Short communication

Contrasting impact of whole-tree-harvesting on chemical quality of plant foliage in coastal vs inland forest

Sigmund Fjære[a], Nicholas Clarke[b], Line Nybakken[a], Hilde Karine Wam[b*]

[a] Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, 1432 Ås, Norway (sigmund.fjare@nmbu.no; line.nybakken@nmbu.no)
[b] Norwegian Institute of Bioeconomy Research, 1431 Ås, Norway (nicholas.clarke@nibio.no)
* Correspondence: e-mail: hilde.wam@nibio.no)

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Abstract

Whole-tree-harvesting (WTH) is gaining support as a means to obtain more bioenergy from forests. One aspect that is scarcely addressed is its impact on the chemical quality of post-harvest plant growth, which may initiate ecological cascade effects through, e.g., altered patterns of herbivory and decomposition. We measured C: N ratios and phenolic compounds in foliage from birch *Betula* spp. that had grown naturally after WTH and conventional harvest (CH) on two boreal sites in inland and more coastal Norway, three or five years after harvest. We found that carbon concentrations were higher after WTH compared to CH on the near-coastal site in spring and summer, but not on the inland site. The only observed change in nitrogen concentration after WTH was that it was lower compared to CH on the near-coastal site in autumn. In line with these changes, the C: N ratio was higher with WTH throughout the season on the near-coastal site, ostensibly favouring production or accumulation of plant defence metabolites. Expectedly, we observed altered concentrations of several phenolic compounds with WTH, particularly at the near-coastal site. Further studies are needed to clarify patterns, but our data strongly suggest that sustainability assessments of WTH should not ignore impact on plant chemical quality, and its potential consequences for trophic interactions.

Keywords: bioeconomy; biofuel; browsing; logging; plant defence; trophic cascade

Introduction

Boreal forests have a substantial bioenergy potential (Ericsson & Nilsson 2006; Bostedt et al. 2015) and consequently, whole-tree-harvesting (WTH) is gaining support. Studies on the ecological effects of such intensified biomass removal are accumulating (Berger et al. 2013). Yet, one aspect that is scarcely addressed is its impact on the chemical quality of plants left or regenerated after harvesting. One major group of interest is phenolic compounds, which are carbon-based secondary metabolites ubiquitous in terrestrial plants and serving functional roles as diverse as herbivory deterrents (e.g., Bryant et al. 1983; Coley et al. 1985), antioxidants (Iason & Hester 1993; Close & McArthur 2002), pathogen protection (Witzell & Martín 2008; Tomova et al. 2005), UV-filtration (Lois 1994), frost hardiness and drought resistance (Samanta et al. 2011), chemical- (Mandal et al. 2010), visual- or aromatic signalling (Samanta et al. 2011) and allelopathy (Inderjit 1996). Phenolic compounds may also affect decomposition rates (Kraus et al. 2003; Asplund et al. 2013; Smolander et al. 2012).

In this study, we measured C: N ratios and phenolic compounds in foliage from birch *Betula* spp. plants grown naturally after WTH and conventional stem-only harvest (CH) on two boreal sites; one inland and one more coastal. Based on principal theories of element turnover, we postulated that:

1) Plant foliage in forest plots recently subjected to WTH would have lower nitrogen compared to foliage in CH plots, due to lack of a soil nitrate flush from decomposed harvest residue (Mattson 1980), and possibly, reduced wet deposition of atmospheric N caused by lower infiltration on more bare land (Prescott 2002). Plant carbon would not be noticeably affected by WTH, as terrestrial plants assimilate more than 95% of their carbon from aerial CO_2 (Livingstone & Beall 1934).
2) Thus, plant foliage in WTH plots would have a higher C: N ratio. As boreal plants are normally N-limited (Vitousek & Howarth 1991), this should favour the allocation of surplus carbon to phenolic compounds, in accordance with the *growth-differentiation* (Loomis 1932), the *carbon: nutrient* (Bryant et al. 1983) and the *protein competition* (Jones & Hartley 1999) hypotheses.
3) Due to higher impact of rainfall near the coast, differences between WTH and CH would be more pronounced coastally than inland, as water access strongly influences plant allocation of resources (Lambers et al. 1998).

Materials and methods

Study area and plant sampling

The study was conducted in two semi-natural boreal forests dominated by Norway spruce (*Picea abies* (L.) Karst.) on intermediate to high Site Index (H40 scale: G14, G17 and G20, Tveite 1977). The inland site (Gaupen) and the near-coastal site (Vindberg) had similar latitude (60°51′45″N vs 60°35’18″ N), mean annual temperature (3.2 vs 4.3˚C) and quaternary geology (moraine), but different annual precipitation (585 vs 1550 mm) and sun exposure (slope 9° W-SW vs 23° N-NW).

Controlled WTH was conducted at Gaupen on frozen, snow-covered ground in Mar 2009 (6 plots with adjacent CH controls, each 30x30 m with 5 m buffer zone between plots) and at Vindberg in Jan 2011 (5 plots 20x20 m, 4 m buffer). Norway spruce trunks were removed after clear-cutting from both WTH and CH plots, using harvesters and forwarders. Other tree species were not intentionally removed, and harvesting was carried out in accordance with the PEFC standards for Norway. In WTH plots, harvest residue was piled for 6-8 months to allow needles to fall off before being removed (in September 2009 at Gaupen and October 2011 at Vindberg). Thus, during these months there were areas on the WTH plots where the residues were piled and other areas from which the residues had been removed. We estimate that we managed to pile 62-63% of the residue on the WTH plots. After harvesting, new vegetation, including our sampling birch plants, regenerated on the sites.

During the growth season 2014, we repeatedly (spring = late May, summer = early July, autumn = late August) collected leaves from upper crown shoots (defoliating the outer 15-20 cm, avoiding the apical shoot) of five individually marked birches in each WTH and CH plot, >5 m from former residue piles (on three plots less than five suitable birches were available). Each tree was sampled on each of the three sampling occasions. We chose birch as our focal species because it dominates regrowth on clearcuts in much of the boreal forests (Renecker & Schwartz 1998), and is staple forage for large herbivores in these forests (e.g., Wam & Hjeljord 2010). We sampled the first and subsequently available target tree upon entering the plot. A target tree had to have a height of approximately 150±30 cm, and approximately 20-30% of shoots damaged by herbivory, and spaces at least 5 feet away from other target trees. Leaves were collected in paper bags, placed in a portable cooler in the field and later forced-air dried at 30°C for 48 hours.

Chemical analyses

We determined total N and C with a Micro Cube (Elementar Analysen, Hanau, Germany). We conducted low molecular phenolic analysis of the birch foliage according to Nybakken et al. (2012) (compounds listed in Table A1). Briefly, we ground the leaf samples, conducted four series of cold-methanol extractions and then ran the samples through High Pressure Liquid Chromatography (HPLC, 1100 series, Agilent USA). We quantified phenolic acids and flavonoids at 320 nm. We calculated individual compound concentrations based on available commercial standards. To reduce extraction time and solvent use, we analyzed condensed tannins from the HPLC-extract (MeOH-soluble fraction) and from the dried residue after phenolic extractions (MeOH-insoluble fraction) with the acid butanol assay (Hagerman 2002). Purified condensed tannins (according to Hagerman 2002) from *Betula nana* (dwarf birch) leaves were used as standards to calculate these concentrations. We chose not to proceed with more specific analyses of hydrolysable tannins, as there were no signs of such compounds (pentagalloylglucose or related compounds) in the HPLC chromatograms.

Statistical analyses

We analysed contents of carbon, nitrogen and phenolic compounds as responses in a mixed effects setting (R version 2.15.3, R Core Team, 2013), with site, time of season and treatment as categorical fixed predictors. For condensed tannins, 16 samples were omitted due to technical lab failure. Homogeneity of variances across each predictor was investigated by graphical inspection (Zuur et al. 2007). Exploratory modelling suggested Gaussian distributions were appropriate, which is not uncommon for proportional data (McCullagh & Nelder 1989). As there were only a few marginal cases of heterogeneity, we applied a linear model (‘lme’ in nlme package) for all responses. TreeID was kept as a random intercept in all models (optimal random structure verified by AIC from ‘anova’, REML estimation). We determined the least parsimonious fixed structure by AIC (ML estimation) (Table S1). Best subset models were validated by lack of patterns in plots of residuals against fitted values and QQ plots of standardized residuals.

Results

Plant contents of carbon were higher after whole-tree-harvesting (WTH) compared to conventional harvest (CH) at the near-coastal site (Tables 1 and A1). The same applied to nitrogen, but only during autumn. The C: N ratio and several phenolic compounds were also higher with WTH than CH at the near-coastal site (Fig. 1). The concentrations of MeOH-insoluble tannins were related to WTH both at the inland and the near-coastal site, but the direction of the relationship varied with season. Mainly, these condensed tannins were lower with WTH compared to CH in spring, but higher with WTH compared to CH in autumn. Practically all phenolic compounds significantly related to WTH were also associated with an interaction term between WTH and time or place (Table A1, supplementary material), underpinning the complexity of the topic.

Discussion

The removal of logging residues by WTH influenced both C: N ratios and phenolic contents of birch foliage, but not always through the predicted pathways. As postulated, we found higher C: N ratios in plants growing at WTH plots at the near-coastal site, but this seemed to be partly due to variation in carbon concentrations rather than a general decrease in the contents of nitrogen. A likely explanation for the lack of a clear reduction in nitrogen concentrations (only observed at the near-coastal site in autumn) is the time lapse of 3 and 5 years from harvesting until we sampled plants. The nitrate flush in the soil normally starts within one year of forest harvesting (Kreutzwizer et al. 2008) and is suggested to last for only 3-5 years (Prescott 2002). In addition, nitrate on the WTH plots could have originated from needles shed by the piles before their removal.

A plausible explanation for the inconsistent changes in carbon concentrations between study sites is the impact of harvesting method on water stress. With more of the ground being exposed, as is the case with WTH compared to CH, plants are more likely to be water constrained due to increased run-off and evaporation from the bare ground (Lambers et al. 1998). However, the opposite can also occur because residue litter may actually limit water infiltration to the soil (Prescott 2002), possibly explaining the higher carbon concentrations with WTH compared to CH at the near-coastal site. Either way, water constraint induces stomatal closure and subsequently lower CO_2 assimilation, and this is more likely to occur later in summer as stored winter precipitation in the soil diminishes (Mahli et al. 1999). This is in line with our study, where significant WTH vs CH differences in carbon concentrations were only observed in spring and summer. Interestingly, the lower nitrogen concentration with WTH at the near-coastal site in autumn was not accompanied by a higher carbon concentration. More studies are needed to elucidate these patterns.

The altered C: N ratios were accompanied by increased levels of several individual phenolic compounds as well as in condensed tannins in foliage from the WTH plots, but again mainly on the near-coastal site. The ecological functions of most individual compounds are poorly known (but see Barbehenn & Kochmanski 2013), but phenolic compounds in general have been shown to serve several protective functions in plants (see introduction). For example, tannins normally reduce the available nutritional value of plant protein to large herbivores (Hagerman & Robbins 1993), which is relevant to our findings. Because these herbivores are nearly always N-limited, at least in parts of the season (Parker et al. 2009), increased levels of tannins may act as a bottom-up constraint (McArt et al. 2009, but see also Adamczyk et al. 2013), changing large-scale browsing patterns. Such perturbations may subsequently contribute to modify the ecosystem community assembly. The latter may also occur if a phenolic component slows decomposer activity (e.g., Kraus et al. 2003; Asplund et al. 2013), and in that way perturbs the element turnover through, e.g., altered litter quality and soil C: N ratios.

In conclusion, sustainability assessments of WTH should not ignore its impact on the chemical quality of post-harvest plant growth. More studies are needed to clarify the relevant patterns, and potentially cascading effects, across environmental gradients.

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Table 1. Coefficient estimates (mg/g dry matter ± 95% REML estimated confidence intervals) in best subset model ('lme', TreeID as random intercept) of birch *Betula* spp. chemical responses (per dry matter) to whole-tree-harvesting (WTH) vs conventional harvest in boreal forest in inland and more coastal Norway (*N*=98 trees resampled three times during growth season). More responses given in Table A1. Sequential coefficient contrasted against reference level = inland, spring, conventional. The most influential coefficients in bold (as indicated by approximated Wald statistics). Note that coefficients should be interpreted in conjunction with both the reference level (the intercept) and other coefficients in the subset (e.g., a negative coefficient may be outweighed by a positive interaction).

Fixed terms	Carbon	Nitrogen	C: N	MeOH-soluble condensed tannins	MeOH-Insoluble condensed tannins	Chlorogenic acid	Apigenin
Intercept	45.2 [44.4,46.0]	3.2 [3.0,3.3]	14.6 [13.4,15.8]	16.8 [14.9,18.7]	19.7 [17.8,21.7]	1.9 [1.4,2.5]	3.9 [3.3,4.5]
Time (ref. level: spring)							
summer	**1.8 [0.9,2.7]**	**-1.4 [-1.5,-1.2]**	**12.2 [11.1,13.3]**	**8.9 [6.7,11.2]**	**-4.9 [-7.5,-2.3]**	0.3 [-0.2,0.7]	**-0.7 [-1.2,-0.1]**
autumn	**-1.3 [-2.2,-0.5]**	**-1.1 [-1.3,-1.0]**	**7.4 [6.4,8.5]**	**6.5 [4.2,8.8]**	**-2.5 [-5.1,0.1]**	0.1 [-0.4,0.5]	**-0.5 [-1.1,0.1]**
Place (ref. level: inland)							
coastal	-0.3 [-1.7,1.0]	**-0.4 [-0.6,-0.1]**	0.7 [-1.3,2.7]	**4.0 [0.8,7.1]**	**-6.6 [-9.0,-4.2]**	**5.1 [4.2,6.1]**	-0.1 [-1.0,0.9]
Treatment (ref. level: CH)							
WTH	-0.4 [-1.3,0.5]	0.1 [-0.1,0.3]	-0.8 [-2.2,0.7]	-	**-2.0 [-4.4,0.3]**	-0.2 [-1.0,0.6]	-0.1 [-0.8,0.5]
Time*Place							
summer near-coastal	**-2.0 [-3.4,-0.5]**	**0.3 [0.0,0.6]**	-1.2 [-2.9,0.6]	**-13.0 [-16.7,-9.4]**	**5.0 [1.8,8.2]**	**0.9 [0.2,1.7]**	**-1.0 [-2.0,-0.1]**
autumn near-coastal	-1.2 [-2.6,0.2]	**0.7 [0.4,1.0]**	**-3.1 [-4.9,-1.4]**	**-3.8 [-7.5,-1.3]**	-0.3 [-3.6,3.0]	**-1.0 [-1.8,1.7]**	0.4 [-0.5,1.4]
Time*Treatment							
summer WTH	-	-0.1 [-0.3,0.1]	-	-	1.6 [-1.5,4.8]	0.1 [-0.5,0.7]	-
autumn WTH	-	-0.0 [-0.2,0.2]	-	-	**4.0 [0.8,7.2]**	-0.1 [-1.0,0.6]	-
Place*Treatment							
coastal WTH	**1.4 [0.0,2.9]**	-0.0 [-0.3,0.3]	**2.7 [0.3,5.0]**	-	-	**-1.8 [-3.1,-0.5]**	**1.2 [0.1,2.3]**
Time*Place*Treatment							
summer near-coastal WTH	-	-0.0 [-0.4,0.3]	-	-	-	-0.4 [-1.5,0.6]	-
autumn near-coastal WTH	-	**-0.4 [-0.8,-0.0]**	-	-	-	**1.0 [-0.1,2.0]**	-

Figure 1. Contents (median, quartiles with 1.5 cut-off) of carbon, nitrogen and phenolic compounds in birch leaves in relation to whole-tree-harvesting vs conventional harvest in two boreal forests; near-coastal (C) and inland (I) Norway. Individual trees were resampled in spring (1), summer (2) and autumn (3).

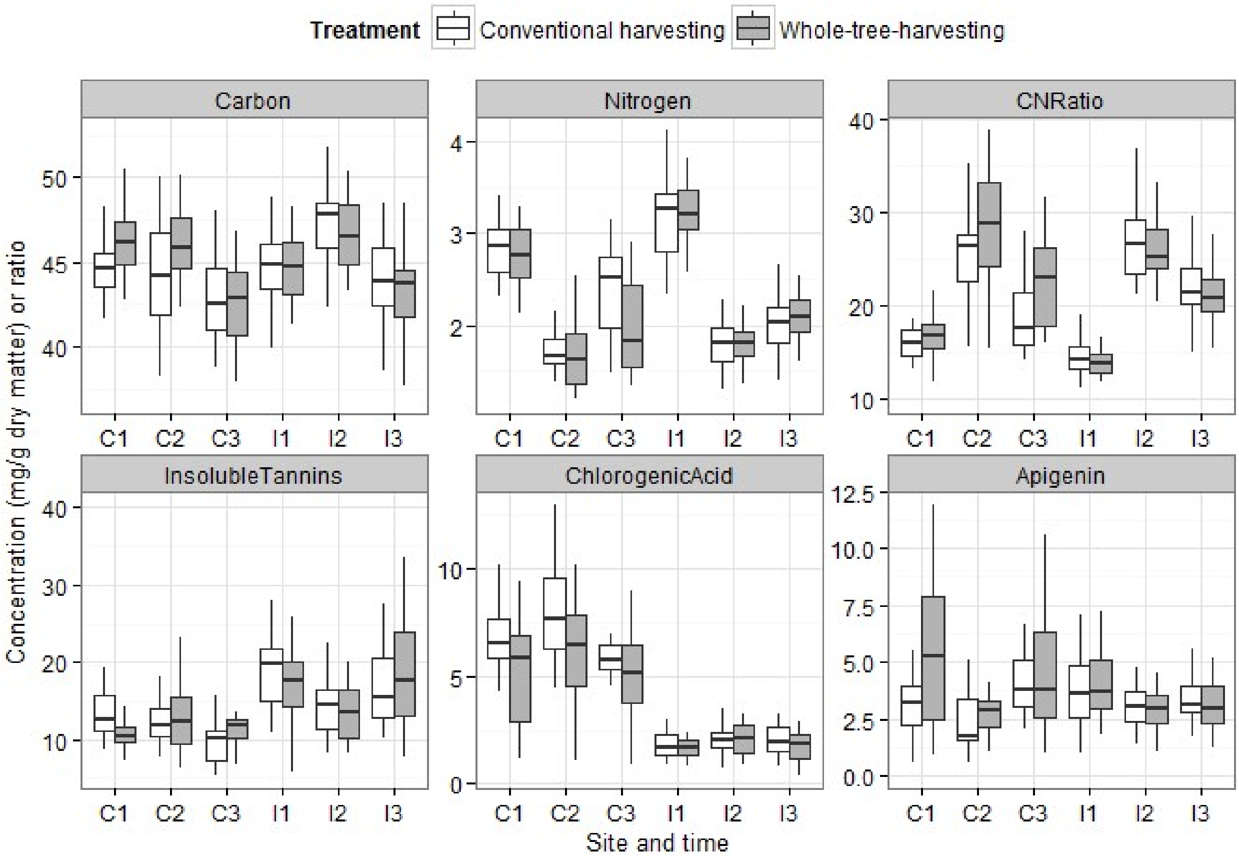

Table A1. Three best subsets of candidate models for plant responses to whole-tree-harvesting (WTH) vs conventional harvest (CH) in boreal forest on two experimental sites in Norway; one near-coastal and one inland (measured in spring, summer and autumn). Mixed effect setting ('lme', ML estimation) with treID as random intercept. Single terms are not shown, but were included whenever involved in a significant interaction term.

	Fixed terms					
Response	Time*Place	Time*Treatm	Place*Treatm	3-way	AIC (weights)	AICc (weights)
Carbon	x		x		-1288.2 (0.44)	-1287.4 (0.43)
	x				-1288.0 (0.39)	-1287.5 (0.44)
	x	x	x		-1284.7 (0.08)	-1283.6 (0.06)
Nitrogen	x	x	x	x	-2442.5 (0.35)	-2441.0 (0.26)
	x				-2442.5 (0.34)	-2442.0 (0.43)
	x		x		-2440.2 (0.11)	-2439.2 (0.12)
C: N ratio	x		x		-1576.8 (0.50)	-1577.6 (0.51)
	x				-1578.2 (0.25)	-1578.7 (0.29)
	x	x	x		-1579.7 (0.12)	-1580.8 (0.10)
Soluble tannins	x				-697.2 (0.62)	-696.7 (0.67)
	x		x		-695.2 (0.22)	-694.4 (0.21)
	x	x			-692.7 (0.07)	-691.8 (0.06)
Insoluble tannins	x	x			-795.9 (0.42)	-794.9 (0.39)
	x				-795.5 (0.35)	-795.0 (0.41)
	x	x	x		-793.9 (0.16)	-792.7 (0.13)
Chlorogenetic acid	x	x	x	x	-1639.2 (0.57)	-1637.5 (0.48)
	x		x		-1638.0 (0.31)	-1637.1 (0.39)
	x	x	x		-1635.9 (0.11)	-1634.7 (0.11)
Naringenins	x	x	x	x	-2007.8 (0.28)	-2006.2 (0.20)
	x				-2007.8 (0.28)	-2007.2 (0.35)
	x		x		-2007.1 (0.20)	-2006.3 (0.22)
Kampferols	x				-2057.6 (0.58)	-2057.0 (0.66)
	x	x	x	x	-2054.8 (0.15)	-2053.2 (0.10)
	x	x			-2054.7 (0.14)	-2053.7 (0.12)
Quercetins	x				-1080.1 (0.72)	-1079.5 (0.76)
	x		x		-1077.2 (0.17)	-1076.4 (0.16)
	x	x			-1075.5 (0.07)	-1074.5 (0.06)
HPCA	x				-2077.4 (0.77)	-2076.9 (0.80)
	x		x		-2073.5 (0.11)	-2072.7 (0.10)
	x	x			-2073.0 (0.09)	-2072.0 (0.07)
Myricitrins	x				-950.4 (0.76)	-949.9 (0.79)
	x		x		-947.3 (0.16)	-946.5 (0.14)
	x	x			-945.2 (0.05)	-944.2 (0.05)
Flavonoids	x				-745.3 (0.51)	-744.7 (0.56)
	x		x		-744.6 (0.37)	-743.8 (0.35)
	x	x	x		-741.0 (0.06)	-739.8 (0.05)
Apigenin	x		x		-1443.2 (0.37)	-1442.3 (0.40)
	x	x	x		-1442.9 (0.32)	-1441.7 (0.29)
	x				-1440.9 (0.12)	-1440.3 (0.15)