

Differential survival and growth of stumps in 14 woody species after conservation thinning in mixed oak-rich temperate forests

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Abstract Many trees sprout after cutting and other disturbances, and individuals may persist for a long time. In 25 forests in Sweden subjected to thinning for biodiversity values, we tested whether survival and growth of sprouts are related to stump diameter. Stem diameters vary under conservation thinning and earlier work had indicated high survival of stumps of small diameter. We also tested whether a continuum of responses in sprouting existed among the 14 species, as predicted by earlier work. We cut on average 26 % of the basal area (mean basal area 28 m²/ha) and analysed 1,044 stumps (diameters 10–76 cm). The response of the species after 9 years ranged along a continuum from weak to strong sprouting. Survival was highest for *Corylus avellana* (95 % of cut individuals survived) and *Tilia cordata* (85 %), then decreased as follows; *Crataegus* spp. > *Alnus glutinosa* > *Prunus avium* > *Fraxinus excelsior* > *Quercus robur/Q. petraea* > *Salix caprea* > *Sorbus aucuparia* > *Acer platanoides* > *Betula pendula*, to *Betula pubescens* (8 %) and *Fagus sylvatica* (8 %). Within species, stump survival was unrelated to stump diameter. Mean maximal sprout height of surviving stumps varied from about 1 to 4 m among the species after 9 years. Sprout height was unrelated to stump diameter. Stump survival (%) and mean sprout height were positively correlated across species. In conclusion, stem

diameter had no effect on sprouting, but the 14 species could be clearly ranked in regrowth. Our results are useful in planning thinning of mixed forests for biodiversity conservation, for biomass harvest, or combined purposes.

Keywords Sprouting · Forest management · Conservation · Coppice · Stool · Succession

Introduction

Bond and Midgley (2001) identified sprouting among the woody plants as an important ecological process. Many angiosperm trees can survive cutting and other damages by sprouting from buds on stem, stump, or roots (the ‘persistence niche’). In Appalachian forests in the USA, Shure et al. (2006) quantified woody regrowth in gaps of different sizes 18 years after clear-cutting. They found that sprouting was much more important for the regrowth than advanced regeneration and seedling growth (for similar results, see also Dietze and Clark 2008). Studies of sprouting have focused on the effects of fire and natural disturbances, while studies of effects of conservation-oriented thinning for biodiversity are rare.

In a review, Del Tredici (2001) concluded that sprouting is more common in seedlings/saplings than in mature temperate trees (see also Bellingham and Sparrow 2000). This is supported by or is consistent with coppicing—repeated harvesting of stems of small diameter from stumps (‘stools’), earlier practiced in many areas (Rackham 1998; Del Tredici 2001; Szabo and Hedl 2013). There are many studies of coppicing of one or a few species of trees/shrubs (for references, see Matula et al. 2012; Splichalova et al. 2012; Albert et al. 2014) but none or few similar or related studies of whole communities of temperate trees in

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mixed forests. The negative relationship between tree size (seedling–sapling–mature tree) and degree of sprouting may not be true for all species in mixed communities (see, e.g. Weigel and Peng 2002; Johansson 2008). After thinning of semi-natural mixed forests, interspecific competition, browsing by e.g. deer, and other processes influence the survival and growth of stump sprouts. Stumps from small trees (small diameter) are younger and sprouts from them may be more vigorous (e.g. Harrington 1984; Johnson et al. 2002), but in mixed high forests, these trees have faced competition from large trees and other species.

Bond and Midgley (2001: Box 1) tentatively classified the woody species as sprouters or non-sprouters, but subsequent work has revealed complex patterns and responses. In a review, Vesik and Westoby (2004) analysed sprouting in relation to intensity and type of disturbance. Clear or fairly clear separation of species into sprouter or non-sprouter was evident after intense disturbances, such as some wildfires that kill most stems. In contrast, there seemed to be a continuum of species responses in degree of sprouting following less intense disturbances where much live above-ground woody biomass was left. After thinning, many trees usually remain in the forest and the disturbance can be classified as less intense.

Reforestation and secondary succession in formerly more open habitats have in many cases led to dense mixed forests in the temperate zone (Sitzia et al. 2010; Götmark 2013). Studies of thinning and other forms of partial cutting in mixed forests have increased and are often concerned with conservation or restoration (e.g. Singer and Lorimer 1997; McGee et al. 1999; Stanturf and Madsen 2005; Keton 2006; Bauhus et al. 2009; Gronewold et al. 2010; Dwyer et al. 2010; Brudvig et al. 2011; Neill and Puettmann 2013). Minimal intervention is one option, and options where thinning may be needed include management with historical reference, non-traditional management, and species management (Pykälä 2000; Götmark 2007; Bauhus et al. 2009; reviewed by Götmark 2013). The present study was done in the Swedish Oak Project, where we compare minimal intervention and non-traditional management (conservation thinning) in a long-term experiment begun in 2000. The aims of our thinning are to (potentially) favour regeneration of oaks, *Quercus robur* L. and *Quercus petraea* (Mattuschka) Liebl. and to evaluate the response of forest biodiversity to alternative management (both light-demanding and shade-associated taxa are studied, e.g., Nordén et al. 2008, 2012; Götmark 2009, 2013). In the present study, we examined the survival of stumps and growth of stump sprouts 9 years after conservation thinning.

We tested the hypothesis that survival of the stumps and sprout height growth from stumps decrease with increasing stump diameter (cf. Bellingham and Sparrow 2000; Del

Tredici 2001). This is of interest to evaluate regrowth after conservation thinning in mixed high forest (as opposed to coppice) and no earlier such study existed. Moreover, we tested whether the woody species range along a continuum in degree of sprouting after conservation thinning, i.e. after a less intense disturbance where many trees remain standing in the forest (Vesik and Westoby 2004). If there is a continuum in stump survival and growth after conservation thinning, the most successful sprouters may influence successional patterns and management decisions.

Materials and methods

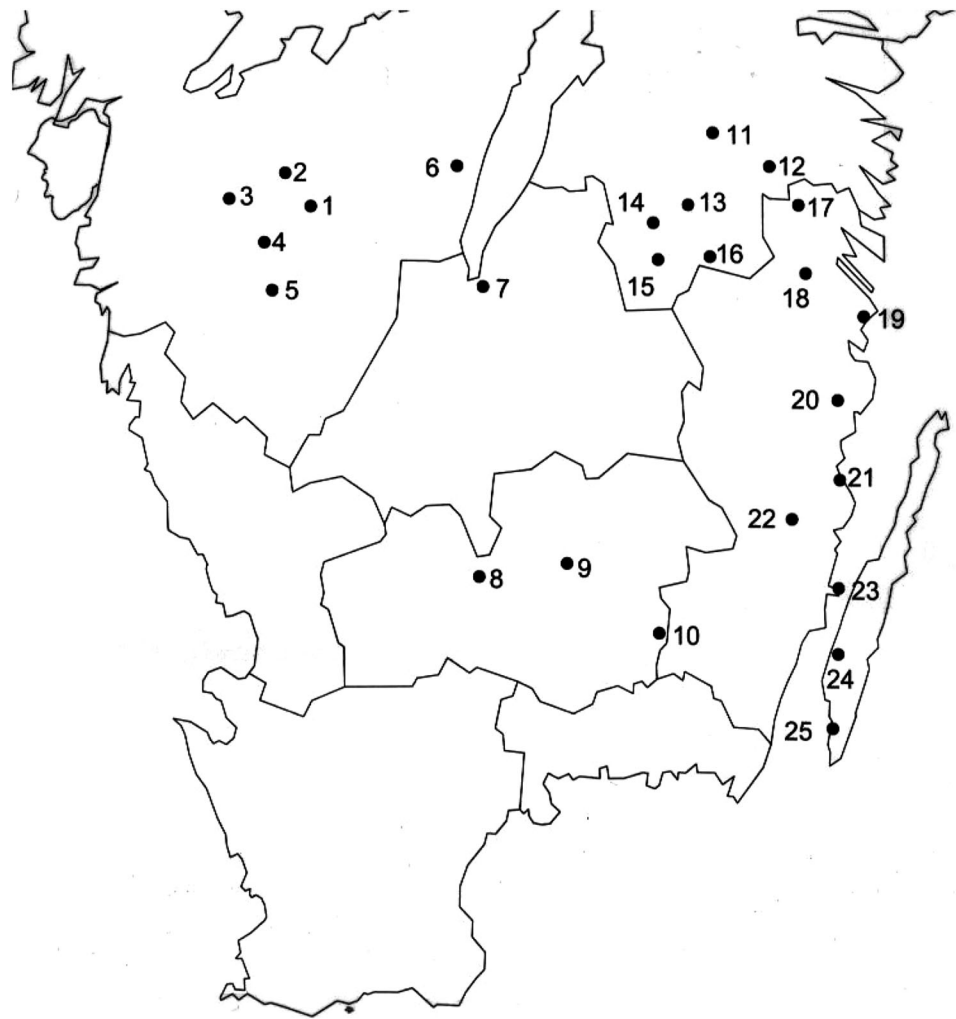
Study sites and plot characteristics

The 25 study sites are located in southern Sweden (Fig. 1), south of the boreal forest. Production forests of *Picea abies* (L.) H. Karst and *Pinus sylvestris* L., with a minor component of *Betula* spp., dominate the land and the forests (Swedish Statistical Yearbook of Forestry, www.skogsstyrelsen.se). Smaller forests with many broadleaved tree species, like the ones we study, form about 3 % of the total forest area.

We studied 25 closed-canopy mixed forests with large oaks (about 80–200 years old), located 5–230 m above sea level at sites where agriculture was abandoned 50–80 years ago. In the study area (Fig. 1), mean precipitation for July decreases from 80 mm at the western sites to 55 mm at the eastern coastal sites; variation among months is small (Swedish Meteorological and Hydrological Institute, www.smhi.se). The mean temperature in July varies from 14 °C in the west to 17 °C in the east (www.smhi.se). Our study sites are nature reserves or part of the Forest Agency's woodland key habitat network (Timonen et al. 2010). The 25 forests had mesic moraine (till) and relatively level, partly stony ground. Brown earth soils dominated, with some podsol at four sites with much *P. abies* (>30 % of basal area). A large clay fraction (10 %) in the soil was recorded only at one coastal site, Vickleby (Fig. 1). Browsing animals (especially roe deer *Capreolus capreolus* L., moose *Alces alces* L., and hares *Lepus* spp.) are common in southern Sweden and also occurred within our plots.

In each forest, we delimited two plots in 2000 (each 1 ha, at most sites 100 m × 100 m). One plot was randomly assigned as treatment plot (conservation thinning) and the other as reference plot, with minimal intervention (not used in the present study). To document the composition of trees before treatment, we measured basal area (stems >5 cm in diameter at breast height, dbh) along transects (10 × 100 m) covering the central 60 % of each treatment plot (0.6 ha), where we later studied stumps. As

Fig. 1 Map of study area in southern Sweden, with location of the 25 forests studied. Lines indicate county borders. Names of study sites: 1 Skölvene, 2 Karla, 3 Östadkulle, 4 Sandviksås, 5 Rya åsar, 6 Strakaskogen, 7 Bondberget, 8 Långhult, 9 Bokhultet, 10 Kråksjö by, 11 Stafsäter, 12 Åtvidaberg, 13 Fagerhult, 14 Aspenäs, 15 Norra Vi, 16 Fröåsa, 17 Ulvsdal, 18 Hallingeberg, 19 Ytterhult, 20 Fårbo, 21 Emsfors, 22 Getebro, 23 Lindö, 24 Vickleby, 25 Albrunna



the two *Quercus* species are morphologically and ecologically similar and were rarely identified to species, they are pooled in this study. For information on tree species composition in each forest, see Table 1 in Götmark (2007).

Experimental treatment and sampling of stumps

In the winter 2002/2003, thinning with chainsaws was conducted near large oaks (>40 cm diameter) that may suffer from competition in this kind of forest. Harvesting was motivated by biofuel research, and the relatively low harvest rate (ca. 25 % of basal area, see below) was also motivated by the precautionary principle. We cut almost all *P. abies*, broadleaved trees of intermediate size (stems 5–35 cm) in the canopy and subcanopy, and oaks of intermediate size if they were common. Old, large trees of other broadleaved species were usually retained. Although more trees were cut near large oaks, the cut trees were distributed fairly evenly across each plot. On average,

about half of the stems of the shrub *Corylus avellana* L. were cut (not quantified). Cut stems were removed by forwarders, large vehicles that transport logs. Branches of trees, and two oak logs per plot, were left as dead wood. We measured canopy openness (% visible sky) from 20 cm above the ground before cutting and after cutting in 2003 and 2009 (for methods, see Götmark 2007). Before thinning, the mean basal area per hectare and plot was 28.2 m² (SD = 4.1, Table 1). The dominant canopy trees were about 22–30 m tall (only range estimated). *Q. robur/Q. petraea* accounted for 49 % of the summed basal area; *P. abies* 11 %; *Populus tremula* L. 8 %; and 11 other species between 1 and 6 %. With respect to number of stems (>5 cm dbh), *C. avellana* dominated (mean: 27 % of stems per site), with *Q. robur/Q. petraea* as second most common (mean 15 %). On average, 23 % of the basal area was cut and harvested (Table 1). Understory trees and shrubs, with diameter of 0–4.9 cm, were not measured; about 50–90 % of these were cut and harvested (a higher proportion if

Table 1 Basal area^a at breast height (1.3 m) before cutting, percentage removed basal area and canopy openness (% visible sky from ground) before (2001) and after conservation thinning (2003) in treatment plots at the 25 study sites

Site ^b	Trees and shrubs, basal area		Canopy openness (%)		No. of stumps
	(m ² ha ⁻¹)	% removed	Before cutting	After cutting	
25. Albrunna	26.5	28.4	12.2	27.1	39
14. Aspenäs	28.5	27.5	11.3	40.6	38
12. Åtvidaberg	31.7	22.9	9.4	23.8	35
9. Bokhultet	28.8	20.5	15.5	30.7	46
7. Bondberget ^c	24.5	9.3 ^c	8.1	22.3	18
21. Emsfors	25.5	15.8	11.6	32.2	29
13. Fagerhult	22.6	22.8	10.2	31.9	74
16. Fröåsa	35.9	32.6	18.6	45.9	28
20. Färbo	31.3	37.4	18.6	35.6	23
22. Getebro	31.5	18.9	14.2	32.2	39
18. Hallingeberg	27.3	16.1	12.4	19.9	65
2. Karla	25.5	28.1	19.6	35.6	52
10. Kråksjö	33.3	23.9	9.4	25.0	29
23. Lindö	25.5	15.2	10.2	29.1	38
8. Långhult	23.9	27.3	16.1	28.3	26
15. Norra Vi	34.3	21.6	10.5	29.4	17
3. Östadkulle	31.4	26.5	12.4	31.0	67
5. Rya Åsar	30.4	15.6	18.2	37.8	39
4. Sandviksås	34.3	31.2	19.4	56.9	6
1. Skölvene	26.1	20.3	17.5	42.8	77
11. Stafsätter	19.4	11.5	9.2	28.1	47
6. Strakaskogen	28.0	34.5	16.2	40.6	78
17. Ulvsdal	26.6	21.6	18.9	33.2	80
24. Vickelby ^c	28.1	2.8 ^c	9.3	23.5	31
19. Ytterhult	23.4	31.6	23.1	45.8	23
Mean ($n = 25$)	28.2	22.6	14.1	33.2	41.8
SD	4.1	8.3	4.3	8.6	21.0

^a Trees and shrubs more than 5 cm in diameter at breast height

^b Numbers refer to site location, see Fig. 1

^c Many *Corylus avellana* stems, less than 5 cm at breast height, removed. These were not included in basal measurements, but their removal caused clear changes in canopy openness

there were many stems). This increased the mean basal area harvested at the sites to about 26 %. Canopy openness from ground level increased from a mean of 14 % before cutting to 33 % after cutting in 2003 (Table 1). In 2006, the thinning had increased the mean stem diameter growth rate of large oaks by 22 % compared with minimal intervention plots (Götmark 2009). Due to regrowth, in 2009, the canopy openness had decreased to a mean value of 25 % (\pm SE 2.1, $n = 25$).

In 2010, eight summer seasons after thinning, we began sampling stumps along transects (10 \times 100 m) placed

across each plot of 1 ha. This was extended in 2011 by more sampling, such that 65 % of the total stump data come from 2011 and 35 % from 2010. To obtain good sample sizes for species analyses, we pooled the 2 years and refer to ‘9-year survival/growth’. We included stumps in the diameter range of 10–76 cm. Since smaller stumps were examined in a different type of regeneration study (J. Leonardsson and F. Götmark, in preparation) and were difficult to find and more often decomposed, they are not included in the present study. The range in stump diameter was large for 12 of the 14 species analysed (Table 2).

In total, we surveyed 40 % of the area of each plot (0.4 ha) for stumps in 2010–2011. We searched carefully for stumps that were more than 10 cm in diameter, cut 20–30 cm above the ground. Note that for these stumps, the diameter at breast height of the trees was smaller, from about 5 cm up to 10 cm. The conifers in Sweden (*P. abies* and *P. sylvestris*) do not survive when the trees are cut near the ground, and they were excluded from the sampling. In both years, we recorded species of stump, diameter (with diameter measuring tape), number of live sprouts and height of the tallest sprout from the position of bud growth on stump or from the ground if the sprout emerged from stump below the ground. Sprouts emerging through soil close to the stump were checked by digging (they can be, and were often seedlings). A stump was defined as dead if we found no live sprout on it. Species identification of dead stumps was based on bark, wood characteristics, and protocols from 2002 with data on trees to be cut along transects. For multi-stemmed cut trees and shrubs, we recorded the diameter of each stump.

In 2011, we also recorded for each stump its height above the ground; proportion of the bark remaining on the stump; proportion of stump that was decomposed in four classes (1: 0–25 %, 2: 25–50 %, 3: 50–75 % and 4: 75–100 % fully soft wood); and number of dead sprouts on stump at time of sampling. All species (except *Populus tremula*) sprout from buds in the bark and bark loss and decomposition might reduce the sprouting of the stumps over time, which we tested. In *P. tremula*, the sprouts came from the cambium on the top of the stumps. The total number of sprouts that died is probably underestimated, as dead sprouts tend to fall off (also due to bark loss). We did not examine root sprouts (root suckers) from two trees known to have such sprouts far from stumps (*P. tremula* and *Prunus avium* L.). Our results therefore refer to stumps and growth of sprouts from stumps.

Calculations and statistical analyses

Each *C. avellana* individual consisted of multiple stumps (from multiple stems), whereas such individuals were uncommon in the other species (0–10 % of the

Table 2 Characteristics of stumps recorded in 2011, 9 years after thinning

Species	Mean \pm SD					Diameter min–max (cm)	N ^c	No. of sites
	Height (cm)	Bark lost (%)	Decomposition (1–4) ^a	Sprouts, no. live	Sprouts, no. dead ^b			
<i>Alnus glutinosa</i>	31 \pm 18	4 \pm 8	1.6 \pm 1.3	2.4 \pm 4.7	8.3 \pm 18	11–76	34	6
<i>Acer platanoides</i>	22 \pm 13	59 \pm 33	2.2 \pm 1.2	0.6 \pm 1.9	7.0 \pm 13	10–52	48	9
<i>Betula pendula</i>	30 \pm 15	13 \pm 19	1.7 \pm 0.8	0.1 \pm 0.6	0	10–72	48	9
<i>Betula pubescens</i>	26 \pm 10	19 \pm 25	2.2 \pm 1.1	0.4 \pm 1.3	2.3 \pm 8.6	10–63	49	11
<i>Corylus avellana</i>	26 \pm 12	22 \pm 22	1.8 \pm 0.9	8.6 \pm 6.0	4.8 \pm 5.2	11–62	49	9
<i>Crataegus</i> spp.	20 \pm 8.1	39 \pm 47	1.7 \pm 1.3	1.1 \pm 1.7	11 \pm 4.2	11–22	7	2
<i>Fagus sylvatica</i>	23 \pm 12	60 \pm 29	2.4 \pm 1.4	0.05 \pm 0.2	0.1 \pm 0.4	15–70	20	2
<i>Fraxinus excelsior</i>	22 \pm 10	46 \pm 33	1.4 \pm 0.8	1.4 \pm 3.3	7.5 \pm 15	10–65	90	11
<i>Populus tremula</i>	25 \pm 11	15 \pm 20	2.2 \pm 1.1	0.07 \pm 0.4	0.3 \pm 1.7	10–64	118	16
<i>Prunus avium</i>	20 \pm 8.9	30 \pm 35	1.6 \pm 0.6	1.7 \pm 2.6	5.3 \pm 7.1	10–27	13	1
<i>Quercus robur/petraea</i>	26 \pm 15	43 \pm 35	1.3 \pm 0.7	2.2 \pm 6.1	4.4 \pm 17	10–76	97	22
<i>Salix caprea</i>	29 \pm 13	25 \pm 36	1.0 \pm 0	0.8 \pm 1.6	4.1 \pm 5.1	14–52	10	3
<i>Sorbus aucuparia</i>	22 \pm 17	55 \pm 39	1.6 \pm 1.0	0.4 \pm 1.4	2.9 \pm 10	10–34	45	11
<i>Tilia cordata</i>	23 \pm 12	30 \pm 31	3.1 \pm 1.2	15 \pm 12	2.8 \pm 3.9	10–73	39	11

^a 1 is 0–25 % decomposition; 2 is 25–50 %; 3 is 50–75 %; and 4 is 75–100 %

^b The number of dead sprouts was probably underestimated

^c Sample size from 2011 (number of stumps)

individuals). To be able to use one overall stump diameter for each individual as explanatory variable, we transferred each multi-stemmed stump to a corresponding single-stem stump, as follows. The basal areas of the stems of the multi-stemmed stump were summed to obtain a total basal area for each individual, and we then calculated an overall diameter from the given total basal area.

We analysed 14 taxa (referred to as ‘species’ below), for which the number of stumps included varied from 11 to 187 (sample sizes for species are given in Fig. 3). *C. avellana* is a shrub but may reach 10 m in height or more. The other species were trees, usually less than 20 m tall (*Sorbus aucuparia* L., *Crataegus* spp.) or taller (*Quercus robur/Q. petraea*, *P. tremula*, *Fraxinus excelsior* L., *Betula pendula* Roth, *Betula pubescens* Ehrh., *Tilia cordata* Mill., *Alnus glutinosa* (L.) Gaertner, *Salix caprea* L., *Acer platanoides* L., *Fagus sylvatica* L., *Prunus avium*). From about 2005, *F. excelsior* has suffered severely from a fungal disease (Enderle et al. 2013) that affected many *F. excelsior* stump sprouts in this study.

To analyse survival among species and relation to diameter, the package lme4 with a mixed logistic model in the software R (R Development Core Team, 2010; <http://www.r-project.org>) was run by expertise at the Department of Mathematical Statistics, University of Gothenburg. In addition, glm in R was used (generalized linear model with

binomial error distribution). In the models, both pooled data (sites pooled) and data where site was included as random factor were used, to account for possible effects of site. For each species, one model with pooled data, and one model with site as random factor, was run. Tests of pairwise differences in survival among species were conducted. In addition, we computed the mean diameter of surviving and dead stumps.

To analyse growth of sprouts on surviving stumps, we used the height of the tallest sprout (maximal height). We assume this is a good measure of individual success; studies of growth rate in trees often report that individual height predicts future survival (e.g. Götmark 2007 and reference therein) and self-thinning of stems (sprouts) occurred within individuals. We analysed the influence of diameter and site on maximal sprout height in the species using the general linear model in SPSS (IBM 2011). In models for species, height was the dependent variable, diameter a covariate and site a random factor. Levene’s test was used to assess heteroscedasticity. Because we used only surviving stumps in this analysis, sample sizes were smaller than in the analysis of survival (sample sizes for species in Fig. 4). We judged that for four species with fewer than 10 (live) stumps, models were not meaningful to run (*B. pendula*, *Crataegus* spp., *F. sylvatica*, *S. caprea*). For the remaining ten species, sample sizes ranged from 10

to 71 (mean value: 31 stumps). The range in diameter of stumps within species was considerable, between 10 and 66 cm (mean 41 cm, $n = 10$ species).

With respect to sites included in the analyses, for stump survival the following numbers of sites were used: *Acer platanoides* (11), *Alnus glutinosa* (7), *Betula pendula* (10), *Betula pubescens* (11), *Crateagus* spp. (2), *Corylus avellana* (10), *Fagus sylvatica* (2), *Fraxinus excelsior* (11), *Populus tremula* (18), *Prunus avium* (2), *Quercus robur/Q. petraea* (22), *Salix caprea* (4), *Sorbus aucuparia* (13), *Tilia cordata* (11). For stump growth, the following numbers of sites were used: *Acer platanoides* (11), *Alnus glutinosa* (7), *Betula pubescens* (11), *Corylus avellana* (10), *Fraxinus excelsior* (11), *Populus tremula* (18), *Prunus avium* (2), *Quercus robur/Q. petraea* (22), *Sorbus aucuparia* (13), *Tilia cordata* (11).

Results

Characteristics of stumps

The average sample size of stumps per site was 42 (SD = 21, range 6–80, $n = 25$, Table 1). Stump height did not vary much among the 14 species; the trees were cut at average heights of 20–31 cm (Table 2). After 9 years, *S. aucuparia*, *A. platanoides* and *F. sylvatica* stumps had lost the highest proportions of the bark (mean values 55–60 %, Table 2). These species have thin bark and had few live stump sprouts (Table 2). *A. glutinosa*, *B. pendula* and *P. tremula* lost least bark (4–19 %). Degree of bark loss was not correlated with stump decomposition rate among species ($r = 0.04$, $n = 14$). *T. cordata*, with highest stump decomposition, produced the highest number of live sprouts (Table 2).

Production of sprouts was highly variable within and among the species. *T. cordata* and *C. avellana* had highest mean production of live sprouts after 9 years (Table 2). These two species had more live than dead sprouts, while all other species had more dead than live sprouts.

Stump diameter and survival

The mixed logistic regression models showed no significant relationship between diameter and stump survival, irrespective of whether site was included as random factor or not. For two species, the models gave P values between 0.05 and 0.1, in *A. glutinosa* with weak tendency for lower survival of larger stumps ($P = 0.098$, with site as random factor: $P = 0.073$), and in *S. caprea* with weak tendency for higher survival of larger stumps ($P = 0.054$, with site as random factor: $P = 0.076$). The model statistics for remaining species (P values 0.20–0.90) can be obtained

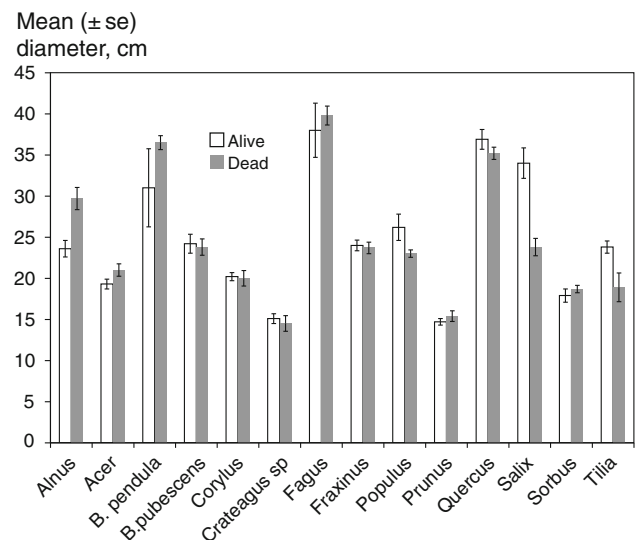


Fig. 2 Mean \pm SE diameter (cm) for live and dead stumps of 14 species 9 years after thinning in 25 mixed oak-rich forest. Full names of species: *Quercus robur/Q. petraea*, *Populus tremula*, *Betula pendula*, *Sorbus aucuparia*, *Betula pubescens*, *Fagus sylvatica*, *Acer platanoides*, *Alnus glutinosa*, *Fraxinus excelsior*, *Prunus avium*, *Salix caprea*, *Tilia cordata* and *Corylus avellana*

online as supplementary material (see first page of this article; can also be obtained from the authors).

Figure 2 shows mean diameter of live stumps and dead stumps for each of the 14 species, with the tendency for differences in *A. glutinosa* and *S. caprea* (non-significant with logistic regression). With respect to direction of differences, in 6 species, the stumps that were alive had on average smaller diameter than had the dead ones and in 8 species the stumps that were alive had on average larger diameter than had the dead ones (Fig. 2).

Survival in different species

Nine-year survival rate of stumps differed markedly between species and was lowest for *P. tremula*, *F. sylvatica* and *B. pendula* (8–10 %) and highest for *T. cordata* and *C. avellana* (85–95 %); the other species formed a continuum between these extremes (Fig. 3). Because stem diameter had no relationship to survival, we excluded diameter as variable when we compared the species. Species survival was analysed with site as random factor. Pair-wise differences between species in stump survival were significant in 55 of 91 tests; 33 of the 55 with $P \leq 0.001$ (Table 3), suggesting that most of the differences are reliable.

Sprout height of surviving stumps

We found no effect of stump diameter on maximal sprout height; P values for diameter effect ranged from 0.31 to 0.91

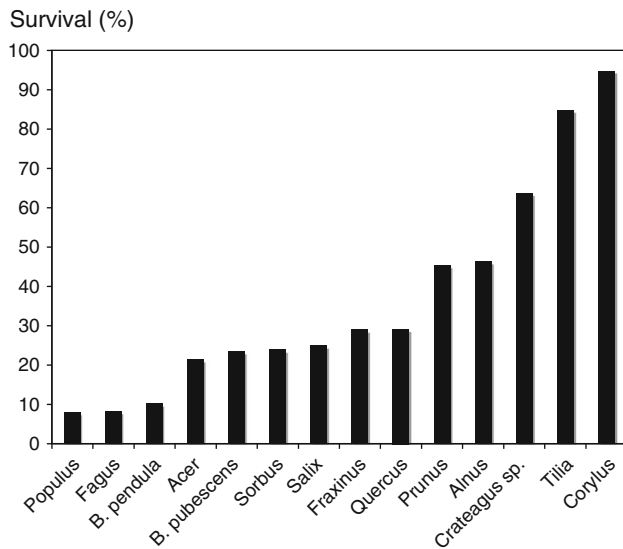


Fig. 3 Nine-year survival of stumps of 14 species after thinning in 25 mixed oak-rich forests. For full names of the species, see legend of Fig. 2. Sample sizes of stumps: *Populus* 187, *Fagus* 36, *B. pendula* 59, *Acer* 85, *B. pubescens* 81, *Sorbus* 67, *Salix* 24, *Fraxinus* 124, *Quercus* 161, *Prunus* 22, *Alnus* 54, *Crateagus* sp. 11, *Tilia* 59, *Corylus* 75

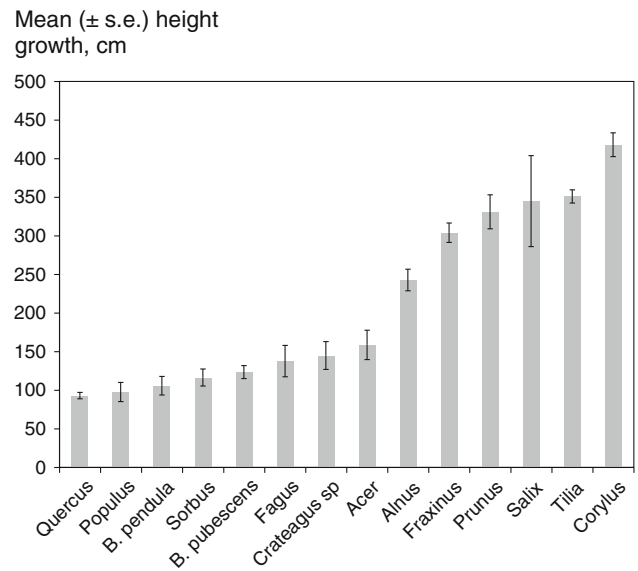


Fig. 4 Mean \pm SE maximal height growth of stumps (sprouts, cm) in 14 species 9 years after thinning in 25 mixed oak-rich forests. For full names of the species, see legend of Fig. 2. Sample sizes of stumps: *Quercus* 45, *Populus* 15, *B. pendula* 6, *Sorbus* 16, *B. pubescens* 18, *Fagus* 3, *Crateagus* sp. 7, *Acer* 18, *Alnus* 25, *Fraxinus* 39, *Prunus* 10, *Salix* 6, *Tilia* 49, *Corylus* 71

(mean value 0.56). Maximal sprout height varied among the sites for five species, i.e. in five of ten models where site was included as random factor; for *F. excelsior* ($P = 0.04$), *P. tremula* ($P = 0.00$), *Q. robur/Q. petraea* ($P = 0.02$), *C. avellana* ($P = 0.00$) and *T. cordata* ($P < 0.01$).

Mean maximal sprout height of surviving stumps varied markedly among species, with lowest height in *Q. robur/Q.*

petraea (mean value 93 cm), highest in *C. avellana* (mean value 419 cm) and with the other eight species in a continuum between these extremes (Fig. 4). Across the 14 species, stump survival and mean maximal height were positively correlated (Spearman’s $r_s = 0.65$, $P = 0.012$), which is illustrated in Fig. 5.

Table 3 Pair-wise tests of differences between stump survivals for 14 species, in mixed logistic regression models with site as random factor

	Alnus	Acer	B. pend.	B. pub.	Coryl.	Crat.	Fagus	Frax.	Pop.	Prun.	Querc.	Salix	Sorb.	Tilia
Alnus		0.000	0.000	0.002	0.000	–	0.005	0.001	0.000	–	0.004	–	0.006	0.001
Acer			–	–	0.000	0.001	–	–	0.010	0.004	–	–	–	0.000
B. pen.				0.000	0.000	–	–	–	0.001	0.013	–	–	0.000	
B. pub.					0.000	0.007	–	–	0.000	0.032	–	–	0.000	
Coryl.							0.025	0.000	0.000	0.000	0.001	0.000	0.000	–
Crat.								0.003	0.003	0.000	–	0.008	0.025	0.008
Fagus									–	0.011	–	–	–	0.000
Frax.									0.000	0.019	–	–	–	0.000
Pop.										0.000	0.000	0.007	0.000	0.000
Prun.											0.041	–	0.039	0.030
Querc.												–	–	0.000
Salix													–	0.000
Sorb.														0.000

P values below 0.05 are given; for estimates of survival of species, see Fig. 3

Full latin names are given in Table 2

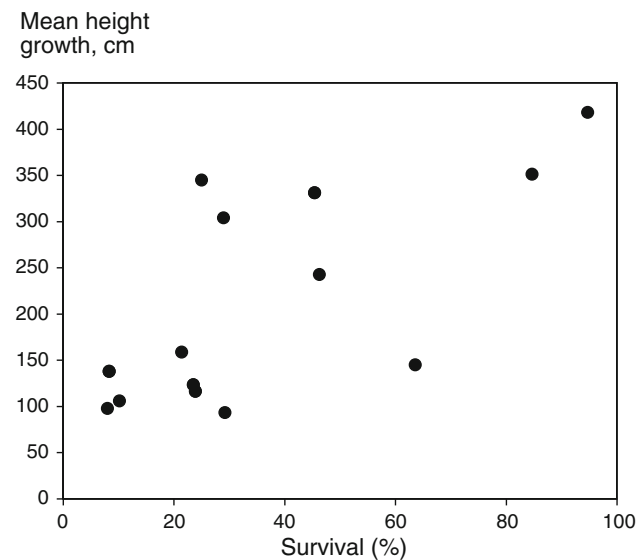


Fig. 5 Correlation between survival and maximal height growth of stump sprouts among 14 species after thinning in 25 mixed oak-rich forest. Each dot represents one species (for species included, see legend of Fig. 2)

Discussion

Nine years after thinning, stump diameter of the woody species was not correlated with the degree of sprouting, but the species differed markedly in survival and sprout growth, and thus formed a continuum in degree of sprouting. These species should therefore not be classified as ‘sprouters’ or ‘non-sprouters’, at least not in their response to thinning. The results support Vesik and Westoby’s (2004) conclusion that woody species form a continuum of sprouting response after less intense disturbances (after strong disturbances, the dichotomy ‘sprouter’ or ‘non-sprouter’ may be useful, see Vesik and Westoby 2004). One could argue that conifers such as *P. abies* may be classified as ‘non-sprouters’ and angiosperms might broadly be classified as ‘sprouters’. However, if we added *P. abies* and *P. sylvestris* in our dataset, they would extend the continuum of sprouting response to thinning in the mixed forests studied.

Stump diameter versus survival and growth

The absence of effect of stump diameter is consistent with a recent study of *T. cordata*, *Quercus petraea*, and *Carpinus betulus* L. (Matula et al. 2012). An 85-year-old forest was harvested to recreate coppice, with residual *Q. petraea* basal area of 0–10 m² ha⁻¹. A negative effect of increasing stump diameter on survival was found for *Q. petraea* only, all *T. cordata* (except one) survived and survival in *C. betulus* tended to increase with stump

diameter. Sprouting was strong in *T. cordata* and clearly lower in *Q. petraea*, like in our study. Residual basal area had only marginal effect on survival and growth, but it was 35 % or less of the remaining basal area at our sites.

Stumps were studied 9–10 years after cutting in *Betula pubescens* and *B. pendula* (Johansson 2008) and in North American *Quercus* spp. (Weigel and Peng 2002). Both studies were of clear-cuts and the *Betula* site was planted with *Picea abies*. Nine-year survival of *Betula* stumps (55–61 %) was much higher than in our study, and sprouting ability and biomass production increased with stump diameter. In contrast, in the *Quercus* spp., sprouting and competitive success decreased with increasing parent tree age and diameter at breast height (Weigel and Peng 2002; see also Splichalova et al. 2012).

One possible explanation for the absence of diameter relationships in our study is that small diameter stumps, 9 cm or less, were not included. In his review, Del Tredici (2001) stated that many trees sprout more vigorously as saplings (defined by him as >2 cm and <15 cm in dbh) than as mature trees (defined as >15 cm dbh). If this is generally true, one expects a similar pattern for the 14 species in our study, which is not the case. Most earlier studies concern forests with a single species and/or coppicing with small diameter stems/stumps (e.g. Harrington 1984; Rackham 1998; Weigel and Peng 2002). In contrast, our mixed initially closed-canopy forests contained many tree and shrub species, and about 74 % of the original basal area remained after conservation thinning. Inter- and intraspecific competition is therefore likely to be important. Some or many small trees are suppressed in such forests and are in worse condition than large trees. Therefore, we suggest that survival probability within species may become relatively equal across diameters after thinning, when cut individuals compete with the remaining overstory trees that expand their roots and canopy. More work is needed to evaluate this general hypothesis.

Differences between species, and factors influencing growth

The sprouts may be supported by resources in the root system and/or in above-ground parts, but this has been studied in few species (Sakai and Sakai 1998; Del Tredici 2001; Luostarinen and Kauppi 2005). We found that *C. avellana* was the most successful species. This was the case also when we quantified regeneration by recording stems growing above breast height after the thinning (J. Leonardsson and F. Götmark, in preparation). *C. avellana* was common in the undergrowth at our sites (Götmark et al. 2005) and has colonized many abandoned pasture woodlands—in one Swedish site where grazing ended in 1922, crown cover of *C. avellana* increased from 10 to 80 % in

70 years (Kardell and Fiskesjö 1999). *C. avellana* may be persistent in the understory, expand into gaps, and its shoots are not much browsed (Götmark et al. 2005; Szymura et al. 2010).

The growth of *C. avellana* sprouts varied among sites; variation in competition, productivity, and browsing by roe deer, moose, and cattle (one site) contribute to this variation (see also Joys et al. 2004). Strong sprout growth occurs also in the North American *Corylus americana* after cutting, and the growth was four times higher in relatively open than in shaded habitats (Pelc et al. 2011). *T. cordata* survived best and grew tallest among the trees, and its growth also varied among the sites. At some of our sites, a few large stumps of *T. cordata* produced lots of tall sprouts, which may explain part of this variation. Pigott (1991) stated that stump sprouts of *T. cordata* form roots separated from old roots.

Susceptibility to competition from remaining trees and shrubs, and increasing cover of herbaceous plants after thinning, was probably important in the differential growth rate among the species. In addition, fungi often attacked *F. excelsior*, *P. tremula* and *Q. robur/Q. petraea* leaves (oak wilt). Many studies have shown that browsing negatively affects growth rate of seedlings and saplings of especially *Q. robur/Q. petraea*, *P. tremula*, *S. aucuparia*, and *S. caprea* (e.g. Wam and Hjeljord 2010; Månsson et al. 2007). We observed sprouts that had been browsed by ungulates, but we have no browsing data for stumps covering 9 years. Before thinning at our sites, the browsing pressure was generally higher on seedlings/saplings of *Q. robur/Q. petraea*, *S. aucuparia*, *A. platanoides*, and *F. excelsior* than on seedlings/saplings of *C. avellana* and *T. cordata* (Götmark et al. 2005; the other species had few seedlings/saplings). Pigott (1991) stated that the leaves of *T. cordata* contain cyanin.

The stumps in our study were more or less shaded, and shade tolerance in the species might influence growth. One shade-tolerant tree (*T. cordata*) was successful, but two other such trees (*F. sylvatica*, *A. platanoides*) were not more successful than shade-intolerant trees (*B. pendula*, *B. pubescens*, *P. tremula*) and mid-tolerant trees (*Q. robur/Q. petraea*, *S. aucuparia*). *A. platanoides* sprouted, but most sprouts had died after 9 years, while *F. sylvatica* had few live sprouts. Shade-tolerant trees often have thin bark and the bark of *A. platanoides* and *F. sylvatica* (and *S. aucuparia*) had partly fallen off the stumps, which might contribute to weak sprouting if many buds in the bark then die.

In Sweden, *A. glutinosa* is known to be difficult to kill by felling. The bark of *A. glutinosa* was almost intact after 9 years. Yet, more than 50 % of the *A. glutinosa* stumps died, and five other species had higher growth rate than *A. glutinosa*. This may be due to a high level of competition after thinning, when many trees/shrubs remain and sprout.

Normally, *A. glutinosa* sprouts vigorously after felling on moist soils, where it often dominates the forests. *P. tremula* and *Prunus avium* also have root suckers, which were not measured in our study. *P. avium* is not common at our sites and the root suckers of *P. tremula* tended to die back due to shade and fungal attack (pers. obs.). In a clear-cut in Canada, dieback in root suckers of two related trees (*Prunus pensylvanica* and *Populus tremuloides*) was much faster than in two species that sprouted from stumps there, *Corylus comuta* and *Alnus ciridis* (Mallik et al. 1997). The authors suggested that this result could be explained by competition between the two groups of trees.

Implications for management

Our 9-year study is useful for management that seeks to shape particular forest types or that seeks to favour (or disfavour) certain species. Conservation thinning to favour oak regeneration by sprouting may fail if *C. avellana*, *T. cordata*, and other strongly sprouting species occur in the forest. If the focus is oak regeneration by sprouting, cutting more of the overstory to provide more light, and fencing against ungulates, may be necessary (Matula et al. 2012; Pyttel et al. 2013). For combinations of careful thinning and biodiversity, shifting some mixed oak-rich forests to contain more of *T. cordata*, *C. avellana*, *Crataegus* spp., and other species can be valuable for biodiversity in a regional or local context (Kennedy and Southwood 1984; Koorem and Moora 2010; Jonsell 2012). Finally, our results also have relevance for biomass harvest based on the species and forest types studied, and for combinations of biodiversity conservation and biomass harvest.

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