Establishment and Early Management of *Populus* Species in Southern Sweden

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Cover: Hybrid aspen regenerated through root suckers. The root suckers were first corridor harvested and later thinned.
Photo: Rebecka Mc Carthy

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Abstract

Populus species are among the most productive tree species in Sweden. Interest in growing them has increased during the 21st century due to political goals to increase the share of renewable energy and to increase the proportion of hardwood species in forests. *Populus* species have been shown to be potentially profitable, but currently they are mostly planted on abandoned agricultural land. There is a lack of knowledge about the establishment of *Populus* species on forest sites. There is also a lack of knowledge of how second generations can be established by root and stump sprouts, and about management of young stands. The main objective of this thesis was to focus on these issues.

Site properties are important for successful establishment of *Populus* species and factors such as soil pH and soil moisture should be considered. Site preparation is important to control weed competition and to modify the microclimate, including soil moisture.

In this thesis, mounding in relation to patch scarification, soil inversion and no intervention, were found to provide the highest survival and growth. Hybrid aspen was in most cases found to be more robust than other *Populus* species, but poplar plants or long unrooted cuttings showed similar survival and faster growth at the site where soil pH was high. In general, short unrooted poplar cuttings showed high mortality on forest sites. In water saturated soils, the growth of poplar cuttings was inhibited and roots were located closer to the soil surface. This was mainly caused by the absence of callus roots originating at the base of the cutting.

Poplar stump sprouts can be used successfully for regeneration if the clones can produce living straight sprouts. Variability in this trait was found in one of the studies in this thesis.

A second generation of naturally-regenerated hybrid aspen can produce over 100,000 root suckers per hectare. If no early management is conducted, biomass will be lost through self-thinning. It was shown in this study that a substantial amount of biomass can be harvested schematically through corridors or cross-corridors, resulting in stimulated stem diameter development. An additional early thinning further increased the diameter on crop trees.

In this thesis, site-adapted management of *Populus* species is suggested to be the most important measure to achieve successful regeneration. In particular, this includes choosing species and clones adapted to specific site properties. A second generation can be established either by stump sprouts (poplars) or root suckers (hybrid aspen). If larger-dimensioned trees are desired, early thinnings are important in the second generation.

Keywords: biomass harvest, clonal forestry, hybrid aspen, poplar, regeneration, root sucker, second generation, site properties, stump sprout, thinning

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To my family

Everything you can imagine is real

Pablo Picasso

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 Mc Carthy, R., Rytter, L. & Hjelm, K. Effects of soil preparation methods and plant types on the establishment of poplar and hybrid aspen on forest land (manuscript).

II Mc Carthy, R., Löf, M. & Gardiner, E. Early root development on nine poplar (*Populus* spp.) clones in relation to moist and saturated soil conditions (manuscript).

III Mc Carthy, R., Ekö, P.M. & Rytter, L. (2014). Reliability of stump sprouting as a regeneration method for poplars: Clonal behavior in survival, sprout straightness and growth. *Silva Fennica*, 48, 1-9.

IV Mc Carthy, R. & Rytter, L. (2015). Productivity and thinning effects in hybrid aspen root sucker stands. *Forest Ecology and Management*, 354, 215-223.

Papers III-IV are reproduced with the permission of the publishers.

The contribution of Rebecka Mc Carthy (RMC) to the papers included in this thesis was as follows:

I RMC conducted most of the field work, did 70 % of the data analysis, and 80 % of the writing.

II RMC contributed 50 % to develop the idea and study design, did 50 % of the measurements, and 80 % of the writing.

III RMC conducted the main part of the field work and data analysis, and did 80 % of the writing.

IV RMC conducted the field work for the last measurement, did the data analysis of study parts A and B, and did 70 % of the writing.

Abbreviations

dbh	Diameter at breast height
DM	Dry mass
D_Q	Quadratic mean diameter

1 Introduction

1.1 Biology and distribution of *Populus* species in the world

Species from the genus *Populus* (family *Salicaceae* Linnaeus) occur naturally over large areas in the northern hemisphere (Dickmann & Kuzovkina, 2014). The genus is divided into six sections: *Abaso* Eckenwalder (Mexican poplar), *Aigeiros* Duby (cottonwoods and black poplar), *Leucoides* Spach (swamp poplars), *Populus* (white poplars and aspens, formerly called *Leuce* Duby), *Tacamahaca* Spach (balsam poplars), and *Turanga* Bunge (arid and tropical poplars).

Populus spp. are light-demanding deciduous pioneer tree species. Some of the species are among the fastest growing tree species in the world and height growth can exceed 4 m $year^{-1}$ (Isebrands & Richardson, 2014).

Soil properties that are known to affect the vitality of *Populus* spp. are pH, soil moisture, soil bulk density, soil nutrient composition and soil temperature (Marron *et al.*, 2014; McIvor *et al.*, 2014; Stanturf & van Oosten, 2014; Zalesny *et al.*, 2005a; DesRochers *et al.*, 2003; Landhäusser, 2003; Stanturf *et al.*, 2001). The fast growth requires good water availability and well-drained soils to avoid oxygen deficit.

Poplars and aspens have a natural vegetative regeneration which is the reason why dense stands of clone groups often are found in their natural habitats (Dickmann & Kuzovkina, 2014) (definition of clone: Box 1). Stump sprouts are more common among poplars in the second generation, while root suckers are more common among aspens (definitions of stump sprout and root sucker: Box 1).

Populus spp. are a desired food source for ungulates and rodents, especially when the trees are young (Richardson *et al.*, 2014; Stanturf & van Oosten, 2014; Myking *et al.*, 2011).

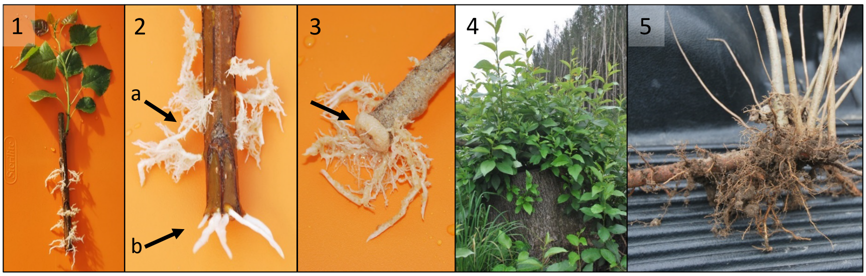
Many of the *Populus* spp. are commercially valuable due to their growth rate and the versatile use of their wood. *Populus* spp. are planted for various uses including veneer, pulp, timber, bioenergy, phytoremediation (absorption of contaminating substances through plants), soil erosion control, agroforestry and as wind breaks. Thus, they are planted widely over temperate and boreal regions. The latest country report from the International Poplar Commission (IPC) reported 8.6 million ha planted with *Populus* spp. in 24 reporting countries, while the total occurrence of *Populus* spp. is estimated to be around 87 million ha (IPC, 2012). China holds the largest share of *Populus* spp. plantations (7.6 million ha), while France, Spain and Italy have between 100,000 to 235,000 ha each. North America has approximately 90,000 ha of *Populus* spp. plantations.

The fact that many of the species are easy to propagate has led to numerous breeding programs, where hybridization is common, resulting in the wide spread use of the species (Isebrands & Richardson, 2014; Dickmann, 2006). *P. deltoides* Marshall, *P. nigra* Linnaeus, *P. maximowiczii* Henry and *P. trichocarpa* Torrey & Gray are often included in breeding programs due to their silvicultural importance. Some of the most well-known interspecific poplar hybrids are *P. deltoides* × *P. nigra* (also known as *P.* ×*canadensis* Moench or *P.* ×*euramericana* Guinier), *P. deltoides* × *P. trichocarpa* (also known as *P.* ×*generosa* Henry or *P.* ×*interamericana* van Broekhuizen), and recently also *P. nigra* × *P. maximowiczii* (Dickmann & Kuzovkina, 2014).

The first controlled crossings of European and North American poplar species started in the early 1900s (Isebrands & Richardson, 2014), while breeding of hybrid aspen started in northern Europe in the 1920s (Tullus *et al.*, 2012). Since then, the breeding work has focused on growth, timber quality and tolerance against diseases such as leaf rust (*Melampsora larici-populina* Klebahn), leaf blight (*Marssonina brunnea* (Ellis & Everhart) Magnus), bacteria cankers (*Xanthomonas populi* Ridé) and other cankers (*e.g. Septoria* spp., *Entoleuca* spp. former *Hypoxylon* spp.). The search for disease tolerant genotypes is the main reason to why clones are used in *Populus* spp. plantations (Ostry *et al.*, 2014).

In this thesis, the focus is on commercially important species from the sections *Aigeiros*, *Tacamahaca* and *Populus*. Species and hybrids from the first two sections will be referred to as ‘poplars’. The focus in the latter section lies on the hybrid between *P. tremula* Linnaeus × *P. tremuloides* Michaux (also known as *P.* ×*wettsteinii* Hämet-Ahti), and will be referred to as ‘hybrid aspen’. Some of the terminology that will be treated in this thesis is defined in Box 1.

Box 1.	**Terminology**
Clone	An asexually-reproduced tree that is genetically identical. Can be produced from *e.g.* roots, stumps, cuttings and micropropagation (Isebrands & Richardson, 2014)
Ramet	A replicate of a clone (clonal copy), *i.e.* clones produced vegetatively such as cuttings (Isebrands & Richardson, 2014)
Cutting	A cut part of a shoot, branch or root (in this thesis a one-year-old shoot from a stump sprout), planted in purpose to produces shoots and roots (1)
Primordia root	Root produced by preformed root primordia at the side of the cutting (Zalesny & Zalesny, 2009; Haissig, 1974b) (2a)
Callus root	Root produced from induced callus tissue at the bottom of the cutting (Zalesny & Zalesny, 2009; Haissig, 1974b) (2b)
Callus tissue	Undifferentiated tissue capable of cell division. Produced as a response to wounding, *e.g.* at the base of cuttings or at the cut surface of stumps (Dickmann & Kuzovkina, 2014; Zalesny & Zalesny, 2009; Haissig, 1974b) (3)
Stump sprout	Natural, asexual, regeneration from callus tissue or dormant buds in stumps after harvest (common among poplars) (Zasada et al., 1981) (4)
Root sucker	Natural, asexual, regeneration from adventitious buds in roots, especially after harvest (common among aspens) (Isebrands & Richardson, 2014) (5)



1.2 Swedish historical background

In Sweden, interest in *Populus* spp. began with the discovery of a large triploid common aspen (*P. tremula*) that had very large leaves. This discovery also led to the start of the Swedish forest tree breeding program in 1936 (Werner, 2010). The first hybrid aspen crossing was done in 1939 at the Ekebo research station located in southernmost Sweden (Werner, 2010; Johnsson, 1953). The research station is today part of the Forestry Research Institute of Sweden (Skogforsk).

Populus spp. are dioecious, and the female species selected for the hybrid aspen crossings was the North American quaking aspen (*P. tremuloides*), while the male species was the native common aspen. At that time, only two female trees growing in Sweden were used for the first hybrids. After World War II, male *P. tremuloides* trees and their pollen became possible to import, resulting in hybrids with both species as the female and male parent (Johnsson, 1953). Today, most hybrids have *P. tremula* as the female species, but all crosses are referred to as *P. tremula* × *P. tremuloides*.

The interest in hybrid aspen increased when the Swedish Match Company (Svenska Tändsticks AB) became concerned that there would be a lack of timber for the match industry. Therefore, the company established progeny trials at the Mykinge trial area (near Jönköping, Sweden). In 1946, hybrid aspen trials were established at both Mykinge and Ekebo (also including one *P. alba* × *P. tremula* hybrid) (Johnsson, 1953). Additionally, some testing of poplars occurred during this period (*e.g. P. trichocarpa* × *P. deltoides* and *P. alba* × *P. nigra*). Due to the introduction and wide-spread use of cheap gas lighters, the industry lost interest in new fast-growing *Populus* spp., and the breeding work stopped around 1960 (Stener, 2004; Christersson & Sennerby-Forsse, 1995).

In response to the oil crisis, the interest in poplars started again in mid-1970s. This time the focus was on bioenergy production as an alternative to fossil fuels (Stener, 2004; Christersson & Sennerby-Forsse, 1995). Additionally, some agricultural land which had been abandoned due to rationalizations in agriculture was planted with poplars in the 1990s when the government offered subsidies for afforestation. The poplar clones (definition of clone: Box 1) tested in Sweden have mainly been imported clones adapted to conditions in other European countries or North America (Stener, 2010; Christersson & Sennerby-Forsse, 1995). The hybrid aspen clones have been bred in Sweden or Finland.

1.3 Present situation in Sweden

Recently, the European Union stressed the importance of renewable energy to reduce global greenhouse gas emissions (European Commission, 2015). Previously, the European Union had set national goals for the EU-28 to increase their share of renewable energy by year 2020 (European Commission, 2009).

Further, the Nordic countries have a vision to become carbon neutral by year 2050 (IEA, 2013; Nordenergi, 2010). In Sweden, the national vision is to become independent of fossil fuels in the transport sector by year 2030 and to have zero net greenhouse gas emissions by the year 2050 (Regeringskansliet, 2012). Hence, bioenergy from renewable sources is of great interest in northern Europe (Rytter *et al.*, 2015). In Sweden, the energy use coming from renewable sources was 53 % in year 2014, of which 34 % came from bioenergy (Swedish Energy Agency, 2016). Most of the biomass comes from forest residues, mainly tree tops and branches. However, since the beginning of the 21st century, the interest in growing poplar and hybrid aspen for bioenergy on agricultural land has increased. Additionally, severe storm damage occurred in conifer-dominated forests in 2005 and 2007. This resulted in subsidies, offered by the government, to promote forest owners to plant trees other than Norway spruce (*Picea abies* (Linnaeus) Karsten), especially deciduous tree species. The purpose was to spread the risks and increase biodiversity in previously conifer-dominated forest stands (Skogsstyrelsen, 2013). Furthermore, ash dieback, caused by the pathogen *Hymenoscyphus fraxineus* (Kowalski) Baral *et al.*, increased the interest in alternative tree species that can be planted on moist and wetter soils. This has raised the question of if and where *Populus* spp. can also be used on forest land.

Currently, 15 hybrid aspen clones and 12 poplar clones are well-tested and registered at the Swedish Forest Agency and are thereby commercially available. The poplar species or hybrids used in Sweden are *P. trichocarpa*, *P. nigra*, *P. maximowiczii*, and *P. deltoides*. However, the poplar plantations have until 2010 been dominated by the clone OP 42 (*P. maximowiczii* × *P. trichocarpa*) (Rytter *et al.*, 2011). In 2010, other tested clones became commercial available, but OP 42 is still the most common clone in southern Sweden. This clone originates from the breeding program initiated by the Oxford Paper Company and the New York Botanical Garden in the 1920s (Schreiner, 1949).

The trend to plant *Populus* spp. is still increasing. To date, the area planted with poplar and hybrid aspen is approximately 2,000 ha each, of which most are planted on former agricultural land (estimates from the Swedish Forest Agency and the Swedish Board of Agriculture).

Although the interest in *Populus* spp. is growing due to promising economic forecasts, there are several factors holding back investments. The Swedish Forestry Act classifies poplar and hybrid aspen as exotic tree species and restricts the area that is allowed to be planted with clone material to 5 % of a forest estate, or 20 ha (Skogsvårdslagstiftningen, 2015). Commonly applied certification schemes (FSC and PEFC) restrict the use of exotic tree species, but do not further restrict the area that the law allows for planting of cloned plant material (Programme for the Endorsement of Forest Certification, 2011; Forest Stewardship Council, 2010).

Further, private forest owners are interested in increased productivity in their forests, but are at the same time reluctant to plant exotic tree species and to practice intensive forestry (Hemström *et al.*, 2013; Lindkvist *et al.*, 2012). The major reason behind this is lack of knowledge concerning the economic, management and environmental consequences.

On agricultural land in Sweden, restrictions differ from forest land and there are few, if any, rules against planting *Populus* spp. Subsidies are currently available if the trees are grown as an energy crop with a rotation age below 20 years. The extent of these plantations is mostly inhibited by high investment costs (*i.e.* plant material and fencing), lack of knowledge or a disturbed landscape view compared to open fields (Hannerz & Bohlin, 2012; Lindkvist *et al.*, 2012).

From a biodiversity perspective, it has been reported that *Populus* spp. can be of importance (Gustafsson *et al.*, 2016; Isacsson, per. comm. 2016; Felton *et al.*, 2013; Weih *et al.*, 2003). An increased share of hardwoods, including *Populus* spp., has also been in focus in Sweden to enhance biodiversity in conifer-dominated forests.

1.3.1 Establishment and management of *Populus* species in Sweden

Both poplar and hybrid aspen have shown to be among the most productive tree species in Sweden when planted at suitable sites (Tullus *et al.*, 2013; Christersson, 2008; Elfving, 1986; Eriksson, 1984; Persson, 1974). On fertile sites in southern Sweden and Denmark, the stem volume production of poplars has reached over 25 m^3 ha^{-1} $year^{-1}$ (Nielsen *et al.*, 2014; Johansson & Karačić, 2011; Christersson, 2010; Karačić *et al.*, 2003). Including branches, this corresponds to approximately 10 ton dry mass (*DM*) ha^{-1} $year^{-1}$. The growth of hybrid aspen has been reported to be somewhat lower; 20-25 m^3 ha^{-1} (7-9 ton *DM* ha^{-1} $year^{-1}$) (Rytter & Stener, 2014; Tullus *et al.*, 2012).

Poplars and hybrid aspen are commonly planted with stand densities between 1,100 and 1,600 stems ha^{-1} (approximately 3 × 3 m or 2.5 × 2.5 m spacing) on agricultural land in Sweden (Rytter *et al.*, 2013; Tullus *et al.*, 2013; Tullus *et al.*, 2012). Site preparations are made through plowing, harrowing and herbicide treatments. Recently other vegetation control methods, such as mulching, have been tested with promising results (Böhlenius & Övergaard, 2015a; Böhlenius & Övergaard, 2015b). The rotation length is commonly between 15 to 25 years. Stand density, number of commercial thinnings and rotation lengths are adapted to the production goal. Wider spacing makes it possible to avoid pre-commercial thinning and its associated cost.

On forest land in Sweden, the use of herbicides is restricted, which stresses the importance of using suitable soil preparation and plant material to achieve fast establishment.

Poplars and hybrid aspen have, in general, good survival and growth on agricultural land. On forest land, the survival of poplar has varied, but several types of damage have been reported for both poplar and hybrid aspen (*e.g.* browsing by ungulates or rodents, pathogens, insects, and abiotic damage) (Stener & Westin, 2015; Engerup, 2011). However, hybrid aspen has been observed by these authors to establish more successfully than poplar on forest land, but knowledge is lacking in this perspective.

Hybrid aspen, which is difficult to root from cuttings (definition of cutting: Box 1), is commonly planted with micropropagated containerized plants (Stenvall, 2006; Haapala, 2004). Poplars are easier to root and are commonly planted with rooted containerized plants or bare root plants. Plants of *Populus* spp. are, in general, more expensive in comparison to mass produced conifer plants, mostly due to the small quantities demanded by the forest industry. In addition, fencing is almost always needed to avoid browsing damage from ungulates and soil preparation is needed to enhance the growing conditions and to ensure fast establishment. All these measures lead to high establishment costs.

Thus, the methods to establish *Populus* spp. on forest land need to be further developed due to lack of experience, and more solid planting recommendations are essential to increase the share of *Populus* spp. in practical forestry.

Due to the their resprouting ability after harvest, there is also an interest in using the second generation of *Populus* spp. as a regeneration method in plantations instead of planting a new stand after harvest. Interest is growing in attaining a new generation without the expense of plant material and soil preparation. Under Swedish growing conditions, it has been reported that poplar stumps can produce between 18 and 37 stump sprouts per living stump (Johansson & Hjelm, 2012). Hybrid aspen can produce over 50,000 root suckers ha^{-1} and root suckers tend to be more productive than the first generation (Rytter, 2006; Rytter & Stener, 2005). This is mostly related to the fast initial growth that is supported by the already existing root system (Frey *et al.*, 2003). However, little has been reported concerning the performance of poplars and hybrid aspen in the second generation and management alternatives are still missing. Cost-effective methods are especially needed to reduce the number of stems in these initially very dense stands without jeopardizing the future stand development.

1.4 Objectives

The main objective of this thesis was to further investigate the establishment of *Populus* spp. The individual studies aimed to explore the possibility to establishing *Populus* spp. on forest land, and how the second generation from stump sprouts or root suckers can be obtained and managed. The specific objectives were:

- To find secure methods for establishment of poplars and hybrid aspen on forest land by investigating the effects of mechanical soil preparation, plant material and site properties on survival and growth (Paper I).
- To study the effects of high water table on early root growth of poplar cuttings (Paper II), since *Populus* spp. are often planted on sites that, at times, can have a high water table (*i.e.* saturated soil condition).
- To study the survival, quality and growth of stump sprouts of poplar clones to assess the reliability of stump sprouting as a regeneration method (Paper III).
- To study the initial productivity and the effects of different thinning regimes on the growth development of hybrid aspen stands established by root suckers (Paper IV).

2 Materials & methods

The studies in this thesis were based on randomized block designs or a totally randomized design established in field or greenhouse experiments. The field sites were located in southern Sweden (Figure 1). Two of the experiments were located on agricultural land in the southernmost Sweden where growing conditions are favorable. All poplar clones have been bred abroad and originate from nurseries in Europe or North America. The hybrid aspen clones were Swedish or Finnish breeds. Additional description of the sites and clone material used in this thesis are found in the appendix.

This section is an overview of the materials and methods used to fulfil the objectives. Detailed descriptions are provided in each individual paper (I-IV). Shoots referred to in this thesis originate from buds on cuttings or stool beds for production of new cuttings. When referring to stump sprouts, the aim is to regenerate vegetatively and create a new stand. When referring to cuttings, the origin was stem cuttings from one-year-old shoots.

2.1 Establishment of poplar and hybrid aspen after planting (Paper I & II)

Three sites in southern Sweden (Brattön, Dimbo and Duveholm) were used to study the establishment of poplar and hybrid aspen on forest land (Figure 1) (Paper I). Four treatments containing four rows each were applied in a random block design: *a*) control with no soil preparation, *b*) patch scarification, *c*) mounding, and *d*) soil inversion (Figure 2). Within each treatment and row, one of four plant types was randomly used: *i*) short poplar cuttings (ca. 20 cm), *ii*) long poplar cuttings (ca. 50 cm), *iii*) rooted containerized poplar cuttings (ca. 47 cm) (referred to as poplar plants), and *iv*) containerized hybrid aspen (ca. 57 cm) (referred to as hybrid aspen). Clones were randomly assigned a position within each row of a plant type. Growth characteristics were registered after each growing season during three consecutive years.

The effect of treatment was analyzed with split-plot mixed models and survival was assessed by a generalized split-plot mixed model with a logit link.

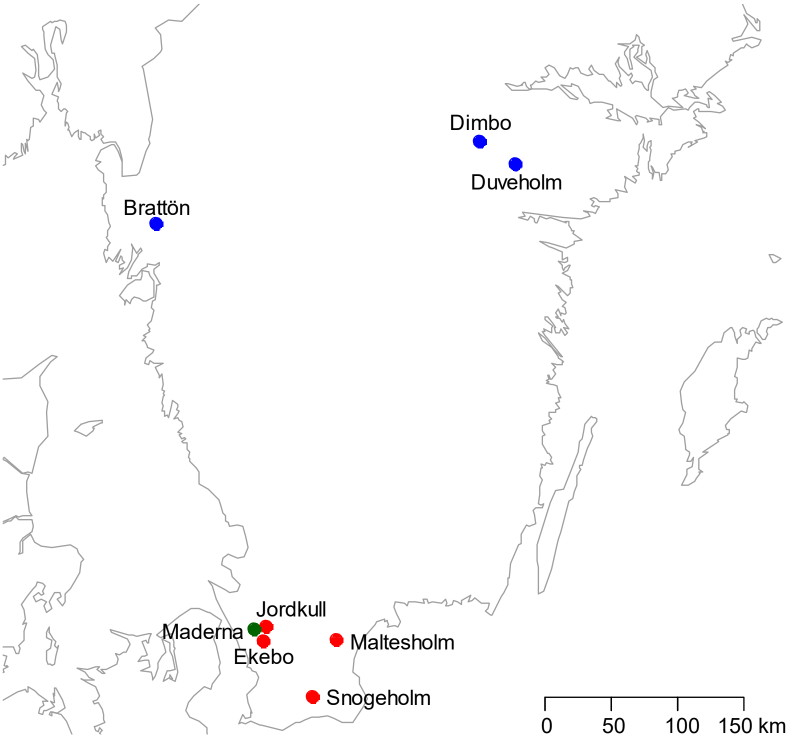


Figure 1. Locations of the study sites in southern Sweden used in Paper I (blue), Paper III (green), and Paper IV (red).

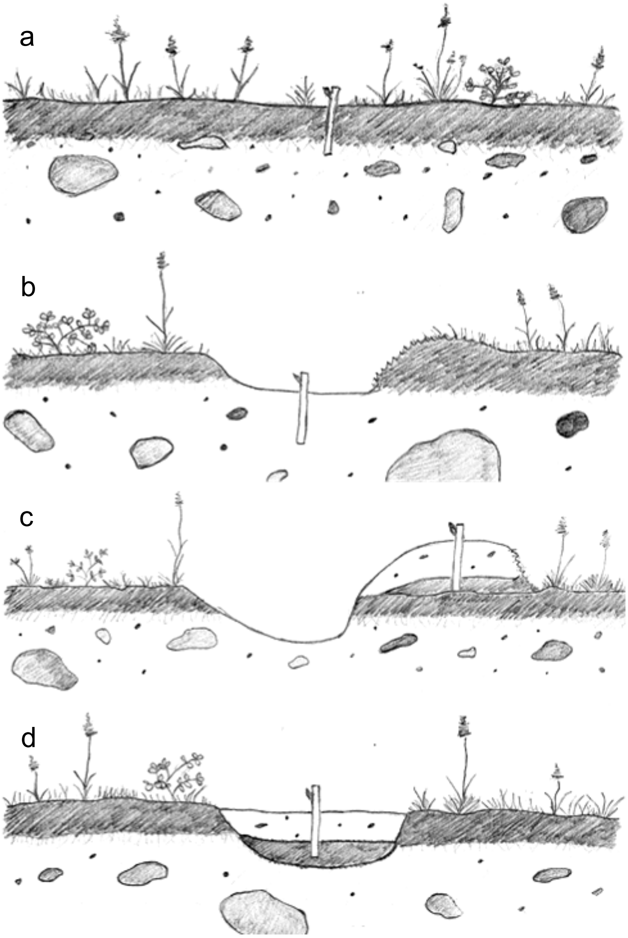


Figure 2. Illustration of the four soil preparation methods used for planting *Populus* spp. on forest land in southern Sweden (Paper I). No scarification (a), patch scarification (b), mounding (c), and soil inversion (d). Planting was done with short poplar cuttings (ca. 20 cm), long poplar cuttings (ca. 50 cm), poplar plants (ca. 47 cm), and hybrid aspen plants (ca. 57 cm). The illustration shows planted short poplar cuttings.

To study the effects of high water tables during the initial establishment phase of poplar, root growth of cuttings (20 cm) was studied under two treatments: moist and saturated (flooded) soil conditions (Figure 3) (Paper II). Both treatments were imposed with nutrient solution. The experiment took place in a greenhouse at the USDA Forest Service's Center for Bottomland Hardwoods Research in Stoneville, Mississippi, USA. The two soil moisture treatments were applied in a random block design and nine clones replicated with four ramets (definition of ramet: Box 1) were randomly placed within each treatment. The planting took place in sand-filled containers and growth characteristics were recorded 18 days after planting.

Treatment effects were analyzed by split-plot mixed models at the whole plant level, or in sections of the cutting (apical, middle and basal) (Figure 3). Correlations among growth characteristics were calculated with Pearson's correlation coefficient for each of the treatments.

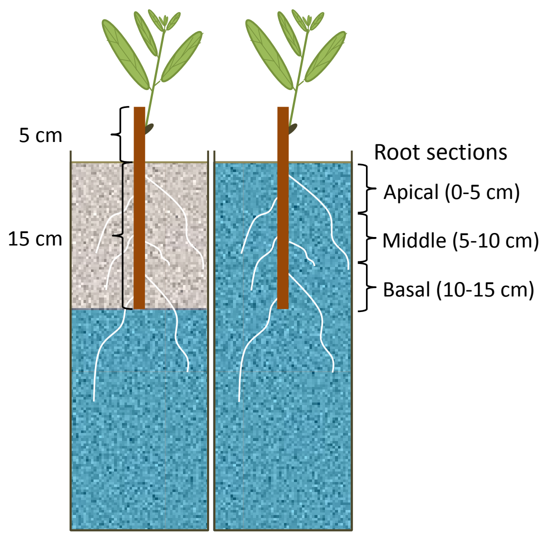


Figure 3. Illustration of the two soil moisture treatments conducted in sand-filled containers in a greenhouse experiment (Paper II). Water levels represent moist (left) and saturated (right) soil conditions. Rooting was studied in three separate 5 cm rooting sections (apical, middle, and basal) of the cutting.

2.2 Stump sprouting of poplar clones (Paper III)

To investigate the ability of stump sprouting after harvesting poplars, stump sprouts from 23 different clones located in a former clone test in southern Sweden were used (Figure 1). Growth characteristics were recorded after one year. Stump survival was defined as stumps having living sprouts. Sprout straightness was recorded in three classes: *i*) straight, *ii*) crooked, and *iii*) very crooked (Figure 4). The clones were represented by three to 10 stumps each and were regarded as randomly distributed within the site. Clones consisted of three groups: eight clones commercially available in Sweden, seven candidate clones (*i.e.* candidates to become commercial), and eight additional clones (*i.e.* clones excluded from further selection).

Analyses of survival of clones and clone groups were conducted with a generalized mixed model with a logit link. Clones having less than two living stumps were excluded from further analysis. Straightness was analyzed by frequency analysis using Fisher's exact test (PROC FREQ in SAS®). Other growth characteristics were analyzed by ANOVA for clones and clone groups.

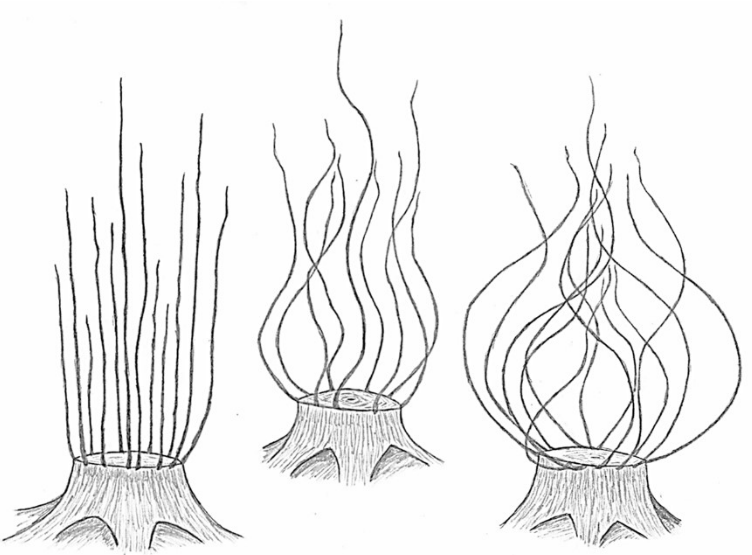


Figure 4. Illustration of straightness of poplar stump sprouts (Paper III) in three classes; straight (left), crooked (middle), and very crooked (right).

2.3 Productivity and management of hybrid aspen root suckers (Paper IV)

Paper IV comprised three study parts (A-C) of the productivity of hybrid aspen root suckers conducted at four sites in southern Sweden (Figure 1).

In study part A, the initial growth of root suckers was studied at all four sites. Each site contained one to four blocks. Growth characteristics were recorded annually or every other year up to the age of four years. Site effects were analyzed by generalized linear models.

Study part B was conducted at one site (Figure 1: Jordkull), where effects of early harvests on the stand development were investigated. Three treatments were applied after two years of growth (Figure 5); *i*) control with no harvest, *ii*) corridor harvest, and *iii*) cross-corridor harvest. Growth effects were studied every two years up to the age of 12 years using a random block design. Analyses of harvest effects were performed by mixed models with block as a random effect.

In study part C, the effects of thinning after harvest were investigated. Half of the experiment used in study part B was thinned to 1,100 stems ha^{-1} at the age of four years. Larger trees were selected within ca. 3 × 3 m spacing. The three treatments in this study part were; *iv*) control with no harvest followed by thinning, *v*) corridor harvest followed by thinning, and *vi*) cross-corridor harvest followed by thinning. These treatments (*iv*-*vi*) are hereafter called second thinning, although one treatment was thinned for the first time. This study part also had a random block design. Growth characteristics were recorded for all remaining trees every two years for 12 years. Harvest effects on growth after the second thinning were analyzed in the same way as in study part B.

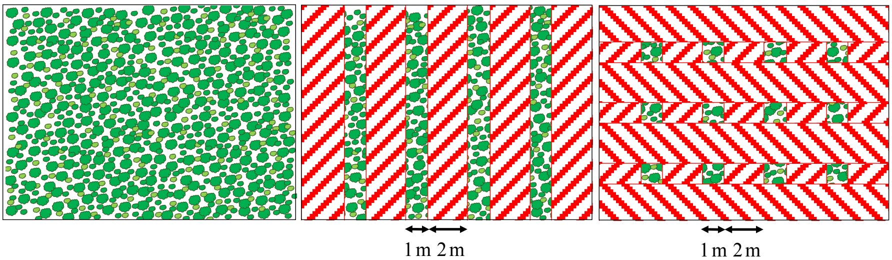


Figure 5. Illustration of treatments performed on two-year-old hybrid aspen root suckers (Paper IV). Left panel: no harvest. Middle panel: corridor harvest - 2 m corridors (striped areas) harvested, leaving 1 m wide rows of root suckers. Right panel: cross-corridor harvest - 2 m wide corridors harvested in two directions (striped areas), leaving 1 × 1 m patches of root suckers.

3 Main results

3.1 Establishment of poplar and hybrid aspen after planting (Paper I & II)

3.1.1 Survival and plant damage

Survival and growth of *Populus* spp. plants on forest land were effected by site, soil preparation methods and plant types, but interactions showed that the effects of soil preparations and plant types differed among sites (Paper I). After three growing seasons, the Dimbo site had the highest survival rate (73 %) for all soil preparation methods and plant types (Figure 6). The Brattön and Duveholm sites showed, in general, lower survival (46 and 51 %, respectively). In general, mounding provided the best survival (67 %), while patch scarification had the lowest (49 %). Hybrid aspen generally showed the highest survival (75 %), but at Duveholm poplar plants and long cuttings showed similar survival. Short cuttings showed the lowest survival (35 %) at all sites.

Damage was observed during the three-year study period. Despite the damage, most living plants still had positive growth. At Dimbo, the fence was damaged and 34 and 25 % of the plants were browsed by ungulates during the first and second seasons, respectively. At Duveholm, 34 % of plants had vole damage at the end of the second season. In most cases the cause of damage could not be assessed, but other obvious damage sources were weather (*e.g.* frost) and competing vegetation. However, concerns that a high water table in some areas caused poor plant development were raised.

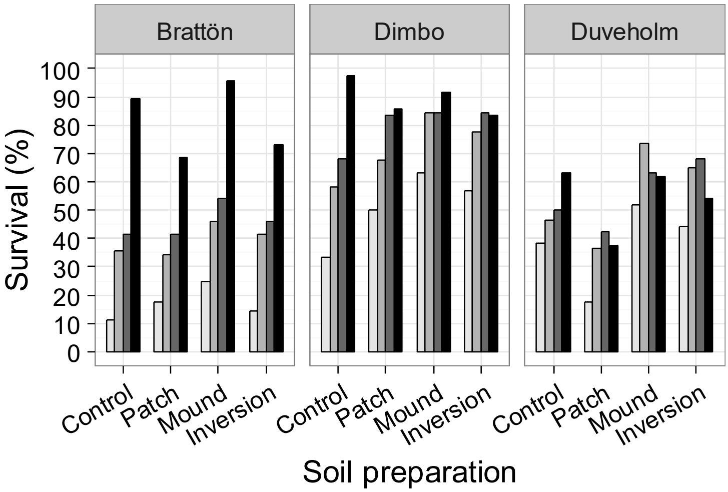


Figure 6. Survival of *Populus* spp. after three growing seasons (Paper I). The three forest sites (Brattön, Dimbo and Duveholm) were treated with four soil preparation methods and four plant types. The soil preparations were: control, patch scarification, mounding, and soil inversion. The plant types were (from light grey to black): short cutting (20 cm), long cutting (50 cm), containerized poplar plant (47 cm), and containerized hybrid aspen plant (57 cm).

Though the study on forest land was not designed to evaluate clonal performance, differences in survival of poplar clones were apparent. This was not statistically analyzed, due to low replication of clones, but only interpreted. Some additional indications of clone survival are discussed in section 4.1.6.

3.1.2 Plant growth

In Paper I, soil preparation and plant type showed site interacting effects on plant growth and height (Figure 7). The Duveholm site had the fastest height growth (76 cm year^{-1}) and the tallest plants (192 cm) in the third season, but this site did not differ from the growth found at Dimbo (52 cm year^{-1}) for all soil preparations and plant types.

In general, mounding provided the fastest growth (63 cm year^{-1}) and tallest plants (161 cm) after three seasons (Figure 7a). Patch scarification showed the slowest growth and shortest plants after three seasons (47 cm year^{-1}, 129 cm, respectively). The control (*i.e.* no soil preparation) and soil inversion treatments showed great variability in their performance over the sites.

Hybrid aspen showed no site effects, but generally had the fastest growth (62 cm year^{-1}) and tallest plants (162 cm) in the third season (Figure 7b). Short cuttings had the slowest growth and shortest plants (51 cm year^{-1} and 123 cm).

However, at Duveholm poplar plants and long cutting showed faster growth (82 cm year^{-1}) and taller plants (210 cm) compared to hybrid aspen (71 cm year^{-1} and 177 cm, respectively).

Plant diameter (at 50 cm above ground) followed a similar response to soil preparation and plant type as plant height in the third season.

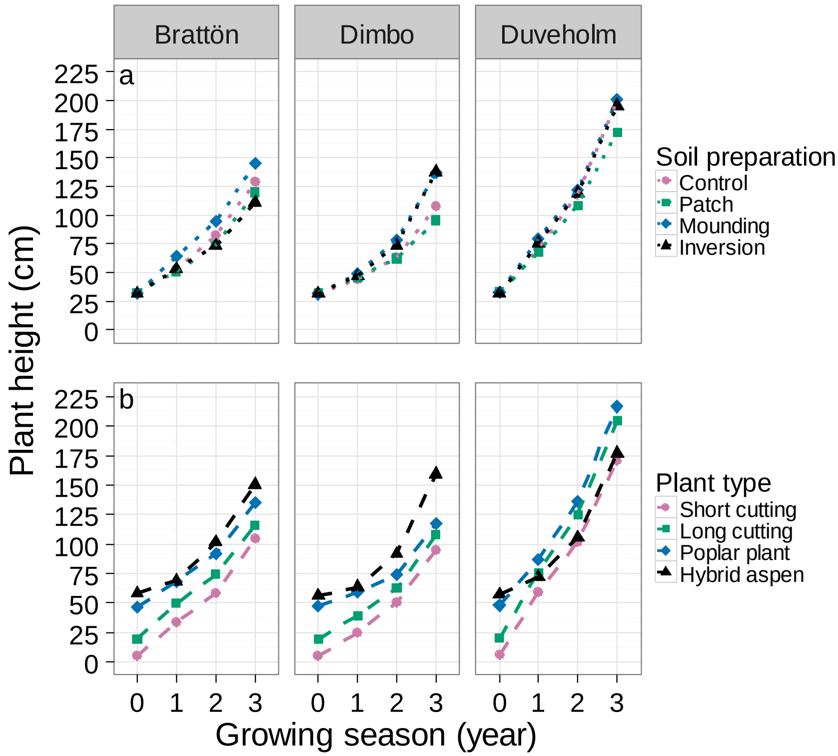


Figure 7. Plant height (cm) of *Populus* spp. during three growing seasons planted at three sites (Brattön, Dimbo and Duveholm) (Paper I). (a) Mean height of plants planted with four soil preparations: control, patch scarification, mounding, and soil inversion. (b) Mean height of four plant types: short poplar cutting (20 cm), long poplar cutting (50 cm), containerized poplar plant, and containerized hybrid aspen plant. Mean height in growing season zero represents the above-ground portion of the cutting or plant at planting.

3.1.3 Rooting of poplar cuttings

In the greenhouse study (Paper II), cuttings grown under moist soil conditions had roots located in all three sections of the cutting (Figure 8), while cuttings grown under saturated soil conditions did not produce roots that originated from callus tissue at the base of the cutting (definitions of callus tissue and callus root: Box 1). The response to soil saturation differed between clones and not all clones showed treatment effects in root dry mass (*DM*), number of roots, and total root length. In general, the number of all types of roots and primordia roots decreased in the saturated soil (definition of primordia root: Box 1). Cuttings grown in saturated soil had a shallower root system. The relative distribution of roots differed between treatments in all sections of the cutting (Figure 8). Approximately 14, 30 and 60 % of the roots were found in the apical, middle and basal sections respectively in moist soil. In saturated soil, these numbers were 27, 40 and 34 %. The mean and total root length was also greater in the apical section when the soil was saturated. The moist treatment had more roots than the saturated treatment in the basal section. Soil saturation, in comparison to moist soil, also resulted in reduced shoot and leaf growth.

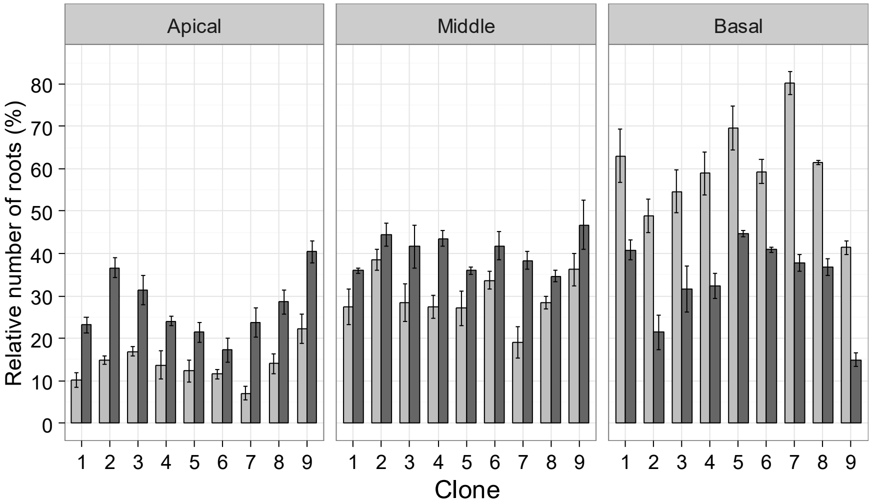


Figure 8. Relative number of roots of nine poplar clones in moist (light grey) and saturated (dark grey) soil in three sections of the cutting (Paper II). The depths of the three sections below the soil surface were: apical (0-5 cm), middle (5-10 cm), and basal (10-15 cm). The cuttings were 20 cm long.

Plants accumulated most biomass in leaves (ca. 65 %), followed by stems (ca. 26 %) and roots (ca. 9 %), although these numbers differed among clones. Only one clone showed a treatment effect, increasing the share of biomass in the stem when the soil was saturated.

This study showed a significant correlation between root *DM* and shoot characteristics in moist (Pearson's $r = 0.48$-0.67) and saturated ($r = 0.39$-0.64) soils. Cutting *DM* and diameter showed significant positive correlations with above ground growth characteristics ($r = 0.41$-0.76), but not with roots.

3.2 Stump sprouting of poplar clones (Paper III)

Regeneration of poplar through stump sprouting differed among the tested poplar clones after one year of growth (Paper III). Clones differed in stump survival (proportion of stumps with living stump sprouts), sprout straightness, mean basal diameter and sprout height. The height of the tallest sprout did not differ significantly among clones (range among clones from 91 to 275 cm). Almost half of the clones had 100 % stump survival, while two of the clones had no living stumps at all (Figure 9). For two clones 100 % of the stumps had straight sprouts, but the other clones varied in sprout straightness (Figure 10). Candidate clones (Ca) had a higher stump survival (93 %) than additional (62 %) and commercial clones (Co) (55 %). No other differences in sprout characteristics were found among these groups of clones.

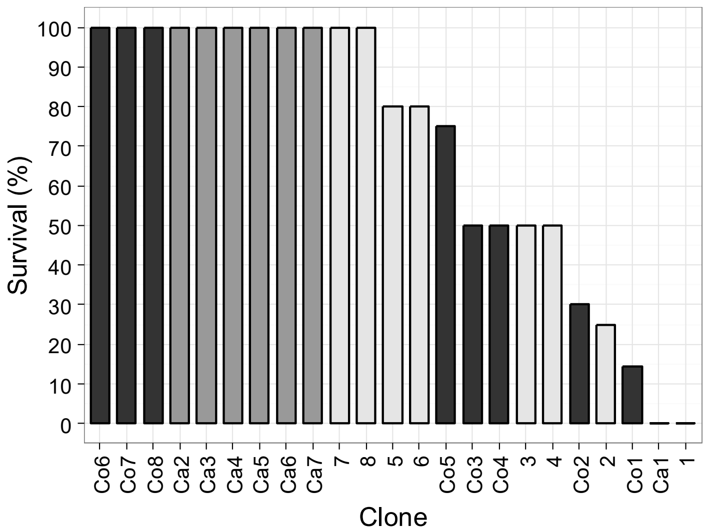


Figure 9. Stump survival of 23 poplar clones (percentage of stumps having living stump sprouts) (Paper III). The clones were divided into three groups: commercial (black - Co), candidate (grey - Ca) and additional clones (light grey). The number of stumps per clone ranged between three and 10.

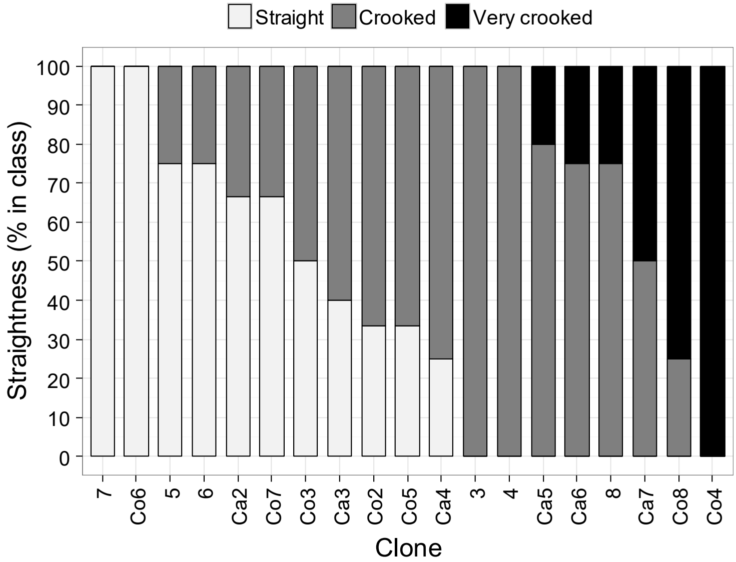


Figure 10. Percentage of poplar stumps with sprouts in three straightness classes: straight, crooked, and very crooked (Paper III). The clones were divided into three groups: commercial (Co), candidate (Ca) and additional clones (indicated by numbers only). Only clones having at least two living stumps were included.

3.3 Productivity and management of hybrid aspen root suckers (Paper IV)

This paper consists of three separate study parts (A-C). In study part A, the initial growth of hybrid aspen root suckers was analyzed. Regeneration of hybrid aspen through root suckers differed among sites. After one year of growth, the most productive site had 110,000 root suckers ha^{-1}. After two years, all four sites showed high production of root suckers (47,000 to 73,000 living root suckers ha^{-1}). The number of living root suckers started to decrease due to self-thinning (*i.e.* mortality due to competition) after one or two years. The standing biomass increased steadily and was on average 36 ton *DM* ha^{-1} (range among the sites from 26 to 44 ton *DM* ha^{-1}) after four years.

In study part B, the harvest in corridors and cross-corridors after two years corresponded to 9.2 and 15.3 ton *DM* ha^{-1}, respectively. The harvests, of course, reduced the stand density compared to the control, but due to self-thinning this effect could no longer be distinguished at the age of 12 years (Figure 11a). The harvest had a positive influence on the quadratic mean diameter at breast height (D_Q) (Figure 11b), but tree height was not influenced. The obtainable biomass (*i.e.* harvested biomass and standing biomass) did not differ significantly among the treatments over the study period. At the age of eight years, all treatments had a mean annual increment of obtainable biomass above 9 ton *DM* ha^{-1} $year^{-1}$.

In study part C, after plots were first harvested (study part B) and later thinned to 1,100 stems ha^{-1}, a strong effect of the first harvest was found. Plots that were previously left without harvest had a smaller crown ratio (Figure 11c), smaller D_Q (Figure 11d), and lower mean annual increment of stem wood (10 m^3 ha^{-1} $year^{-1}$ at the age of 12 years). The opposite was found for plots that were previously cross-corridor harvested. After 12 years this treatment produced over 14 m^3 stem wood ha^{-1} $year^{-1}$. The previously corridor harvested plots ended up in between the other two treatments. At the age of 10 years, the effect of harvest on crown ratio had declined, but the effect on D_Q remained unchanged over the study period. The mean annual increment was still steadily increasing at this age.

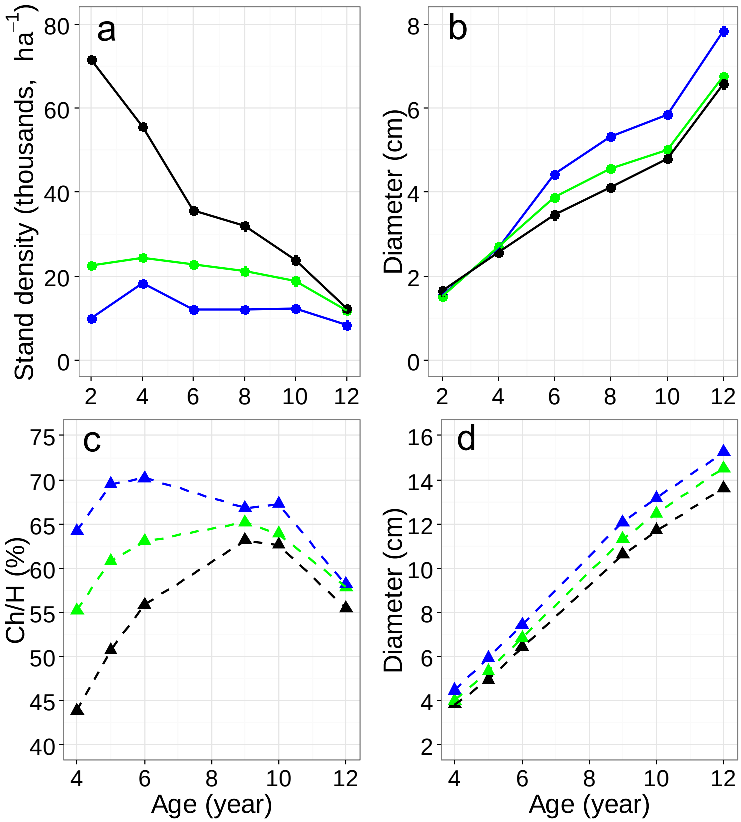


Figure 11. Growth development of hybrid aspen root suckers in study parts B and C (Paper IV). Treatments after two years were: no harvest (black), corridor harvest (green), and cross-corridor harvest (blue). a) Number of root suckers (thousands per hectare), b) quadratic mean diameter at breast height (D_Q), c) ratio between green crown height and tree height, and d) quadratic mean diameter at breast height (D_Q). Panels a) and b) are results from thinning only through harvest at the age of two years (study part B) while panels c) and d) show results after an additional thinning to 1,100 stems ha^{-1} done at the age of four years (study part C).

4 Discussion

4.1 Establishment of poplar and hybrid aspen

For successful establishment of *Populus* spp., soil preparation, plant material, including choice of clone, must be adjusted to the site conditions (Papers I and II).

4.1.1 Survival and plant damage

Site properties were indicated to have had the largest influence on survival and growth in Paper I. *Populus* spp. need nutritious soils with pH above five to grow well (Stanturf *et al.*, 2001; Ericsson & Lindsjö, 1981). Different soil properties, including soil fertility, also affect the growing conditions for competing weeds (Hedwall *et al.*, 2010; Stanturf *et al.*, 2001; Löf, 2000). Vegetation control is therefore of great importance when growing light-demanding tree species such as poplars (Böhlenius & Övergaard, 2015b; Löf *et al.*, 2012; Bilodeau-Gauthier *et al.*, 2011; Hytönen & Jylhä, 2005; Czapowskyj & Safford, 1993).

Damage from voles was rather frequently seen during the first two years at the Duveholm site, which may have been one of the main causes of the lower survival at this site. We ocularly observed that the weed competition differed between the sites and Duveholm was the only site having areas with clover (*Trifolium* spp.). The populations of voles related to the amount and composition of ground vegetation (Hytönen & Jylhä, 2005; Manson *et al.*, 2001). Due to the rate of vole-damaged plants at Duveholm (over 30 %), the weed situation seems to have been favorable for voles at this site.

The survival rate at the Brattön site was also low. This site had some areas that were rather wet. The soil moisture affected the weed composition, but probably also decreased the soil temperature. Landhäusser (2003) and Hansen (1986) showed that survival, rooting and shoot growth of poplar cuttings are strongly inhibited when the soil temperature is low. They did not recommend planting poplar cuttings in soil temperatures below 5 to 10° C. Additionally, the greenhouse experiment (Paper II) showed that root and shoot growth were negatively affected by a high water table (section 4.1.4). The short cuttings showed a very low survival (17 %) at Brattön. This may have been influenced by the high water table in combination with the low planting height (5 cm above soil surface). However, hybrid aspen showed reasonably good survival (82 %) at this site.

At Dimbo the survival rate was, in general, highest for all soil preparations and plant types. The fence was damaged during the first two seasons, resulting in browsing by moose (*Alces alces* Linnaeus). This did not affect the survival, but only growth. Several other studies have reported that browsing by ungulates can be severe on hardwood species in the northern Europe (Edenius & Ericsson, 2015; Bergqvist *et al.*, 2014; Edenius *et al.*, 2011; Myking *et al.*, 2011; Bergquist *et al.*, 2009; Härkönen *et al.*, 2008; Zakrisson *et al.*, 2007; Viherä-Aarnio & Heikkilä, 2006). The importance of fencing and maintenance of the fence should therefore not be ignored.

4.1.2 Growth and soil properties

The Duveholm site showed the highest growth. The soil pH was also highest (5.3) at this site compared to Brattön (4.7) and Dimbo (4.5). In the literature, soil pH above five is commonly recommended to achieve sufficient growth of *Populus* spp. (Stanturf *et al.*, 2001; Boysen & Strobl, 1991; Timmer, 1985; Ericsson & Lindsjö, 1981).

Hybrid aspen showed the best and most stable performance (*i.e.* survival, growth and plant height) over the sites, indicating that these hybrids are not as sensitive to changes in soil characteristics. This is probably influenced by the origin of the species. For hybrid aspen, the hybridized species originate from northern latitudes, compared to poplars which commonly originate from lower latitudes and where none of the species are native to Sweden. However, when soil pH was high, long cuttings and poplar plants grew better than hybrid aspen. It has also been found by Hjelm and Rytter (2016) that poplars are sensitive to low soil pH and their study included soils from the sites in this paper.

The Dimbo site had, in addition to the lowest pH, a coarser soil structure (sandy moraine). It has been observed that the growth of poplar increases if the soil contains some sand, but too much sand degrades the growing conditions (Pinno *et al.*, 2010). Medium soil textures, *e.g.* sandy loam, are commonly recommended for poplars in order to grow well (Stanturf *et al.*, 2001). Soil texture and a lower pH likely resulted in the general lower growth at this site, but, of course, the fact the plants were browsed should also be taken into account.

Several authors have reported that soil properties other than pH, soil moisture content and texture affect the growth of poplars. For example, the composition of nutrients such as phosphorous, potassium and the source of nitrogen have been shown to influence the growth of poplars, but it has also been observed that the effect of nutrient composition can differ between clones (Guillemette & DesRochers, 2008; DesRochers *et al.*, 2006; Brown & van den Driessche, 2005; DesRochers *et al.*, 2003; Czapowskyj & Safford, 1993). Therefore, the choice of sites for poplar growth should not be based only on the site characteristics explored in this thesis.

4.1.3 Effects of soil preparation and plant type

Among the soil preparation methods, mounding showed the most promising results in terms of survival, growth and plant height (Paper I). The elevated planting spots reduce soil moisture, increase soil temperature and delay colonization of weeds (Löf *et al.*, 2012; Sutton, 1993; Örlander *et al.*, 1990). Patch scarification, on the other hand, was found not to be suitable for establishment on these often moist sites with high weed competition. It has also been observed that patch scarification is not particularly effective to improve growth of young seedlings in southern Sweden (Bergquist *et al.*, 2009). The results indicated that it could even be better to leave the organic layer intact (control) than to perform soil preparation methods that lower the planting spot (*i.e.* patch scarification and sometimes soil inversion) when the water table is high.

Hybrid aspen was the most reliable plant type in Paper I (section 4.1). Short cuttings were found to be unsuitable to plant on forest land, while long cuttings, in most cases, performed as well as poplar plants in terms of survival and growth. Higher survival and growth of longer poplar cuttings compared to shorter cuttings have also been demonstrated on agricultural land (Rossi, 1991), as well as in controlled experiments (Schuler & McCarthy, 2015; Vigl & Rewald, 2014; DesRochers & Thomas, 2003; Allen & McComb, 1956). The reason for this is related to the size of the cuttings. Longer cuttings can provide more stored carbohydrate and a larger surface area available for rooting (Schuler & McCarthy, 2015; DesRochers & Thomas, 2003; Dickmann *et al.*, 1980; Haissig, 1974a). It has been shown that longer cuttings increase the number of basal roots and shoot growth of cuttings, but also that a larger above ground part of long cuttings is favorable (Schuler & McCarthy, 2015; Kaczmarek *et al.*, 2014; Rossi, 1991).

Böhlenius and Övergaard (2015a) found that 30 cm cuttings initially grew better than bare root plants. In Paper I, it was also seen that the two types of cuttings grew faster than containerized plants during the first growing season, but this effect declined, especially for the short cuttings, during the second growing season (Mc Carthy *et al.*, 2016). This indicates a planting shock in containerized plants and that a better balanced root to shoot ratio may be favorable. However, long poplar cuttings can be a good alternative to poplar plants if they have a sufficient length.

4.1.4 Influence of soil moisture on root growth

When establishing cuttings, the greenhouse study showed that rooting and shoot growth were influenced by soil moisture regime and clone. Callus roots (*i.e.* roots originating from callus tissue: Box 1) were lacking at the bottom of the cutting. Consequently, the relative distribution of roots was shifted toward the soil surface when the soil was saturated. Others have shown that soil saturation has a negative influence on growth of poplars, and that clones respond differently to this soil condition (Guo *et al.*, 2011; Cao & Conner, 1999; Liu & Dickmann, 1992). On the contrary, Allen and McComb (1956) found the highest growth when cuttings were planted in saturated soil. However, at the end of their study the growth had started to decline and leaves started to turn yellow. Pezeshki *et al.* (1998) also found that roots located closer to the soil surface of black willow (*Salix nigra* Marshall) cuttings when the soil was saturated. At deeper levels these cuttings did not produce any roots.

Callus roots emerge from callus tissue as a reaction to wounding. Heilman *et al.* (1994) reported that callus roots dominated the first-season growth, but Bloomberg (1963) suggested that primordia roots (*i.e.* roots originating from preformed root primordia: Box 1) are of greater importance for early survival and growth. The lack of callus roots (and callus tissue formation) in the saturated treatment could later have an influence on the overall plant growth, but the long-term effects need to be studied further. It is possible that callus roots could emerge later, since it has been observed that callus roots can emerge much later than primordia roots (Haissig, 1974b; Bloomberg, 1963). However, this occurrence was not reported for cuttings exposed to soil saturation. Thus, it is possible that callus roots could emerge later when soil saturation decreases. Deep-growing roots are of importance for hydraulic control (*i.e.* regulation of water in the tree) and may affect tree resistance to windthrow (Zalesny & Zalesny, 2009; Kozlowski, 1986). Therefore, having roots shifted toward the soil surface at establishment may result in plants being less adaptable to changes in soil moisture regimes and later make them more susceptible to windthrow. On the other hand, when callus roots are lacking, the growth of primordia roots is essential for plant establishment and survival (Bloomberg, 1964). It is important to note that when stands become older the soil moisture conditions will also change.

4.1.5 Influence of cutting characteristics on the rooting of poplars

The location and age of the shoot from which cuttings are made, cutting size and cutting moisture content have also been shown to influence survival, and growth of roots and shoots (DesRochers & Thomas, 2003; Zalesny *et al.*, 2003; Dickmann *et al.*, 1980; Allen & McComb, 1956). In Paper II, the cutting diameter (7-15 mm), as well as cutting *DM*, showed positive correlations to shoot growth, and the importance of early shoot growth together with root growth is essential for successful establishment (Krabel *et al.*, 2015; Branislav *et al.*, 2009; Zalesny *et al.*, 2005b; Rhodenbaugh & Pallardy, 1993; Tschaplinski & Blake, 1989; Pallardy & Kozlowski, 1979). This indicates that smaller cuttings should be used with care, especially when the growing conditions are tougher. This was also seen among the short cuttings planted on forest land (Paper I), which were both ca. 30 cm shorter and ca. 1 mm smaller in diameter compared to long cuttings. However, in both Paper I and II cuttings came from dormant one-year-old shoots, and cuttings from these shoots are generally recommended (Zalesny & Zalesny, 2009; Allen & McComb, 1956).

Generalization of results for practical use from Paper I and II should be made with caution. Root growth in saturated soil needs to be studied in longer-termed field trials, and the influence of soil properties on establishment needs to be further defined. Nevertheless, these two papers indicate that the site conditions influence survival and growth, and that a high water table affects the growth of cuttings negatively.

4.1.6 Clonal effects on the establishment of *Populus* species

Clonal differences are common among *Populus* spp., providing a basis for breeding and selection of clones (Stanton *et al.*, 2014; Zalesny & Zalesny, 2009; Stener & Karlsson, 2004; Bisoffi & Gullberg, 1996). Thus, it is important to use well-tested clones when planting *Populus* spp., but also to plant them under site conditions they have been tested for (Dickmann, 2006).

In Paper II, the effect of clones was strong on root growth under different soil moisture regimes (*i.e.* in root *DM*, number of roots, presence of callus roots, and root length). Additionally, above-ground growth showed differences in response depending on clone (*i.e.* in shoot *DM*, leaf *DM* and total leaf area). Some clones were less affected by soil moisture regime, while other clones showed a strong response.

The study on forest land (Paper I) indicated that clones also had an influence on establishment and interacted with the site conditions. The number of replicates was low for poplar clones (two ramets per experimental unit) and higher for hybrid aspen (eight ramets per experimental unit) (definition of ramet: Box 1). Therefore, it is difficult to provide a solid figure for the clone survival of poplar and hybrid aspen, and the following discussion should be regarded as a preliminary indication of the clonal differences.

To demonstrate the clonal influence on survival after three growing seasons, the most successful and comparable plant types (*i.e.* containerized poplar and hybrid aspen plants) and soil preparation method (mounding) were selected (Figure 12).

Hybrid aspen clones generally performed more consistently among the sites compared to most poplar clones (Figure 12). Nevertheless, these hybrid aspen clones had lower survival at Duveholm. The vole population was also highest at this site, which probably influenced the survival (section 4.1.1). Two poplar clones (no. 4 and 10) showed a more stable survival than the other poplar clones and had a similar survival rate to hybrid aspen at all sites. The other poplar clones had a great variability in survival and some of them did not show a convincing suitability to these sites.

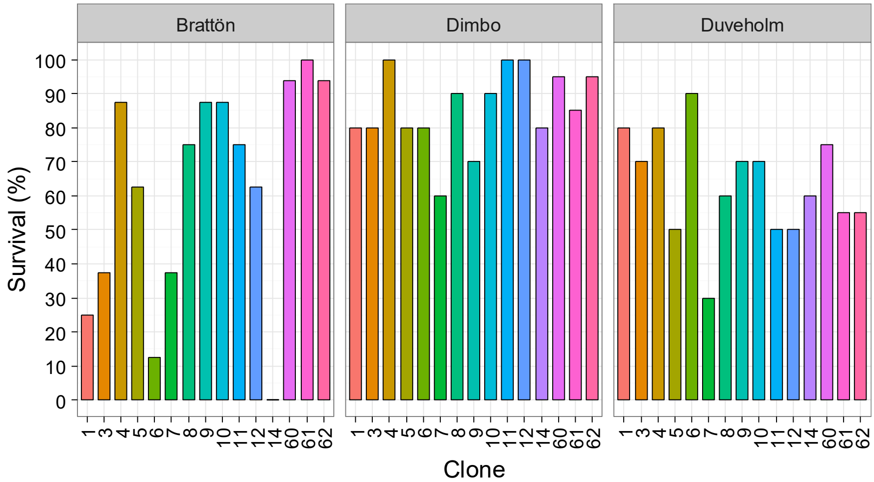


Figure 12. Clone survival of containerized poplar and hybrid aspen plants when mounding was performed at three forest sites after the third growing season (unpublished data, Paper I). Clones 1-14 are poplars, and clones 60-62 are hybrid aspens. Nine of the poplar clones were *P. trichocarpa* (clones 1, 4, 5 and 8-14), two *P. maximowiczii* × *P. nigra* (clones 3 and 7), and one *P. maximowiczii* × *P. trichocarpa* (clone 6). Hybrid aspen clones 60 and 61 were Swedish breeds, while clone 62 originated from Finland. Each site contained 8-10 ramets per poplar clone and 32-40 ramets per hybrid aspen clone.

Containerized poplar and hybrid aspen from Paper I were also selected to interpret clone survival dependence on soil preparation (Figure 13). The survival of clones also tended to differ among soil preparations. Poplar clone no. 4 showed a more stable performance across the different soil preparation methods compared to the other clones. The hybrid aspen clones had a higher survival compared to most of the poplar clones in the control (no soil preparation) or when mounding was performed. The survival of most clones was lower in the control and patch scarification treatments.

The variation in clonal survival, indicated in Paper I and observed in Paper II, emphasizes the importance of testing and selecting clones tolerant to site-specific soil conditions when planting *Populus* spp.

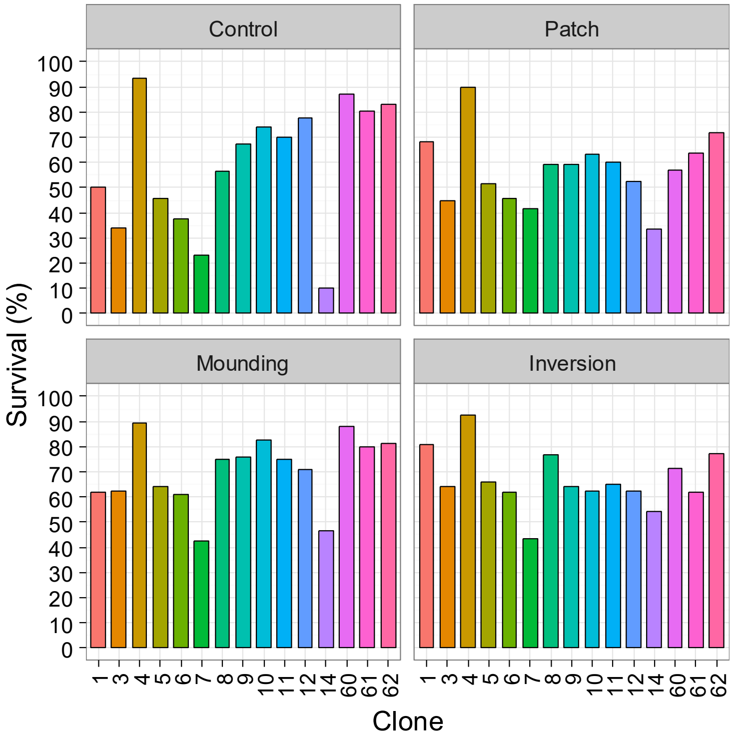


Figure 13. Survival of clones from containerized poplar and hybrid aspen plants for four soil preparations (averaged over three sites) after the third growing season (unpublished data, Paper I). Clones 1-14 are poplars and clones 60-62 are hybrid aspens. Nine of the poplar clones were *P. trichocarpa* (clones 1, 4, 5 and 8-14), two *P. maximowiczii* × *P. nigra* (clones 3 and 7), and one *P. maximowiczii* × *P. trichocarpa* (clone 6). Hybrid aspen clones 60 and 61 were Swedish breeds, and clone 62 originated from Finland. Each soil preparation method contained 28 ramets per poplar clone and 112 ramets per hybrid aspen clone.

4.2 Stump sprouting of poplar clones

The first step for finding reliable clones for stump sprouting is the establishment and success of the first generation (Paper I and II). If this succeeds, there is a good possibility to find clones suitable for the second generation of poplars (Paper III). However, several clones showed poor performance in the sense of survival and straightness and may not be suitable for regeneration through stump sprouts in the second generation. Differences in stump sprouting among poplar clones have previously been reported (Laureysens *et al.*, 2003; Dickmann *et al.*, 1996; Herve & Ceulemans, 1996).

Zasada *et al.* (1981) observed differences in stump sprouting in poplars depending on harvesting technique and time of harvest. The ability to produce stump sprouts can also vary among balsam poplars (Zasada *et al.*, 2001). Most of the clones commercially available in Sweden belong to the balsam poplar group (mostly *P. trichocarpa*). It is therefore important to test the capacity of current clones to produce stump sprouts. Stump sprouts originate from dormant buds or callus tissue (Zasada *et al.*, 1981; DeBell & Alford, 1972). Callus sprouts seem to be more commonly produced, but do not always develop into dominant sprouts when sprouts originating from dormant buds are present (Zasada *et al.*, 1981; DeBell & Alford, 1972). The dominant sprout type in this study was callus sprouts (determined by visual inspection) and many of the sprouts were still very small after one year of growth.

Important characteristics for clones suitable for regeneration through stump sprouts are the production of living, straight and fast-growing sprouts. It is likely that crooked sprouts will negatively affect stability and future stem form. Johansson and Hjelm (2012) also observed problems with crooked sprouts that tended to break at the intersection with the stump. Two clones that produced 100 % living stumps with 100 % straightness were found in this study. One of these clones had been phased out from the clone testing program due to undesirable characteristics (*e.g.* susceptibility to leaf rust). The focus in the breeding programs has been on growth rate, stem quality and disease resistance (Stanton *et al.*, 2014; Stener, 2004; Bisoffi & Gullberg, 1996). In this study, a few other clones had a high survival rate and a rather high frequency of straight sprouts. However, more clones need to be tested to provide a sufficient base of plant material for use in practical forestry.

The studied clones also differed in number of sprouts produced per stump. This may not be of great practical importance since a sharp decrease of sprouts during the first years has been reported (Johansson & Hjelm, 2012; Ceulemans & Deraedt, 1999; Zasada *et al.*, 1981). The growth of the largest sprout per stump should be of greater importance, but at this early stage (one-year-old sprouts) no differences were found among the clones.

It is important to note that this study did not cover all commercially available clones and that further sites and clones need to be studied over a longer period. Additionally, due to different experimental conditions in Papers I and III, it is difficult to draw parallels between the clone performance in these two papers even though some of the clones were the same.

4.3 Productivity and management of hybrid aspen root suckers

Paper IV showed that when a healthy stand of hybrid aspen is harvested, a high biomass production could be achieved in the new generation of root suckers, often based on 50,000 to 100,000 root suckers ha^{-1}. For common aspen, 70,000 root suckers ha^{-1} has been reported in Norway (Børset, 1956), and at the age of 8 years about 30,000 root suckers ha^{-1} has been observed in Sweden (Nilsson & Wasielewski, 1987). Bachmann *et al.* (2015) found 60,000 trembling aspen root suckers ha^{-1} after one year of growth, but this number was further increased to 90,000 root suckers ha^{-1} when the soil was disturbed. Increased soil temperature and light availability have been reported to affect vigor and growth of root suckers (Frey *et al.*, 2003; Wan *et al.*, 1999; Peterson & Peterson, 1992; Eliasson, 1971; Sandberg & Schneider, 1953). Soil compaction and wounding of roots, on the other hand, has been suggested to decrease the vigor of root suckers (Frey *et al.*, 2003). When aiming for vigorous root sucker generation, the entire overstory should be removed, and the number of strip roads made by harvesting machines and soil preparation should be considered. However, knowledge of the effects of soil compaction and soil preparation on growth are still missing for hybrid aspen.

A sharp decline in the number of living root suckers is common among aspens since the often dense root sucker stands cause competition, leading to self-thinning (*i.e.* natural mortality) (Frey *et al.*, 2003; Peterson & Peterson, 1992). This sharp decline was also observed in Paper IV when no thinnings were performed in the root sucker stand. Stronger and more frequent thinnings, on the other hand, resulted in larger D_Q and hence a larger individual tree volume. When no harvest was conducted, this resulted in loss of biomass due to self-thinning. If larger dimensions are desired the stand has to be thinned.

A strong increase in *dbh* and crown size in response to thinning is common among pioneer hardwoods such as *Populus* spp. (Rytter & Stener, 2014; Rytter, 2013; Simard *et al.*, 2004; Rice *et al.*, 2001; Miller, 2000; DeBell & Harrington, 1997; Cameron *et al.*, 1995; Niemistö, 1995; Hibbs *et al.*, 1989; Erdmann *et al.*, 1975; Allen & Marquis, 1970; Steneker & Jarvis, 1966). It has also been suggested that fast-growing hardwoods should have a living crown of at least 50 % of the tree height to have good growth (Cameron, 1996; Niemistö, 1996). In the unthinned plots, the crown length after 4 years was below 45 % of the tree height. This further stresses the importance to space hybrid aspen root suckers early. Obtainable biomass (*i.e.* harvested and standing biomass) was the same over the 12-year-period whether or not harvesting was done in the second year. Instead of leaving the stand to self-thinning, this harvested biomass could give an income. However, efficient machinery with techniques that could perform this harvest have, so far, not been tested in Sweden (Bergkvist & Fogdestam, 2011).

4.3.1 Diameter development of the largest trees

The study in Paper IV was not designed to compare the largest trees remaining after the different harvest and thinning and regimes. However, this is a relevant comparison when designing treatments for practical application. Therefore, the approximately 1,100 largest trees ha^{-1} were selected in the plots that were only treated once (control, corridor harvest and cross-corridor harvest) (study part B). These trees were then compared to the trees in the study where a second thinning was conducted two years after the first harvest, leaving about 1,100 trees ha^{-1} (study part C).

More intense thinning regimes result in larger D_Q among the largest trees ($p < 0.0001$) (Figure 14). The plots that were cross-corridor harvested and later thinned had the largest D_Q after 12 years of growth. Cross-corridor harvest without further thinning reached the same level as the treatment that was first left unthinned and later thinned to 1,100 stems ha^{-1}. Further, these two treatments did not differ from the corridor harvest that was later thinned, or from the corridor harvested that was not further thinned. Plots that were never thinned had a significantly lower D_Q among the 1,100 largest trees ha^{-1} compared to all other treatments (Figure 14). Significance levels were tested with the same model as in previous analyses of treatment effects on growth characteristics (section 2.3).

This comparison further emphasizes the importance of early thinnings in hybrid aspen root suckers if larger-dimensioned trees are desired.

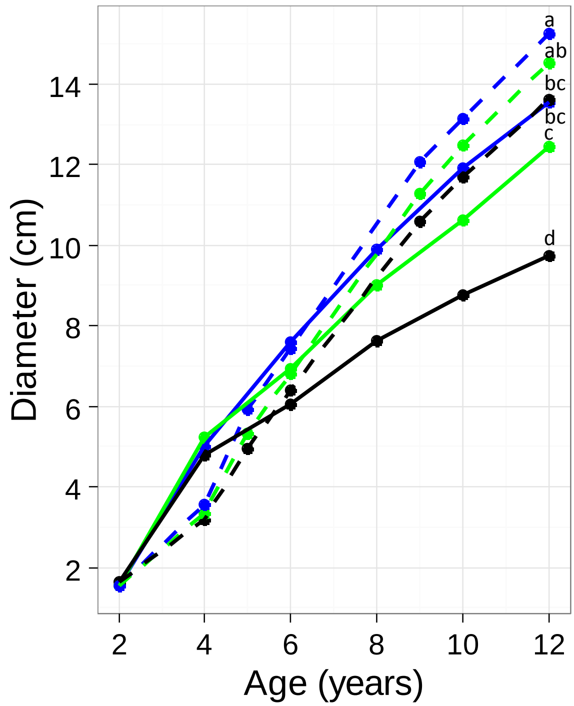


Figure 14. Development of quadratic mean diameter at breast height (D_Q) of hybrid aspen root suckers after selecting the largest trees (1,100 stems ha^{-1}) under six different thinning treatments (unpublished data, Paper IV). After two years three harvest regimes were applied (study part B): no harvest (black solid line), corridor harvest (green solid line), and cross-corridor harvest (blue solid line). At the stand age of four years, half of the plots were thinned to 1,100 stems ha^{-1}, resulting in the last three thinning treatments (study part C): no harvest and thinned (black dashed line), corridor harvest and thinned (green dashed line), and cross-corridor harvest and thinned (blue dashed line). Different letters show statistically significant differences among treatments after 12 years according to Tukey's test ($\alpha = 0.05$). Means in year two are after harvest, but before selection of the largest trees.

4.4 General considerations in clonal forestry of *Populus* species

It has been common in many countries to plant only a few clones on a large scale (Zsuffa *et al.*, 1993). Failure after widespread use of a few promising clones has been reported, and can result in catastrophic failure including economic losses. Many monoclonal plantations in Europe suffered economic losses when the Italian poplar clone I-214 showed susceptibility to the pathogen *Marssonina brunnea* (Zsuffa et al., 1993; Heybroek, 1978). In this thesis, several clones have been included in each paper. The reason behind this was the risk of using only one clone, but also to study differences among clones. The results showed differences in growth and survival among clones (Paper I-III), including interacting effects where treatments were applied. In Paper IV root suckers were studied, which makes it difficult to study clonal effects without genetic analyses of the root suckers to determine clonal origin.

At present, there is no regulation concerning the number of clones that must be used in Swedish forestry. The preference to choose the commonly used clone OP 42 in Sweden should therefore be considered by the forest owner. This may be especially important when establishing new large-scale plantations, or if the area planted with *Populus* spp. clones significantly increases in Sweden.

Some authors have tried to determine how many clones should be used in a plantation (Bishir & Roberds, 1999; Libby, 1982). However, it is a complex problem where several known and unknown factors need to be taken into account. Libby (1982) suggested adapting the number of clones to the level of losses one is willing to accept, not to minimize the risks. Libby (1982) also suggested that the use of one clone should be optimal in a plantation, while polyclonal plantations containing seven to 25 clones may provide more safety (with the restriction that the clones are not relatives). Mixtures of two to three clones were suggested to be the worst strategy. Bishir and Roberds (1999) predicted that the number of clones should be reduced as harvest time increase, or as the intensity of pest attacks increases. However, Lindgren (1993), suggested that the number of clones could be lower when more intense systems with shorter rotations are applied. The number of clones should also be decided at a landscape level rather than at a stand level (Lindgren, 1993; Zsuffa *et al.*, 1993).

In the last two decades, some authors have advocated clone mixtures to support the growth of more disease tolerant genotypes, while less tolerant clones in the mixture will attract the pathogens (Ostry *et al.*, 2014).

One way to draw benefits from superior clones, but reduce the possibility that different clones compete with each other, is to adapt the choice of clone to specific site requirements (Lindgren, 1993; Zsuffa *et al.*, 1993). This can be done by planting different clones in separate sections of the stand, or to vary which clones are planted in different plantations (Lindgren, 1993; Zsuffa *et al.*, 1993). As discussed in section 4.1.6, site-specific requirements for *Populus* spp. clones currently used in Sweden are still missing, but would be valuable for site-specific deployment. This would also be a highly relevant way to plant these species in Sweden, since this thesis showed high variability among clones at various site properties. However, DeBell and Harrington (1997) failed to show differences in production between monoclonal and polyclonal plantations when studying four poplar clones. On the other hand, they found that weak clones were supressed in polyclonal plantations and monoclonal plantations showed greater uniformity in tree size.

Hybridization with native species is a risk of using exotic species. In Sweden, the only native *Populus* spp. is the common aspen (*P. tremula*). Hybrid aspen can hybridize with the native common aspen (Felton *et al.*, 2013; Latva-Karjanmaa, 2006). This could be a threat to the conservation of genes of native aspen. Hybridization has also been predicted to be more common in warmer climates, but it is still a matter of debate whether this would be an advantage or a threat (Latva-Karjanmaa, 2006). However, aspens more often reproduce clonally by root suckers rather than seeds (Dickmann & Kuzovkina, 2014; Latva-Karjanmaa, 2006; Peterson & Peterson, 1992).

It has been reported that *Populus* spp. have a positive influence on biodiversity in Sweden, and common aspen is a desired host of vulnerable species (*e.g.* lichens, epiphytic bryophytes, fungi, insects and birds) (Gustafsson *et al.*, 2016; Felton *et al.*, 2013; Weih *et al.*, 2003). It has also been observed that poplars can serve as a host to red-listed beetles (Isacsson, per. comm. 2016). However, further research is needed to provide more knowledge of which species hybrid aspen and poplars can host.

5 Conclusions

If the right sites, methods and clones are chosen, *Populus* spp. can be highly productive, with a variety of uses, such as bioenergy, fiber production, furniture and construction.

Soil properties, such as pH and soil moisture, should be considered when planting *Populus* spp. However, other soil properties, like nutrient composition are also likely to affect the growth of these species.

Soil saturation inhibits root and shoot growth of poplar cuttings. When planted in saturated soils, the roots were more concentrated toward the soil surface. This was mainly caused by the absence of roots originating from callus tissue at the base of the cutting.

At the sites in this thesis, mounding gave the most promising and stable results when planting *Populus* spp. on forest land. Hybrid aspen showed better establishment compared to other *Populus* spp.

Short poplar cuttings and patch scarification cannot be recommended on moister sites with high abundance of competing weeds. Instead, poplars should be planted as containerized plants or long cuttings. However, the long-term effects of a shallow root system at root initiation are still uncertain.

The choice of suitable clones is important when planting *Populus* spp., since the clones respond differently to different soil properties.

The choice of clones also affects the potential to regenerate poplar via stump sprouts in the second generation. Among the tested clones in this study, a few produced stump sprouts with desired properties.

Damage to plants was rather common during the first years of growth. To avoid browsing from ungulates, fencing or use of repellents should be considered. It is more difficult to find measures to avoid damage from voles. A key measure should be weed control to reduce the amount of suitable vole habitat.

Clear-felled stands of hybrid aspen have a high initial production of root suckers. The new generation needs early thinning for reasonable *dbh* development. Early thinnings can be made schematically in corridors or cross-corridors, followed by selective thinnings. However, there are still technical limitations for an efficient harvest. If no thinnings are made there will still be a considerable reduction in the number of stems due to competition.

6 Future research

Further studies are required to explore suitable site conditions for *Populus* spp., especially concerning nutrient composition on forest land.

To study the economy of *Populus* spp. plantations is essential to provide forest owners with reliable economic forecasts and will most likely affect the future development of *Populus* spp. in Sweden.

It is essential to study how long-term stand development is affected by the cutting type, especially properties of the root system.

There are only a few poplar and hybrid aspen clones used in practical forestry in Sweden. Tests of new clones are therefore needed, especially for finding good material adapted to different site conditions.

The stump sprouting ability of different poplar clones needs more research to provide solid recommendations on how to establish second generations based on stump sprouts. The long-term development of stump sprout regenerations must also be investigated.

Root sucker regeneration of hybrid aspen is highly productive and could be used as a source of bioenergy. Development of efficient harvest techniques combined with adapted silviculture models is essential to be able to use this potential in practice.

Measures that could affect the productivity of hybrid aspen root suckers need to be further studied. For example, how is the initiation of hybrid aspen root suckers influenced by soil compaction, soil preparation and forest residues left at the forest floor?

The endurance of hybrid aspen root suckers' productivity after repeated harvests needs to be studied with different rotation ages to provide more knowledge about the third and fourth generations.

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Appendix

Descriptions of the study sites

Complementary site descriptions from Paper I-IV are provided in table A1.

Table A1. *Description of the sites used in Papers I-IV. Site name, experimental type (Exp. type) (F = forest land, G = greenhouse, and A = agricultural land), stand size (in Paper I: area of the experiment), age of the previous stand (Prev. stand age) (NS = mature Norway spruce stand) (year), stand age at the end of the study period (growing season, year), coordinates (Coord.), elevation (masl), soil structure, stand density at planting (Paper I) or at harvest of the first generation (Papers III and IV), mean annual precipitation (Prec.), mean annual temperature (Temp.), annual vegetation length (Veg.), number of blocks, and number of plants/cuttings at planting (Papers I and II) or number of stump sprouts (Paper III) or root suckers in the second generation after one year of growth (Paper IV). Climate data are provided from the Swedish Meteorological and Hydrological Institute (SMHI).*

Site	Exp. type	Stand size (ha)	Prev. stand age	Stand age	Coord.	masl	Soil structure	Stand density (stems ha^{-1})	Prec. (mm)	Temp. (°C)	Veg. (days)	No. of blocks	No. of plants
Paper I													
Brattön	F	0.7	NS	3	58°35N, 11°50E	135	Clay-silt moraine	2500	900	6-7	190	4	1536
Dimbo	F	0.8	NS	3	59°07N, 15°43E	90	Sandy moraine & surged gravel	2500	500	6-7	190	5	1920
Duveholm	F	0.8	NS	3	58°58N, 16°09E	55	Glacial clay & silty moraine	2500	500	6-7	180	5	1920
Paper II													
USA	G	-	-	18 days	33°25N, 90°55W	37	Sand	-	-	21	-	3	216
Paper III													
Maderna	A	0.7	19	1	55°59N, 12°59E	75	Clayey moraine	276	700	7-8	210	1	16,000*

Paper IV													
Ekebo	A	0.2	22	2	55°57N, 13°06E	88	Clayey moraine	530	700	7-8	210	1	50,000
Jordkull	A	0.7	11	12	55°59N, 13°02E	80	Clayey moraine	750	700	7-8	210	4	72,000*
Maltesholm	A	0.5	21	4	55°55N, 14°00E	40	Sandy sediment	740	600-700	7-8	200	1	51,000
Snogeholm	A	3.5	12	4	55°33N, 13°43E	45	Clayey moraine	950	600-700	7-8	200	4	106,000

* Estimated number of stump sprouts ha^{-1} of the stumps included in the study (Paper III) or number of root suckers at Jordkull after two years (Paper IV).

Clone information

The *Populus* spp. clones used in Papers I-III are presented in tables A2 to A4 below. Paper IV investigated hybrid aspen root suckers which were not identified by clone in the second generation. At harvest of the first generation, the sites Jordkull, Maltesholm, Snogeholm and Ekebo consisted of 4, 47, 8 and 35 clones, respectively.

Table A2. *List of the 12 poplar clones and three hybrid aspen clones used in Paper I. Clone represents the identifier used in this paper, Clone ID is the identity assigned by the Forestry Research Institute of Sweden (Skogforsk). All clones are commercially available in Sweden. Six of the poplar clones were also used in Paper III (bold).*

Clone	Clone ID	Taxon	Additional information
1	S21K766049	*P. trichocarpa*	
3	**S21K766003**	*P. maximowiczii* × *P. nigra*	Commercial name ‘Rochester’
4	S21K82604	*P. trichocarpa*	
5	**S21K766048**	*P. trichocarpa*	
6	**S23K9040086**	*P. maximowiczii* × *P. trichocarpa*	
7	S23K9040089	*P. maximowiczii* × *P. nigra*	
8	S23K9040073	*P. trichocarpa*	
9	S23K9040025	*P. trichocarpa*	
10	**S23K9040019**	*P. trichocarpa*	
11	**S23K9040011**	*P. trichocarpa*	
12	**S23K9040006**	*P. trichocarpa*	
14	S216PPL52	*P. trichocarpa*	
60	S21K894012	Hybrid aspen	Commercial name ‘KL-003’
61	S21K884012	Hybrid aspen	Commercial name ‘KL-001’
62	S21K0940201	Hybrid aspen	Finnish clone ‘C05-99-34’

Table A3. *List of the nine poplar clones used in Paper II. Clone represents the identifier used in this paper, Clone ID is the commercial identity or the identity assigned by the University of Minnesota's experimental research nursery (UM NCROC), Grand Rapids, MN, USA. Clones 1 to 6 are currently tested in Germany, Lithuania, Poland, Russia, Sweden and Ukraine.*

Clone	Clone ID	Taxon	Additional information
1	99007115	*P. deltoides* × *P. nigra*	
2	99008002	*P. deltoides* × *P. nigra*	
3	99038013	*P. deltoides* × *P. nigra*	Full-sib with clone 4
4	99105008	*P. deltoides* × *P. nigra*	
5	9732-24	*P. deltoides* × *P. nigra*	Full-sib with clone 6
6	9732-31	*P. deltoides* × *P. nigra*	
7	D110	*P. deltoides*	Open-pollinated, WI, USA
8	DN5	*P. deltoides* × *P. nigra*	Commercial clone in the USA and Canada
9	NM6	*P. nigra* × *P. maximowiczii*	Commercial clone in the USA and Canada

Table A4. *List of the 23 poplar clones used in Paper III. Clone represents the identifier used in this paper. The clones were divided into three groups: commercial clones (Co) are commercially available in Sweden, candidate clones (Ca) are candidates to become commercial, and additional clones (no prefix) not included in the other two groups. Clone ID is the identity assigned by the Forestry Research Institute of Sweden (Skogforsk). Number (No.) of stumps represents the number of replicates in this paper. Six of the clones were also used in Paper I (bold).*

Clone	Clone ID	Taxon	Additional information	No. of stumps
Co1	S21K766005	*P. maximowiczii* × *P. trichocarpa*	Commercial name 'Androscoggin'	7
Co2	**S21K766003**	*P. maximowiczii* × *P. nigra*	Commercial name 'Rochester'	10
Co3	**S23K9040086**	*P. maximowiczii* × *P. trichocarpa*		4
Co4	**S21K766048**	*P. trichocarpa*		4
Co5	**S23K9040019**	*P. trichocarpa*		4
Co6	**S23K9040011**	*P. trichocarpa*		4
Co7	**S23K9040006**	*P. trichocarpa*		3
Co8	S21K82601	Balsam type × *P. trichocarpa*		4
Ca1	S23K9040059	*P. trichocarpa*		3
Ca2	S21K766007	*P. deltoides* × *P. nigra*		3
Ca3	S23K9040035	*P. trichocarpa*		5
Ca4	S23K9040032	*P. trichocarpa*		4
Ca5	S23K9040046	*P. trichocarpa*		5
Ca6	S23K9040009	*P. trichocarpa*		4
Ca7	S23K9040041	*P. trichocarpa*		4
1	S23K9040002	*P. trichocarpa*		4
2	S21K766024	*P. deltoides* × *P. trichocarpa*	Commercial name 'Barn'	4
3	S23K9040056	*P. trichocarpa*		4
4	S23K9040058	*P. trichocarpa*		4
5	S23K9040001	*P. trichocarpa*		5
6	S23K9040010	*P. trichocarpa*		5
7	S23K9040003	*P. trichocarpa*		4
8	S23K9040051	*P. trichocarpa*		4

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WERNER
KATHRIN & MICHA
MALIN & JONATAN
GIULIA & CLÉM
TAGE
ROGER & YVONNE
MÅRTEN
ANNA & LILL
ANDERS & RUNE
TORBORG & KALLE
LOTTA & JONAS
KARIN
EWA & ROLAND
IDA
LUCI RUGBY
ANNA
NILS & TAMARA
MARTIN & LOVISA
TARA & JULIA
NIELS
EMMA
ERIK
MARINA
JOHAN & HANNA
JAKOB
HILD & TOM
FLORIAN
ERIK, PETRA, MELKER, KLARA & ALVA
NINA
PER & KATTIS
RENATS & IRYNA
GUN
GUILLERMO & MARIA
MARTA
IAIN
LENNART