

Swedish beech forests and the storm gap theory

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The storm gap theory of forest dynamics was developed by Sernander largely as a result of his investigations of the Norway spruce *Picea abies* forests of Fibyurskog and Granskär following the great storms of 1931 and 1932. This theory is reviewed in the light of subsequent investigations and its relevance to forests of common beech, *Fagus sylvatica*, which Watt had also investigated in southern England; developing his theory of pattern and process in the plant community as a result.

Ancient unmanaged Swedish beech forests are extremely important as they enable us to ascertain how such forests develop in a state of nature. They are often important in terms of biodiversity and the veteran trees they contain are especially valuable in the conservation of rare epiphytic lichens and bryophytes.

The history of *Fagus sylvatica* and variations in its extent in Swedish forests during the Holocene is illustrated by a review of articles concerning a number of important forest areas.

Keywords: *Fagus sylvatica*; old-growth forest; biodiversity; storm gaps; wind; veteran trees; influence of fire on forest history; climate change

Introduction

In Scandinavia common beech, Bok in Swedish, grows in Denmark, southern Norway, and southern Sweden as the map in Jonsell (2000) demonstrates. When in leaf, *Fagus sylvatica* is very vulnerable to gales, and old unmanaged beech forests that have been left to grow naturally contain trees of many different ages. Investigation shows that very many of the trees involved developed from shade-tolerant dwarf trees that began to grow rapidly when the mature trees which formerly overshadowed them were destroyed by gales that created gaps in the forest.

Working in southern England, Watt (1925) first described a reproduction circle that had developed in a beechwood in which a formerly dominating tree had been destroyed. In his second paper (Watt, 1947) he termed the repeated system of development, death, release of dwarf trees which eventually matured and later died only to be themselves replaced in terms of “pattern and process” expressed as cyclic change. His views on the processes influencing the structure of ancient forests of tree species with shade-tolerant seedlings were essentially in agreement with the storm gap theory of forest dynamics developed by Sernander (1936) largely as a result of his investigations of the Norway spruce *Picea abies* forests of Fiby urskog and Granskär following the great storms of 1931 and 1932.

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Following a review of this theory in the light of modern developments and the underlying basis of storm damage and mortality, the paper goes on to discuss the value of veteran beech trees and ancient beech-dominated forests in conservation terms. The final section is concerned with the way in which *Fagus* invaded Sweden during the Holocene and the ways in which the extent and nature of its communities have changed since then.

Tree gap formation and the gap dynamics theory

Tree gaps in forests occur when trees are either blown over and uprooted, or snap, or die, usually after being weakened by such factors as drought or attack by insects and/or fungi. Scientific interest in forest gaps and their formation has elicited reports for well over a century but the earliest papers of real significance in the context of this paper are those of Watt (1925, 1947) dealing primarily with beech, and Sernander (1936) who studied the ancient Swedish forests of Fiby urskog and Granskär following the great storms of 1931 and 1932. As a result of his studies of these two boreal forests, in which the majority of the trees were of Norway spruce *Picea abies*, Sernander produced his gap dynamics theory of forest regeneration in which the importance of dwarf trees, whose existence had been noted by foresters such as Cnattingius (1888) many years before, is a prominent feature. This theory, which is in many respects applicable to forests of other species, has recently been reviewed by Hytteborn and Verwijst (2011).

Shade-tolerant dwarf spruce commonly occur growing very slowly beneath the dense shade of mature trees. When gales create forest gaps, such previously shaded and suppressed dwarf trees receive abundant light and their roots are subject to less competition for water and mineral nutrients. This release is shown clearly by the much wider annual rings that develop in the years after the gale. Sernander found release dates related to a number of gales, including the great gale of 1795. Fiby urskog still contains spruce developed from dwarf trees released by this great storm, of which a tree 28 m high when cored in 1981 is an example (Hytteborn, Moberg, & Packham, Transect 1, in Packham, Harding, Hilton, & Stuttard, 1992, pp. 121, 145).

In the 1931 storm most of the trees destroyed in the forests of Stockholm and Uppsala fell in the storm direction, but in some places the trees lay in whirls, having apparently been felled by a tornado. As such storms blow in waves, the ellipsoidal or rectangular gaps created are formed in the direction of the gale. Trees at forest margins are often more resistant to gales than those deep within the forest. Trees are less resistant to gales from an unfamiliar direction, while the soil type and previous climatic conditions make a considerable difference to number and size of gaps developed.

Sernander's gap dynamics theory applies also to beech, as he concluded that although spruce was the conifer most sensitive to gales, before leaf fall deciduous trees may be even more at risk, a view confirmed by records of storm damage to *Fagus sylvatica* woodlands in Great Britain.

Old beechwoods that have been left to themselves for long periods come to consist of trees of many ages as a result of repeated gap formation (see Figure 1). The whole floor of narrow gaps may be covered by beech seedlings and saplings that are not in competition with any other tree. Watt (1925) provides a map showing a typical reproduction circle from southern England resulting from the fall of previous mature trees in which the position is more complex. Saplings of ash *Fraxinus excelsior*, whose seed is wind-dispersed, typically occupy the well-lit centre of the gap with beech and other species such as oak and spindle *Euonymus europaeus* round the margins. In the main forest the seed of beech falls almost vertically, so young beech may be restricted to



Figure 1. A storm gap in a beech forest with several fallen beeches probably felled on different occasions with very little field layer vegetation. Their stems have been snapped by gales whereas beeches growing on the shallow soils of the South Downs, England, are often completely uprooted. Söderåsen National Park, Scania province. Photograph by Jörg Brunet.

the margins of large gaps unless there had previously been a mast year which had augmented the seed bank of this species. The outcome of competition between the seedlings and saplings of these species in wider gaps varies, dependent on various factors described in Packham et al. (1992, p.151), who give a copy of Watt's map of a reproduction circle. They also give a figure from Watt (1947), which shows the distribution of phases in an old beechwood and illustrates his concept of pattern and process in the plant community. In heavily shaded areas beneath dense beech the ground is bare. As a little more light enters, wood-sorrel *Oxalis acetosella* provides the understorey, while bramble *Rubus fruticosus* takes over as the amount of light increases still more. This sequence is repeated many times in particular places in the process of cyclic change.

Storm damage and mortality

Figure 1 shows typical storm damage in a Swedish beech forest. The stems have snapped well up the trunks, whose remnants remain as fungus-ridden dead hulks. If the stumps remaining after trunks have snapped well above ground are healthy, and not subject to significant fungal infection, they may produce new leafy shoots and continue to grow as living high stumps. In other cases, including wooded pasture in eastern Scania, the trunks snap much closer to the ground.

Summer drought is an important factor in promoting ill health that can tip the balance between life and death in the long run. Despite its northern location, southern Sweden is

subject to summer droughts which affect tree biomass accumulation in following years. A recent reconstruction of a regional drought index starting in 1750 (Drobyshev et al., 2011) in two areas of southern Sweden, one on the southwest Atlantic coast (SW) and the other in an area close to the Baltic coast including the island of Gotland (NE), gives an important long-term insight into this factor. The major part of the study region is a transition between boreal and temperate biomes in which both coniferous and deciduous trees are common. Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* are the main coniferous species, while the commonest deciduous trees are beech *Fagus sylvatica*, oak (both *Quercus robur* and *Q. petraea*), downy birch *Betula pubescens* and aspen *Populus tremula*. Dendrochronological samples were taken at breast height using two radii from each tree and chronologies were built up for both oak and pine, both of which were sensitive to summer drought. The results were complex and differed from place to place but those for the period 1945–1975, in which the SW area had a trend towards a drier growing season but the NE did not, are of particular interest.

Fuentes, Niklasson, Drobyshev, and Karlsson (2010) studied tree mortality in the semi-natural beech forest of Biskopstorp, south western Sweden. The mortality rate did not differ among size classes, but were related to different tree condition classes. Their results highlighted the importance of the living high stump stage in the dynamics of the beech forest and suggest that the main cause of mortality in this stand was a combination of wind and infection by the fungus *Fomes fomentarius*. Living high stumps seem to be common in beech forests developed on stony moraines. As living high stumps are of high conservation value for both invertebrates and epiphytes, they should receive special consideration in the conservation-orientated management of southern Swedish beech forests (see Figure 2).

Investigations of storm damage and long-term mortality in the unmanaged semi-natural, temperate deciduous forest of Draved, southern Denmark, by Wolf, Møller, Bradshaw, and Bigler (2004) following the severe storm of 1999 are particularly interesting as they contrast the mortality patterns of *Fagus sylvatica* with other species characteristic of the boreal forests of Scandinavia. Storms killed many large trees, while a large number of the smaller individuals were killed by competition; standing dead individuals have narrower growth rings than the live survivors. Mortality patterns of *Fagus* and *Betula* differed. The former died less frequently than would be expected from its abundance, while the reverse was true of birch. Dead trees of *Fagus*, *Betula pubescens* and *Tilia cordata* were mainly wind-thrown, whereas half of the dead of *Alnus glutinosa* and *Fraxinus excelsior* were hulks (standing dead trees).

The long-term influence of fire on European forests

Fire has had an important long-term influence on the structure and tree species composition of forests, but there are almost no cases in southern Scandinavia where the fire history is known. As Niklasson et al. (2010) point out, this is due to a lack of intact forests containing old trees and dead wood from which the fire history can be reconstructed. However, these authors have been able to reconstruct the fire history of a 13 ha conifer-dominated area from which 886 tree ring samples were collected in the Białowieża Primeval Forest in Poland. From 1653 to the late 1700s fires were very frequent. After 1781 the length of intervals between fires increased dramatically, and since 1874 no major fire has been recorded. When fires were frequent *Pinus sylvestris* established only sporadically. When fires became less frequent *P. sylvestris* and *Picea abies* established on a very large scale, but now only *P. abies* and a few deciduous trees



Figure 2. Leafy living high stump of common beech. This high stump is unusual in that it has survived despite being split right to the ground. Photograph by Örjan Fritz.

regenerate: in a fire-free landscape *P. sylvestris* will be confined to the most oligotrophic and xeric soils. Although this paper by Niklasson et al. (2010) does not involve *Fagus sylvatica* it is quoted here because of its methodological importance and the way in which the combination of fire scars and tree rings can be used to reconstruct forest fire histories. It would be good if a similar fire history could be reconstructed for a large beech forest. Unfortunately, there appears to be no recorded fire history of common beech forests in Sweden or elsewhere.

Ohlson et al. (2011) examined a set of 75 macroscopic charcoal records that showed that invasion of northern Europe by *Picea abies* in the late Holocene diversified the fire regime, previously considered to be predominantly controlled by the macroclimate. As the Norway spruce invaded boreal European forests, it significantly reduced wildfire activity. This had an important influence on *Fagus sylvatica*, which invaded Sweden at the same time as Norway spruce with which it was often associated on a sub-continental scale.

Working in the Siggaboda Reserve in southern Småland, Sweden, Niklasson, Lindbladh, and Björkman (2002) established a long-term record of *Quercus* decline, logging and fires in this southern Swedish *Fagus-Picea* forest. Using tree-ring data, pollen and charcoal analysis they reconstructed forest development and disturbance by fire and logging over the last thousand years. The fire of 1652 was particularly severe, affecting most of the reserve including the core area. *Quercus* was common in the whole area until the late eighteenth century. *Quercus* disappeared completely at the end of the eighteenth century, when almost all the *Pinus* went also. No oaks have regenerated in the core area since the last fire in 1748, although a few single *Pinus sylvestris* established in the neighbouring managed forest around 1920. Norway spruce on the other hand has greatly increased since 1748 while *Fagus* became particularly abundant in the late nineteenth century and is still prominent today. The influence of human intervention still overshadows the effects of climate change.

The importance of veteran beech trees and ancient forests in Sweden

Tree age is very important when considering biodiversity in beech forests. Fritz, Niklasson, and Churski (2008) working in the Biskopstorp Reserve in the county of Halland, south western Sweden found that rare epiphytic lichens and bryophytes were mainly found on old trees of which examples are shown in Figure 3. The rarity of lunglav, the lung lichen *Lobaria pulmonaria*, described by Moberg and Holmåsen (1982) and shown in Figure 3 is emphasised by Thomas and Packham (2007) who also list several lichens found on ancient beech but not in more recent plantations.

Churski and Niklasson (2010) were concerned that low numbers of old-growth beech here would have an adverse effect on the conservation of epiphytic and saproxylic species in this 900 ha southern Swedish beech-dominated forest landscape, with its spatially and temporally disjointed old-growth structures in which there are few trees in the 150–240 year age group. They made the interesting suggestion that active measures should be taken to induce senescence and micro-habitat formation, such as the induction of rot-holes in vital trees close to old-growth patches. Some veteran Swedish beech are very large, one in the Torup forest of western Scania has a dbh of 1.6 m.

Quercus and *Fagus* are often found growing together in southern Sweden, particularly in forests which have been left untouched for centuries. Veteran trees of both frequently grow together under such circumstances. Even the largest specimens of *Quercus* in Scania are unlikely to be one thousand years old, although it is difficult to be exact as ancient oaks are so often hollow (Drobyshev & Niklasson, 2010) and the relationship between size and age is poor. The ages of 18 oaks that had not become hollow varied between 400 and 600 years. In contrast, *Fagus* seldom reaches more than 300 years. The oldest specimen of *Fagus sylvatica* in the northern hemisphere, at a little over 500 years, is growing on calcareous parent material in the Valle Cervara site, central Apennines, Italy, at 1750 metres above sea level (Piovesan, Biondi, Di Filippo, Alessandrini, & Maugeris, 2008). Many of the trees growing in the uneven aged primary old-growth site here were 300 years old.



Figure 3. Lung lichen, *Lobaria pulmonaria*, growing on a veteran beech in a forest whose herb layer is dominated by *Anemone nemorosa*, and with a few *Melica nutans*, *Galium odoratum* and *Lamiastrum galeobdolon*. Tromtö, Blekinge province. Photograph by Svante Hultengren.

History of Swedish beech forests

Lindbladh et al. (2007) report the investigation of forest and land use history of the 2000 ha Fulltofta estate which is situated in Scania, southernmost Sweden, and has been publicly owned since 1920. Until well into the twentieth century the estate was mainly used for timber production, but now conservation, recreation and economic factors are regarded as equally important and the availability of the land use survey of the estate made in 1772 is very useful in this regard. The ways in which various tree species and forest types have dominated different parts of the estate over the past 2000 years was established using historical sources, pollen analysis of the deposits in large lakes and small hollows, plant macro-fossils and dendrochronological investigations. The methods employed allowed differences in the types and openness of the vegetation to be distinguished with

considerable certainty. The estate has been dominated by broad-leaved deciduous trees over most of the last 2000 years. When the lime *Tilia*, hazel *Corylus* and oak *Quercus* forest started to decline around a thousand years ago it was largely replaced by beech. Despite the extensive planting of Norway spruce *Picea abies* which began in the mid-nineteenth century, both oak and beech have still remained common. *Fagus sylvatica* first became established in Scania around 2000 years ago (Berglund, 1991), and was important in the Ageröds moss from around AD 800, though with a slight decrease in the sixteenth century.

The development of *Fagus* on the Fulltofta estate was less pronounced and came much later. In 1772 three unconnected blocks of beech on the estate were admixed with other broadleaves, particularly oak and lime, but now these blocks consist almost exclusively of beech. The ability to distinguish spatial and temporal variations in the vegetation of sites such as this is clearly important when attempting to restore the vegetation of former plantation sites.

Hannon, Niklasson, Brunet, Eliasson, and Lindblad (2010) documented the fossil pollen and plant macrofossils over the last 2000 years for three small forest hollows in the Siggaboda nature reserve. The whole area has been forested for at least the last 2000 years but the forest has been subject to continuous change for the whole of that time, especially in the last 200 years during which *Fagus* and *Picea* have become very prominent and *Quercus*, *Tilia*, *Alnus* and *Corylus* have declined. *Fagus* and *Quercus* have been significantly more common in these “hotspot” areas than in the surrounding forest, of which the most important is in a five hectare area of old-growth mixed *Fagus* and *Picea abies* forest of high biodiversity.

In the future climate change with its accompanying increases in summer droughts and atmospheric CO₂ will affect Swedish beech just as it will those in Britain, where Broadmeadow, Ray, and Samuel (2005) show the overall results will be adverse although there will be considerable variations locally.

Conservation value of ancient Swedish beech forests

The numbers of animal, plant and fungal species associated with these ancient Swedish forests are much higher than in young beech plantations. This diversity extends to the ecosystem as a whole, but ancient beech also have large numbers of epiphytes growing on their trunks and dead wood as Packham, Thomas, Atkinson, and Degen (in press) note. Much is known and more is being discovered about the history and function of these ecosystems, which are often visited by the general public as well as woodland experts.

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