Immediate Response to Artificial Burning and Cutting in Young Trees of Beech (*Fagus sylvatica* L.) and Oak (*Quercus robur* L.)

- Survival, resprouting ability and tree vigour

Omedelbara effekter av bränning och nedklippning hos unga träd av bok (*Fagus sylvatica* L.) och ek (*Quercus robur* L.)

- Överlevnad, skottskjutningsförmåga och vitalitet

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Sammanfattning

Målet med studien var att se hur bränning med propanbrännare och klippning av huvudstammen påverkade överlevnad, skottskjutning och vitalitet hos unga bokar (*Fagus sylvatica* L.) och ekar (*Quercus robur* L.) under första säsongen efter behandling. Behandlingarna utfördes vid två tillfällen under vegetationssäsongen – i maj och i juli – för att se om tidpunkten hade någon betydelse för hur träden påverkades. De nya skotten räknades och mättes två gånger på de tidigt behandlade träden och en gång på de träd som behandlades sent. Vitaliteten bedömdes genom att jämföra bladfärgen med en färgskala som gick från grönt via gult till brunt. Eftersom mätningarna gjordes under första vegetationssäsongen efter behandlingarna var det svårt att avgöra överlevnadsfrekvens och vitalitet hos de avsågade träden. Möjligheten finns att träd som inte gjorde några nya skott under första vegetationssäsongen kommer att göra det i framtiden. Överlevnaden hos brända bokar och ekar skilde inte mycket mellan arterna under den första säsongen, men grövre träd visade en betydligt högre överlevnad än klenare. Förmågan att skjuta nya skott, liksom vitaliteten, var bättre hos ek än hos bok under första säsongen.

Abstract

Young trees of European beech (*Fagus sylvatica* L.) and pedunculate oak (*Quercus robur* L.) were burned with a propane-flamer or cut with a hand-saw with the intention to study their response, in terms of survival, ability to resprout and tree vigour during the first vegetation season after disturbance. An early burning/cutting was performed in May and a late one in July, to see if the response was different because of the time of the year. New sprouts were counted and measured twice on the early treated trees and once on those treated late. The vigour of the trees was determined through comparing the leaf-colour of the trees to a colour-scale. In such an early stage the survival and vigour of the cut trees was hard to determine, because they may need more than one season to start resprouting. The survival of the burned beech and oak trees did not differ much during the first season, but larger trees survived to a much higher extent than thin ones. The ability to make new sprouts as well as the tree-vigour was better for the oaks than for the beeches during the first season.

Introduction

Two thousand years ago, southern Sweden was covered by deciduous forests with lime (*Tilia*), Oak (*Quercus*), alder (*Alnus*) and birch (*Betula*) in mixture with pine (*Pinus*) (Björse & Bradshaw 1998). At that time, the dominants in the region today – Norway spruce (*Picea abies*), Scots pine (*P. sylvestris*) and European beech (*Fagus sylvatica* L.) (Björse & Bradshaw 1998; Lindbladh 1998; Björse 2000), had a very different distribution and abundance in southern Sweden. Norway spruce had its southernmost outpost in Östergötland and Dalsland in mixtures with Scots pine and birches. Scots pine was more common in the eastern parts of the region, closely linked to areas with frequent fires (Björse & Bradshaw 1998), and the European beech had not yet entered the scene from the south (Hannon et al. 1999).

Webb (1987) and Huntley & Webb (1989) claim that, in North America and Europe, climatic change has been the main factor for alteration of plant communities over the last thousands of years. Others (Abrams 1992; Clark et al. 1989; Tinner et al. 1999; Svenning 2002) claim that fire (human and natural) has been shaping the landscape for millennia. In Europe it has also been suggested that human activities (directly and indirectly), climate change and natural disturbances have acted together in driving the alterations that have occurred (Björse & Bradshaw 1998), and that human impact has been the primary factor for the last one thousand years (Lindbladh et al. 1998).

From studying pollen diagrams, it can be seen that pedunculate (*Q. robur* L.) and sessile (*Q. petraea*) oak and hazel (*Corylus avellana*) were much more common in the virgin forests of Europe than they are today (Vera 2000). Vera (2000) claims that what made it possible for them to persist, was heavy grazing by large wild herbivores, such as aurochs (*Bos primigenius*), European bison (*Bison bonasus*) and red deer (*Cervus elaphus*). Those animals contributed to create an open park-like landscape with big trees, where succession of young trees took place in thorny scrubs (e.g. *Crataegus*, *Juniperus*). Some (Tinner et al. 1999; Vázquez et al. 2002) suggest instead that different oak-species (among others pedunculate oak) and partly also hazel (Clark et al. 1989; Tinner et al. 2000; Svenning 2002) benefited from fires, while European beech was disfavoured (Tinner et al. 1999; Tinner et al. 2000; Vázquez et al. 2002). Many of the fires were human-caused that later ceased due to migration and changes in agricultural practises (Clark et al. 1989).

It is well known and accepted that pines have adaptations to frequent fires (Agee 1998), but whether also pure deciduous stands has been burning occasionally is still debated (Lindbladh & Bradshaw 1998; Hannon et al. 1999; Tinner et al. 1999; Vera 2000; Vázquez et al. 2002). In North America, suggestions have been made that many of their oak-species are adapted to, and even dependent on, forest fires for their large-scale existence (Crow 1988; Abrams 1992; Dey & Guyette 2000; Brose et al. 2001). Important morphological features, which make them successful competitors after fire in comparison with other deciduous species, have been detected in American oaks. For example the oaks have thick bark which provides good insulation for the cambium during fires (Lorimer 1985; Crow 1988; Abrams 1996; Dey & Guyette 2000), good resprouting ability after heat stress (Huddle & Pallardy 1996; Huddle & Pallardy 1999) and a great number of dormant/adventitious buds situated just under the surface of the mineral soil, where they are protected from the heat of fires (Dey & Guyette 2000). The removal of grass in the fire takes away the protection for rodents, which are main predators on acorns (Lorimer 1985). Oaks do not rot easily after cambial damage, their roots go deeply into the soil, and ground conditions after fire provide good growing-ground for acorns (Abrams 1996). Whether some of this is also true for central-European oaks (pedunculate and sessile oak), is little investigated, but there are indications that they possess at least some degree of adaptation to fire (Lindbladh & Bradshaw 1995; Lindbladh & Bradshaw 1998; Tinner et al. 1999; Vázquez et al. 2002; Niklasson et al. 2002).

Today, in forests left to free development, light-demanding trees like pedunculate and sessile oak have problems to compete with more shade tolerant species, when domestic animals and fire are banned from the forests (Niklasson et al. 2002). Pedunculate and sessile oaks are crucial as host trees and feeding-places for many threatened species, for example for a great number of wood-living insects (Jonsell et al. 1998), and therefore it is important that oaks remain a common member in our tree flora.

In North America a decline in oak regeneration coincides with effective fire suppression programs, which were initiated during the early 1900's. American researchers are now trying to reintroduce fire as a means of management, to secure the regeneration and to stop the loss of oaks that is taking place. (Abrams 1996; Brose et al. 1999; Dey & Guyette 2000) It is often proposed that both American and European oaks have problems to regenerate under closed canopies (Abrams 1996; Löf et al. 1998), and Abrams (1996) suggests that the competition from seedlings of more shade-tolerant species is an important reason for this. The remedy for the regeneration problem might be the use of fire to reduce the number of competing species like for example American (*F. grandifolia*) and European beech that, some suggest, has seedlings that are more fire-sensitive than oak-seedlings (Barnes & Van Lear 1998; Brose & Van Lear 1999; Brose et al. 1999). Experiments with the aim to test this hypothesis have come up with ambiguous results. Barnes & Van Lear (1998), Brose & Van Lear (1999) and Brose et al. (1999) found that seedlings of American oaks would benefit from fire treatment, while the opposite was true for McGee et al. (1995), who found that American beech seedlings increased more than northern red oak (*Q. rubra*) after fire. Besides the shade and competition problem for oak regeneration, there is the problem of predation of acorns (Watt 1919; Abrams 1996; Löf et al. 1998). Abrams (1996) suggests that using fire may also reduce this loss.

The subject of oak regeneration also has implications for forest restoration. One of the aims of forest restoration is to bring back disrupted ecosystems to their 'natural' state, or at least to make them resemble such an ideal state as much as possible. The idea is that humans should mimic natural processes to speed up the transformation to the 'original' state on a particular site. The restoration is thought to reduce the risk of losing rare and fragile ecosystems, which earlier has been altered by man. (Moore et al. 1999; Stanturf & Madsen 2002) It is previously known that many conifer species have adaptations to fire (Weaver 1974; Kimmins 1987; Moore et al. 1999), and burning with different intensities can therefore be used as a tool when restoring conifer plant communities. When considering alternative ways of restoration of hardwood ecosystems, it is important to know if some of these species, for example oaks, also show characteristics for fire adaptation.

Interestingly, very little research on fire adaptations in different tree-species has been performed in Europe, and therefore the main goal of this study was to analyse if young trees of pedunculate oak and European beech respond differently to fire-disturbance. The specific objectives were: (1) to analyse differences between young oak and beech in sprouting capacity in the season following artificial burning and cutting (2) to examine survival and tree vigour in young oak and beech during the season following artificial burning and cutting. The results are discussed with the aim of providing guidance to forest managers in forest restoration efforts.

Material & Methods

Experimental design

For the study formerly established experimental blocks, located on former agricultural land on the grounds of the Swedish University of Agricultural Sciences at Alnarp (55°40′N/13°10′E, 15m a.s.l.), were used. The site was flat and the soil texture was sandy loam. Bare-rooted seedlings were planted, and seeds of beech and oak were sown, in April 1995 and 1996, in four blocks (figure 1). In each block four rows of beech and four rows of oak were randomly placed. The distance between the individual trees in each row was 0.5 m, and between the rows 1.25 m. (Löf 1999) Since the planting and sowing there have been a certain rate of mortality among the trees, why the spacing was more irregular when the present study started. Before this study began the blocks had been left unattended since 1998.

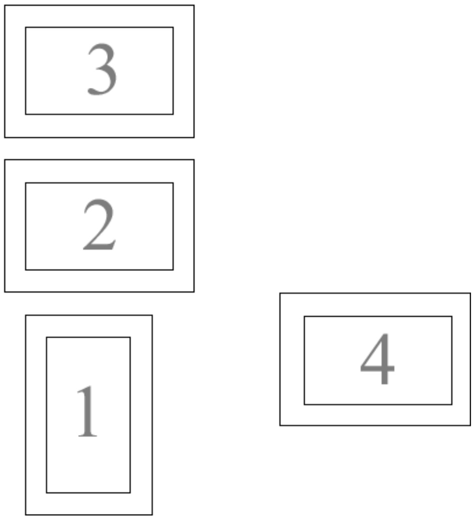


Figure 1. The experimental blocks at Alnarp, with four rows of beech and four rows of oak in each block.

For the present experiment only the former untreated control and mowing-treatment were used. The pre-conditions in those two did not differ considerably from each other, and changes that occurred after abandonment of the former experiments have made them very similar.

Today the ground in the experimental blocks is covered by grass. The trees vary in height from approximately 0.5 - 4 m. The great variation in tree-height might be due to dense initial spacing or to the competition from the grass.

Climate

Climate-data were taken from a SMHI (Swedish meteorological and hydrological institute) weather station in Malmö, ca. 8km southeast of the study area. The average temperature during the vegetation period (March - September in southern Sweden) was 13.0°C, and the total rainfall was 330 mm. The normal average temperature between 1961-1990, for the same months, was 11.5°C, and the normal total rainfall (1961-1990) was 290 mm. From this it can be seen that it was warmer during the vegetation season year 2003, than it normally is in the area. For average temperatures and rainfall month-wise see table 1.

Table 1. Climate data from Swedish meteorological and hydrological institute (SMHI) (2003) in Malmö.

	Average temperature 2003 (°C)	Rainfall 2003 (mm)	Normal temperature 30 years (°C) 1961-90	Normal rainfall 30 years (mm) 1961-90
March	3.1	11	2.0	40
April	6.9	45	6.0	38
May	12.7	58	11.3	41
June	16.5	54	15.3	52
July	18.9	90	16.5	61
August	18.3	36	16.4	58
September	14.5	36	13.0	59

Selection of trees for the treatments

The diameters of the trees were measured to the nearest mm, at 30 - 50 mm height above ground, with a calliper or a slide-calliper. Oval trees were measured somewhere between the thickest and the thinnest place of the stem. Stems with gnaw-marks were treated as the oval ones and trees with multiple stems were removed from the sample. A small number of stems were divided close to the ground or had branches very low. They were measured under the division, or only the main stem was measured.

Two diameter-classes were chosen for further treatment: 5 - 35 mm (thin) and 40 - 70 mm (coarse). A gap was left between the diameter-classes to make the two classes more different from each other. Five trees of each species, in each diameter-class and for each treatment were selected from each block. In block number 4, there were not enough beech trees in the thin diameter-class, why there were only ten instead of twenty-five trees in that class. This means that 100 trees from each block (85 from block 4) were included in the study (5*2*2*5*4), making a total of 385 trees.

Treatments

The five treatments in the study were BE-burn early, CE-cut early, C-control, BL-burn late and CL-cut late (figure 2). All treatments were performed on both beech and oak. Treatments were randomly selected in MINITAB (Minitab Inc., USA) (Calc - Random data - Sample from columns). Each tree was marked with a specific number and a letter-code for the treatment.

The cutting was done at a height of 50-100 mm above the ground, with a handsaw or a pair of secateurs. The equipment used for the burning was a propane-flamer with open burners (Ascard 1995). A stopwatch was used to note the time during which each plant was burned. Larger individuals (>30 mm) were in the flame around one minute and small ones about thirty seconds. The burning was done just above the ground and the nozzle was directed towards the stem from all sides (figure 3).

Figure 2. All treatments in the study – BE, BL, CE and CL.
Photo: Sven Birkedal

Figure 3. The nozzle of the burner directed towards the stem from all sides.
Photo: Sven Birkedal

The early cutting (CE) was performed on May 7th and the early burning (BE) on May 8th. At the time when CE and BE treatments were done the beeches were flushed to approximately 80%, and the oaks had just started to open the buds. The late cutting (CL) was done on June 30th and July 3rd. The late burning (BL) was started on July 3rd., but as a consequence of the heavy rain that day the burning was completed on July 5th. At the time of the late treatments both tree-species were fully flushed and in a stage of shoot elongation.

Measurements

In the first measurement, on July 19th, all new sprouts were measured from the stem/ground to the outermost tip of the longest leaf. The number of sprouts on each tree was counted, except where the sprouts were so small and so many that separate counting was impossible. In that case their numbers were estimated in classes of ten and their length in classes of 5 mm. The origination-point of the new sprouts was recorded to either S – stem over the soil surface, or M – stem in the mineral soil. (On September 23rd twenty trees of the burn treatments (BE, BL) were checked to see where the sprouts appearing from the mineral soil, originated from. The soil around the sprout was dug away to find out whether the sprout started from the roots, or from the stem below ground. Only four of the investigated trees were beeches.) The original stem of some trees seemed to have died as a result of their treatment; if that was the case it was noted. To be considered as dead the leaves on the original stem should be either brown or missing. Whether the tree had made new sprouts or not, was not taken into account when deciding if it had survived – just the original stem was considered. In this study only immediate mortality was measured, which means that only the mortality during the first season after the treatments was recorded. In the first measurement only treatments BE and CE, were included, because the trees in the late treatments (BL, CL) had not shown any sign of response.

In the second measurement, September 24th to 26th, the response of trees in all treatments (BE, CE, C, BL and CL) was analysed. This time survival, sprout-lengths, number of sprouts and point of origin of sprouts was noted, but also leaf-colour and if the cambium on the burned trees had grown over the burned area. Leaf-colour was compared with a scale of eight colours, from green via yellow to brown. For this colours from Butinox (Jotun Paints Europe Ltd.) were used:

1: 7020-G30Y (dark green)
2: 5040-G30Y (green)
3: 2060-G70Y (light green)
4: 2040-G70Y (yellow-green)
5: 1040-Y (light yellow)
6: 4551 (sun-yellow)
7: 3050-Y20R (grey-brown)
8: 5040-Y60R (red-brown)

The incoming light - photosynthetic photon flux density (PPFD) in $\mu mol\ m^{-2}\ s^{-1}$ was measured with a photometer (LI-190 SA, LiCor, NE, USA), at a height of approximately one meter above ground, by each tree. The light-availability was taken as a measurement of the aboveground competition. The measurements were performed on October 28, which was a cloudy day. The sun appeared for about fifteen minutes, while the measurements for the last part of block 3 were taken.

Statistical analysis

The statistical analysis was done in MINITAB. Mean values were calculated from each block and put into the model. Samples where the values were close to a normal distribution were analysed in ANOVA - General linear model, and the rest were analysed in Nonparametrics - Friedman. The computer produced a value for the level of significans. If the P-value was less than 0.05, pedunculate oak and European beech were considered to respond differently to the treatment.

Results

The survival after burning did not differ considerably between pedunculate oak and European beech. There were by far more dead trees (ca. 70 %) in the thin diameter class than in the coarse class (ca. 5 %) for both species. The resprouting after disturbance started faster in the oaks than in the beeches, and the oak-sprouts grew much longer.

Survival

Pedunculate oak and European beech showed no significant difference in immediate mortality within diameter class and treatment. The immediate mortality of the original stem (figure 4), among the burned trees, was considerably higher for the thin trees than for the larger trees (figure 5). The mortality of the control trees in the thin diameter class was much lower (ca. 5 %) than the mortality of thin burned trees (ca. 70 %). There was no significant difference in survival between early and late burned trees for either species.

Figure 4. Beech tree in thin diameter class where the original stem is dead.
Photo: Sven Birkedal

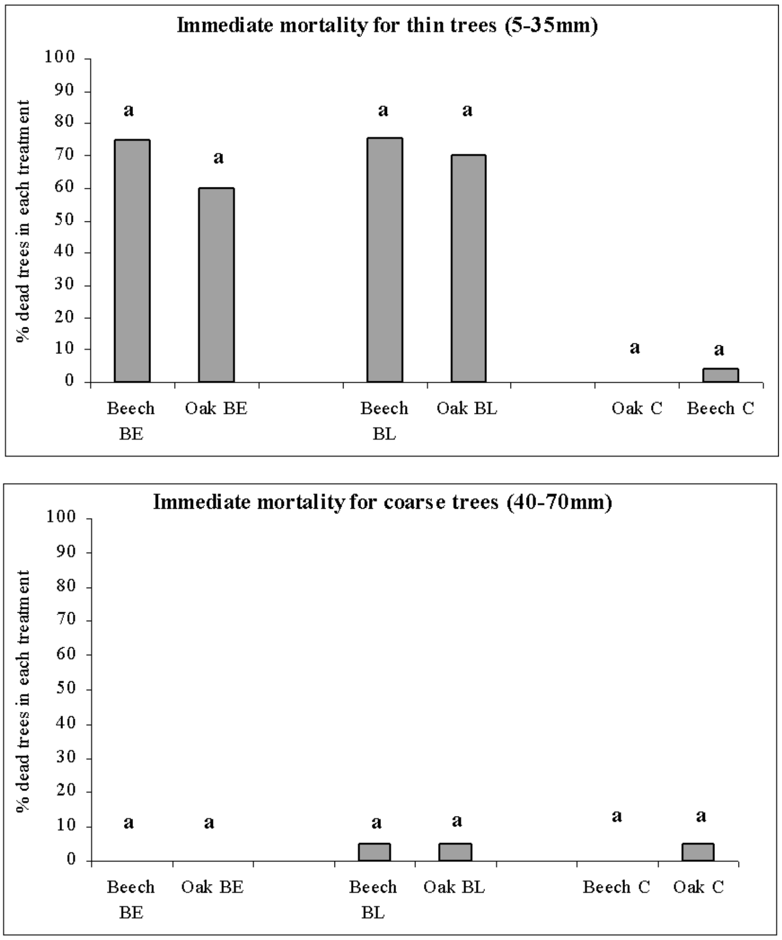


Figure 5. Percent of trees (mean value of blocks 1-4) in burn treatments (BE-burn early, BL-burn late) and control (C), where the original stem died during the first vegetation season. Different letters above the columns indicate statistically significant differences (P<0,05) between beech and oak.

Resprouting ability

In general oak (figures 6a & b) produces more biomass (total length of sprouts) than beech during the first vegetation season after disturbance (table 2). It is most visible for the burn-treatments, where oak has greater length of sprouts per tree, in both July and September and for both diameter classes (Only strictly significant for the thin diameter class ($P<0,05$)). Oak also responded quicker than beech did.

Table 2. Mean number of sprouts and mean length of sprouts per tree (mean value of blocks 1-4), in July and September, for all treatments (BE-burn early, BL-burn late, C-control, CE-cut early, CL-cut late). Statistically significant difference ($P<0,05$) between beech and oak, for the same treatment and diameter class, indicated with different letters.

∅ 5-35mm	Mean no. of sprouts/ tree (July)		Mean no. of sprouts/tree (Sept)		Mean length of sprouts/tree (July) (cm)		Mean length of sprouts/tree (Sept) (cm)	
Beech BE	0	a	2,4	a	0	a	25,7	a
Oak BE	4,3	b	3,9	a	153,5	b	206,3	b
Beech BL			3,4	a			14,2	a
Oak BL			3,2	a			110,1	b
Beech CE	4,3	a	9,8	a	51,9	a	268,8	a
Oak CE	6,9	a	5,8	a	217,0	b	250,3	a
Beech CL			17,3	a			100,8	a
Oak CL			3,6	b			89,7	a
Beech C			0				0	
Oak C			0				0	

∅ 40-70mm	Mean no. of sprouts/ tree (July)		Mean no. of sprouts/tree (Sept)		Mean length of sprouts/tree (July) (cm)		Mean length of sprouts/tree (Sept) (cm)	
Beech BE	0	a	2,9	a	0	a	23,1	a
Oak BE	2,7	b	2,4	a	86,5	a	158,7	a
Beech BL			0,9	a			2,6	a
Oak BL			3,6	b			116,2	b
Beech CE	3,5	a	32,1	a	45,9	a	557,2	a
Oak CE	15,1	b	15,1	b	652,0	b	917,2	a
Beech CL			9,9	a			65,4	a
Oak CL			17,4	b			540,0	b
Beech C			0				0	
Oak C			0				0	

Figure 6a. New sprouts in cut oak.
Photo: Sven Birkedal

Figure 6b. New sprouts in burned oak.
Photo: Sven Birkedal

Some of the trees with great diameter have produced considerable amounts of biomass. There are also large trees that have produced short or no sprouts at all, but there are no thin trees, which have produced a lot of biomass (figure 7). The same relation holds for both investigated tree species. No control trees sprouted during the whole season.

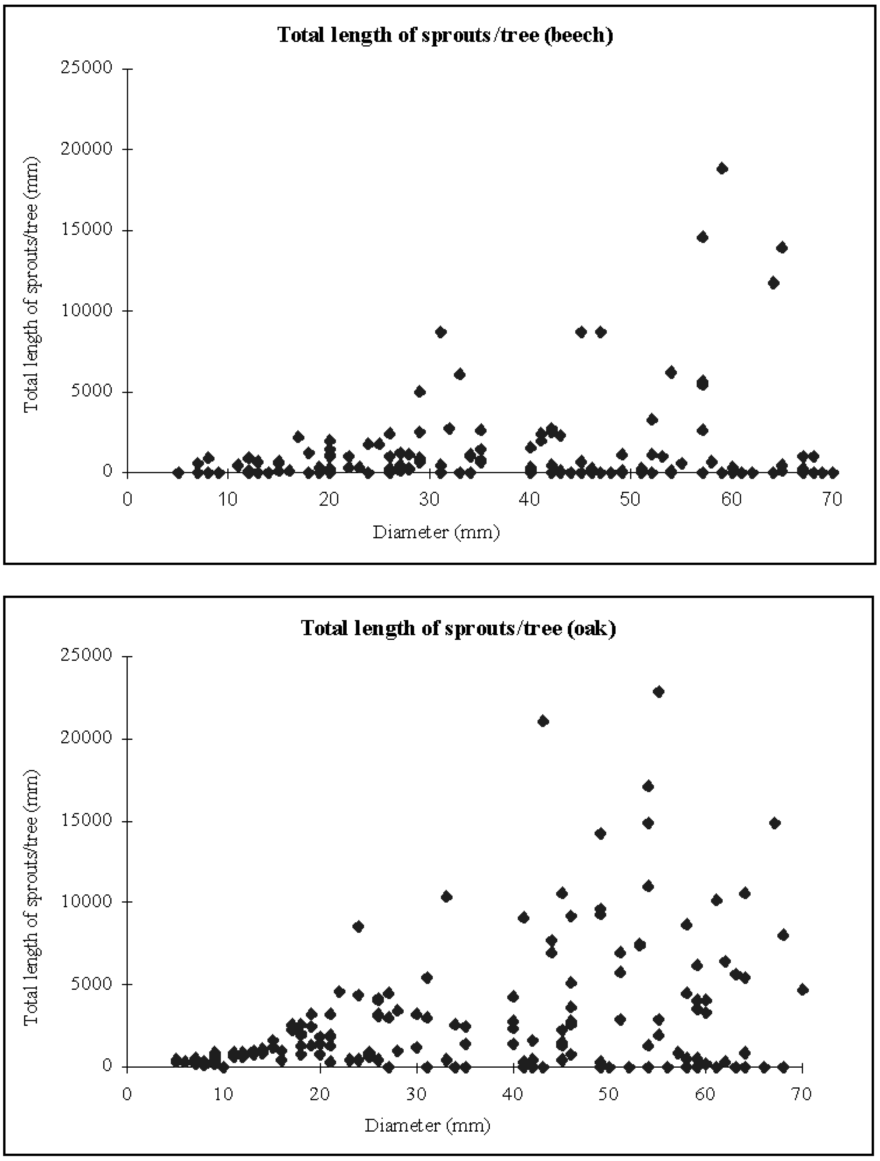


Figure 7. Effect of initial diameter (mm) of the tree on total sprout length/tree (mm). All treatments (BE-burn early, BL-burn late, CE-cut early, CL-cut late) and both diameter classes (5-35mm & 40-70mm) are included.

There were differences in the location of new sprouts in the two species. This also differed between the treatments (figure 8). Most of the cut trees made new sprouts from the stem above the soil, and for beech this was true also for the burn treatments. Oaks, to a larger extent, seemed to form new sprouts under a layer of mineral soil after being burned. Only one tree, a beech where the roots were partly over the soil, had new sprouts starting from the roots.

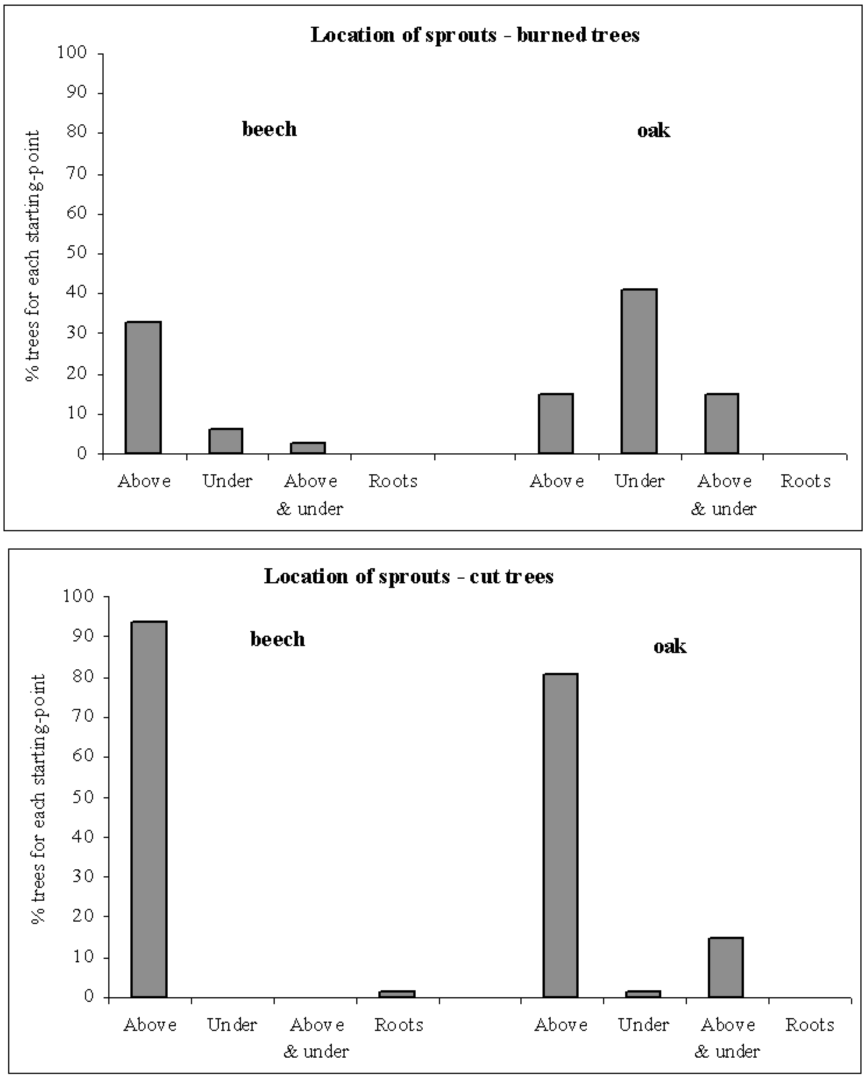


Figure 8. Percent of trees (mean value of blocks 1-4) in burn treatments (BE-burn early, BL-burn late) and cut treatments (CE-cut early, CL-cut late), on which the sprouts originate from the stem above or under the soil surface, both from above and under the soil surface or from the roots of the tree.

The availability of light had no influence on the length of sprouts the trees were able to produce during the first season after treatment (figure 9).

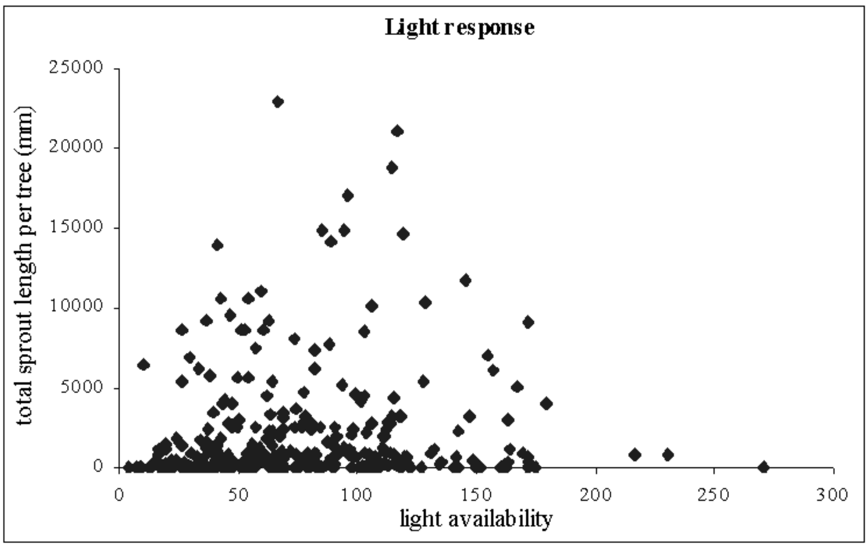
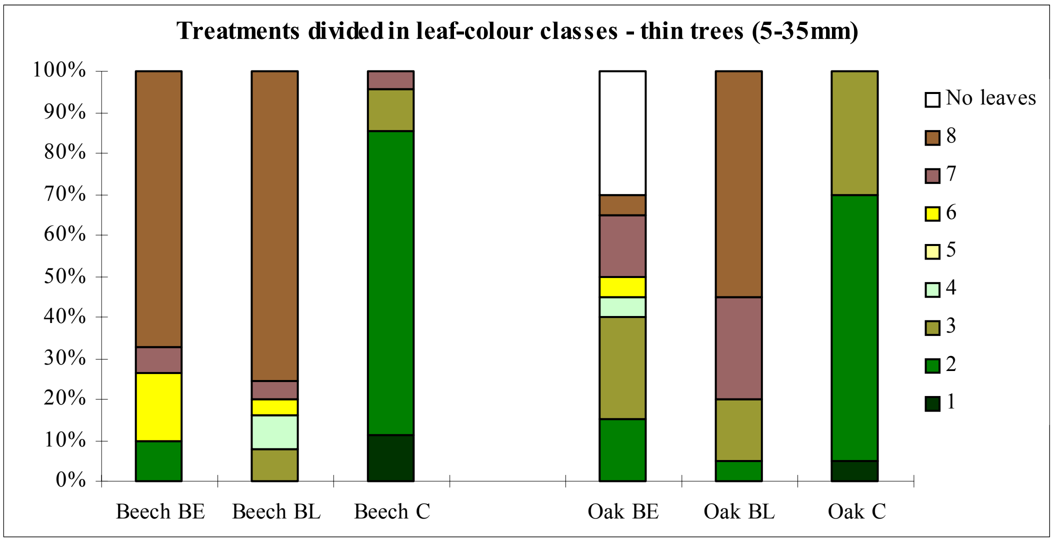


Figure 9. Effect of light availability (photosynthetic photon flux density (PPFD) in μmol m^{-2} s^{-1}) on total sprout length per tree (mm). Treatments BE (burn early), BL (burn late), CE (cut early) and CL (cut late) are included, as well as both diameter classes (5-35mm & 40-70mm).

Tree vigour and cambial regrowth

The leaves of the burned beeches were more yellow (figure 10) than the leaves of the burned oaks (figure 11), and trees in the coarse diameter class had greener leaves than those in the thin class. In general, control trees had more vigorous crowns than burned trees.

Figure 10. Yellow-green colour of leaves in a burned beech.
Photo: Sven Birkedal



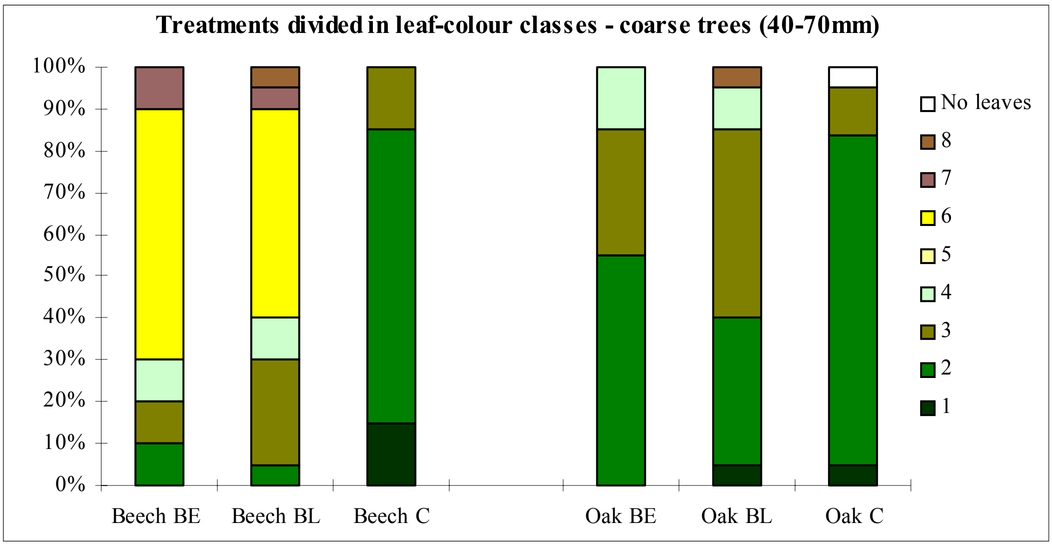


Figure 11. Percent of trees (mean value of blocks 1-4), in each treatment (BE-burn early, BL-burn late, C-control), in leaf-colour classes 1-8 (1-dark green, 2-green, 3-light green, 4-yellow-green, 5-light yellow, 6-sun-yellow, 7-grey-brown, 8-red-brown) or without leaves.

There was no general result of one species showing more cambial regrowth (figure 12) than the other (figure 13). There were, though, more trees in the coarse (40-70mm) diameter class, which had started to grow over the burned area on the stem, than there were in the thin (5-35mm) diameter class. No uniform trend, concerning whether the early or the late burned trees grew the most over the burned area, could be found.

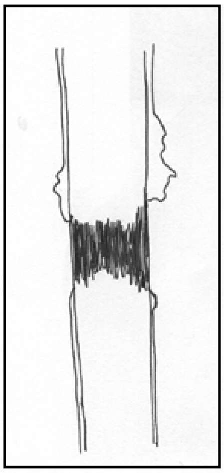


Figure 12. Regrowing of the cambium after burn-damage.

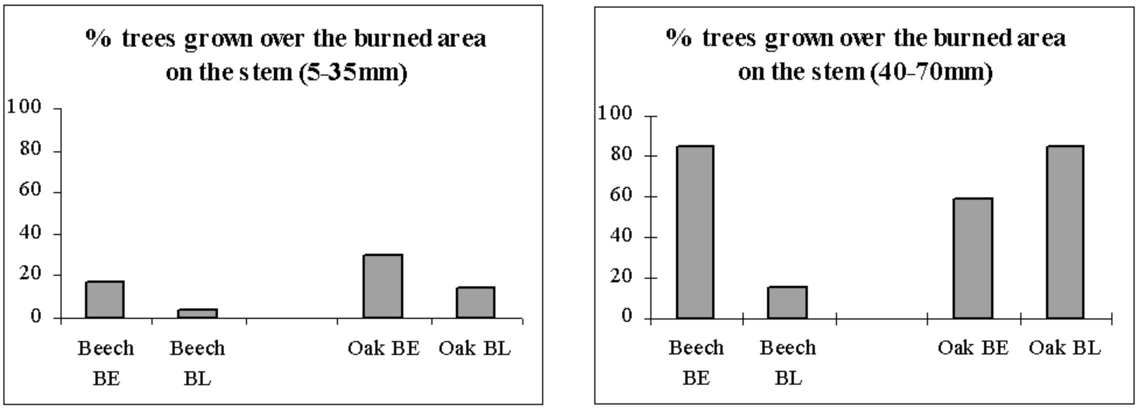


Figure 13. Percent of trees (mean value of blocks 1-4) in the burn treatments (BE-burn early, BL-burn late), which have grown over the area on the stem where the cambium was killed by the burner.

Discussion

Survival

The survival of the original stem during the same season as the trees were burned, did not differ considerably between European beech and pedunculate oak or between early and late treatments. There are though, markedly more dead trees in the thin diameter class than in the coarse class. This is consistent with previous results (Regelbrugge & Smith 1994; Pausas 1997), and might be due to the greater thickness of bark in bigger trees (Vines 1968; Kimmins 1987; Hengst & Dawson 1993). The thicker the bark, the more insulation it can provide for the cambium during an ongoing fire (Kozlowski et al. 1991, Pausas 1997; Dey & Guyette 2000). The intention with the burning was to kill the cambium completely on both coarse and thin trees, but it is possible that this was not fully achieved. Another reason for the better survival in the coarse trees might be that the xylem was harmed more severely in the thin trees and therefore the water transport to the leaves was disrupted (Mats Niklasson, pers. comm.). The survival is higher for both beech and oak among the control trees than in the burn treatments. If cut/burned but unsprouted trees have survived their treatment is hard to tell after only one season. The same criterion as for the burned and control trees - that the original stem is dead - cannot be used for the cut trees. On the cut trees the original stem has been removed and whether or not they will resprout in the future cannot be determined during the first season. There are cut trees for both beech and oak, which have resprouted already, and by this, have proven their survival through the first season. No guarantees can be made for the future survival of neither cut nor burned trees. Gardiner & Helmig (1997) has found that only after seven years do the mortality of water oak (*Q. nigra*) sprouts cease, and therefore it will be risky to try and determine the final survival of the trees until at least seven years have passed since the treatments were performed.

Resprouting ability

After the burn treatment in May (early), European beech needed more time to start resprouting than pedunculate oak. A similar result was visible also after the cut treatment in May, where the beeches indeed had started to make new sprouts, but to a lesser extent than oak. When measurements were repeated later during the season, the beeches had somewhat caught up with the oaks, but still the oaks had a greater sprout-length than beech in all early treatments but the early cut (thin diameter class). Burning and cutting was performed a second time, in July, and when the new sprouts on those trees were counted and measured it was found that, again, oak was the faster resprouter. The fact that oak started the resprouting faster than beech is probably due to oak (northern red oak and white oak (*Q. alba*)) having greater reserves of starch in the roots than many other tree species (Huddle & Pallardy 1999). Huddle & Pallardy (1999) and Ziegenhagen & Kausch (1995) have also found that starch levels in roots are at their minimum in May, why it was expected that the trees in the late treatments would resprout faster than those in the early treatments. European beech does react this way, while pedunculate oak does not. The reason might be that the fluctuations in root starch levels in oak (northern red oak and white oak) are smaller than for other tree species (Huddle & Pallardy 1999). Pedunculate oak has, because of its faster resprouting and its longer sprouts, an advantage compared to European beech when re-colonising an area after disturbance.

Concerning the mean number of sprouts it can be said that the beeches that had resprouted had made a great amount of sprouts, but they were in general not as long as the oak sprouts. The fact that some beeches had made so many sprouts is a possible source of error in the study, because it was hard to be sure that every individual sprout was counted and measured, and only once. The mean number of sprouts per oak tree was higher in July than in September, which might seem a little strange. The reason probably was that some trees had been struck quite hard by oak mildew, which had killed some of the sprouts. The mean length of sprouts per tree was however, greater in September than in July, which suggests that the mildew has not severely disturbed the total biomass production.

After being cut, both European beech and pedunculate oak formed most of their new sprouts from dormant/adventitious buds on the stump, generally from the cambium ring in the cut, but sometimes also from further down on the stump (more common for oak). After burning of beech the largest part of the new sprouts originated from the stem under the burned area, but from over the soil surface. Burned oaks on the other hand, resprouted most frequently from under the surface of the mineral soil, or from both under and above the soil. The strategy to have dormant buds in this location gives northern red oak an advantage after surface fires, because the soil protects the buds from some of the heat during the fire (Dey & Guyette, 2000), while the high temperatures kill buds on the stem. It has been suggested in earlier studies (Malanson & Trabaud 1988) in yet another oak-species, *Q. coccifera*, that after fires new sprouts appear from well-protected buds located under the surface of the soil.

In this study trees which had an initially great diameter occasionally produced large amounts of biomass, while none of the trees with a small diameter reached the same level of biomass production. That trees which are bigger before the disturbance-occasion have a better ability to make many and long new sprouts afterwards, is consistent with some previous research (Pausas 1997; Espelta et al. 2003), and contrary to other (Gardiner & Helmig 1997).

Yet another factor, which might contribute to variation in resprouting frequency and length of sprouts after disturbance, is light availability. From what can be found from this study light availability does not affect any of the studied variables, while other studies (Ziegenhagen & Kausch 1995) show that undisturbed pedunculate oak seedlings under shaded conditions respond to the lower light level with an increase in shoot length. Gardiner & Helmig (1997) found that different thinning regimes in the overstory did not affect the number of sprouts which *Quercus nigra* was able to produce initially. Mortality in the sprout clumps was not affected either. During the coming vegetation seasons sprouts with better availability of light grew taller in the Gardiner & Helmig (1997) study, why the sprouts in the present study can be expected to show a greater response to different light levels in a couple of years.

Tree vigour and cambial regrowth

Tree vigour after the burn treatments were estimated through determining the colour of the leaves and through checking whether the cambium had continued to grow over the burned area on the stem. Neither leaf-colour nor cambial growth is a good estimator of vigour of the cut trees. Therefore the leaf-colour will be related only to the control trees, and the cambial growth can speak only for the burned trees.

The leaf-colour test indicated that pedunculate oaks show less tendencies of yellowing and wilting after burning than do the European beeches. The difference was more apparent in the coarse diameter class. Generally it can be said that the coarse diameter class, in both species, had managed better than the thin class when it came to crown vigour. As discussed above, this is probably due to greater bark thickness in bigger trees or to damage caused to the xylem in thin trees. Others (Barnes & Van Lear 1998) have found that mature oaks in North America can withstand fires very well compared to many other hardwood species, and that is probably what we see in this study as well. It has also been shown earlier (Brose & Van Lear 1999) that American beech, on the other hand, is quite sensitive to fires. The response to fire-damage on the beech stem is, according to the results of Brose & Van Lear (1999), a less vigorous crown. The crowns of the control trees in the present study did not show any great tendencies of wilt or yellowing. Any considerable difference in leaf-colour between the early and the late burned trees cannot be detected.

The cambial growth over the scorched place on the stem was a little greater in pedunculate oak than in European beech, but it was generally quite much greater in the coarse than in the thin trees. If the fire scar is not very broad, and if the cambium grows much enough after the damage, there might be a possibility that the cambium above and under the scar can connect again. If a new connection is formed the tree might survive even if the scar originally stretched all around the stem (Mats Niklasson, pers comm.). Unfortunately, no literature has been found on this subject. The difference in cambial growth between early and late burns showed no consistency.

Management suggestions

There are a couple of ways to use the knowledge about oaks/beeches and fire in practical forestry or in forest restoration. The use in forest restoration may be a bit more obvious since the aim there is to reintroduce natural disturbance regimes in different forest ecosystems (Moore et al. 1999; Stanturf & Madsen 2002). If it is so that, as this and many other studies suggest, oak forests formerly depended upon frequent fires for their survival, the aim of forest restorers should be to burn oak forests at short intervals to keep the competition from more shade tolerant species down.

The results could also give guidance to commercial forest managers who have problems with the natural regeneration of oak. Not necessarily to use fire in the regeneration, but to try and imitate the results of a fire. One example is that the removal of grass in oak regenerations will render difficulties for some of the worst acorn predators - the voles (Lorimer 1985). Another result of frequent fires is the creation of open forests (Lorimer 1985) with, for oak, favourable light conditions (Crow 1988), why shelter-woods should be preferable for oak regeneration.

In North America research (Brose & Van Lear 1999) has been performed to try and find out how much damage fire in shelter-woods will cause to overstory trees. The results showed that the damage was great in American beech, while most of the damage to the oak stems were due to large accumulation of slash around the stem base.

Conclusions

The conclusions to be drawn from this study cannot stretch further than one season after the burning and cutting, why it is hard to say anything about how well the pedunculate oaks will manage in competition with the European beeches in a longer perspective. From what can be seen during the first season however, the oaks start making new sprouts faster than the beeches and the oak sprouts are also considerably longer than the beech sprouts. The survival, as it has been estimated such a short time after the disturbances, does not differ between the two species, but the larger trees have survived to a much greater extent than the thin ones. The vigour of the beech trees is worse during the first season than the vigour of the oaks. The results that have been found can give a little indication of what will happen in the future, but to know the long-term implications further studies are needed.

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References

Abrams, M.D. (1992) Fire and the Development of Oak Forests. *BioScience*, **42**(5), 346-353.

Abrams, M.D. (1996) Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. *Annales des sciences forestières*, **53**, 487-512.

Agee, J.K. (1998) Fire and pine ecosystems. *Ecology and Biogeography of Pinus*, ed. Richardson, D.M. Camebridge University Press, Camebridge. 527 pp.

Anonymous (2003) Väder och vatten. Swedish meteorological and hydrological institute, Norrköping.

Ascard, J. (1995) Thermal Weed Control by Flaming: Biological and Technical Aspects. Doctoral thesis. Sveriges lantbruksuniversitet. Alnarp. Department of Agricultural Engineering. Report 200.

Barnes, T.A. & Van Lear, D. (1998) Regenaration in Mixed Hardwood Stands. *Southern Journal of Applied Forestry*, **22**(3), 138-142.

Björse, G. & Bradshaw, R. (1998) 2000 years of forest dynamics in southern Sweden: suggestions for forest management. *Forest Ecology and Management*, **104**, 15-26.

Björse, G. (2000) Near-Natural Forests in Southern Sweden. Doctoral thesis. Sveriges lantbruksuniversitet. Alnarp. Southern Swedish Forest Research Centre. Silvvestria 134.

Brose, P. & Van Lear, D. (1999) Effects of Seasonal Prescribed Fires on Residual Overstory Trees in Oak-Dominated Shelterwood Stands. *Southern Journal of Applied Forestry*, **23**(2), 88-93.

Brose, P., Schuler, T., Van Lear, D. & Berst, J. (2001) Bringing Fire Back. *Journal of Forestry*, **99**(11), 30-35.

Brose, P., Van Lear, D. & Keyser, P.D. (1999) A Shelterwood-Burn Teqnique for Regenerating Productive Upland Oak Sites in the Piedmont Region. *Southern Journal of Applied Forestry*, **23**(3), 158-163.

Clark, J.S., Merkt, J. & Muller, H. (1989) Post-glacial Fire, Vegetation, and Human History on the Northern Alpine Forelands, South-western Germany. *Journal of Ecology*, **77**, 897-925.

Crow, T.R. (1988) Reproductive Mode and Mechanisms for Self-replacement of Northern Red Oak (Quercus rubra)-A Review. *Forest Science*, **34**(1), 19-40.

Dey, D.C. & Guyette, R.P. (2000) Anthropogenic fire history and red oak forests in south-central Ontario. *The Forestry Chronicle*, **76**(2), 339-347.

Espelta, J.M., Retana, J. & Habrouk, A. (2003) Resprouting patterns after fire and response to stool cleaning of two coexisting Mediterranean oaks with contrasting leaf habits on two different sites. *Forest Ecology and Management*, **179**, 401-414.

Gardiner, E.S. & Helmig, L.M. (1997) Development of water oak stump sprouts under a partial overstory. *New Forests*, **14**, 55-62.

Hannon, G., Bradshaw, R. & Emborg, J. (2000) 6000 years of forest dynamics in Suserup Skov, a seminatural Danish woodland. *Global Ecology & Biogeography*, **9**, 101-114.

Hengst, G.E. & Dawson, J.O. (1993) Bark properties and fire resistance of selected tree species from the central hardwood region of North America. *Canadian Journal of Forest Research*, **24**, 688-696.

Huddle, J.A. & Pallardy, S.G. (1996) Effects of soil and stem base heating on survival, resprouting and gas exchange of *Acer* and *Quercus* seedlings. *Tree Physiology*, **16**, 583-589.

Huddle, J.A. & Pallardy, S.G. (1999) Effect of fire on survival and growth of *Acer rubrum* and *Quercus* seedlings. *Forest Ecology and Management*, **118**, 49-56.

Huntley, B. & Webb, T. (1989) Migration: species' response to climatic variations caused by changes in the earth's orbit. *Journal of Biogeography*, **16**, 5-19.

Jonsell, M., Weslien, J. & Ehnström, B. (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation*, **7**, 749-764.

Kimmins, J.P. (1987) *Forest Ecology*. Macmillian Publishing Company, New York. 531 pp.

Kozlowski, T.T., Kramer, P.J. & Pallardy, S.G. (1991) The physiological ecology of woody plants. Academic Press. San Diego.

Lindbladh, M. & Bradshaw, R. (1995) The development and demise of a Medieval forest-meadow system at Linnaeus' birthplace in southern Sweden: implications for conservation and forest history. *Vegetation History and Archaeobotany*, **4**, 153-160.
Lindbladh, M. & Bradshaw, R. (1998) The origin of present forest composition and pattern in southern Sweden. *Journal of Biogeography*, **25**, 463-477.
Lindbladh, M. (1998) Long Term Dynamics and Human Influence in the Forest Landscape of Southern Sweden. Doctoral thesis. Sveriges lantbruksuniversitet. Alnarp. Southern Swedish Forest Research Centre. Silvvestria 78.
Lindbladh, M., Bradshaw, R. & Holmqvist, B.H. (1998) Pattern and process in south Swedish forests during the last 3000-years sensed at stand and regional scales. Doctoral thesis. Sveriges lantbruksuniversitet. Alnarp. Southern Swedish Forest Research Centre. Silvvestria 78.
Lorimer, C.G. (1985) The role of fire in the perpetuation of oak forests. *Challenges in oak management and utilization*, ed. Johnson, J.E. Cooperative Extension Service, University of Wisconsin, Madison. 8-25.
Löf, M. (2000) Establishment and growth in seedlings of *Fagus sylvatica* and *Quercus robur*: influence of interference from herbaceous vegetation. *Canadian Journal of Forest Research*, **30** (6), 855-864.
Löf, M., Gemmel, P., Nilsson, U. & Welander, N.T. (1998) The influence of site preparation on growth in *Quercus robur* L. seedlings in a southern Sweden clear-cut and shelterwood. *Forest Ecology and Management*, **109**, 241-249.
Malanson, G.P. & Trabaud, L. (1988) Vigour of post-fire resprouting by *Quercus coccifera* L.. *Journal of Ecology*, **76**, 351-365.
McGee, G.G., Leopold, D.J. & Nyland, R.D. (1995) Understory response to springtime prescribed fire in two New York transition oak forests. *Forest Ecology and Management*, **76**, 149-168.
Moore, M.M., Covington, W.W. & Fulé, P.Z. (1999) Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecological Applications*, **9** (4), 1266-1277.
Niklasson, M. Lindbladh, M. & Björkman, L. (2002) A long term record of *Quercus* decline, logging and fires in a southern Swedish *Fagus-Picea* forest. *Journal of Vegetation Science*, **13**, 765-774.
Pausas, J.G. (1997) Resprouting of *Quercus suber* in NE Spain after fire. *Journal of Vegetation Science*, **8** (5), 703-706.
Regelbrugge, J. C. & Smith, D.W. (1994) Postfire Tree Mortality in Relation to Wildfire Severity in Mixed Oak Forests in the Blue Ridge of Virginia. *Northern Journal of Applied Forestry*, **11** (3), 90-97.
Stanturf, J.A., Madsen, P. (2002) Restoration concepts for temperate an dboreal forests of North America and Western Europe. *Plant Biosystems*, **136** (2), 143-158.
Svenning, J.-C. (2002) A review of natural vegetation openness in north-western Europe. *Biological Conservation*, **104**, 133-148.
Tinner, W., Hubschmid, P., Wehrli, M., Ammann, B. & Conedera, M. (1999) Long-term forest fire ecology and dynamics in southern Switzerland. *Journal of Ecology*, **87**, 273-289.
Tinner, W., Conedera, M., Gobet, E., Hubschmid, P., Wehrli, M. & Ammann, B. (2000) A palaeoecological attemt to classify fire sensitivity of trees in the southern Alps. *The Holocene*, **10** (5), 565-574.
Watt, A.S. (1919) On the causes of failure of natural regeneration in British oakwoods. *Journal of Ecology*, 173-203.
Vázquez, A., Pérez, B., Fernández-González, F. & Moreno, J.M. (2002) Recent fire regime characteristics and potential natural vegetation relationships in Spain. *Journal of Vegetation Science*, **13**, 663-676.
Weaver, H. (1974) Effects of Fire on Temperate Forests: Western United States. *Physiological ecology*, ed. Kozlowski, T.T. Academic Press, New York. 542 pp.
Webb, T. (1987) The appearance and disappearance of major vegetational assemblages: Long-term

vegetational dynamics in eastern North America. *Vegetatio*, **69**, 177-187.
Vera, F.M.W. (2000) Grazing Ecology and Forest History. CABI Publishing, Oxon, UK.
Vines, R.G. (1968) Heat transfer through bark, and the resistance of trees to fire. *Australian Journal of Botany,* **16**, 499-514.
Ziegenhagen, B. & Kausch, W. (1995) Productivity of young shaded oaks (*Quercus robur* L.) as corresponding to shoot morphology and leaf anatomy. *Forest Ecology and Management,* **72**, 97-108.