REVIEW PAPERS

Development and Traits of Wolf Trees in Scots Pine (*Pinus sylvestris* L.): A Literature Review

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Abstract

This article reviewed studies from Germany, Russia, Lithuania, Sweden and Finland about wolf trees in Scots pine (*Pinus sylvestris* L.) forests and examined the definition of a wolf tree. In addition, we analyzed the main traits and parameters of these trees, such as lower crown ratio, more conical stem taper, partly deformed crown, and thicker and longer branches. The analysis revealed changes in the definition of a wolf tree during the XX century and different definitions over various regions. The differences between wolf trees and common trees were found in growth patterns, stress sensitivity and genetics. Also this article reviewed several possible reasons for the occurrence of wolf trees in forest stands.

Key words: b-type trees, tree development, morphological types, competition, crown form, growth patterns, thinning.

Introduction

Scots pine (*Pinus sylvestris* L.) is naturally occurring tree species found in the boreal forest region and high-altitude forests along a large belt from north-west Europe to Siberia (Critchfield and Little 1966, Nikolov and Helmisaari 1992). In Europe, Scots pine is one of the most important tree species for commercial use (Mason and Alia 2000). For biodiversity, native pinewoods have a high conservation value (Lust et al. 2001, Kuuluvainen and Ylläsjärvi 2011).The management of Scots pine has a long history (Cotta 1821, Schwartz 1991), which is reflected by various thinning programs developed over the last centuries (Schwappach 1908, Wiedemann 1943, Erteld 1960, Nilsson et al. 2010). In current silvicultural programmes, the quality of pine timber (Liziniewicz 2014), the role of tree species admixtures (Agestam 1985), and the potential for developing more heterogeneous stand structures (Mason 2000) are often emphasized.

A key point in managing this tree species with its rapid early growth has been the removal of trees with undesirable form ('wolf trees') during the early stages of stand development. Wolf trees grow faster than the surrounding trees, have a larger crown and other tree parameters, and utilize a larger growing space, thus reducing stand timber volume.

Figure 1. Wolf tree (indicated with an arrow) in a 17-year old self-regenerated Scots pine stand in Lithuania

Such trees are not favoured by foresters due to their lower timber quality and because they hinder the development of better quality trees, which can negatively influence future timber harvests. However, trees of this type could benefit biodiversity due to the provision of increased stand structural complexity compared to stands composed solely of trees that are regular in size and crown (McElhinny et al. 2005). Given the importance of biodiversity questions for modern forestry, we summarize existing information on wolf trees and their features as the first step for further research. The objectives of our literature review were (1) to examine how Scots pine wolf trees were distinguished from other pine trees in the stand; (2) to explore reasons for the occurrence of wolf trees, and (3) to explain their development.

Methods

The literature search for relevant articles consisted of three steps:

1. Web-based literature search to collect studies which could refer to wolf trees in Scots pine;
2. Identification of the potentially relevant studies by reading the title and abstract of each collected article;
3. Analysis of the potentially relevant studies and extraction of information related to our three original research questions.

The web-based literature search was performed through the search engines and databases provided by the Web of Science and Google Scholar. During the search with the Web of Science the syntax was:

Topic=("wolf tree*") OR Topic=(b-typ*)
AND Title=("scots pine") OR Title=("pinus sylvestris")
NOT Title=(canis) NOT Topic=(Mediterranean)
NOT Topic=(population*) NOT Topic=(fung*)
NOT Topic=(treat*) NOT Topic=(*preservat*)
NOT Topic=(expos*) NOT Topic=(chem*)
NOT Topic=(pollut*) NOT Topic=(strobus)
NOT Topic=(herbivor*)

Refined by:

Research Areas=(FORESTRY) AND Document Types=(ARTICLE OR ABSTRACT OR BOOK OR REPORT)
Timespan=All years.
Search language=Auto

The search in Google Scholar was performed using the key words "Scots pine wolf trees", "scots pine b-type" and excluding the word "canis".

In step two, studies that referred to wolf trees in Scots pine were selected directly. Studies referring to larger or more vigorous trees or other classifications like hierarchy, social classes or quality classes were also selected for reading. Later, the accepted publications were divided into those relevant for our three research questions concerning wolf trees, and those where general patterns of Scots pine stand development could be linked to our findings and ideas about wolf trees. In addition, silvicultural textbooks and management guidelines used in Germany, Sweden, Russia and Lithuania were examined in their native language to include other relevant studies. We also used snowball sampling – non-probability chain referral sampling (Patton 1990) by using the literature references provided in selected studies to find other relevant literature.

During the reading and analysis of the literature, definitions and characteristics of wolf trees and possible reasons (hypothesized, studied or concluded) for their emergence were recorded and later summarized in tables and figures. The statements of different authors about the characteristics of wolf trees were divided into three categories, depending on whether these were stated (assumed/hypothesized), measured in field, or tested in a long-term experiment.

Results

In total 401 studies were collected using the Web of Science, when the syntax listed above was used. After confining the results to the research area of forestry, 16 studies were collected. 11 additional studies were collected after the search using Google Scholar. Ten studies, directly relating to wolf tree issues, and seven more studies about general development of Scots pine were analyzed in the results section of our paper; other papers were considered in the discussion.

Development of wolf trees in Scots pine

As stated by Spathelf and Ammer (2015), Scots pine shows the best growth on fertile sites but it is mainly found on poorer soils due to the lower competitive abilities of the species. Vaartaja (1950) discovered that on richer soils massive germination occurred later, which could be explained by greater competition from the ground vegetation. However, some seedlings germinate earlier than others and genetic differences between growth rate and micro-site variation initiated subsequent size stratification (Kellomäki and Hari, 1980). These differentiation processes were strengthened by the resulting size difference between the trees. Those trees which germinated earlier than others had extra time to develop, so they experienced less competition (Kuuvulainen and Rouvinen 1997).

Hafemann and Stähr (2007) showed, that Scots pine seedlings need large gap openings to develop a good quality stem. The optimal gap diameter for successful regeneration should be similar to a mature tree height (20-30 m.)

Such gap size provides the optimal microclimatic and lighting conditions for seedlings. In smaller gaps, lower quality branchy stems with poorer form are often found. However, bigger gaps can also create unfavourable conditions for regeneration, such as stronger direct sunlight and bigger temperature fluctuations in the upper layers of the soil. The lower capacity of Scots pine to self-prune also provides greater opportunity for seedlings to develop into wolf trees (Spathelf and Ammer 2015)

Productivity during stand development is the highest for trees with long and small crowns (Spathelf and Ammer 2015). This also corresponds to the study of Stähr and Hainke (2009), who stated that the relationship between tree growth and crown diameter decreases with age. The issue about wider crowns and lower productivity with age is also mentioned in thinning guides as the reason for early removal of wolf trees (Kerr and Haufe 2011).

Analysis of the studies regarding wolf trees

These studies showed that wolf trees have been mentioned and described in the silvicultural literature for a long time. However, for a long time this term was used to describe solitary trees. By the beginning of the 20th century the term had an important part in forest classifications. For example, Lönnroth (1925) distinguished two types of wolf trees: i) "better wolf", strongly developed trees with larger branches, and ii) "worse wolf", trees, which were especially twisted and branchy, or had other low quality traits. Interestingly, he also classed forked trees in the "worse wolf" tree type. The study of Lönnroth (1925) is the first mention of wolf trees in scientific literature.

By the middle of the 20th century, the classifications had become briefer, and two wolf trees' classes were united into one. Schädelin (1942) presented wolf trees as vigorous individuals that differ from other trees by superior height or diameter growth and a poor growth form (forks, thick branches, crooked or bent stem axis). However, the understanding of wolf trees in Scots pine stands was developing, and the second term for them, namely b-type trees appeared in the German silvicultural literature. In contrast to that, target trees with good stem quality and small amount of branches were called a-type trees. Thus, several names for the same wolf tree phenomenon can be found (see Table 1). Kräuter (1965), Pofahl et al. (1979) and Lockow (1992) defined b-type Scots pine trees as having a low crown ratio, relatively long and thick branches, small branch angles in the lower part of the stem and a mostly irregular, partly one-sided crown. These studies also identified an intermediate a/b type: trees with parameters close to common trees but with longer and thicker branches. Other definitions were provided by Smith et al. (1997), who described wolf trees as poorly formed dominants, and Matthews (1989), who presented wolf trees as trees with straggling crowns and low branching, together with defective stems.

Table 1. Different terms describing wolf trees, and authors using them

Term	Description	Authors
Wolf trees	Super-dominant trees with wide crowns and thick branches	Lönnroth (1925), Schädelin (1942), Matthews (1989), Smith et al (1997), Gedminas and Ozolinčius (2006), Hagner (2012)
b-type trees	Trees having low crown ratio, relatively long and thick branches, small branch angles in the lower part of the stem and a mostly irregular, partly one-sided crown.	Kräuter (1965), Pofahl et al. (1979), Lockow (1992), Hertel and Kohlstock (1994), Beck (2000)
Deformed seedlings	Seedlings of abnormal form	Freyberg and Stetsenko (2009)

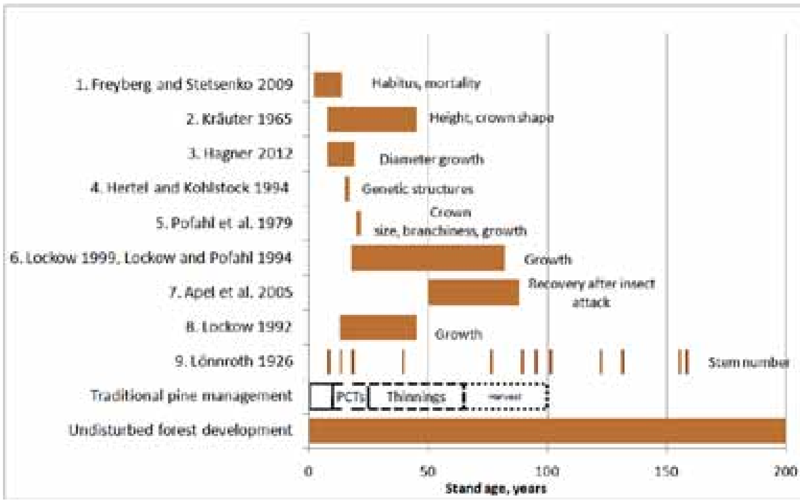

Figure 2. Empirical studies on Scots pine wolf trees in Northern Europe and ages of the study stands. For comparison, the timing of pre-commercial thinnings (PCTs), thinnings and harvest in typical Scots pine forest management as well as the natural forest development with more than 200 years old trees (see Lassila 1920 or Edwards and Mason 2006) are included in the Figure

Table 2. Tree parameters of Scots pine wolf trees in comparison to other trees in the stand as presented by Kräuter (1965) and Hertel and Kohlstock (1994) and complemented by other studies (* tested in combination with other features)

Morphological Trait	Tree parameter	Tested/measured/ stated	Study
Tree crown	Lower crown ratio	Tested	Pofahl et al. 1979*; Hertel and Kohlstock1994
		Measured	Kräuter 1965;
		Stated	Gedminas and Ozolinčius2006
	Partly one-sided, more flat crown	Tested	Hertel and Kohlstock 1994
		Stated	Beck 2000
Branches	Thicker branches in the lower part of stem	Tested	Pofahl et al. 1979*; Hertel and Kohlstock 1994
		Measured	Kräuter 1965;
		Stated	Gedminas and Ozolinčius 2006; Beck 2000
	Longer branches	Tested	Hertel and Kohlstock 1994
		Measured	Kräuter 1965;
		Stated	Gedminas and Ozolinčius 2006; Beck 2000
	Smaller branch angle in the lower part of stem	Tested	Hertel and Kohlstock 1994
		Stated	Gedminas and Ozolinčius 2006
Needles	Lighter color of needles	Stated	Gedminas and Ozolinčius 2006
	Smaller amount of needles	Tested	Lockow 2007;
		Stated	Gedminas and Ozolinčius 2006
	Drier needles	Stated	Gedminas and Ozolinčius 2006
	Larger dry needle biomass	Tested*	Pofahl et al. 1979*
Stem	More conical stem taper	Tested	Hertel and Kohlstock, 1994
	Lower wood density due to wider annual rings	Stated	Lockow 2007
Growth	Super-dominant	Stated	Gedminas and Ozolinčius 2006; Beck, 2000
	Faster growth as a young tree	Tested	Hertel and Kohlstock 1994
		Stated	Gedminas and Ozolinčius 2006
	Distinguishable from the early age	Tested	Freyberg and Stetsenko2009
	Faster growth	Tested	Pofahl et al. 1979*; Lockow 1992
	Smaller photosynthetic efficiency	Stated	Gedminas and Ozolinčius 2006
Genetic aspects	Less genotype variation	Tested	Hertel et al. 1998
	Smaller heterozygosity	Tested	Hertel et al. 1998
Stability	More sensitive to stress	Tested	Beck 2004; Apel et al. 2005
	Less stable	Tested	Freyberg and Stetsenko2009
		Stated	Beck 2004; Lockow 2007

For the purpose of our study, we will use a very general understanding of wolf trees as described by Beck (2004). He characterizes wolf trees as super-dominant trees with wide crowns and thick branches. This definition summarizes the most important points of the previous ones.

However, it is important to mention that the characteristics of wolf trees are relative and can only be compared with other trees within a particular stand.

The studies, selected for our analysis, cover a range of tree ages between 2 and 159 years (see Table 3 and Figure 2). They will be described below in the order of the increasing tree age.

The youngest wolf trees were mentioned by Freyberg and Stetsenko (2009), who described the influence of pesticides on the development of Scots pine seedlings. In their study, seedlings of Scots pine were treated with pesticides, and then planted. The description of the seedling appearance was very similar to the description of a wolf tree. Their results showed development into several morphological types in the early growth stages, and the percentage of the wolf tree type was higher among the seedlings grown from the treated seeds, than this from non-treated ones. Another observation was that seedlings with an abnormal morphological type had a much higher

Table 3. Analyzed studies, concerning Scots pine wolf trees, with publication year, location and experimental stand age.

Authors	Year	Location	Stand age, years
Lönnroth	1925	Finland	14 to 159
Kräuter	1965	Germany	8 to 45
Pofahl et al.	1979	Germany	22
Lockow	1992	Germany	10 to 100
Hertel and Kohlstock	1994	Germany	17
Hertel et al.	1998	Germany	20
Beck	2000	Germany	2 to 65
Beck	2004	Germany	61 to 122
Apel et al.	2005	Germany	50 to 78
Gedminas and Ozolinčius	2006	Lithuania	2 to 100
Lockow	2007	Germany	10 to 86
Freyberg and Stetsenko	2009	Russia	2 to 14
Hagner	2012	Sweden	8-19

probability of mortality compared to seedlings with a normal morphological type.

The study by Hertel and Kohlstock (1993) was performed in 17-year old Scots pine stands with trees from 72 progenies from Central and Eastern Europe. 90 trees of the normal morphological type and 95 wolf trees were chosen from these stands according to crown ratio, branch thickness and crown width. Lateral buds were taken from them, and a genetic analysis was performed. The results of this analysis showed only a minor polymorphism difference between the two morphological types. However, trees of the wolf tree type had a significantly lower genotype variation while trees of a normal morphological type had a higher level of heterozygosity based on a high number of rare alleles. However, Hertel and Kohlstock (1993) also stated that the classification of Scots pine trees into these two types was due to a combination of several effects, not only genetics.

Knowledge about pine wolf trees in Germany was summarized by Lockow (2007), who referred to long-term observations covering stand ages from 10 to 86 years. Trees classified as b-type had stronger branches and a smaller crown length/crown width ratio than trees classified as a-type. B-type trees were not the tallest trees in the stand; however, their diameter growth was faster. In principle, the largest individuals at the beginning of the study remained the largest trees over time, often characterized by non-concentric crown projections. For the same crown size (vertically projected on the stand area), b-type trees had a smaller crown surface than other trees, and hereby less needle biomass (Lockow 2007). Therefore, Lockow (2007) concluded that a-type trees used the total stand area more efficiently in terms of stand growth than b-type trees. For b-type trees, there was also a lower ability to recover after *Lymantria monacha* attack and higher mortality (Apel et al. 2005). Beck (2004) concluded that after Scots pine trees stopped growing as an immediate response to drought and high temperature, dominant and co-dominant individuals in general would continue to grow, while suppressed trees are less or not able to continue. In addition, more juvenile wood, more uneven year-rings, and less self-pruning were mentioned by Lockow (2007).

The study of Gedminas and Ozolincius (2006) covers a wide range of tree ages, almost from germination until the mature forest stage. The authors state the same issue about the wolf trees' position in the forest, as Lockow (2007): usually wolf trees are not the tallest trees in the stand. The main trait of wolf trees, as stated in the study, was comparatively wide and branchy crown, lower branch angle and thicker branches. Due to this fact, wolf trees take super-dominant position in the stand. Another important issue was the productivity of wolf trees. For example, if we assign the relative solar energy usage efficiency coefficient of 1.0 for trees of a normal morphological type, then for the wolf trees it would be only about 0.5-0.7

Concerning the silvicultural promotion of larger pine individuals, Degenhardt (2009) simulated the growth response on the base of solitary trees and found relatively small effects on growth compared to individuals of average size. Stähr and Hainke (2009) showed that a fourfold increase in growing space during the thicket stage resulted in twofold increased crown surface and growth. In the pole stage, the effect was even smaller (Stähr and Heinke 2009).

The economic impacts of the removal or promotion of wolf trees was explored by Hagner (2012), who studied two stands, planted at the same time in the same conditions. One stand was managed in a traditional way and in the second stand, individual wolf trees were promoted. It is important to note, that smaller healthy pines were left between the wolf trees. The study showed a bigger diameter variation in wolf trees at the age 19. Still, the mean diameter of wolf trees was at least 2 cm bigger than the mean diameter of regular trees. Using the software program "Tree", an economical model was built to examine the effects of future stand tending. The results showed that removing wolf trees with a diameter of 11-22 cm, stimulated growth of the smaller pines, which would be subsequently ready for final felling at 90 years of age. This is 15 years later than in traditionally managed stands. However, wolf trees could also be sold as low quality wood by the age 20. The total income in a wolf-tree stand was 115%, compared to a traditionally managed stand.

Based on the reviewed studies describing the morphological differences between wolf trees and common trees, we created the following figure; summarizing the main traits of a wolf tree and compared it with a common Scots pine tree (see Figure 3).

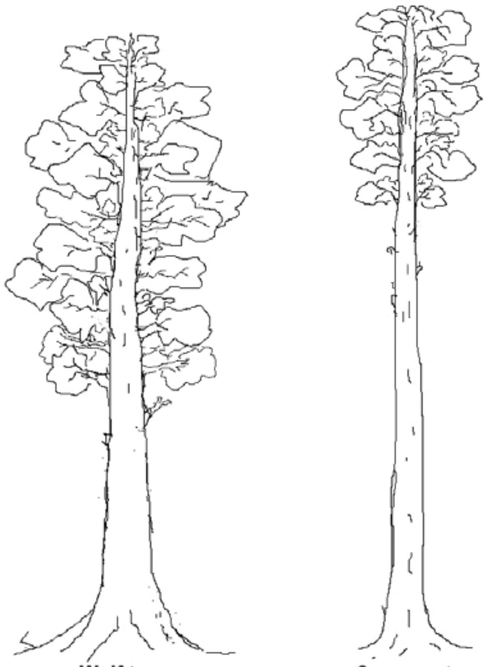

Figure 3. Comparison of wolf tree's and common tree's morphological traits

Discussion and conclusions

Usually the silvicultural literature only mentions wolf trees in relation to thinning rules. Therefore, the identification of wolf trees depends on subjective judgments. Considering this fact, we used both information from wolf tree studies and general literature about the development and growth of Scots pine forests.

Main features of the wolf trees described in the literature were wide crowns, thick branches, low branch angle and a super-dominant position in the stand. In the thinning guidelines the super-dominant position is the key feature for distinguishing a wolf tree in a stand. However, definitions vary between regions and the variations in conditions do not allow for a homogeneous picture of individual wolf tree development. But there does appear to be a common understanding about those features, which define a wolf tree.

Our analysis showed that most authors distinguished wolf trees by their lower crown ratio and more one-sided, branchy crown. Uusvara (1991) showed that on more productive sites more Scots pine trees with thick branches, bigger branch number and branch angle – typical features of wolf trees – were found. This corresponds to the studies by Kräuter (1965) and Kohlstock (1982) who pointed out that earlier removal of wolf trees is required on more productive sites to promote healthy individuals with fewer branches. However, in young stands on moderate sites silvicultural interventions may not always be necessary (Kohlstock 1982). Haapanen et al. (1997) observed low to moderate heritabilities for most stem parameters. However, the heritabilities of branching angle and branchiness were among the highest observed. Based on these six studies, we suppose that seedlings established earlier on richer soils are more likely to develop into a/b intermediate type trees, and the seedlings with a tendency to inherit low branching angle and branchiness are likely to develop into b-type wolf trees.

Regarding the stability of wolf trees, we found contradictory statements. Apel et al. (2005) found a higher sensitivity to stress, at least a year after heavy insect attacks. However, in the studies of Augustaitis (1998, 2007) and Juknys et al. (2003) we can see a clear tendency of faster recovery of dominant trees after different types of stress. In the study of Augustaitis (1998) the most dominant trees had the biggest loss of foliage after a pest outbreak. However, during the next 3 years the dominant trees showed much faster recovery after the stress event than the other tree classes. The explanation could be found in older trees classifications, where wolf trees were divided into two morphological types (Lönnroth 1925). The trees of a "better wolf" type, which are super-dominant, could be less sensitive to stress than normal trees, while the trees of a "worse wolf" type were most likely removed earlier from the stands described in the studies of Beck (2004) and Lockow (2007).

In the study of Ferris and Humphrey (1999) the wide range of tree diameter distribution and canopy complexity were listed among the most important factors, which affect biodiversity in the stand. Wolf trees, with their fast diameter growth at a younger age, and thick long branches, could definitely benefit biodiversity by adding complexity to the stand structure and creating a wider range of possible habitat from the earlier stages of the stand development.

In conclusion, we expect differences between the number of wolf trees on fertile and poor sites: fertile soils can promote a higher frequency of wolf trees and their fast development. Considering the number of wolf trees and the soil type, forest managers can decide how many wolf trees to leave. This decision can also be based regarding the amount, quality and perspective of the trees around the wolf tree and the distance from the wolf tree to the neighbouring trees. For example, more free-standing wolf trees could be left to provide future habitat, because they would cause less effect on future crop trees.

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