Forest Ecology and Management 363 (2016) 200–211

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Unearthing the roots of degradation of *Quercus pyrenaica* coppices: A root-to-shoot imbalance caused by historical management?

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ARTICLE INFO

Article history:
Received 21 October 2015
Received in revised form 23 December 2015
Accepted 24 December 2015
Available online 6 January 2016

Keywords:
Biomass partitioning
Grafting
Multi-stemmed tree
Resprouting
Forest decline
Vegetative regeneration

ABSTRACT

Slow growth, branch dieback and scarce acorn yield are visible symptoms of decay in abandoned *Quercus pyrenaica* coppices. A hypothetical root-to-shoot (R:S) imbalance provoked by historical coppicing is investigated as the underlying driver of stand degradation. After stem genotyping, 12 stems belonging to two clones covering 81 and 16 m^2 were harvested and excavated to measure above- and below-ground biomass and nonstructural carbohydrate (NSC) pools. To study root system functionality, root connections and root longevity were assessed by radiocarbon analysis. Seasonality of NSC was monitored on five additional clones. NSC pools, R:S biomass ratio and fine roots-to-foliage ratio were higher in the large clone, whose centennial root system, estimated to be 550 years old, maintained large amounts of sapwood (51.8%) for NSC storage. 248 root connections were observed within the large clone, whereas the small clone showed comparatively simpler root structure (26 connections). NSC concentrations were higher in spring (before bud burst) and autumn (before leaf fall), and lower in summer (after complete leaf expansion); they were always higher in roots than in stems or twigs. The persistence of massive and highly inter-connected root systems after coppicing may lead to increasing R:S biomass ratios and root NSC pools over time. We highlight the need of surveying belowground organs to understand above-ground dynamics of *Q. pyrenaica*, and suggest that enhanced belowground NSC storage and consumption reflect a trade-off between clonal vegetative resilience and aboveground performance.

1. Introduction

Quercus pyrenaica Willd. is a marcescent oak located in siliceous sub-Mediterranean regions from northern Morocco to south-western France, generally in montane slopes unsuitable for agriculture. *Q. pyrenaica* has been traditionally coppiced for firewood, charcoal and woody pastures. The vigorous root-resprouting ability of this species has determined its intense coppice use, consisting on short cutting cycles ranging from 7 to 15 years. Abandonment of historical coppicing in 1970s has revealed the current degradation state of most of stands, where overaged multi-stemmed trees present low stem growth, absent acorn yield, and high branch and stem dieback (Bravo et al., 2008; Cañellas et al., 2004). Several consequences of long-term coppicing are repeatedly suggested since the 1990's as determinants of such decay: excessive stem density and acute competition among clonal stems, substrate oligotrophication, clonal carbon starvation, low genetic diversity, and disequilibrium between belowground and aboveground tree organs (Serrada et al., 1992; Cañellas et al., 2004; Corcuera et al., 2006; Bravo et al., 2008, and references therein). Although genetic diversity loss has been already discarded (Valbuena-Carabaña and Gil, 2013; Valbuena-Carabaña et al., 2008), actual causes of degradation remain unknown, and forest managers unsuccessfully try to convert coppices into high forests by thinning trials.

Abbreviations: R:S, root-to-shoot ratio; NSC, non-structural carbohydrates; dbh, diameter at breast height; B_{ST}, stem biomass; B_{BR}, branch biomass; B_{FL}, foliage biomass; B_{CR}, coarse root biomass; B_{TP}, taproot biomass; B_{FR}, fine root biomass; DM, dry matter; DOY, day of year.

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http://dx.doi.org/10.1016/j.foreco.2015.12.040
0378-1127/

Table 1
Aboveground features and dry biomass partitioning of 12 measured stems belonging to two different clones of *Quercus pyrenaica*. Aboveground biomass was separated by organs (stem, branches and leaves); and woody biomass (stem and branches) was separated by tissue (heartwood, sapwood and bark).

Clone	dbh[a] (cm)	Height (m)	Annual growth rings[b]	Biomass (kg)				Woody biomass (kg)		
				Stem	Branches	Leaves	Total	Heartwood	Sapwood	Bark
LARGE (81 m^2)	15.75	12.67	48	100.8	31.0	4.8	136.6	33.53	63.50	34.79
	21.75	13.75	50	171.6	95.5	8.6	275.7	72.50	124.12	70.42
	20.38	11.65	44	137.8	105.6	8.4	251.8	64.79	115.27	63.38
	21.50	13.46	46	151.8	69.2	7.0	228	58.25	103.19	59.57
	17.00	12.51	47	112.5	23.7	3.5	139.7	37.04	65.39	33.77
	22.60	13.27	46	191.5	102.7	10.0	304.2	82.45	134.35	77.38
	12.40	10.97	43	55.3	8.1	2.2	65.6	19.75	26.06	17.65
	11.75	9.94	42	41.4	5.7	1.8	48.9	10.32	23.10	13.63
SMALL (16 m^2)	21.28	10.46	45	125.1	43.0	5.8	173.9	47.77	80.45	39.92
	19.30	9.78	48	106.1	22.0	3.5	131.6	35.47	59.80	33.73
	19.18	9.89	44	95.8	33.3	4.4	133.5	39.32	57.53	31.18
	20.05	9.42	47	100.3	43.9	5.6	149.8	41.68	64.73	37.76

[a] dbh: diameter at breast height.
[b] Annual growth rings counted at breast height at the end of 2013 growing season.

Belowground factors are rarely taken into account in ecology and forest management studies. Technical difficulties in surveying belowground attributes and delineating genotypes, unfeasible by naked-eye in this species, lead to disregard the effect of clones in aboveground stem performance. Yet, in a *Q. pyrenaica* coppice, clonal structure and root biomass have shown to have an effect on diametric stem growth (Salomón et al., 2013), and genetic analyses have revealed heterogeneous clonal structures and clones of up to 43 stems covering areas as large as 258.5 m^2 in some *Q. pyrenaica* stands (unpublished data). Since non-structural carbohydrate (NSC) allocation to storage organs can be actively regulated to cope with unfavorable conditions (Dietze et al., 2014; Sala et al., 2012), belowground influence on aboveground performance would partially come from a trade-off between carbon allocation to growth and storage. Accordingly, enhanced NSC storage in roots is consistently displayed by resprouters to support vegetative regeneration after disturbance (e.g. Knox and Clarke, 2005; Paula and Ojeda, 2009; Zeppel et al., 2015; Zhu et al., 2012b), often at the cost of growth and sexual reproductive effort (Bond and Midgley, 2001; Clarke et al., 2013; Iwasa and Kubo, 1997; Poorter and Kitajima, 2007). Moreover, large amounts of living parenchyma needed to store NSC might entail high maintenance costs derived from root respiration processes. In this line, favored NSC allocation to roots may lead to high belowground maintenance costs and constrained aboveground performance, supporting the hypothesis of a root-to-shoot (R:S) imbalance as the main cause

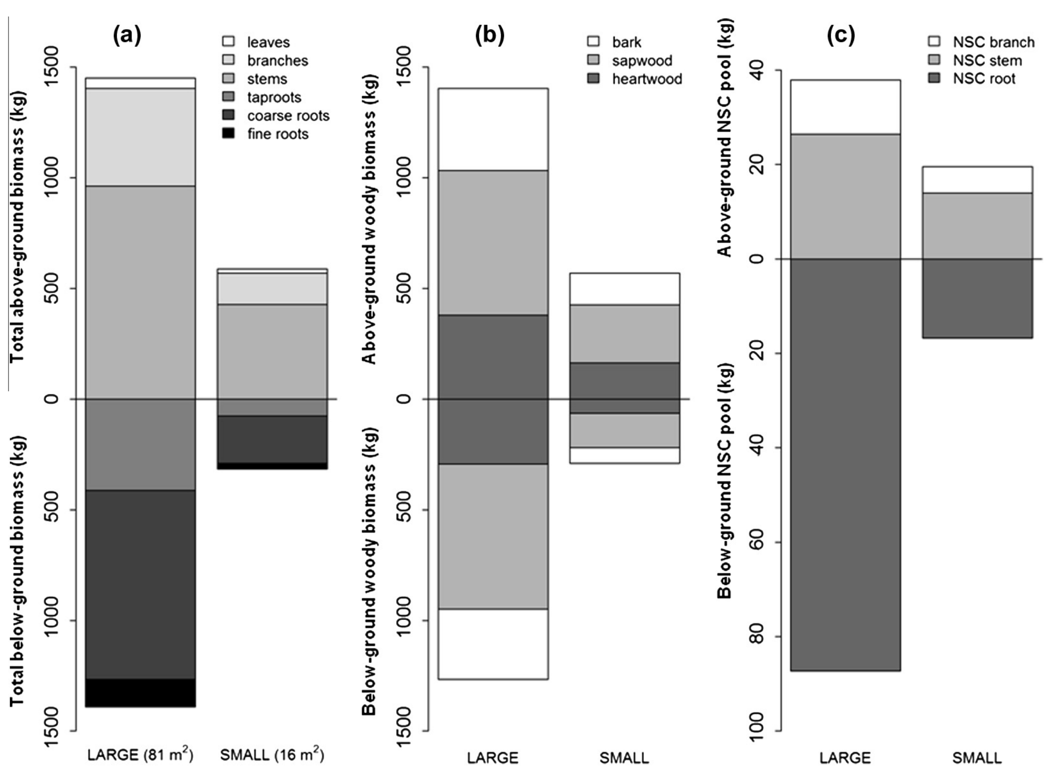

Fig. 1. Biomass partitioning in two clones of *Quercus pyrenaica* of contrasted size, displayed by (a) plant organ (leaves, branches, stems, taproots, coarse roots and fine roots) and (b) plant tissue (heartwood, sapwood and bark) excluding leaves and fine roots. Sapwood non-structural carbohydrate (NSC) pools of the clones (c), calculated as the product of NSC concentration on a dry matter basis by its corresponding sapwood dry biomass. The larger clone was composed by eight stems and it had a clonal extension of 81 m^2, whereas the smaller clone was composed by four stems and it had a clonal extension of 16 m^2.