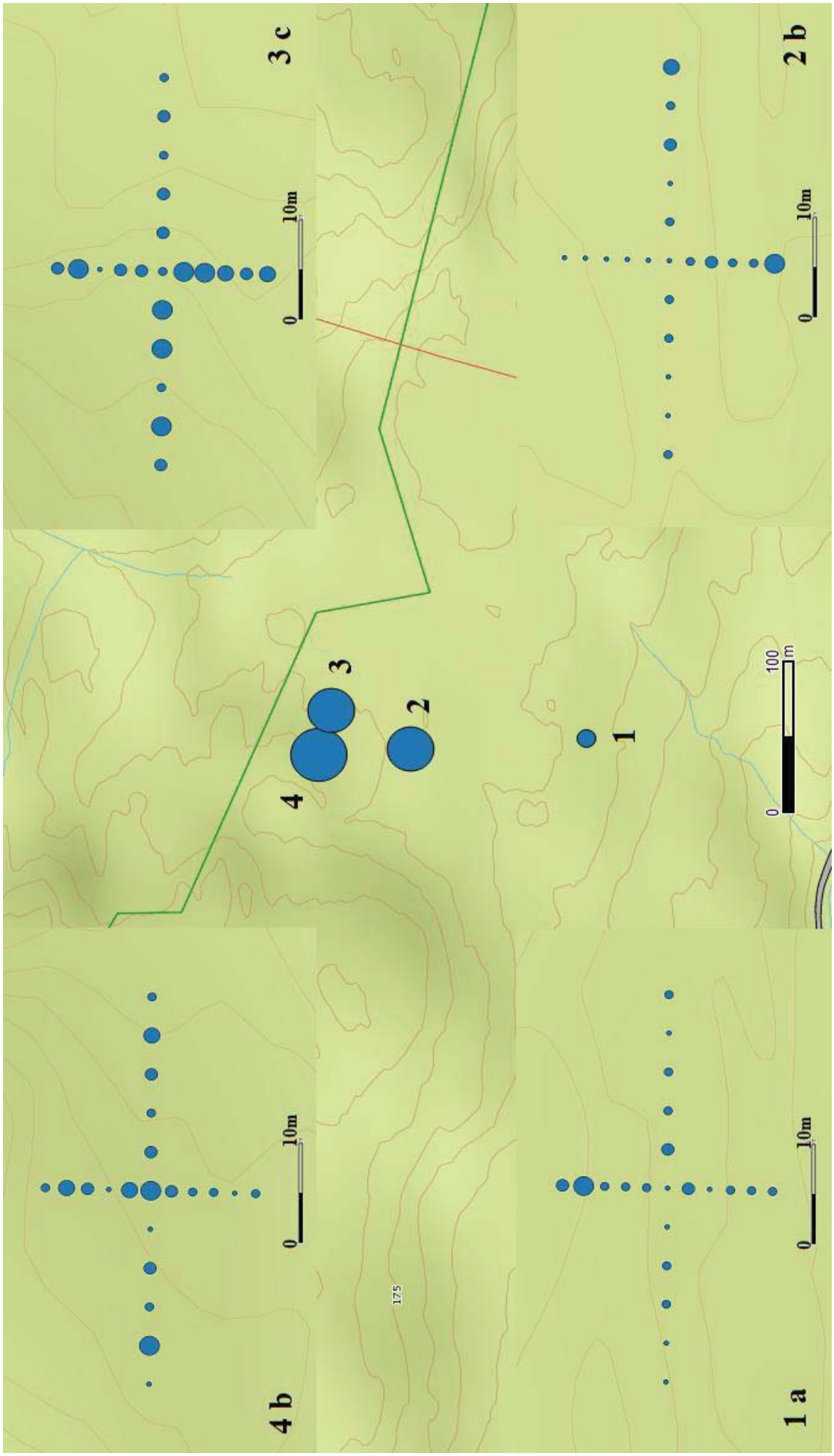


Figure 8. Mean C/N ratios in the SP1 site, and actual C/N ratios of all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of, P <.05. Plots that share a letter are not significantly different in mean C/N ratio.

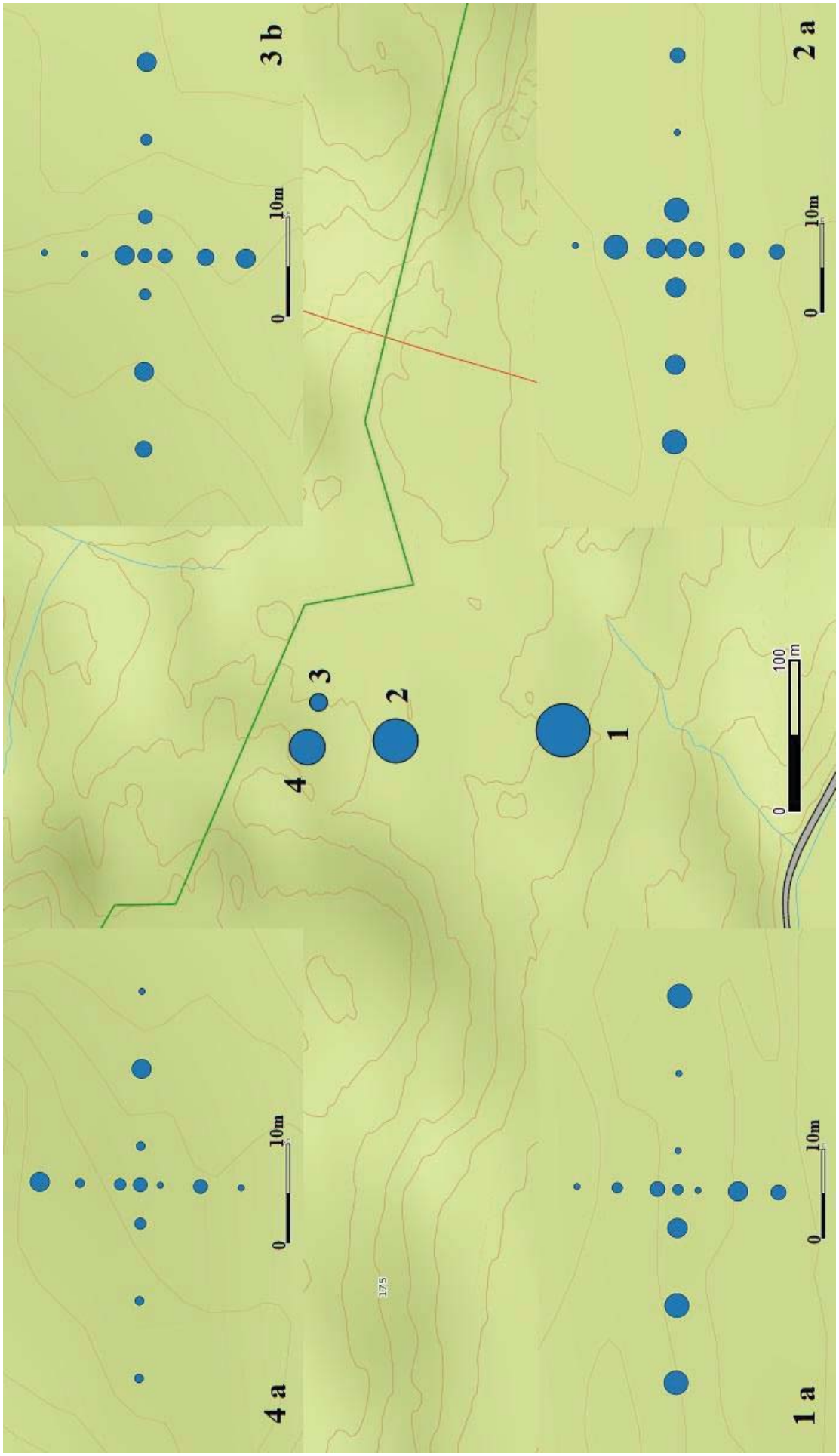


Figure 9. Mean pH in the SP1 site plots, and actual pH for all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of, P <.05. Plots that share a letter are not significantly different in mean pH.

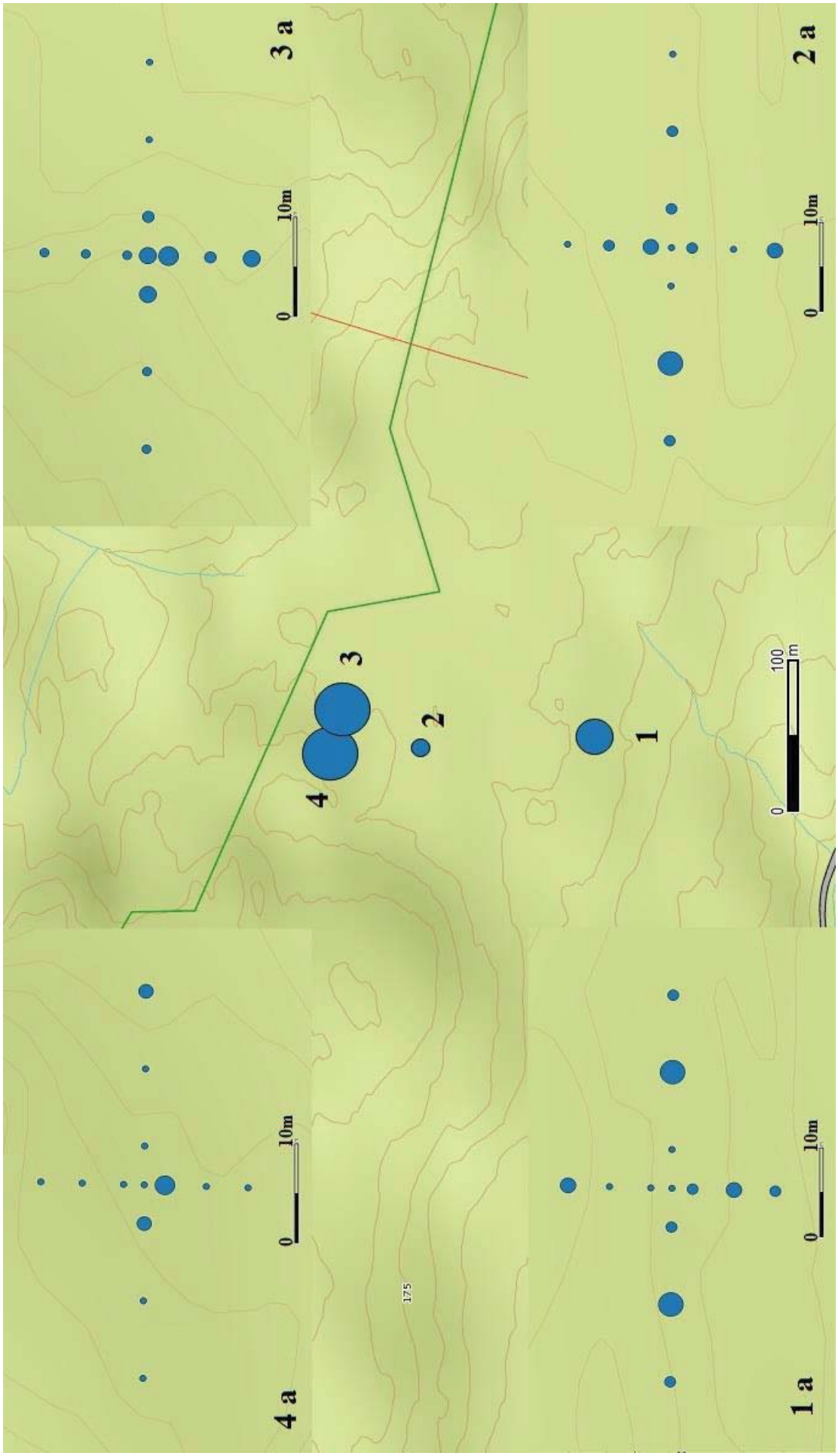


Figure 10. Mean condensed tannin (CT mg/g-1) content in the SP1 site plots, and actual CT content for all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of, P <.05. Plots that share a letter are not significantly different in mean CT content (mg/g-1).

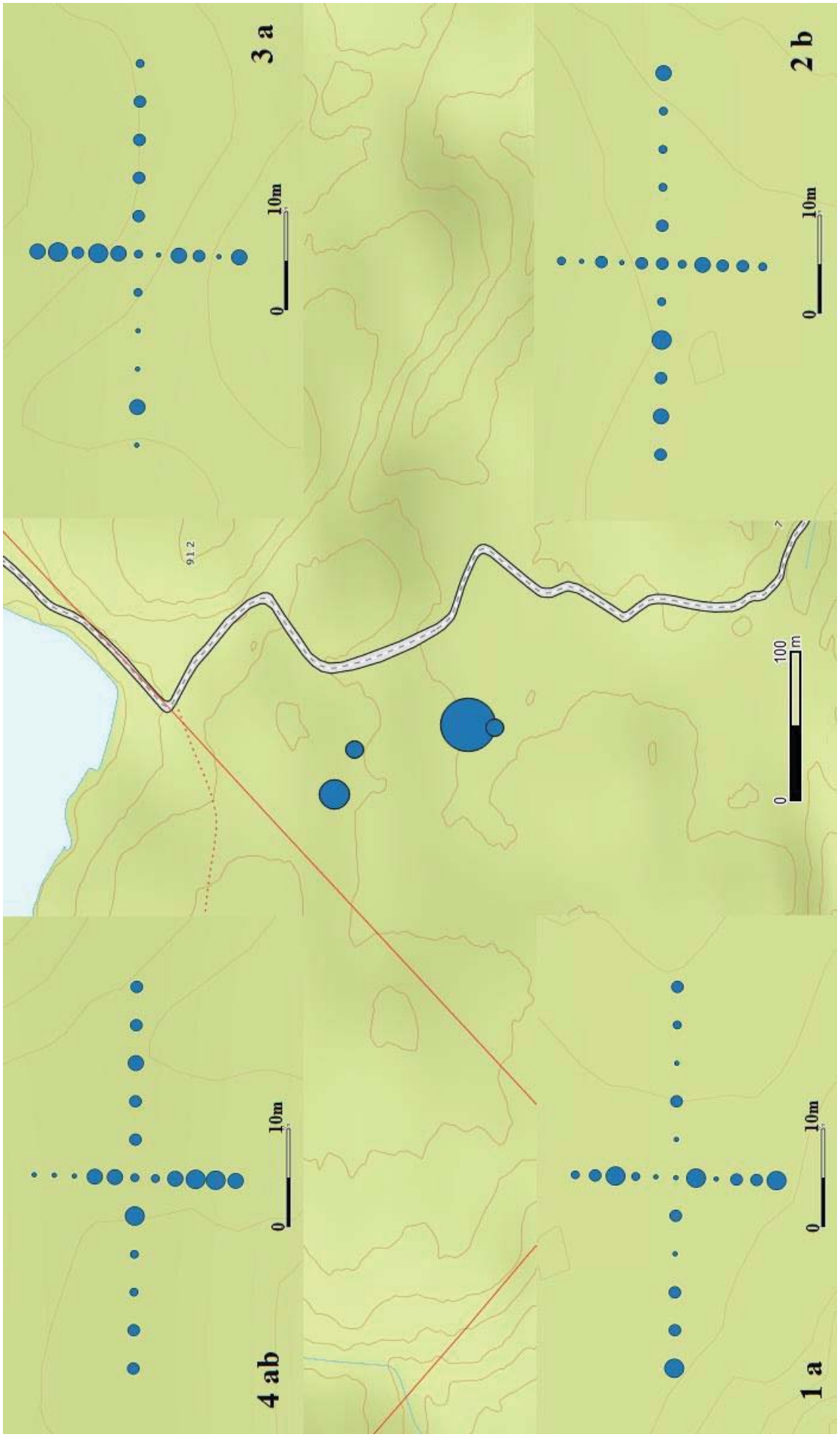


Figure 11. Mean C content for each plot in the SP2 site, and actual C content (%) of all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of, P <.05. Plots that share a letter are not significantly different in mean C concentration (%).

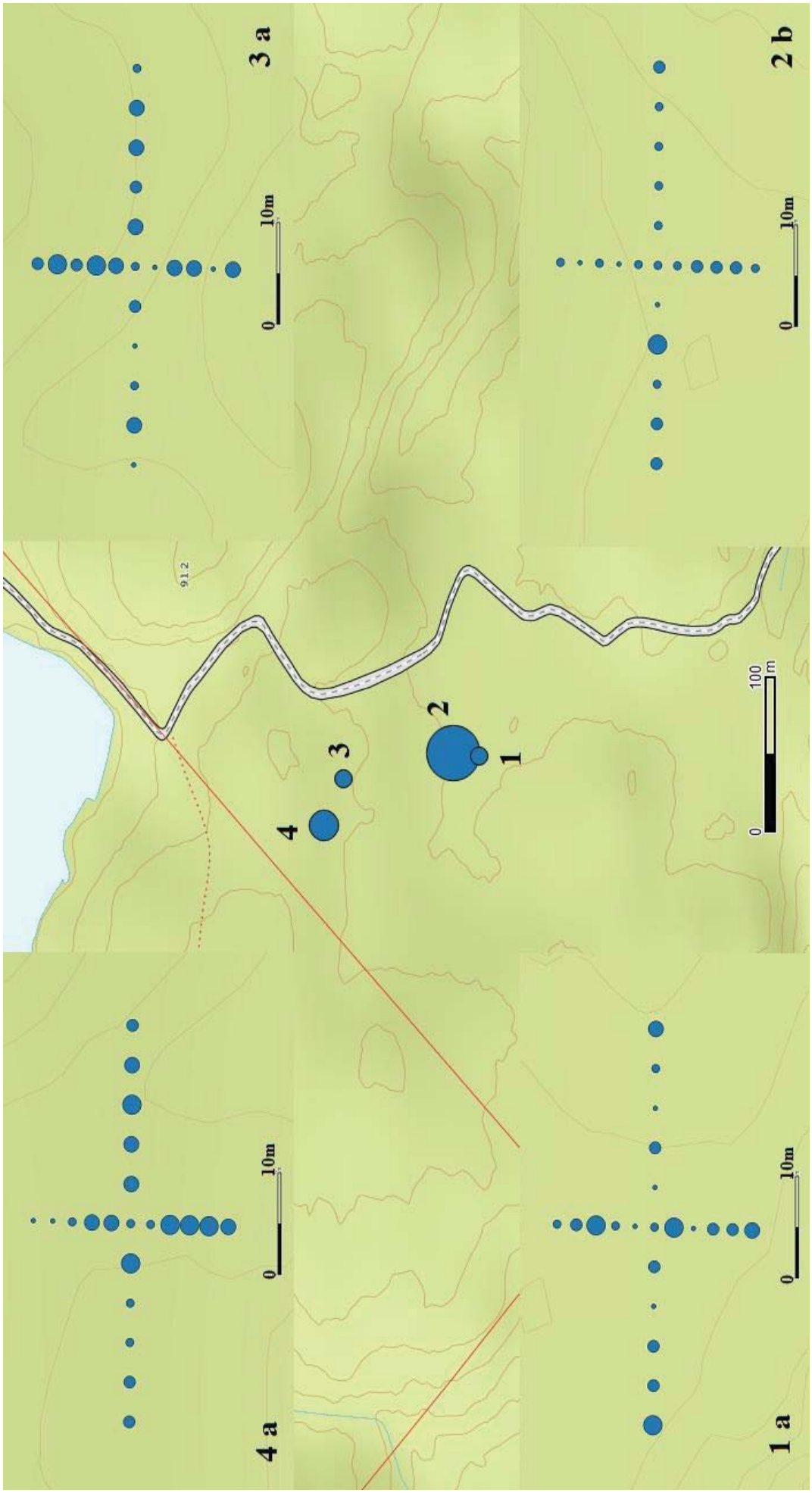


Figure 12. Mean N content for each plot in the SP2 site, and actual N content (%) of all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of, P <.05. Plots that share a letter are not significantly different in mean N concentration (%).

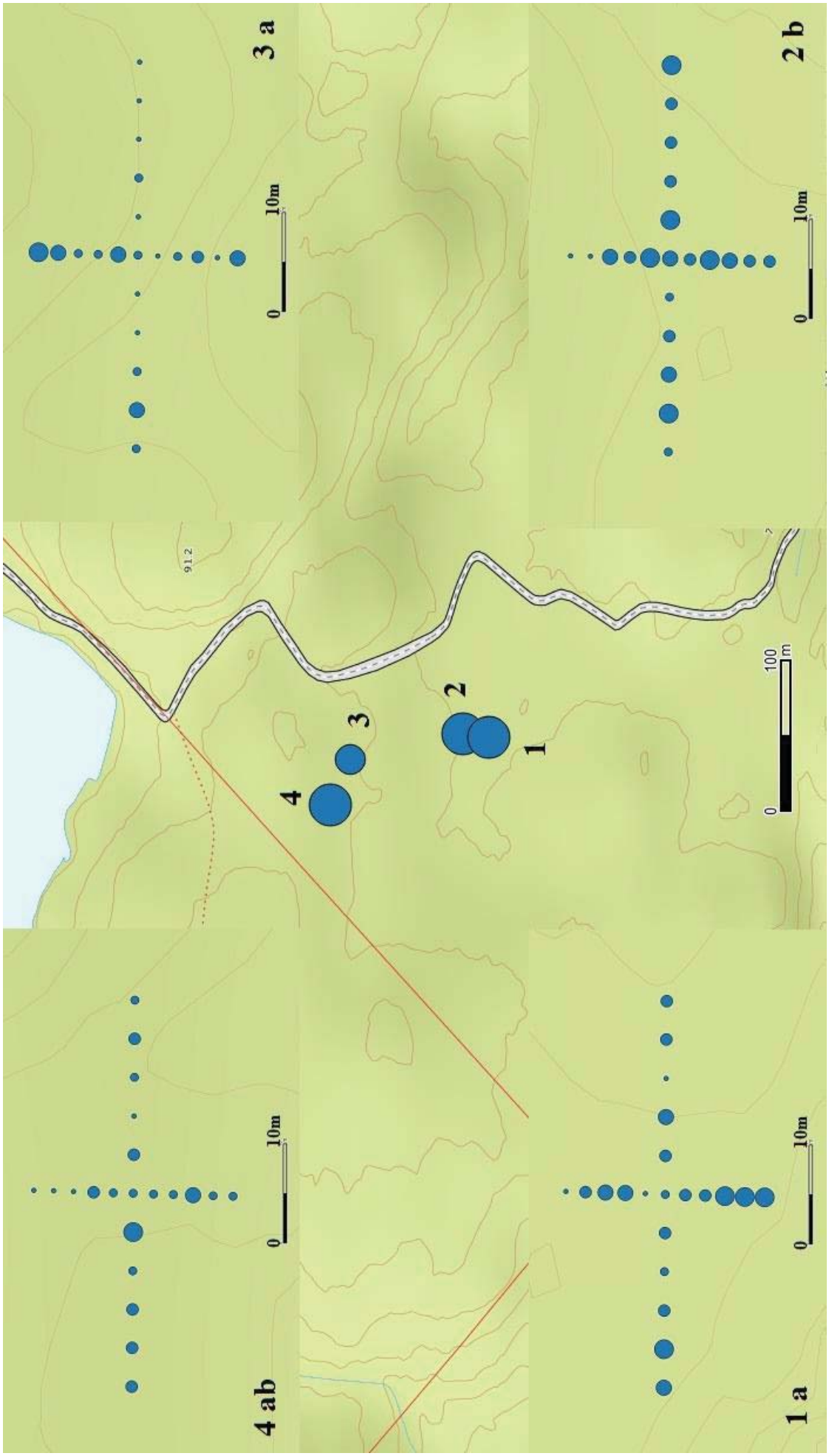


Figure 13. Mean C/N ratios in the SP2 site, and actual C/N ratios of all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of, P <.05. Plots that share a letter are not significantly different in mean C/N ratio.

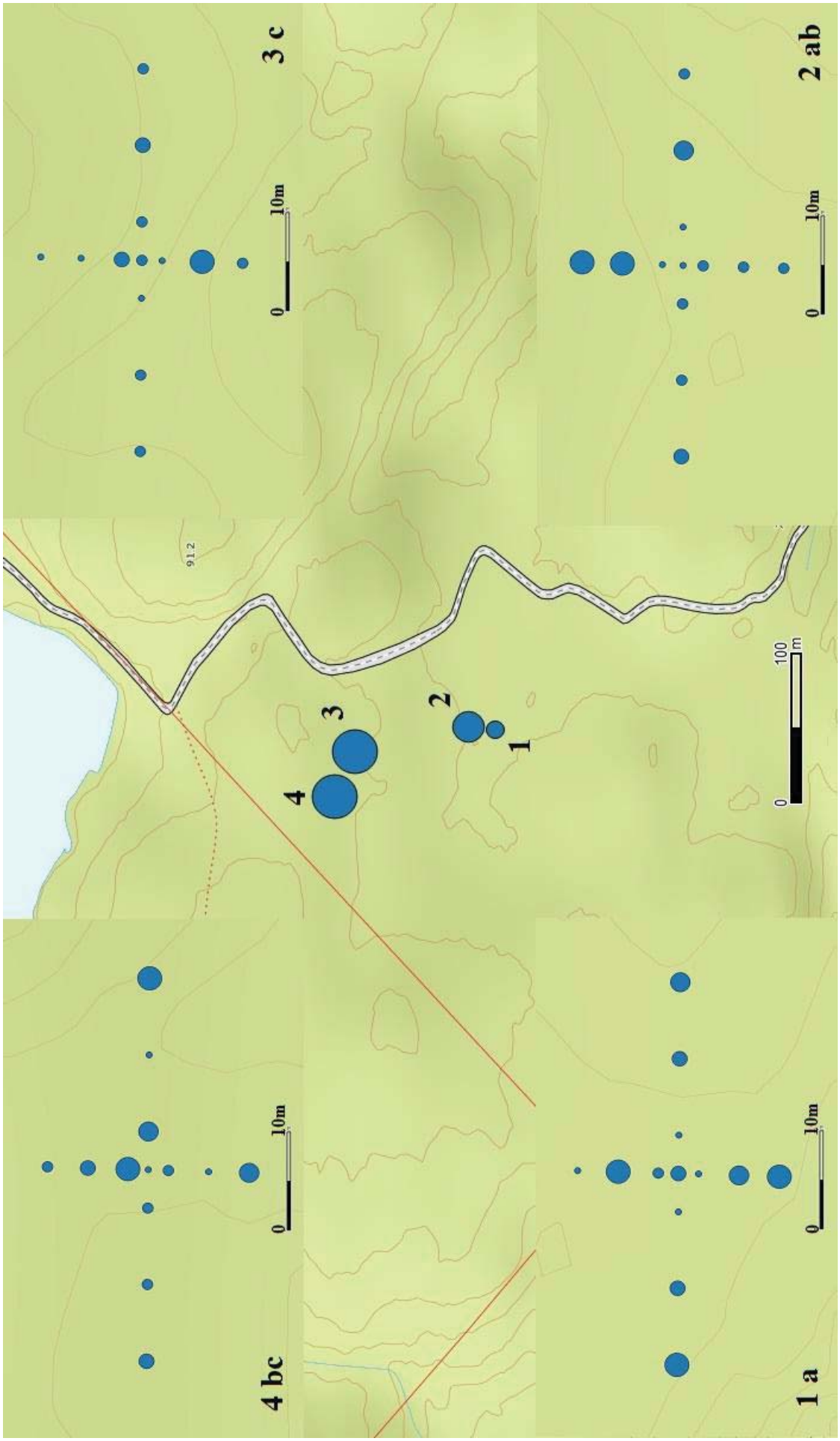


Figure 14. Mean pH in the SP2 site plots, and actual pH for all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of, P <.05. Plots that share a letter are not significantly different in mean pH.

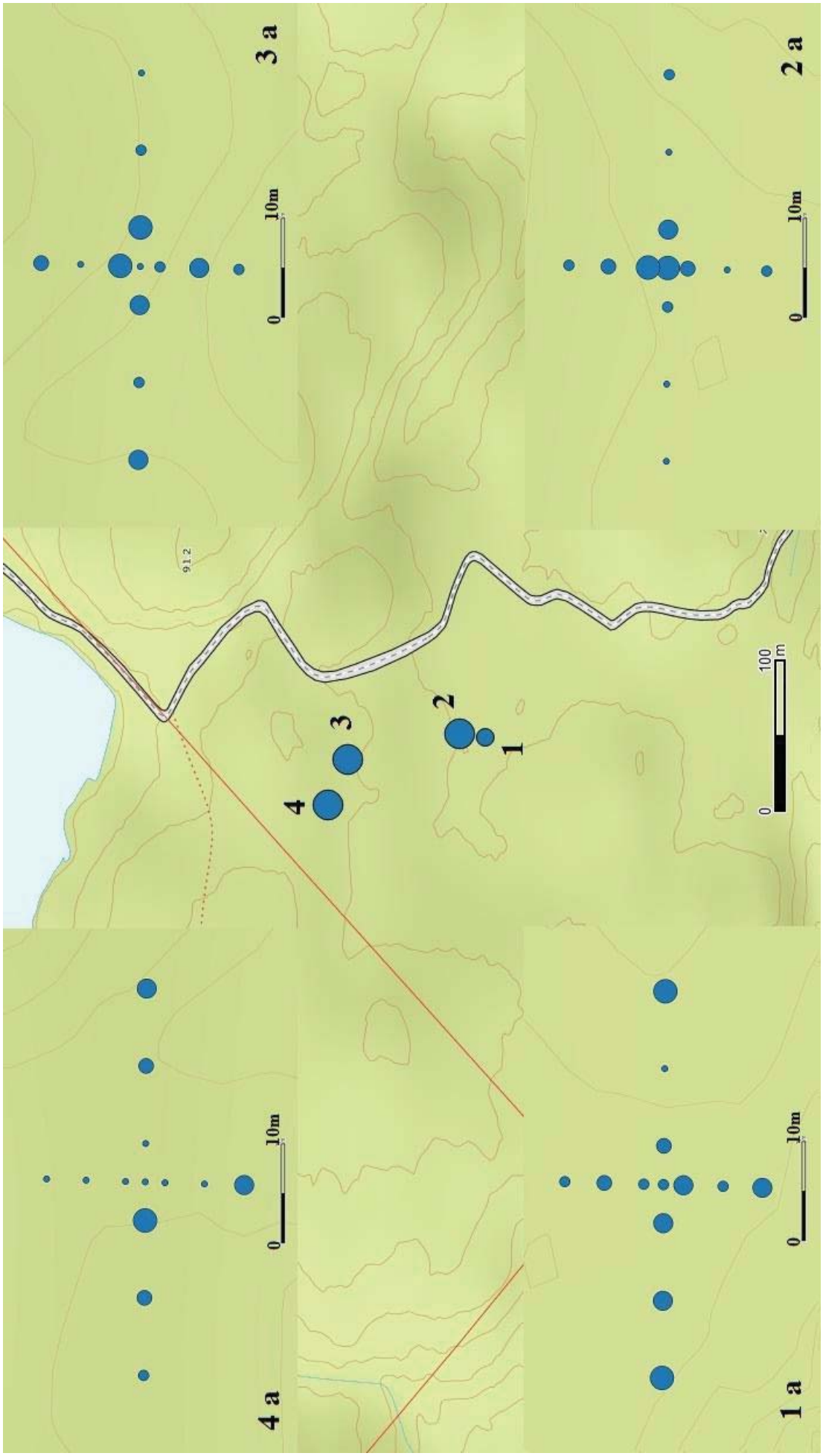
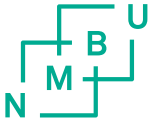


Figure 15. Mean condensed tannin (CT) content in the SP2 site plots, and actual CT content for all top soil samples from each plot. Letters indicate results from the Tukey HSD test, with a significant value of, P <.05. Plots that share a letter are not significantly different in mean CT content (mg/g-1).



Norges miljø- og biovitenskapelig universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway