Ecology of the fire-dependent forest herbs *Geranium bohemicum* and *G. lanuginosum* in Sweden

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Cover: *Geranium bohemicum* at a forest fire site

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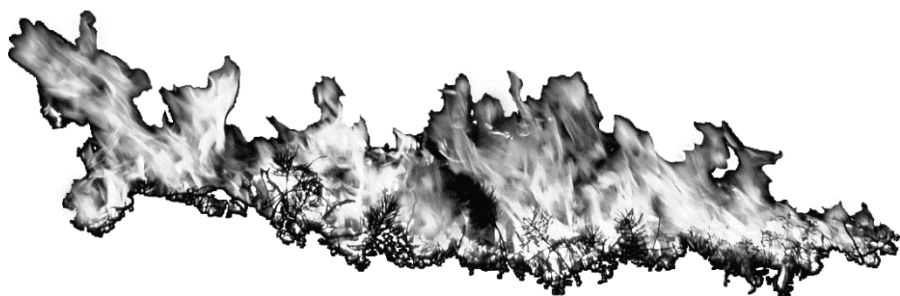
Abstract

Geranium bohemicum and *G. lanuginosum* are the only plant species in Sweden considered fire-dependent, because of their heat-triggered germination. Both are today threatened due to effective fire suppression. An aim with this study was to elucidate their population ecology. These plants have either a summer- or winter-annual life-cycle depending on date of germination. Both at fire sites and in a garden experiment this date occurred in the first half of July, probably determined by day length. Seedlings had a protracted emergence during the fire-year. Winter-annuals in the 15 studied wild populations were more successful than summer-annuals, since they had the whole growing season the year after fire to reproduce. Summer-annuals often germinated too late and were killed by autumn frost before reproduction. Grazing by hare and roe deer was severe during the fire-year and until spring the year after. But plants have an amazing ability to recover successfully. There was large variation in reproductive success between populations, with a positive net return of seeds at all but one site. Almost all seeds were produced by the first generation of plants. Out of this seed crop a few percent germinated within the study period, giving rise to secondary generations. But those plants were small and produced few seeds, probably because of increasing competition in the developing vegetation. Consequently, populations are highly dependent on the first generation, which makes them vulnerable to reproductive failure due to herbivory and winter mortality. But reproductive failure after a fire can be buffered by a remnant seed bank. *Geranium* seed banks were found in the mineral soil below both unburned and recently deep-burned soil. Most of the recently produced seeds seem to add to the seed bank, since only ca 8 % of seeds were lost during a 2-year observation period. These results suggest that to preserve these threatened *Geranium* species it is advisable to burn nutrient rich forests, since that is where seed banks are most likely to be present. Further, the time of burning should be during July and August, to promote winter-annuals which perform better than summer-annuals. Burning should be performed when the humus layer is dry enough to be consumed by the fire, to ensure high enough temperature for seed germination to occur.

Keywords: forest fire, prescribed fire, population dynamics, seed bank, seed dispersal, seed germination, phenology, herbivory, emergence depth, humus consumption, soil nutrients

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Dedication

Till skogen, elden och blommorna

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Risberg, L., Granström, A. 2009. The effect of timing of forest fire on phenology and seed production in the fire-dependent herbs *Geranium bohemicum* and *G. lanuginosum* in Sweden. *Forest Ecology and Management* 257(8):1725-1731.

II Risberg, L., Granström, A. 2014. Exploiting a window in time. Fate of recruiting populations of two rare fire-dependent *Geranium* species after forest fire. *Plant Ecology* 215(6):613-624.

III Risberg, L., Granström, A. 2012. Seed dynamics of two fire-dependent *Geranium* species in the boreal forest of southeastern Sweden. *Botany* 90(9):794-805.

IV Risberg, L. Nutrient availability and plant performance of *Geranium bohemicum* at burnt sites – can it explain its distribution in the landscape? *Manuscript*

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1 Introduction

1.1 Plants and fire

Fire dramatically changes life conditions for plant species and plays an important role in most ecosystems in the world by determining properties such as species composition and nutrient cycling (Bond & Keeley, 2005). Plant species have to adapt to the fire regime in their habitat. The *fire regime* concept is based on several variables such as *intensity, severity, fire return interval, size* and *season* (Conedera *et al.*, 2009; Bond & van Wilgen, 1996; Whelan, 1995). These are also discussed under sections 1.5 and 1.6 for Swedish forests. *Intensity* is defined as heat released per unit length of the flaming front, i.e. fireline intensity sensu Byram (Byram, 1959) and is determined by fuel load and type, fuel moisture content, slope and wind speed. Fire intensity is decisive for tree mortality through canopy damage (Sidoroff *et al.*, 2007). One definition of *severity* is fire consumption of organic matter, both aboveground and belowground (Keeley, 2009). Hence, it can be correlated with intensity that kills aboveground parts, but intensity may have little effect on consumption belowground, which occurs in smouldering combustion. Severity is often defined by depth of burn in the humus layer, which is determined by humus moisture content, density and mineral soil content (Miyanishi & Johnson, 2002; Miyanishi, 2001). This process causes most of the heat release into the soil and is decisive for plant and seed bank mortality and recolonization (Lee, 2004; Schimmel & Granström, 1996). *Fire return interval* (FRI) is the time between individual fire events in any given stand. The FRI is important for populations since it may be shorter than plant age for reproduction or longer than longevity of seeds in seed bank (Menges, 2007). *Size* (i.e. burnt area) and the distance between fires are important for revegetation and seed dispersal. *Season* may also be important since plant growth varies within the year and a fire that occurs when a plant is growing

may be more harmful (Liu & Menges, 2005). Variations in moisture content and fuel load during the season can have effect on intensity and severity of the fire (Knapp *et al.*, 2007). Timing of fire may also be important since length of season remaining affects growth and reproduction of short-lived plants establishing after fire. Microbial biomass and activity is another factor that varies with season, thus spring versus autumn fires can have contrasting effects on microbial communities, which can in turn influence plant nutrient availability (MacKenzie & DeLuca, 2006).

Plant cells can tolerate temperatures of ca 50–60 °C depending on metabolic activity, whereas dehydrated tissues, especially some seeds can tolerate temperatures somewhat in excess of 100 °C (Whelan, 1995; Granström & Schimmel, 1993). Both maximum temperature and duration are critical, and the most important tissues to protect are the growth initiating cells, i.e. the cambium, meristem, and seeds. Common strategies for plants in fire prone ecosystems are to have a protection of thick bark, to resprout from surviving buds, to have a seed bank, to be wind-dispersed or to have a combination of these strategies. These traits may not exclusively be adaptations to fire, but also to drought and browsing (Buhk *et al.*, 2007). Plants susceptibility to fire is increased by high production and retention of dead material, finely divided plant parts, low moisture content, high levels of secondary compounds (oils, fats, waxes, terpenes), and if they are growing in a community which is capable of carrying a fire (Bond & van Wilgen, 1996).

In tree-dominated ecosystems tree layer survival determines the conditions for all other species. Bark thickness and crown architecture are important factors for tree survival (Fernandes *et al.*, 2008). Pine trees (*Pinus sylvestris*) develop a thick bark and a branch-free stem with age. Because of this they are favoured over spruces (*Picea abies*) at low-medium intensity fires, since spruces will easier be killed by fire due to a thinner bark and low branches that easily torch. Older birch and oak trees have thick bark and some protection towards heat, but younger trees have very low protection.

Resprouting species sprout from buds protected from the heat by bark or soil and also humus in ecosystems where organic material is accumulated. Resprouting can occur from the crown, the basal stem, lignotuber, geophyte, leaf sheets, rhizomes, root crown sprouts or root suckers (Bond & van Wilgen, 1996). Species that resprout from parts insulated by humus or soil are affected differently depending on fire severity (depth of burn), i.e. how much of the humus layer that is consumed. Species like *Vaccinium myrtillus, Vaccinium vitis-idaea* and *Deschampsia flexuosa* have their rhizomes in the humus and will be killed by severe fires (Schimmel & Granström, 1996), while *Populus tremula* and *Pteridium aquilinum* often have their roots and rhizomes in the

mineral soil and can survive even if the humus layer is consumed. Resprouting species are good at surviving periods between fires, but may not flourish until resources become abundant, like after a clear-cut or a fire (Jönsson & Nihlgard, 2004; Dolling, 1999). Seed-banking species escape unfavorable growing conditions in time by surviving in the soil, usually close to the parent plant, since they often have short dispersal distance. Most seeds are found in the humus layer and upper 5 cm of the mineral soil (Korb *et al.*, 2005; Granström, 1982), and to germinate they both need to survive the fire and to get the right conditions afterwards. Seeds which have a hard seed-coat often need heat-stimulation to germinate, and there is a narrow zone between too low and too high temperatures (Baskin & Baskin, 2001). Seeds may also require smoke and other chemical compounds produced in the fire for germination; this has been observed mainly in Mediterranean type climates (Baker *et al.*, 2005; Keeley, 1991). Wind dispersed species do not have to survive the fire but can recolonize with seeds from the surrounding landscape, if the distance is within its dispersal capacity. Examples of wind dispersed species are *Senecio* spp., *Taraxacum* spp., *Epilobium* spp., *Salix* spp., *Populus* spp., *Betula* spp., *Pinus* spp., *Picea* spp., and successful establishment of these usually occur on bare mineral soil, i.e. after severe fires (de Chantal *et al.*, 2005; Greene *et al.*, 2004; Romme *et al.*, 1997).

1.2   The studied species

Geranium bohemicum L. and *G. lanuginosum* Lam. (svedjenäva and brandnäva in Swedish) belong to the family Geraniaceae. The genus has 20 species in Sweden, of which seven have been recently introduced. Since *Geranium* species are probably mostly insect pollinated they are poor pollen producers, and rarely found in sediments in paleoecological studies. Therefore it is unknown when *G. bohemicum* and *G. lanuginosum* migrated to this area, and from where. It is also very difficult to distinguish pollen from different *Geranium* species (U. Segerström, pers. comm.). Most of the *Geranium* species are perennial (Mossberg & Stenberg, 2003) but *G. bohemicum* and *G. lanuginosum* grow as summer- or winter annuals (Almquist, 1899). They form dormant seed banks which have heat triggered germination, and are the only herbs considered to be fire dependent in Sweden. Their seed coats are water impermeable and need to be heated to 50–100 °C to take in water so that the seed can germinate (Granström & Schimmel, 1993). At higher temperatures the seed is killed. During heating the 0.2 mm micropyle breaks, creating a permanent opening and allowing water to enter the seed (Gama-Arachchige *et al.*, 2010). The seed can also germinate after mechanical scarification of the

seed coat. Seed-longevity of dormant seeds in soil is unknown, but germination of dry seeds stored for 129 years has been observed (Milberg, 1994). But since longevity most likely is shorter than the current fire-return interval, these species are considered as threatened. *Geranium lanuginosum* is listed as

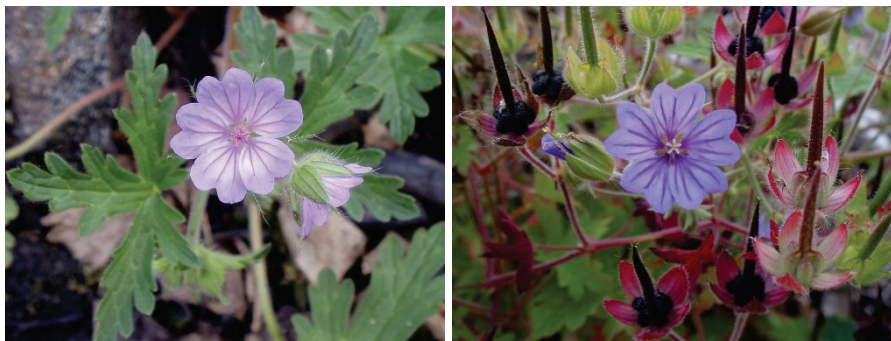*Figure 1*. Seedlings of *G. lanuginosum* (left) and *G. bohemicum* (right).

Figure 2. *G. lanuginosum* (left) and *G. bohemicum* (right).

Figure 3. Rosette leaves of *G. lanuginosum* on the left and *G. bohemicum* on the right (left panel). New seeds, from left: mottled *G. bohemicum*, even-coloured *G. bohemicum* and *G. lanuginosum* (right panel).

vulnerable (VU) on the Red list of threatened Swedish species, whereas the more common *G. bohemicum* is near threatened (NT) (Gärdenfors, 2015). Only 2320 *G. lanuginosum* plants (of which I have found 1536 since 2005) have been registered in Swedish Species Gateway (www.artportalen.se) 1973–2014. But there are also ca 70 additional sites where the species has been noted 1902–2014 with no plant number given.

At flowering both species have erect leafy stems which can reach a height of 50 cm. Both stalks and leafs have glandular hairs, denser on *G. lanuginosum* than on *G. bohemicum*. *Geranium lanuginosum* have red stem nodes on stalks and the leaves are are more lobed (Figure 3). The cotyledons of *G. lanuginosum* have entire margins, while those of *G. bohemicum* have a notch on each side, making species identification easy at this stage (Figure 1 and 16). The flowers are violet and slightly larger for *G. bohemicum,* 15–20 mm wide, compared to 15 mm for *G. lanuginosum* (Figure 2) (Mossberg & Stenberg, 2003). The stigma is red in *G. lanuginosum* but white in *G. bohemicum*. Five seeds are normally produced, each in their own mericarp, but sometimes two in each (Figure 14). When seeds are ripe and air humidity is low the seeds are dispersed ballistically, released from the mericarp when it ejects from the rostrum (Almquist, 1899). *Geranium lanuginosum* have brown seeds with a coarse net, while *G. bohemicum* have mottled seeds with pale brown-greyish and white areas, slightly smother surface texture and slightly larger size (Figure 3) (Mossberg & Stenberg, 2003; Dahlgren, 1943).

The two species are found in scattered populations in the same type of habitat, on disturbed nutrient rich soils, usually on burnt forest sites (Johansson, 2006; Mossberg & Stenberg, 2003). Most observations of the species have been done in eastern Götaland and Svealand, coinciding with the area that has the highest density of lightning ignitions in the country (Granström, 1993; Granström, 1991b). Probably the first map showing the distribution of *G. bohemicum* in Sweden was published by Sterner (1922), and perhaps the first on *G. lanuginosum* by Dahlgren (1943). *Geranium lanuginosum* was first described by Almquist (1916) as a sub-species of *G. bohemicum* (ssp. *deprehensum)* and not separated to its own species until 1926 (Lindman, 1926) which later was shown to be identical with *G. lanuginosum*, known since a long time from southern Europe (Hylander, 1933). More recent distribution maps in Sweden of *G. lanuginosum* shows occurrences from northern Uppland to south-eastern Småland and southern Värmland (Mossberg & Stenberg, 2003) (Figure 4), south of which there is a geographical gap extending to the area around the Mediterranean Sea (Aedo *et al.*, 2007; Hultén & Fries, 1986). *Geranium bohemicum* has a larger distribution area and occurs further north along the east coast of Sweden (Figure 4), into southern Norway

and southern Finland, extending into Russia and middle to eastern Europe down to the Mediterranean sea (Aedo *et al.*, 2007; Hultén & Fries, 1986). No numbers on frequency are available to my knowledge. Habitat descriptions for both species are open areas of *Quercus*, *Fagus*, *Castanea*, *Corylus*, *Abies*, *Picea* or *Pinus* forest, on limestone or acidic rocks, usually on recently burned sites, between sea level and 1800 m (Aedo *et al.*, 2007). Some regional Swedish floras also provide maps and description of locations where it has been found (Bertilsson *et al.*, 2002; Rydberg & Wanntorp, 2001; Nyström, 1993; Mascher, 1990; Malmgren, 1982; Genberg, 1977; Clemedson, 1973; Johansson, 1961; Dahlgren, 1943). Common localities mentioned in these, apart from forest fire sites, are scarified clear-cuts, road clearings, south facing rocks and ruderal areas.
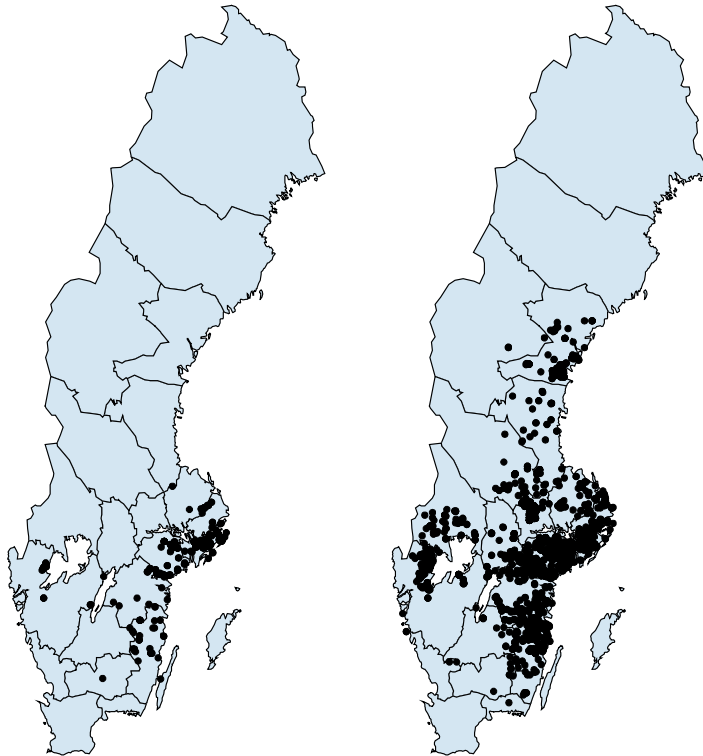

Figure 4. Distribution maps of *Geranium lanuginosum* (left) and *G. bohemicum* (right) in Sweden. From observations reported in Artportalen – Swedish Species Gateway 1900–2014.

1.3   Fire effects on soil nutrients and plants

Mature boreal and hemiboreal forests are characterised by a forest floor consisting of mosses and lichens above a well-defined humus layer. In these forests plant growth is generally limited by plant-available nitrogen, light, and sometimes phosphorus (Giesler *et al.*, 2002; Fisher & Binkley, 2000). Large quantities of nitrogen is present in the organic soil horizon (i.e. the humus layer), but nearly all of it is bound into complex organic forms which are difficult for the plants to access (Näsholm *et al.*, 2009). Plants utilize inorganic N as nitrate and ammonium, but also have the ability to take up organic N, usually as amino acids or peptides (Britto & Kronzucker, 2013; Näsholm *et al.*, 2009; Nordin *et al.*, 2001). Fire dramatically changes the conditions in the forest ecosystem, both for plants that survive and those that establish afterwards. Fire consumes living and dead plants, as well as the humus layer to varying degrees. Dead plants and animals are decomposed by surviving and colonising microbes and bacteria which have a high activity due to increased pH, soil temperature, and the presence of charcoal (Pluchon, 2015; DeLuca *et al.*, 2006). These processes lead to an increase in plant-available inorganic nutrients like nitrate, ammonium and phosphate during a period of a few years after a fire (Certini, 2005; Gundale *et al.*, 2005; Wan *et al.*, 2001). Nutrient levels then return to pre-fire levels due to plant uptake, leaching of nitrate, denitrification and immobilisation by microbes.

Since fire effects are highly variable the spatial heterogeneity of nutrients and light will increase after fire and this causes a spatial pattern of plant establishment (Rodríguez *et al.*, 2009; Gundale *et al.*, 2006; Neèman *et al.*, 1992). The new niches created by fire increase the number of species, and there is a succession of herbs, dwarf shrubs, mosses and lichens (Marozas *et al.*, 2007; MacKenzie *et al.*, 2004). *Geranium bohemicum* and *G. lanuginosum* are two of the few annual plants in the boreal and hemiboreal forests in Sweden, which otherwise mainly consist of long-lived plant species, which can survive as a plant during the long periods that may occur between disturbance events (Ruokolainen & Salo, 2006; Schoennagel *et al.*, 2004; Rydgren *et al.*, 1998; Schimmel, 1993). But these perennials may, like the *Geraniums,* be favoured by, or dependent on fire disturbance (Sandström *et al.*, 2014; Johansson, 2006; Granström, 1991b). In northern America, there is an equivalent fire-ephemeral species: *Geranium bicknelli* (Haeussler *et al.*, 2007; Wang & Kemball, 2005).

1.4   Population dynamics in early successional species

Once established at a fire site there are many factors potentially affecting success for a short-lived (annual or biennial) plant. The composition and

survival of the previous vegetation and time of establishment determines the time frame for growth and reproduction of an establishing plant. Plants establishing early usually have a higher reproductive success (Verdú & Mas, 2006; Verdú & Traveset, 2005). Photoperiod can regulate plant development within a year so that a plant which germinates late in the season may wait to reproduce until the next year, i.e. prolong the time until reproduction (Searle & Coupland, 2004; Simons & Johnston, 2000). This longer time for growth may be an advantage since there is more time to build resources before reproducing, but these plants are also exposed to risks such as grazing and climatic stress during a longer time. Chances for a plant of being eaten may be affected by palatability of the plant and the surrounding plant community (Massad, 2013; Johansson *et al.*, 2010; Bee *et al.*, 2009; Hjältén *et al.*, 1993) and plant size (Boege & Marquis, 2005). The impact of grazing on reproduction may be more severe when grazing occurs late, i.e. on plant reproductive tissues (Massad, 2013; Ramula, 2008; Obeso & Grubb, 1994). Winter survival can also be detrimental for plant success and may depend on plant size (Sletvold, 2005; Gross, 1981).

Fire-ephemeral plants can either be monocarpic or polycarpic (Pate *et al.*, 1985). Monocarpic plants die after reproduction, but some of these have several cohorts of plants after fire (Keeley *et al.*, 2006). Within a few years fire ephemerals have to produce a lot of seeds, which can either be wind-dispersed to new favourable sites or form a seed bank, where the seeds hopefully survive until the next favourable growing opportunity.

1.5 Past and present fire regimes

Forest fire has historically been a major disturbance agent in boreal (Brown & Giesecke, 2014; Niklasson & Granström, 2000; Zackrisson, 1977) and hemiboreal forests in Sweden (Niklasson, 2011; Olson *et al.*, 2010; Niklasson & Drakenberg, 2001). Lightning strike is the only natural fire starter, but there are many anthropogenic causes of fire. People have started fires to improve conditions for cattle grazing and hunting, for slash and burn cultivation, to clear land for permanent cultivation, to improve forest regrowth, and in later years for nature conservation purposes (Ingvarson *et al.*, 2012; Granström & Niklasson, 2008; Emanuelsson & Segerström, 2002; Granström, 2001; Bladh, 1997; Granström, 1991a; Kardell *et al.*, 1980). Historical landscapes, vegetation, fire frequency etc. can only be broadly estimated with paleoecological methods, e.g. by dating pollen and charcoal particles in lake and peat sediments. One difficult, but important task is to separate human influence over fire regimes from that of climate (Brown & Giesecke, 2014;

Conedera *et al.*, 2009). In southern Sweden there are suggestions that fire and vegetation development was controlled by climate during the early and middle Holocene, and by humans during the last ca 4000 years (Olson *et al.*, 2010), 2000 years (Bradshaw *et al.*, 2010) or 900–1000 years (Lindbladh *et al.*, 2000; Lindbladh & Bradshaw, 1998).

Active forest fire suppression began when humans started to value timber higher than other forest "products". The large-scale timber exploitation started earlier in southern than in northern Sweden (Lundmark *et al.*, 2013; Östlund, 1995). This contributed to an earlier decline of fires in most places in southern Sweden; emerging before the 1700s up until the end of the 1800s (Niklasson, 2011; Niklasson *et al.*, 2010) and in the end of the 1800s in the north (Niklasson & Granström, 2000). Around 1 % of the forest in northern Sweden burned annually before this suppression began (Niklasson & Granström, 2000; Zackrisson, 1977), and average fire return interval (FRI, i.e. the time it takes before a fire occur at the same spot again) was 100 years (Table 1). Now a very small area burns annually, on average only 0.001 % of the forest (Skogsstyrelsen, 2010), and FRI is in the range 1000–20 000 years (Drobyshev *et al.*, 2012; Granström, 2001). Interestingly, while the burnt area has decreased, the numbers of fires have increased, to around 10-20 times higher than in a "natural state". This is because most fires are caused by humans (Granström, 2001; Engström, 2000). Probably less than 10 % of fires are caused by lightning today (Granström, 2009).

Table 1. *Estimations of ranges and averages for some fire regime variables in northern Fennoscandia, from Granström (2001).*

Variable	Range fore individual fires	Likely averages
Intensity (kw/m)	10–20 000	500
Severity (depth of burn)	0–100 % of organic soil layer	probably high
Interval (year)	10–500+	100
Season	late May–early September	late June–early July
Size (ha)	0–100 000	>1000
Numbers	n. a.	0.05–10/10 000 ha x year

Former range and averages for the *fire regime* variables in northern Fennoscandia has been put together and estimated by Granström (2001) (Table 1). *Fire return interval* (FRI) is the variable that has been mostly studied, since it is easiest to quantify. The best method to use is dendrochronology, i.e. dating fire scars in tree rings, which has a high resolution (a year or less). Dead or living old trees constitute archives of fire history for up to the last ca 500 years.

Further back in time paleoecology is used, where dating has much lower resolution, and there are uncertainties as to the actual charcoal deposition into sediments after forest fires (Ohlson, 2006). This makes FRI difficult to estimate, but there are attempts suggesting FRI of 200–500 years 4000–9400 years ago (Olson *et al.*, 2010) and 160–410 years 500–10 000 years ago (Brown & Giesecke, 2014). With dendrochronology FRI has been frequently studied, especially in northern boreal Sweden and was effected by factors such as human impact, topography, aspect, proportions of mires altitude and latitude, but with an overall average of 100 years (Drobyshev *et al.*, 2014; Sander, 2005; Hellberg, 2004; Niklasson & Granström, 2000; Engelmark, 1984; Zackrisson, 1977). Vegetation type may also affect interval. Essentially all forests have burned on occasion, even spruce swamp forests (Ohlson *et al.*, 2011; Hörnberg *et al.*, 1995; Engelmark, 1987). Zackrisson (1977) observed large differences in FRI between forests of different vegetation type in the Vindelälven river valley, in that "dryer" forest had shorter FRI than more mesic types.. But a difference between present vegetation types and fire interval is not always found, since fire can cover large areas after long dry periods, when all vegetation types are dry enough to burn (Niklasson & Granström, 2000). It is also under such conditions that lightning ignitions are most frequent (Enoksson, 2011). FRI is further limited by fuel build-up; in northern Sweden fire spread is unlikely the first 20 years after fire (Schimmel & Granström, 1997). Within the hemiboreal zone of Sweden, i.e. within the main distribution area of *G. bohemicum* and *G. lanuginosum* there are fewer dendrochronological studies done on fire history because of lack of datable material due to long-term suppression of fire, heavy utilisation of dead wood for tar- and charcoal production, and a long history of logging. But there are some studies done, mostly in forest reserves. These show a FRI of 20–50 years (Niklasson, 2011; Niklasson *et al.*, 2010; Niklasson, 2006; Lindbladh, 2003; Niklasson *et al.*, 2002; Niklasson & Drakenberg, 2001; Page *et al.*, 1997). These short fire intervals were probably heavily influenced by humans, to improve vegetation for cattle grazing and for slash and burn culture. Humans have caused changes in fire *season* by increasing the proportion of early season fires and extending the fire season relative to a "natural" fire regime (Granström & Niklasson, 2008; Groven & Niklasson, 2005; Niklasson & Drakenberg, 2001; Engström, 2000; Niklasson & Granström, 2000). The season for lightning ignited fires starts in the first half of May and continues to mid October, but the peak is in late June–mid July (Enoksson, 2011; Granström, 1993).

Size of individual fires has also decreased due to humans. Prior to the agricultural colonisation of an area of interior northern Sweden in 1650, 23 %

of fires were over 1000 ha, and 90 % of the area burnt in those large fires, (Niklasson & Granström, 2000). After 1650 the figure was 6 and 55 % respectively. Average size may also drop if there are many fires, since recent fires act as fuel breaks (Niklasson & Granström, 2000; Schimmel & Granström, 1997). Within the hemiboreal zone large fires are more difficult to reconstruct, but fires over 100–200 ha occurred every 9–46 years in four studied areas and the largest detected was 2500 ha (Niklasson, 2011).

Intensity has probably mostly been low–moderate since natural forests had high age distribution of pines, where some evidently survived repeated fires over several hundred years (Niklasson & Granström, 2000; Östlund *et al.*, 1997). Frequent fires also prevent large fuel build-up which otherwise could cause high intensity. Indirect signs of occasional stand-replacing fires was observed in northern Sweden but not in the southern part (Niklasson, 2011; Niklasson & Granström, 2000). There are no quantitative estimates of former *severity* (depth of burn) in past fire regimes, but high severity would be expected in fire regimes dominated by lightning ignitions, since they occur after long dry periods (Enoksson, 2011), causing deep smouldering in the humus layer.

1.6   Slash and burn culture

Slash and burn is a primitive form of cultivation/crop-rotation system which was used during many hundred years on outlying forested land in most of Sweden (Dove, 2015; Emanuelsson & Segerström, 2002; Kardell *et al.*, 1980). The first written sources about slash and burn culture are the *Provincial Law Codes* from 1250–1300 (Eliasson, 1997). But paleoecological studies have shown increasing burn activity, which likely came from slash and burn activity, starting already in the 700s (Lindbladh & Bradshaw, 1998). There are very few quantitative estimations of the extent and importance of slash and burn practice, but it seems to have been very important for both crop production, hay and cattle grazing, and the harvests could be very high, even better than on permanently cultivated area. The system also used a much larger area compared to permanently cultivated area (Larsson, 1989; Weimarck, 1953). Slash and burn culture died out when yields improved on permanently cultivated areas and timber prices increased. In Sörmland it ceased in the first half of 19th century (Schnell, 1946) while in some areas of Småland it continued until the 1930s (Larsson, 1989). Many names of places in the landscape contain references to this practice, telling us that it used to be common. Examples include place names containing words like: *fall*, *svedet*, *svedja*, *göl*, *brännan*, *bråne* and *rödsel*.

Animal husbandry was an important income and the cattle grazed on the outlying land. Burning to improve cattle grazing probably had an even larger extent than slash and burn culture, but this has been little studied. These two land uses are impossible to separate since they were tightly connected, slash and burn fields were left for grazing after a few years (Granström, 1995; Montelius, 1953). It was common that the slash and burn fires slipped out of boundaries, intentionally or not (Larsson, 1989). Perhaps the most extensive pasture lands were the open heathlands in the south-western part of Sweden which lasted for several hundred years and were maintained by repeated burnings (Lindbladh et al., 2011).

Already since the *Provincial Law Codes* 1250 there has been regulations on how to use the outlying land, whether it was allowed to burn to grow crops, or if the forest should be preserved and used for forest products like fuel, timber, potash and tar (Eliasson, 1997). Especially in mining and iron districts, regulations not to burn were enforced early on, since there was a high need for wood for charcoal production from the 16th to the 20th century (Bladh, 1997; Eliasson, 1997; Stridsberg, 1992; Montelius, 1953). But slash and burn and iron-making were not necessarily conflicting, instead they could benefit from each other (Emanuelsson & Segerström, 2002). Burning for growing crops or to improve conditions for forest regrowth could be allowed after removal of the wood for charcoal production (Stridsberg, 1992). The Swedish government also encouraged slash and burn culture during some periods, to establish new settlements in forested areas. These could feed a growing population and bring in more taxes, like the immigration of specialized slash and burn farmers from eastern Finland, starting in the late 1500s (Wedin, 2007; Eliasson, 1997; Bladh, 1995).

Slash and burn culture have been practised more extensively in some regions than in others, and this can probably be explained by topography and climate, where a landscape without stones or boulders was more suitable for permanent cultivation and areas with high precipitation were unsuitable for slash and burn culture (Larsson, 1989). Wet soils as well as, sandy sediments, were also avoided. Instead soils with high fertility were searched for and high places on southern slopes were preferred to reduce risk of frost (Kardell et al., 1980; Montelius, 1953).

The time of the year when land was burned varied depending on what was planned to be cultivated as first crop; end of May–early June for potatoes and turnips and July or end of August for rye. There are examples of forest being felled in spring and then burned already in August the same year (Kardell et al., 1980). But it seems like the forest was more often felled around midsummer or late summer and burned the next year, either already in late

winter or spring (Weimarck, 1979) or between midsummer and mid July (Bladh, 1995; Clemedson, 1973; Bannbers, 1934). The area felled was about 0.5–10 ha (Bladh, 1997; Kardell *et al.*, 1980). The fuel was spread evenly to ensure that the whole site burned (Weimarck, 1968; Weimarck, 1953; Bannbers, 1934), but there is no information on severity, i.e. depth of burn. Wood which was not consumed in the fire could be used for charcoal production in a charcoal kiln or as a fence around the new burn, which was built to stop cattle and wild animals from grazing the crop (Kardell *et al.*, 1980; Montelius, 1953). Crops were cultivated for 1–3 years, sometimes after a new fire at the clearing, then the clearing was left for cattle grazing or hay production for some years or it was brought to permanent cultivation. After 10–40 years, depending on site fertility, when enough vegetation and nutrients had accumulated, the site was burned again (Weimarck, 1979; Montelius, 1953; Weimarck, 1953; Bannbers, 1934).

1.7 Prescribed fires

Several species are dependent on forest fires as a natural disturbance factor. To give these species a chance to survive in the modern forest landscape with its efficient fire suppression, prescribed fires for nature conservation purposes are increasingly used. Different land owners (state, forest companies and private) perform these fires in selected areas. There are no reliable statistics, but total burnt area per year is probably 2000–3000 ha. Prescribed burning is also in the management plan for many nature reserves and in "threatened species action plans" for many red-listed species with different habitat requirements (Forsslund *et al.*, 2011; Wikars, 2006). The first prescribed fires in forest nature reserves in Sweden started in the beginning of 1990s. Since then the knowledge on how to perform prescribed fire, as well as the number of executed fires are increasing (Ingvarson *et al.*, 2012; Nilsson, 2005). In the EU project "Life Taiga", 14 county administrative boards will share 100 million SEK for executing prescribed fires during 2015–2019.

Since 1998 burning of forests is included in the forest certification systems FSC and PEFC (FSC, 2014; PEFC, 2012). Large forest owners which are certified have to burn the equivalent of 5 % of the annually cut forest area on dry and mesic land. There are no specific requirements for how these areas should be selected or the degree of fire impact, e.g. depth of burn or mortality of trees. However, there is a premium for burning forest land with still standing timber. For example, when burning an intact forest stand and leaving it permanently for nature conservation, the burnt area is multiplied by three in the certification scheme.

2 Objectives

The aim of the studies in this thesis was to analyse the ecology of the two fire-dependent, seed-banking, annual forest herbs *Geranium bohemicum* and *G. lanuginosum* in SE Sweden. Focus was on factors important for long-term population survival such as seedling emergence, reproductive success and formation of a seed bank. The plants are considered as threatened since the fire return interval has dramatically increased. Hence, the aim was also that the results can be applied for the management of these two species. The specific objectives were:

- ❀ To elucidate the influence of timing of fire on plant phenology and reproductive success (papers I and II).

- ❀ To analyse important factors for population dynamics following fire such as survival, grazing and seed production for successive cohorts over time (papers II and III).

- ❀ To estimate vertical and spatial seed bank distribution, emergence depth and short-term seed depletion of the soil seed bank (paper III).

- ❀ To analyse the relation between available nutrients and plant performance on burned sites, and thus help explain the distribution of these species in the landscape (papers I and IV).

3 Material and methods

This thesis is based on several studies mostly performed on wild plant populations of *Geranium bohemicum* and *G. lanuginosum* in the field, but there is also a garden experiment, an indoor seed dispersal trial and a lab experiment on seed germination (Table 2). I also planted seedlings of both species at several sites and measured plant available nutrients for some of them. The studied wild populations were located in an area in SE Sweden centred at (59°0'N, 16°15'E) (Figure 1 in paper II), which is within the main distribution area of both species. The populations were found by contacting the fire brigades in all municipalities within an area of 350x100 km in this region, from which information was received on fires they extinguished during the years 2003–2011. I also contacted forest companies for information on prescribed fires within the area. Then I inventoried 86 fire sites over 0.5 ha and found *G. bohemicum* on 19 of the sites, three of these also had *G. lanuginosum*. These 19 sites were used for the different field studies. I also searched for the species on a large number of scarified clear-cuts, either in the year scarification was performed or the year after, to study habitat preferences and abundance.

Sites with *Geranium* populations always had a number of species present that indicate a relatively fertile site type such as *Calamagrostis arundinacea*, *Pteridium aquilinum*, *Veronica officinalis*, *Rubus saxatilis*, *Carex digitata* and *Fragaria vesca*. Frequently occurring species were also a number of short-lived, early successional species like *Cirsium vulgare*, *Senecio vulgaris*, *Moehringia trinervia*, *Galeopsis bifida*, *Vicia* spp. and *Lathyrus* spp. The pre-fire forest stands consisted of *Picea abies, Pinus sylvestris*, *Betula pendula,* and occasionally *Populus tremula* and *Quercus robur* (Figure 5).

Figure 5. Examples of forest sites with *G. bohemicum* and/or *G. lanuginosum*. (a) June 11, 11 months after fire. (b) May 2, 10 months after fire. (c) July 12, 13 months after fire. (d) October 14, 4 months after fire. (e) November 25, 6 months after fire.

3.1 Phenology studies

I observed plant phenology in the end of the first growing season for all *G. bohemicum* and *G. lanuginosum* plants I found at the burnt sites (paper I). In addition I collected phenological observations from people who had observed the species at a few other burns.

I also did a planting experiment at two burnt sites to compare phenology and seed production between over-wintered plants established during the fire-year (i.e. plants exhibiting a winter-annual habit) with plants established the following spring (i.e. summer-annual habit). Approximately 2-week old seedlings were planted in mid May 2005 at a distance of about 1 m from over-wintered wild plants. Five seedlings of both *Geranium* species were planted in each of two plots at the Brevens Bruk site (May 11) and in each of four plots at the Gimo site (May 14).

To have better control of germination date and the associated phenology and reproductive behaviour, I set up a garden experiment outside SLU in Umeå (63°49'N, 20°17'E) in May 2005 (paper I). During the summers of 2005–2007 I then established a total of 14 cohorts of *G. bohemicum* and *G. lanuginosum* under two levels of nutrition. Seeds used were taken from plants established at a fire site 1998 in SE Sweden.

3.2 Plant population studies

On 13 of the 19 sites where I found the species I followed population development (Table 1 and Figure 1 in paper II); eight sites until one year after fire, four sites until the second year and one site until the fourth year after fire. Nine of the studied sites were natural burns (1–5 ha) and four prescribed burns (20–25 ha). In the autumn of the fire-year, all plants at a site or all plants in sub-populations within a site were marked with short <10 cm plastic sticks next to the plants. All sites were also visited in May and July the year after fire, and some sites at longer time intervals. Winter- and summer-survival, grazing and seed production was quantified for all plants. All new plants establishing at a site were marked and observed until death.

3.3 Humus consumption and seedling emergence

I compared depth of moss, humus, and charred humus at unburned sites, burned sites, and locations where *G. bohemicum* plants had germinated (paper III). I examined from which depths *G. bohemicum* plants had germinated by

Table 2. *Burnt sites and populations of Geranium bohemicum and G. lanuginosum used in the different studies in the thesis*

Species	Site	Date of fire	No. of years after fire pop. studied (II)	No. of plants marked year of fire (II)	Soil seed profile sampling (III)	Other (III, IV)	Clear cut=CC Forest=F	Prescribed =P, Wild fire=W
G. boh	Brevens Bruk	25-May-04	2	360	✓		CC	P
G. boh	Hävla	27-May-05	1	15			CC	W
G. boh	Ågelsjön	09-Jun-04	2	367			CC, F	P
G. boh	Rippestorp	10-Jun-08	1	223	✓	Emergence depth, humus consumption	CC, F	W
G. boh	Lövsjön	10-Jun-11	1	50			F	P
G. boh	Gravmark1	16-Jun-06	–	–		Resin capsules	CC	P
G. boh	Gravmark2	25-Jun-07	–	–		Resin capsules		P
G. boh	Valdemarsvik	05-Jul-05	2	148	✓		F	W
G. boh, G. lan	Mosshult	08-Jul-05	1	90			F	W
G. boh	Glupen	08-Jul-05	1	12			F	W
G. boh	Övergivern	10-Jul-06	–	–		Resin capsules	F	W
G. boh	Skirsjön	11-Jul-05	1	10		Resin capsules	F	W
G. boh	Haninge	11-Jul-05	1	107			F	W
G. boh, G. lan	Mörtsjön	24-Jul-06	2	141			F	W
G. boh	Frejdaren	24-Jul-06	1	8			F	W
G. boh, G. lan	Tyresta	03-Aug-99	–	–	✓		F	W
G. boh	Gimo	09-Aug-04	4	302	✓	Seed bank dynamics	CC	P

carefully digging down in the soil until the empty seed coat was located. I also measured the diameter of the seedling leaf rosette to search for a relationship between seed depth and time of emergence. These observations were done at a large fire site from 2008, within the region of the other study sites.

3.4   Seed bank studies

To quantify number and distribution of *G. bohemicum* and *G. lanuginosum* seeds I did a soil profile sampling at four sites (Table 1 in paper III). I sampled 20x20 cm plots in 2 cm layers, down to 8 cm (two sites) or 10 cm (two sites) in the mineral soil. Samples were taken in pairs below deep burned and unburned/surface scorched soil surface, within a meter from each other (n=2–5). I also sampled two more profiles (2 cm-layers down to 8 cm), which was not included in Paper III. That was two unburned patches next to populations of *G. bohemicum* at the Brevens Bruk site.

In addition I studied depletion of recently dispersed seeds at two areas within the Gimo site that burnt August 8, 2004 (paper III). On four occasions during a period of two years after fire I took 2x10 samples of the upper 2 cm of soil (Figure 7). On the first sampling date, i.e. ca 3 months after seed dispersal, I also set up four 50x50 cm wire mesh cages, two at each area, to exclude vertebrate seed predators. Inside these cages I took 20x20 cm samples on September 28, 2006 and October 8, 2007, to compare with the samples outside. Within these two areas, I also marked all germinating plants until July 7, 2008 i.e. ca four years after fire, and counted their seed production in the plant population study (paper II).

After sieving the dried soil samples I searched for all *G. bohemicum* and *G. lanuginosum* seeds under a stereo-microscope with 16X magnification among all particles remaining in a 0.5 mm sieve. I separated seeds into five fractions: recently produced, old, filled, poorly filled (i.e. viable or not), and those that had been eaten on (depredated).

3.5   Germination trial

I tested germination of dried seeds from seven populations of *G. bohemicum* and two of *G. lanuginosum*, sampled from different sites within the study-area (paper III). Time between seed collection and start of the experiment was between 2 and 786 days. I placed two replicates of 50 seeds of each population on moist paper in petri dishes in room temperature and observed them at least once a week during 525 days.

Germination of mature but undried fresh seeds was also observed. These seeds were collected before dispersal and while the carpel was still brown and attached to the rostrum, both from plants grown in greenhouse and natural populations. These seeds were also placed on moist paper in petri dishes at room temperature.

3.6   Seed dispersal

I grew plants of *G. bohemicum* or *G. lanuginosum* to maturity in a greenhouse with high humidity, so that the mature seeds would not disperse. Plants of either species in a pot were then placed, one at a time, in a greenhouse room with low humidity, to let the seeds disperse during 2–3 days (paper III). The size of the room was 4x7 m, and I placed the pot in the middle of a short side 1 m from the wall. The floor and the walls (up to the height of 3 m), were covered with non-woven fabric, which stopped the seeds from bouncing. The distance from the pot was measured for each seed which landed in a 45° sector facing the other short side, since these were the only seeds which for sure had not been stopped by the walls.

3.7   Seed weight and size

I weighed 100 filled seeds dispersed from each of the four plants of *G. bohemicum* and *G. lanuginosum*, which I used in the seed dispersal experiment. I also weighed filled seeds collected from six wild populations of *G. bohemicum* and two of *G. lanuginosum* on burnt sites and clear-cuts, 100 seeds were weighed individually per population. Length and width (90° from the radicle) of the seeds were measured individually on 20 seeds in eight wild populations of *G. bohemicum* and in three wild populations of *G. lanuginosum*.

3.8   Nutrient availability and plant growth at recently burnt sites

I planted seedlings of *G. bohemicum* at four 0–1 year old burns and measured nutrient availability of NO_3^--N, NH_4^+-N and PO_4^+-P with ionic resin capsules (paper IV). Two sites were in SE Sweden and caused by wildfires, one in ca 25-year old surviving pine forest and one at a 10-year old sparse spruce forest which was killed in the fire. The other two were prescribed fires, one at a clear cut and one in a forest, in NE Sweden. The resin capsules were placed in the mineral soil at a depth of ca 5 cm to capture nutrients equivalent to what was available for plant roots. After 61–71 days plants and capsules were harvested and seedling growth was assessed by measuring plant diameter. To study

variation with time the experiment was repeated the following year at one of the northern sites. I also compared plant growth for seedlings planted in spots where smouldering fire had burnt down to the mineral soil, with growth of seedlings planted in the adjacent surface scorched humus layer. Resin capsules were extracted with HCl and content of NH_4^+-N, NO_3^--N and PO_4^+-P were analysed with a flow injection analyser (Tecator 5012, Foss Tecator, Sollentuna, Sweden).

4   Results and discussion

4.1   Plant populations

4.1.1   How date of germination affects phenology and reproductive success

Both species had a fast development and grew very large under high nutrient
and light levels (paper I, II, IV). After appropriate heat stimulation seeds
imbibed water and germinated within 2–3 days. The seedlings then developed
rosette leaves until the first buds became visible in the center of the rosette
after ca 60 days (Figure 3 in paper I). The first flowers opened on a single stalk
after 65 days for *G. bohemicum* and after 70 days for *G. lanuginosum* (Figure
6). Both species had their first mature seeds after ca 90 days, so there are no
important differences between the species in that respect. Nutrition level had
no effect on phenology, despite leading to very large differences in plant size.
Date of germination had no effect on number of days to maturity either, apart
from the last cohort, which bolted (initiated reproduction through induction of
buds) in the season of emergence (germination July 16), resulting in delayed
emergence of flower buds (81–90 days) (paper I).

   Date of emergence determined whether the plants flowered the same year or
delayed reproduction to the following summer, i.e. exhibited a summer- or
winter annual habit. The break-point was in the first half of July in the garden
experiment (Figure 1 and 2 in paper I), suggesting that most plants emerging
after natural fires would be winter-annuals, since lightning-ignited fires peak in
late June–early July (Granström, 1993). The last cohort to bolt in the year of
emergence was July 16 in the common garden experiment, but at field sites
seedlings emerging after burns from July 5 and later never bolted in the same
year. But I do not know the pattern at field sites between June 11 and July 5,
since I found no fire sites with the plants during this period. It is critical that
this break-point is well tuned to the length of the growing season and the

probability of high reproductive success. Possibly the break-point is a little late, since total reproductive failure due to late flowering was observed on sites that burned in the early part of June (Figure 6). For example, a seedling emerging in late June will have its first mature seeds in the beginning of October, when the growing season has almost ended. So then almost no seeds will be produced, since all plants that had bolted died in autumn frosts. Bolting was probably regulated by day-length i.e. photoperiod (long-day requirement), which is a common mechanism for plants in temperate and boreal regions to regulate seasonal flowering time (Simons & Johnston, 2000).

Figure 6. Example of an unsuccessful summer-annual plant which soon after died in autumn frost without producing any seeds. The first flowers have emerged on a single stalk in the center of the rosette of *G. bohemicum* on October 14, four months after fire at site Rippestorp which burnt June 10.

There was a large variation in seedling emergence date in the fire-year at the field sites (Figure 12). At sites which burnt in May–June there were both plants that flowered and set seeds, and plants which still had not bolted by the end of the growing season (paper I, II). At sites that burnt late there were, at the end of the season, seedlings with newly emerged cotyledons as well as plants with several rosette leaves. Possible reasons for this prolonged emergence period are discussed in section 4.2.3.

There was no evidence that winter-annual plants did benefit from stored resources accumulated in the first year, since size in the autumn (for ungrazed plants) was a bad predictor of final size or seed production the following year. But in spring and July (i.e. final size), the correlation between plant size and seed production was significant (Table 2 in paper II).

In the garden experiment in Umeå, plants germinating early (May–June) and late (August–September), had equal final seed production (paper I). This means that length of season does not limit seed production for plants with a summer-annual habit, provided they germinate early enough. This was also observed at the two field sites where I planted seedlings on May 11 and 14 next to winter-surviving plants (paper II). The summer-annuals produced as many seeds in the end of the season as the winter-annuals, even though the summer-annual plants started to flower in the end of July, i.e. when the winter-surviving plants began to senesce after reproducing (Figure 2 in paper II). On the other hand, in the field sites summer-annuals very rarely had as high seed production as winter-annuals. The main reason for this could be that actual seedling emergence could have been delayed, leading to a shortened growing period, even if the date of fire was in the early part of summer. Most summer-annuals died when they were still flowering and setting seeds, compared to winter-annuals which had completed their life-cycle already in the beginning of August. Variations in success for different cohorts are commonly reported for annual plants, where either autumn (Nilsson, 1995) or spring (Bertin, 2001) cohorts can be most successful. Summer-annuals normally germinate in spring and winter-annuals in autumn after losing dormancy during dry summer months and/or cold periods (Assche & Vandelook, 2006; Baskin *et al.*, 2004; Baskin & Baskin, 1985; Håkansson, 1983). But it is also common within plant populations to produce seeds which can germinate during a longer period, to reduce risk of climatic stress and competition among the offspring (Baskin & Baskin, 2001).

Availability of nutrients for the two *Geraniums* was decisive for plant size (paper IV) and seed production (paper I). Plant available nutrients such as nitrate, ammonium and phosphate increase during a period after fire (Certini, 2005; Gundale *et al.*, 2005). The relative proportions between the nitrogen forms may change between years, the peak of ammonium typically comes about one year after fire (Wan *et al.*, 2001) but both are used by the plants, and probably other N-forms too (Inselsbacher & Näsholm, 2012), which I did not measure here. I did not detect any significant difference for any of the three nutrients between the fire-year and the year after at the studied site (paper IV).

4.1.2 Seed production, dispersal and secondary germination

Almost all seeds (92–100 %) were produced by the first generation of winter-annual plants (Figure 3 in paper II). Summer-annual plants in that study were very unsuccessful. Average seed production per seed-producing plant in the year after fire was 244 for *G. bohemicum* and 293 for *G. lanuginosum*, with high variation between sites (4–925 seeds). There was a corresponding high variation in net return to the *G. bohemicum* seedbank (seeds produced per all emerged plants); on average 79 seeds (0.2–395). Thus the net result was positive at 12 of 13 sites. This may be explained by the availability of resources (light, water, nutrients) which seemed to differ a lot between sites, already in the year of fire. The two *Geranium* species grow very poorly in low-light conditions and some sites had almost 100 % cover of other herbs already in the year of fire or the year after (Figure 7). At other sites the tree stand survived intact and should have reduced both available light and nutrients. At sites that burned relatively late in the season (July 5 or later), with only non-bolting plants the year of fire, there was no relationship between time of fire and average plant size in the autumn, so soil nutrient status probably had more effect than time for growth.

Figure 7. In the first post-fire year field-layer vegetation is typically sparse, allowing for good light conditions, but certain species can have rapid regrowth from buried stems. Here *Geranium* plants emerged under a dense canopy of *Pteridium aquilinium*, which obstructed or severely reduced seed production. Two months after a fire on May 8.

On all five sites which were monitored into the second autumn and later, new cohorts of plants established also after the fire-year (Figure 3 in paper II). At the site that was followed the longest, new recruits were observed four years after fire. All plants germinating after the year of fire must be from recently produced seeds, not from the old seed bank since no new seedlings were observed until autumn the year after fire, i.e. after dispersal of new seeds. This may seem contradictory given the heat-triggered germination mechanism.

However, undried seeds were observed germinating both in field, sometimes while still in the carpel attached to the dying plant, and also in germination trials indoor but with a large variation in time to germination, 7–40 days (paper III). This variation probably depended on degree of ripening of the seeds. Further, in the germination trials there was even some germination among filled, ripe and pre-dried seeds which were kept moist in room-temperature, over the 525 days the trial was running. But most seeds, 93 % of *G. bohemicum* and 91 % of *G. lanuginosum* were still dormant (range 74–100 %) (Figure 11 in paper III). It was difficult to keep constant humidity during such a long time, and drying may affect dormancy status (Assche & Vandelook, 2006; Meisert, 2002). But there were very few seeds germinating after dry episodes in my study. Not even mould, which sometimes grew in the petri dishes, seemed to affect the dormancy status of seeds. Age of the dry-stored seeds (2 days to 26 months) when the trial started did not affect germination percentage either.

At field sites most seedlings in secondary cohorts germinated within a few decimeters from the dead or dying mother plants (Figure 8 and 10), which may

Figure 8. Two generations of *G. bohemicum* plants at site Mörtsjön May 20, 2008 which burnt July 24, 2006. Four second-generation plants (marked with orange sticks and circles) which produced 13 seeds in 2008. Nearby the dead mother plant (marked with a blue stick), which produced 1500 seeds in 2007.

be due to a combination of more deposited seeds, and better germination and growing conditions. Seeds germinating in thick humus layers have lower survival rate due to less water holding capacity, but a thin charred duff layer is advantageous (Hesketh *et al.*, 2009; Greene *et al.*, 2004). In area A at the Gimo site two plants in the first cohort growing on a 1x1 m area of mineral soil (upper right corner in Figure 10) produced ca 5800 seeds the year after fire. Within 0.5 m from these two plants ca 150 new plants in total germinated in the following two years. Most germinated in the autumn one year after dispersal, perhaps this portion of seeds needed some after-ripening, i.e. drying during summer (Gama-Arachchige *et al.*, 2012; Assche & Vandelook, 2006). In the dispersal experiment in paper III the density of deposited seeds (seeds/m^2) was highest within a meter from the plant, but 71 % of the seeds were dispersed >3 m for *G. bohemicum* (average 3.67 m) and 62 % for *G. lanuginosum* (average 3.12 m) (Figure 10 in paper III). This would promote establishment of new plants further from mother plants, but this was difficult to confirm in the field. Perhaps seed dispersal was shorter in field because of barriers that may be present, like other plants (Herrera, 1991; Stamp, 1989) and stones. But this is probably only a minor problem since ballistic seed dispersers arrange pods in optimal seed projecting angles which is about 45° for *Geranium* (Garrison *et al.*, 2000; Stamp & Lucas, 1983).

It is common among plants with "hard"/refractory seeds that some of a given seed cohort can germinate without heat stimulation or mechanical scarification (Keeley, 1991). In regions with Mediterranean-type climate there are annuals with heat triggered seeds which have only one or two generations after fire, or have several cohorts if a portion of the newly produced seeds are triggered by some other environmental cue than fire, such as high precipitation (Keeley *et al.*, 2006). Having this ability of secondary germination is functional since there may still be patches free from competition a few years after fire, i.e. more cohorts can succeed with seed production. But usually plants establishing early have higher success (Verdú & Mas, 2006; Verdú & Traveset, 2005; van Baalen, 1982). I found that seed production for secondary cohorts was very low, but at three of four sites they still contributed with a net increase of 7.6 seeds per established plant at the most (Figure 8, Figure 3 in paper II). It is likely that seed production was mostly determined by competition with other plants which dramatically increased over time (Figure 9), but at least in the first two years after fire there was still high spatial variation in vegetation cover. This resulted in that a few plants had high seed production, while those that germinated among other plants, in moss carpets, in downing wood or other unfavourable places, were unsuccessful.
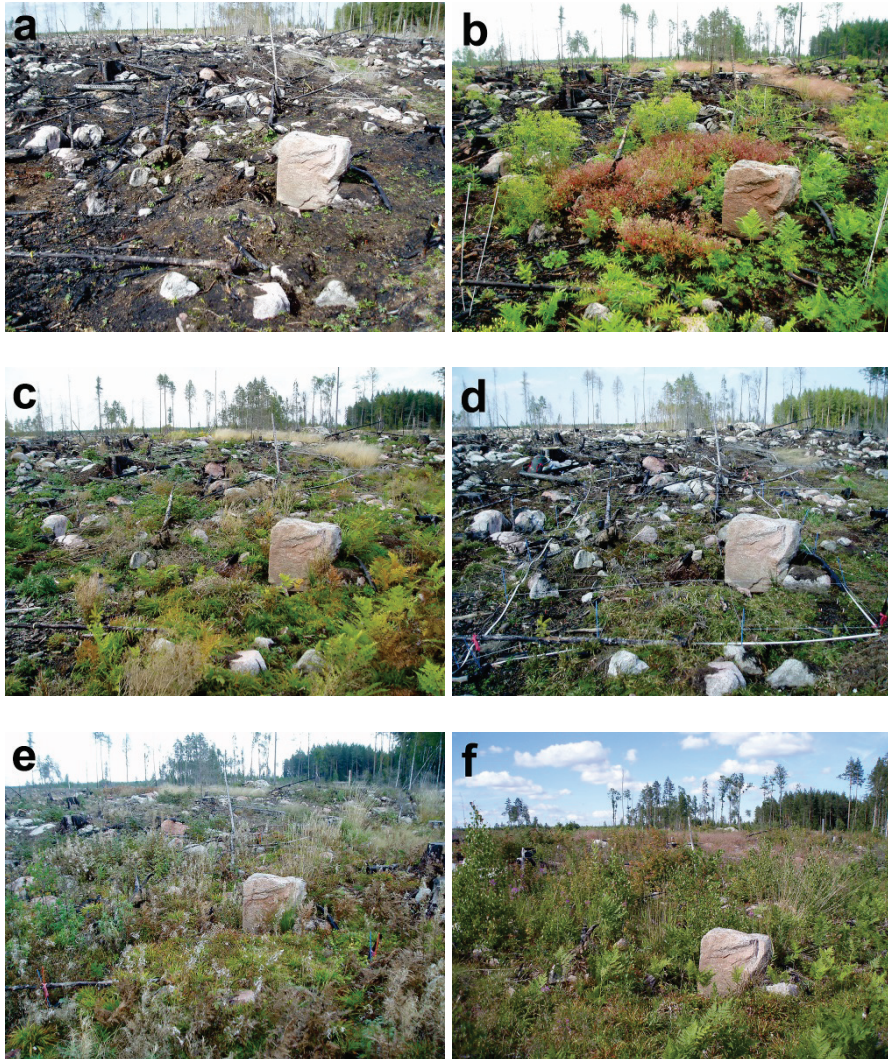
Figure 9. Recolonization of perennial plant species is fast, the *Geranium* plants can only cope with the competition the year of fire and the year after. A plot (ca 7x3 m) at the Gimo site at different dates. This view facing the right side in Figure 10, area B. The site was burned August 9, 2004 (a) May 14, 2005. Small winter-surviving *G. bohemicum* rosettes (b) July 20, 2005. Dense reddish seed-dispersing plants in the middle of the picture (c) September 27, 2005. First generation of plants are dead, some newly produced seeds germinate. In 2005, 35 670 seeds were produced within the plot. (d) May 4 2006. (e) September 29, 2006. In 2006, 203 seeds were produced and 422 in 2007. (f) July 8, 2008. A few, very small plants were observed, but no seeds were produced.
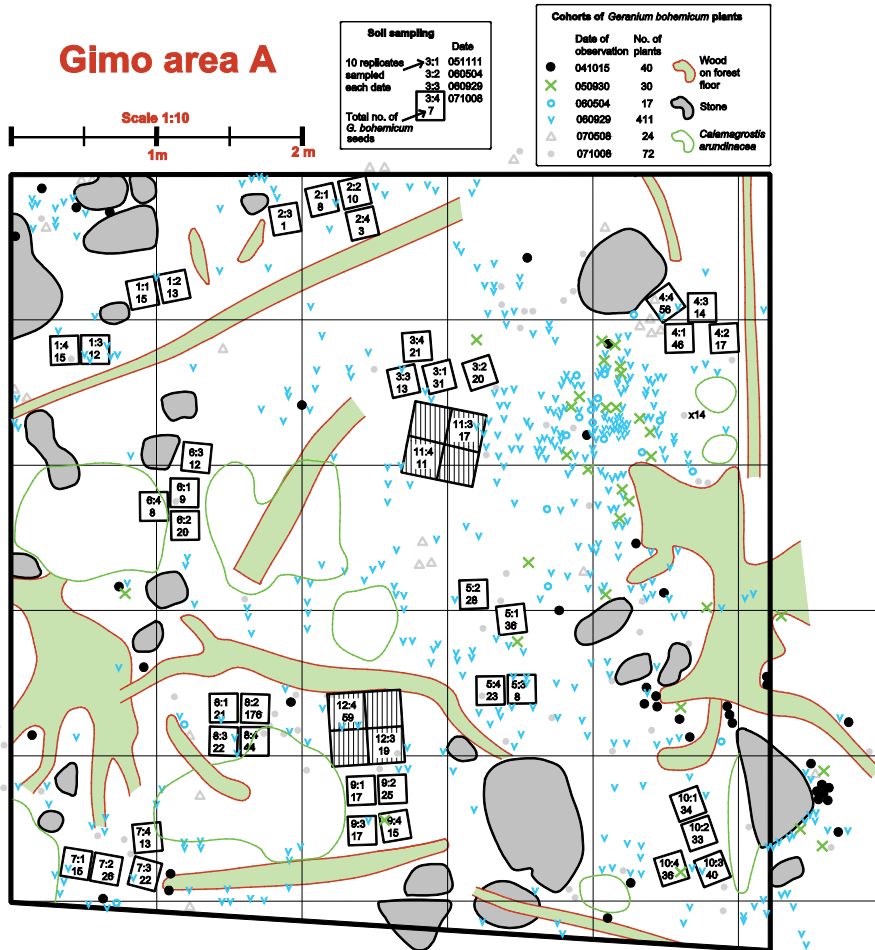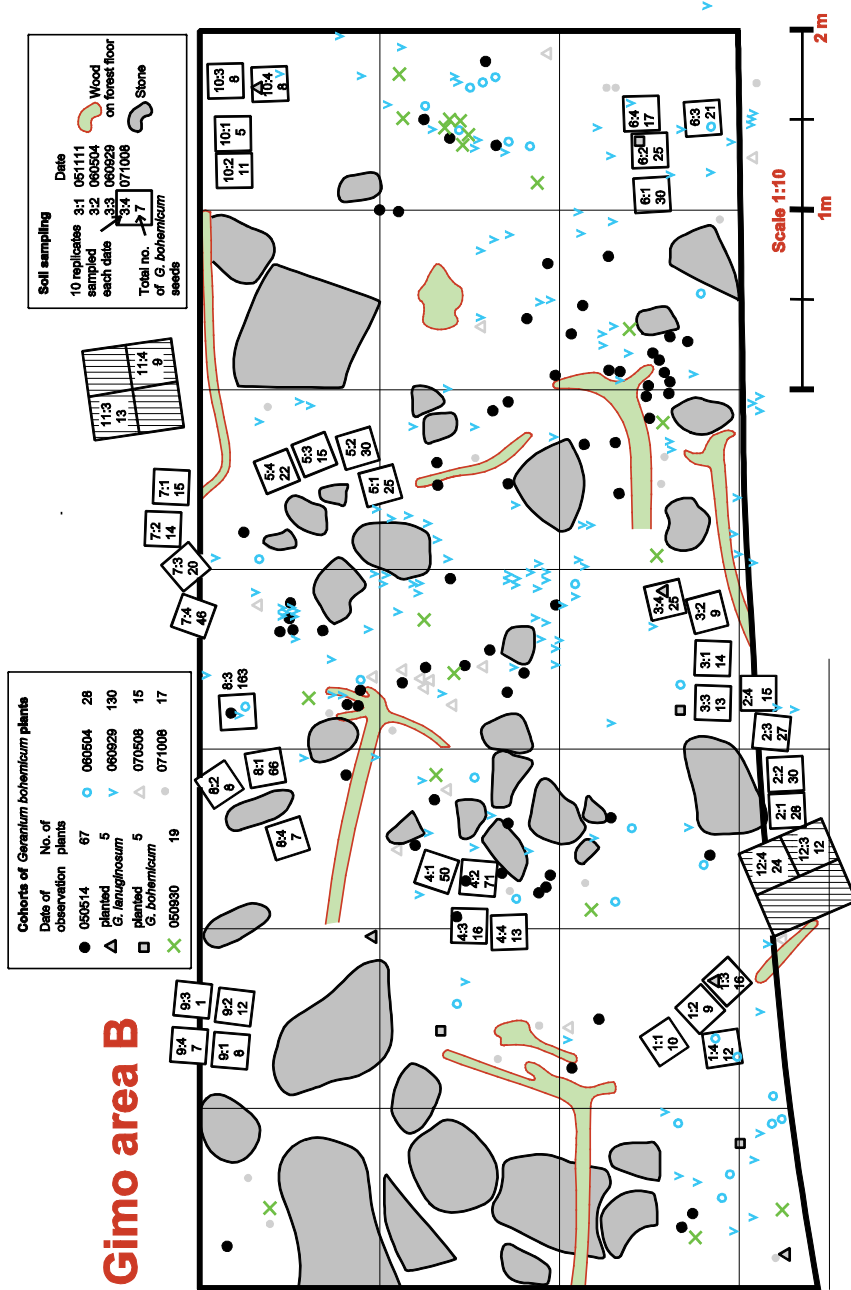
Figure 10. Maps of area A and B at the Gimo site, a clear-cut which was burned August 9, 2004, where the population study (paper II) of *G. bohemicum* plants and the seed bank study (Figure 3-5 and Table 2 in paper III) were performed. Individual plants in different cohorts were marked. Black dots denote seedlings emerging from the "old" seed bank and the other symbols are seedlings of subsequent cohorts, emerging from recently produced seeds. Area B was established in spring the year after fire. Five seedlings of *G. bohemicum* and *G. lanuginosum* were then planted there. Sample plots, also within cages, for the seed bank study are shown with number of *G. bohemicum* seeds found in each.

Gimo area B

Scale 1:10

2 m   1m

Soil sampling

		Date
10 replicates	3:1	051111
sampled	3:2	060504
each date	3:3	060929
	3:4	071008

Total no. 7
of *G. bohemicum*
seeds

Cohorts of *Geranium bohemicum* plants

Date of observation	No. of plants		
050514	67	060504	28
planted *G. lanuginosum*	5	060929	130
		070508	15
planted *G. bohemicum*	5	071008	17
050930	19		

Wood
on forest floor

Stone

4.1.3 Factors affecting survival and seed production

Already during the first few months following fire, an average 31 % (0–80 %) of the seedlings died. Suspected causes were drought, herbivory and litter fall. Winter survival for non-bolting plants varied much between sites with an average of 40 % (0–87 %) for *G. bohemicum* and 69 % (54–83 %) for *G. lanuginosum* and because of this it was decisive for population success. Frost heaving, trampling and grazing, snow mould (Figure 11) and drought in the spring were the most common causes of death, and some of these have also been observed in other studies of short-lived species (Sletvold, 2005; Bertin, 2001; Nilsson, 1995). There was no significant effect of autumn rosette size (ungrazed plants) on survival (Table 4 in paper II). In other studies on rosette-forming short-lived plants larger rosettes had higher survival (Sletvold, 2005; Bertin, 2001; Gross, 1981), or high population density decreased survival (Nilsson, 1995). Survival during summer was higher than during winter, 47–100 % of plants alive in May the year after fire survived to reproductive stage. Causes of death seemed to be drought, uprooting/grazing and competition with other plants. Water availability at fire sites may be scarce, since severely hydrophobic substances are produced by heating of organic matter and contributes to the decrease in water infiltration (DeBano, 2000).

Another factor affecting survival was herbivory which is common at fire sites (Allred *et al.*, 2011; de Chantal & Granström, 2007), since animals are attracted by plants with higher nutrient concentrations, which often establish after fire (Pearson *et al.*, 1995). We observed grazing by hare and roe deer at all 13 sites and at one site also red deer. Grazing was abundant in the year of fire and the following spring, but later became almost absent, probably because other plants had become available to eat that were preferred by the herbivores, or that palatability of the *Geranium* plants decreased (Elger *et al.*, 2009).

Larger plants had a higher risk of being grazed than small ones at the three sites studied in October the fire-year (Figure 11, Table 1 in paper II). Causes could be longer exposure time due to earlier emergence and higher attraction of grazers to larger plants (Boege & Marquis, 2005). However, plants not only survived but also had an amazing ability to recover after grazing, initiated from several apical buds in the center of the rosette. But many plants failed to do so (Figure 4 in paper II). Plants that were heavily grazed in autumn the year of fire had lower winter survival than less grazed plants, and plants that were severely grazed (>50 % eaten) in spring produced fewer seeds. For summer-annual *Geranium* plants, severe grazing was often observed on the shoots, which they did not manage to regrow before the end of the season, leading to a high risk of reproductive failure. For the winter-annual plants grazing occurred mostly on the foliage the fire-year and the following winter, not so much on the

shoots in the following summer. This shows that timing of grazing is important; plants more often manage to recover after early compared to late grazing (Ramula, 2008; Obeso & Grubb, 1994). Whether the shoot (reproductive tissues) or the foliage (vegetative tissues) is removed may also affect reproductive output, with shoot damage being most harmful (Boalt & Lehtilä, 2007; Gomez, 2005). Plants can escape grazing by growing beneath a protecting barrier produced by other plats (de Chantal & Granström, 2007; Gomez, 2005; Herrera, 1991). This rescued some *Geranium* plants in my studies, which happened to germinate for example below burnt logging residues, wind falls or stones. The spatial arrangement of *G. bohemicum* and *G. lanuginosum*, which often germinate in groups within limited nutrient rich areas, is likely to be a disadvantage, since plants can easily be found and grazed.

Figure 11. Grazing of *Geranium* rosettes is very common, but plants have a great capability of resprouting from the center. Large plants like this, which has lost half of its leaf area, were more often grazed than small plants. October 14, ca 4 months after fire (left). It is common that only the stalks remain. *G. bohemicum* plants which have suffered from both snow-mould and grazing by small rodents under snow cover. March 1, ca 7 months after fire (bottom).

Figure 12. G*eranium. bohemicum* and *G. lanuginosum* sometimes germinates from the soil seed bank on unburned scarified clear-cuts. Two *G. bohemicum* rosettes in May next to a recently planted *Pinus sylvestris* (left). A flowering *G. bohemicum* in July, next to a planted *Picea abies* and surrounding *Deschampsia flexuosa*, i.e. a relatively low fertile site (right).

Figure 13. Large plants of *G. bohemicum* with high seed production at an unburned, scarified clear-cut with a nutrient rich vegetation type, Kvarsebo Östergötland. Picture is taken July 19, in the second growing season after soil scarification was done.

4.1.4 Appearance on clear-cuts

Before planting or sowing a scarification is made on most clear-cuts to remove the humus layer and create a good mineral soil seed-bed for the new tree-

seedlings. Several species use this opportunity for germination and recolonization, but which species that appear depends on vegetation type and previous land use (Jonason *et al.*, 2014; Granström, 1986). If the mineral soil contains a seed bank of *G. bohemicum* and *G. lanuginosum* seeds can germinate after mechanical scarification of the seed coat (Figure 12–14). It is not known if heat from the sun is enough to break dormancy after long time storage in the soil, or if mechanical scarification of the seed coat is required. In several Swedish floras and in Swedish Species Gateway (www.artportalen.se) there are numerous observations of these species at e.g. clear-cuts and road clearings (Mossberg & Stenberg, 2003; Rydberg & Wanntorp, 2001).

This far I have observed *G. bohemicum* on ca 80 scarified clear-cuts in southeastern Sweden, the same year or the year after the scarification. *Geranium lanuginosum* was present on 25 of these. Population success was highly variable, just as it was at the fire sites (Figure 12–13). At most sites vegetation type seemed to determine population reproductive success. Emergence time on clear-cuts seemed to be more spread over time compared to at burnt sites, since some germinated soon after the clear-cut, but most of them later, after soil scarification had been performed. Those germinating first were often most successful (Figure 13), while *Geranium* plants in the scarified strips, sometimes in very high numbers, were often almost covered by surrounding vegetation. This severely reduced plant size and reproductive success causing a reduction in the seed bank. The *Geranium* plants seem to have no advantage of being less visible to grazers compared to at a burnt site. They were often found and selectively grazed.

4.2   Seed banks

Possible fates for seeds after dispersal are incorporation into seed bank and relocation over time, germination, predation, decaying or consumption in the next fire. Results from the study of recently dispersed seeds, the soil profile distribution and the seed germination studies all show that most *G. bohemicum* and *G. lanuginosum* seeds are incorporated into a persistent seed bank (paper III). But seed longevity and the shape of the depletion curve is unknown.

4.2.1   Seed characteristics

It was possible to separate "old" seeds from recently dispersed seeds since old seeds lacked the outer seed coat (Figure 14, Figure 1 in paper III). Usually one seed is formed in each carpel, but sometimes there are two, leading to "half-sized" seeds (Figure 14). In each carpel there are two ovules, usually only one is developed into a seed, but sometimes both (Dahlgren, 1956). In the seed

depletion study in paper III, 34 of 1501 recently produced filled *G. bohemicum* seeds found in the 88 samples were half-sized, i.e. double seeds were produced in 1.1 % of the carpels. Average seed weight was 7.24±0.17 mg (n=6) for *G. bohemicum* populations and 6.50±0.19 mg (n=2) for *G. lanuginosum*. Average seed length was 3.27 ±0.03 mm (n= 8) for *G. bohemicum* and 2.97±0.03 mm (n=3) for *G. lanuginosum*. Average seed width in these populations was 1.66±0.02 mm (n=8) for *G. bohemicum* and 1.67±0.02 mm (n=3) for *G. lanuginosum*.

Figure 14. Two *G. lanuginosum* seeds, where the old seed to the left lacks the outer seed coat of the recently produced seed to the right (left). Seed carpel of *G. lanuginosum*. One seed is usually produced in each carpel, but this one belongs to the ca 1 % that has two (right).

4.2.2 Distribution of the old seed bank

Old *Geranium* seeds were found at all depths down to 10 cm in the mineral soil below both deeply burnt and unburnt/surface scorched soil surface (Figure 2 in paper III). No *Geranium* seeds were found in the humus layer at any of the sites. Average density of old seeds at the sites was 16–163 per m^2 (n=4), but variation between sample points/profiles was high with 0–450 per m^2 (n=18). There was no difference in seed density between unburned/surface scorched (n=4) and deeply burned (n=4) profiles with 85.9±21.4 SE and 81.3±41.6 SE per m^2 respectively. At the two unburned patches the Brevens Bruk site (not included in paper III), average number of old seeds in soil samples was 25 seeds/m^2 (and recently produced seeds 13 seeds/m^2), which is within the range at the other four sampled sites. In the only other seed bank study performed on these species, an average of 21 *G. bohemicum* seeds and 89 *G. lanuginosum* seeds per m^2 were found down to 6 cm in the mineral soil, most between 0–3 cm, (Johansson, 2003).

The small number of samples makes it difficult to statistically test for any difference in number and distribution of seeds in soil seed banks in burned and

unburned areas or between sites. For uncommon species like these, with a patchy distribution, estimating the seed bank can be a problem (Stark *et al.*, 2008; Pickup *et al.*, 2003). I sampled in total 0.16–0.4 m^2 per site. More soil samples would have been preferred, but this estimation technique of physical separation was very time-consuming. Seed bank quantification using seedling emergence techniques takes less time, but then it is not possible to detect non-viable seeds and accurate germination stimuli need to be provided for the seeds (Ferrandis *et al.*, 1999).

Nevertheless the results clearly show that a residual *Geranium* seed bank (that has not been killed or triggered to germinate) should always be expected, even if all humus is consumed in the fire. And further that the seed bank is probably composed of seeds produced after several fires, since seed viability is so long; in 2006 I found viable seeds in soil samples at a site in Tyresta National Park (paper III) that had last burned in 1809 (Niklasson, 2006). But how can seeds be located so deep down in the soil? Re-distribution of seeds dispersed on the soil surface may occur by burrowing animals (Canti, 2003; Chambers & Macmahon, 1994) although earthworm activity in particular is low in podsolized soils. Present depth distribution may also be a result of former slash and burn practice, i.e. crop cultivation followed by cattle grazing/trampling. This caused soil disturbance (Kardell *et al.*, 1980; Weimarck, 1979; Montelius, 1953), which may have helped to incorporate seeds deep into the mineral soil. Slash and burn culture was wide-spread in southern Sweden during 1600–1850 (Montelius, 1953).

4.2.3 Activation of the old seed bank

Geranium bohemicum and *G. lanuginosum* seeds need to be heated above 50 but not above 100 °C to germinate (Granström & Schimmel, 1993). The heat comes from the combustion of the humus layer which will be consumed to a varying degree depending on humus moisture, humus thickness, packing ratio, and amount of surface fuel load (Behenna *et al.*, 2008; Hille & Stephens, 2005; Miyanishi & Johnson, 2002; Wretlind, 1948). Temperature in flames above soil surface is ca 700–1200 °C (Stoof *et al.*, 2013; Odion & Davis, 2000), in smouldering duff 400–600 °C have been reported (Rein *et al.*, 2008). But the *Geranium* spp. seeds will seldom experience such temperatures since no seeds were found in any of the humus layers (Figure 2 in paper III), and soil heating decreases sharply with depth (Odion & Davis, 2000; Bradstock & Auld, 1995). Already 2–3 cm down in the mineral soil peak temperatures are typically less than 60 °C (Schimmel & Granström, 1996). So there will only be a narrow depth zone in the mineral soil where seeds get the right temperature for germination, in all other cases they remain dormant or are killed. But only two

Figure 15. Two seedlings of *G. bohemicum* which have just reached above the soil surface 16 days after a forest fire on July 10. The inserted picture shows an extreme example of how the date of emergence is spread over time. The picture is taken on November 26 in an old spruce forest 6 months post fire! (Burn date May 27).

charred *Geranium* seeds were observed in all of the samples (site Valdemarsvik, at a depth of 4–6 cm).

In the seed distribution study there was an indication of fewer seeds at burnt areas in the upper 4 cm, at least in the upper 2 cm, compared to lower depths (Figure 2 in paper III). More seeds may have germinated or been killed by the fire at those depths (Behenna *et al.*, 2008; Auld & Denham, 2006; Williams *et al.*, 2004; Ferrandis *et al.*, 1999). Emerging plants within the sampled areas were only 0.4–4 per m^2, which is far less than the number of old seeds found in the soil seed bank (16–163 per m^2). This indicates that most seeds in the seed bank remain dormant.

At the burnt sites not all humus was consumed in the fire, and plants of *G. bohemicum* were only found in mineral soil spots or where 1 cm of charred humus remained (Figure 6 in paper III). *Geranium bicknelli* in boreal forests of northern America seems to have the same germination and habitat requirements (Haeussler *et al.*, 2007; Lee, 2004; Granström & Schimmel,

1993; Ahlgren, 1960) but has also been found on forest floor that has only been surface scorched, though with less cover and frequency (Wang & Kemball, 2005), suggesting a more superficially distributed seed bank. *Geranium bohemicum* emerged from 1–6 cm depth in the mineral soil (Figure 7 in paper III). Emergence depth was possible to determine since the seed coat usually remains at the original location in the soil (Figure 8 in paper III). As the hypocotyl grows, the cotyledons are kept folded and bent downwards until it reaches the soil surface (Figure 15). Usually seedlings of varying age are found next to each other. One explanation can be emergence depth, since there was a significant negative correlation between plant size and emergence depth (Figure 9 in paper III). *Geranium bohemicum* is definitely one of the first plant species appearing at a fire site, Figure 15 is taken only 16 days after fire. Only certain resprouting species such as the grass *Calamagrostis arundinacea* are faster.

According to the model by Bond *et al* (1999) 52 mm would be the limit for a seed mass of 7 mg, i.e. the approximate seed weight of the two *Geranium* species This is in agreement with my findings of 6 cm, but it may not be the lower limit, since I found seedlings of both *G. lanuginosum* and *G. bohemicum* successfully germinating from 12 cm in a lab study in fine sand (unpublished material). The rate of hypocotyl growth was 0.3–0.8 cm/day, but the conditions then were very favourable (20°C, continuously moist soil) In the field soil will be more compact, stones and roots may constitute barriers and moisture level (precipitation) and soil temperature may be too low to allow fast growth through the soil.

For preservation of these species there will be a need for prescribed fires in selected areas, since current FRI is 1000–20 000 in Sweden (Drobyshev *et al.*, 2012; Granström, 2001). Climate change may decrease FRI slightly, since length of burning season and number of days with extreme fire risk will increase in Sweden (Sjökvist *et al.*, 2013). Our ability stop fires may though match this higher risk. But several studies suggest climate warming will increase fire intensity and frequency in boreal forests (Boulanger *et al.*, 2014; Bond-Lamberty *et al.*, 2007). It is unknown how long the two *Geranium* species have been in this region, but they have established and survived in former fire regimes. Since their seed longevity and shape of the depletion curve is unknown, so is the required FRI for long-term survival. There is probably no lower limit, since ripe seeds can germinate immediately (paper III). For the upper limit not much is known. Evidently seeds can sometime survive at least close to 200 years, but this does not give evidence for seed depletion patterns over time. Clearly, FRI in this region has been substantially shorter than that in the recent past. Dendrochronological studies within their present distribution

area, have documented FRI of 20–50 years during the last ca 500 years (Niklasson, 2011; Lindbladh, 2003; Niklasson *et al.*, 2002; Niklasson & Drakenberg, 2001). Further back in time FRI is more uncertain.

The requirement of total humus consumption for activation of the *Geranium* spp. seed bank (paper III) implies a long period of drying, which severely restricts the number of suitable burn days in most summers. Instead many fires are executed early in the season and during marginally dry conditions. But such fires will unlikely create the desirable severity. After a less severe forest fire, resprouting species like *Pteridium aquilinium*, *Calamagrostis arundinacea, Vaccinium vitis-idaea*, *Vaccinium myrtillus* and *Deschampsia flexuosa* etc. will rapidly dominate the post-fire colonisation (Schimmel & Granström, 1996), and if any *Geranium* plants germinate they will have almost no chance in the competition (Figure 7).

4.2.4 Short-term seed depletion

As mentioned in section 4.1.2 there were several secondary cohorts of seedlings. But these seedlings represent only 0.2–2.5 % of the total sum of *G. bohemicum* seeds produced at the burnt sites (Paper II, Table 2 in paper III). Low germination of recently produced seeds was also observed at the two sites where I planted seedlings (paper II). There were no wild populations of *G. lanuginosum* so all subsequent seedlings must have been the offspring of the ones I introduced. At the Gimo site only eight seedlings were observed out of 20 415 seeds produced and at the Brevens Bruk site one seedling out of 970 seeds produced. All *G. lanuginosum* seedlings emerged in the year after the seeds were dispersed.

In the seed depletion study depredated *G. bohemicum* seeds were found already on the first sampling occasion, i.e. 3–4 months after seed dispersal. No increase in the proportion of depredated seeds (which was ca 8 %), was found during the three subsequent samplings in the two following years (Figure 3 and 4 in paper III). This shows that predation was a small threat to the seeds and most were eaten shortly after dispersal. I also found depredated seeds in the net exclosures, which obviously did not keep all predators out, unless the seeds were eaten shortly before the exclosures were established, i.e. 3–4 months after seed dispersal. The cages were sampled ca one and two years after the start of the study (third and fourth sample dates) (Figure 3 in paper III). No difference in number of seeds was observed inside or outside the cages, since variation between samples was too high (Figure 10, Figure 5 in paper III). The number of seeds per m^2 from the third and fourth sample dates were 545±185 and 478±78 (n=20) respectively outside the cages, and 356±48 and 563±265 (n=4) respectively inside the cages.

Plants of both species can disperse their seeds more than six meters, but many seeds seem to fall just below the plant. In areas with high seed production the number of seeds found in surface soil samples was higher, giving high variation between samples (Figure 10, Figure 5 in paper III). Also in the indoor seed dispersal study the seed density was higher within one meter of the plant, but then relatively even out to the distribution limit around 6 m (Figure 10 in paper III). In the field, seeds might also have been redistributed by small rodents (Kjellsson, 1985), as mice nests were observed in the study area. But the proportion of eaten seeds was not higher in samples where there were a higher total number of seeds. Perhaps the mice were storing seeds for later. Predation was also observed on seeds which were still in the carpel and not dehydrated. Such seeds are soft compared to the dried seeds which are very hard and may deter predators. Seed predation will probably decrease to even lower levels with time, as litter accumulates. Seeds which have been incorporated into the soil usually have higher survival (Alexander & Schrag, 2003), which can be due to lower predation (Hulme & Borelli, 1999) and less fluctuation in temperature and humidity (van Baalen, 1982).

5 Conclusion and management implications

In this thesis I have identified the most important factors in the population ecology of *Geranium bohemicum and G. lanuginosum*, from a conservation perspective. I have showed that seed production in the first generation is the most important factor for population success. This varied much between sites due to nutrient supply, date of germination, winter mortality and herbivory. Plants which germinated after fires from July and later grew as winter-annuals and usually had highest success, since they had the whole next growing season for growth and reproduction. Very early germinating summer-annuals also had high seed production in the garden experiment, but this was rarely observed in the field. The time for growth and reproduction may have been too short, since emergence date during the fire-year was spread in time, and plants which have entered reproductive phase dies in the autumn frosts. Grazing was a large problem at some sites during the fire-year and the following winter, later almost absent. But plants have an amazing ability to recover successfully. The high requirement of nutrients may explain why the two *Geranium* species are mostly restricted to nutrient rich areas in the landscape. This is required for high seed production which is essential for long-term survival.

Seeds in the old seed bank germinated only during the fire-year. But a few percent of the recently produced seed crop gave rise to secondary cohorts, up to four years after fire. Though these plants contributed little to the new seed bank, they had a positive net result in most cases. Most recently produced seeds added to the new seed bank, since seed predation also was low. Plants germinating in the fire-year were only found at spots with near or total humus consumption, which is needed for the required heat stimulation. Germination of seeds was observed from 6 cm in the mineral soil. The fact that seeds were found below both burned and surface scorched soil surface, and down to 10 cm

depth indicates that the seed bank probably consists of seeds produced after several fires. This will be a buffer if reproduction would fail after a fire.

My results have several direct implications for management aimed at preserving the two threatened *Geranium* species. The current regime of very long fire-return intervals in the forest landscape we have created with effective fire suppression will most likely continue. For the long-term survival of the species, repeated prescribed burning in selected areas will be one solution. Based on the results of this thesis recommendations for the management of *Geranium bohemicum* and *G. lanuginosum* are:

- ✤ Fertile, mesic sites should be selected for burning, within the region where the species are known to be present.

- ✤ Burning should be performed when the humus layer is dry enough for an extensive smouldering fire to occur, since germination of these *Geranium* species only happen where essentially all humus has been consumed in the fire.

- ✤ Burning should preferably be done in July and August, since plants germinating after late fires will follow a winter-annual habit, leading to higher reproductive success.

- ✤ Fire intensity should be high enough to kill the competing tree layer. Alternatively, clear-felled areas can be burned. This ensures ample light and nutrient supply in the post-fire succession.

- ✤ If possible, protect the plants from grazing animals, since they are highly palatable.

6   Acknowledgements

7 References

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