Windthrow, what comes after the storm?

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1. Introduction

The past decades, the vision on the forest and on the forest management in Flanders has been changing most drastically. From different angles, the same but differently formulated demand is heard for forest that is more sustainable managed, that is more divers or just more suspenseful, always though a forest that is more ecosystem and that offers more chances to spontaneous processes. The knowledge of these processes is mostly very limited and superficial. Main problem is that there are almost no forests where these processes dominate and that most of these forest are still very young. One of the big unknowns is the dynamic induced by windthrow. Forests where logs of fallen trees are left untouched are very scarce in Flanders. Normally these trees are sold and removed quickly after their fall. Snags, standing dead trees or dying trees are removed with thinnings or for safety reasons. Nevertheless it is broadly accepted that the presence of dead wood, and the conservation of the ecotypes created by the windthrow (mound, pit, ...) can highly increase the forest dynamic and the forest diversity. The uprooting of trees has implications to all aspects of the forest ecosystem. As the crown layer is opened, a change in micro- and meso-climate is created. Besides this, the soil is disturbed by a mound and pit micro gradients system. This article wants to bring a short review of some of the effects of these changes.

According to White & Picket all biologic systems are dynamic. The dynamic is ensured by processes of germination, of growing, of dying and of replacement (Drury & Nisbet 1971) stimulated by disturbances of the system (Van Miegroet 1994). The frequence, the diversity, the character and the size of disturbances are determining for the further evolution of the system (Van Miegroet 1994). Also woodland ecosystems are dynamic systems that are regularly disturbed by wind, fire or other factors (Dix & Swan 1971, Henry & Swan 1974, Sprugel 1976, White 1979, Lorimer 1980, Hytteborn et al. 1978). Structural and functional equilibria are broken and changes take place in the forest climate and the water and energy cycling (Van Miegroet 1994). Only recently windthrow is no longer seen as a destructive mechanism but as a part of the natural forest dynamic, on which every forest community reacts in its own way. Moreover, forests without windthrow lack development phases that are just partly replaced by human activities (cutting area, soil disturbance, ...).

In a large number of natural forest types uprooting of trees is the main source of exogenous forest disturbance (Cooper 1913, Sernander 1936, Stearns 1949, Webb 1958, Wright 1974, Pritchett 1979). According to Langohr (1993) the apparent fact that windthrow occurs now more frequently than ever, can be explained by three causes: the small size of the forests, the use of monocultures and the planting of (high production) tree species on the wrong sites. Furthermore the change of an intensive

treatment to a more extensive forestry implicates less thinnings and more trees in a sub-optimal condition which are more sensitive to windthrow.
As stated above, uprooting of trees has an important impact on several parts of the forest biocoenoses. Therefore, the changes caused by gaps as well as the new soil situation are briefly reviewed.

2. Windthrow as forest disturbance

2.1. Gaps in the canopy layer

By tree uprooting, gaps are created with specific climatological conditions clearly different from the forest climate. Not only the size of the gap determines the climate, also the shape and the orientation are most important in relation to the impact of wind, sun and rain (Koop 1981).Minckler et al. (1973), March & Skeen (1976), Chadzon & Fletcher (1984) and Vitousek & Denslow (1986) state that the most important ecological changes caused by uprooting are the increase of the amount of light and the improvement of the spectral characteristics of the light.

According to Langohr (1994), in forests where the understorey is lacking, the change in humidity has as more important impact on plant growth than the increase in light. The absence of interception and decrease of water use by roots can double the amount of precipitation reaching the soil and stimulating the plant growth.

Vazquez-Yanes & Orozco-Segovia (1982), Cook & Lyons (1983) and Mladenoff (1987) also mention other shifts: changes in the amount of warmth, allowing a better germination of seeds, larger temperature fluctuations and changes in soil acidity, phosphorous, total nitrogen, nitrate, calcium and potassium.

At the same time windthrow causes the deposition of considerable amounts of organic material (stem, branches, bark, ...) on the soil surface. Because of the increased energy input through the canopy gap, the decomposition of this material as well as of the present organic material will be accelerated (Koop 1981). These logs and crowns of fallen trees (often even sprouting again) prevent the soil from being abruptly exposed to the macro-climate. A diameter of twice or three times the tree height is accepted as a critical size above which the forest climate is replaced by the macro-climate.

2.2. Soil perturbation: mounds and pits

Uprooting of trees creates a so called mound and pit system (Stephens 1956, Karpachevskiy et al. 1968, Kooi 1974, Dwyer & Merriam 1981, Ives et al. 1972, Cremeans & Kalisz 1988). The mound marks the former position of the roots in the soil (Lutz 1940, Armson & Fessenden 1973, Stone 1975, Beatty & Stone 1986, Schaetzl et al. 1989), whereas the pit contains a part of the roots and the uplifted soil.

Fig. 1 shows the main types of soil disturbance by windthrow. The dimensions of the soils disturbance are not indicated since they can be very variable: the depth can fluctuate between 0.3 and 2 meter, the length between 0.5 and 5 meter.

a. Soil profile before windthrow
b. Complete windthrow, with the pit lifted out of the mouth (often found with superficially rooting trees)
c. Complete windthrow, with the pit completely in the mound (often found with deep rooting trees)
d. Complete windthrow, with the pit out of the mound and by which a pronounced relief is created as an important part of the soil of the pit is placed besides the mound (often found on slopes)
e. Incomplete windthrow with a strong disturbance of the original soil profile (often found when the uprooted tree is hanging in the canopies of surrounding trees)
f. Closing windthrow, after the cutting of the tree, the soil profile is almost completely restored (often found in windthrow as in type b1)
g. Closing windthrow, after the cutting of the tree a clear disturbance of the original soil remains (often found in windthrow as in type c1)
h. Complete windthrow as in type c, but a part of the original upper soil layer is lifted with the pit after which it drops back into the mound
i. Complete windthrow, with almost vertical sides of the mound, these disturbances are mostly very deep (up to 2 meter)

Between mounds and pits notable differences in micro-climate are found. The humidity, the thickness of the snow cover and O-, A- and E-layers are mostly highest in the mounds, smallest on the pits and intermediate on the undisturbed forest soil (Beatty & Stone 1986, Schaetzl 1986). In comparison to mounds, pits are exposed to much higher temperature fluctuations. This is mainly caused by the thinner litter and snow layer (Kienholz 1940, Federer 1973).

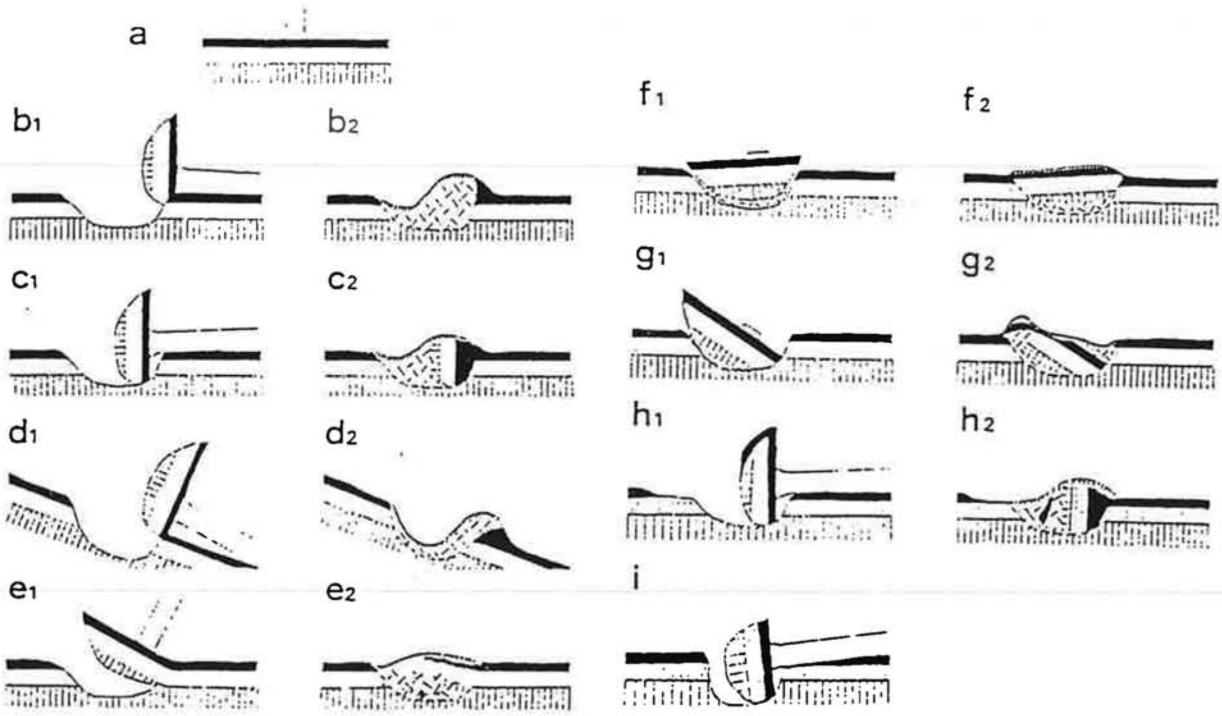

Figure 1. Overview of the most frequently occurring types of soil disturbances created by windthrow, the drawings at the left side (1) show the situation directly after the windthrow, the drawings at the right side (2) show the situation after almost complete decomposition of woody tissue and stabilisation of the slope (Langohr, 1993)

Koop (1981) describes four phases in the process of levelling out (Fig. 2). By erosion and crumbling of of soil originating from the pit, the original soil profile is lost and irregular, incoherent layers are formed in the mound. The rapidity of decomposition of the roots is a key parameter in this proces (Beatty and Stone, 1986). In the case of a slow decay of the roots, the earth is transported from the pit to the mound by precipitation. Soil layers are mixed and the original profile disappears. In the case of a fast decay, clumps of earth will fall of. In the mound, large parts of the original profile is found.

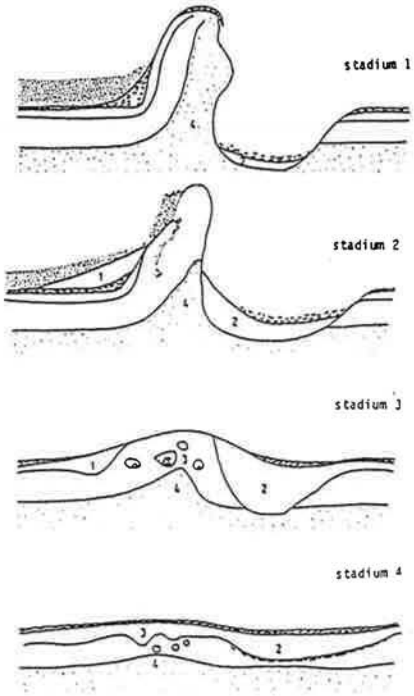

Figure 2. Model for the leveling proces of the uprooting relief with 1 - material originally above the rooting zone, 2 - soil originally beneath the rooting zone and now mixed with organic material in the mound, 3 - loose soil and decaying roots with many cavities and 4 - twisted deeper horizon

3. Impact of windthrow on diversity and species composition of vegetation and regeneration

3.1. Gaps in the canopy layer

Colonisation of open places by vegetation can happen by means of sprouting of trees and shrubs, emergence of suppressed seedlings and by the germination of seeds (Koop 1981). The evolution and development of vegetation and regeneration in open places are in the first place determined by the size of the gap (Minckler & Woerheide 1965, White 1979, Lorimer 1980, Runkle 1982, Hibbs 1982, Brokaw 1985, White et al. 1985, Van Miegroet 1994). Differentiation in gap size implicates a large species diversity (Denslow 1980, Runkle 1984). Koop (1981) states that when the gap becomes too big, the number of species will decrease because ruderal plants will expand and will push away the seedlings and typical forest plant species. Fallinski (1976) concludes more or less the same: the leaf mass in the herbal vegetation of open places can often be divided into two layers, one of the ruderal species and a lower one of the typical forest species. By a strong increase of ruderal species like *Urtica dioica*, species like *Oxalis acetosella* are pushed away (Koop 1981). Spurr (1956) states that the re-colonisation in big gaps is mainly prevented by the presence of logs and branches.

For the regeneration of tree species, Hyttebom et al. (1978) discriminate between group regeneration patterns in large gaps, and tree by tree replacement in small gaps. When the created gap is very small, it is often closed by lateral growth of the surrounding trees (Marks 1974, Oliver & Stephens 1977, Hibbs 1982).

In smaller gaps, the regeneration of trees will mostly depend on the presence of parent trees or of a seed bank. The germinating seeds mostly come from tolerant tree species (Van Miegroet 1994). Depending on the presence and the size of suppressed seedlings before the disturbance, emergence will play a part in the re-colonisation (Brewer & Merrit 1978).

In larger openings though, the presence of local parent trees or seed banks is negligible. The seed of tolerant tree as well as pioneer species is imported by the wind and the gap is rather rapidly colonised. Lateral closure of the canopy layer is no longer possible.

Where large scale disturbances destroy the forest biocoenose over a vast area, the recovery of the ecosystem can take very long time. This situation is comparable with the consequences of a clearcut. All compartments of the biocoenose are affected since the complete local climate is changed. Enormous amounts of organic matter cover the soil with a sudden reduction of the living biomass. Such disturbances affect the site quality and give rise to large scale evenaged forests (Van Miegroet 1994). Of course seedlings of intolerant species benefit most of this situation. According to Koop (1981) this large scale destruction finally results in smaller entities. This happens in a rather uniform way within a period of several decades. Leibungut (1984) defines a temporal plenter phase. Only after several generations of trees, the contours of the early pioneer phase disappears (Derkman & Koop 1977).

Besides the size of the gap, Koop (1981) considers the nutrient state of the site to be an important characteristic for the further evolution of the stand. In nutrient poor conditions, the number of plant species will increase while in nutrient rich conditions there is often no notable change. According to Fallinski (1986), more plant species of nutrient rich and moist conditions are observed than in the closed forest. This can be caused by the higher mineralisation of litter and humus, as well as by the higher amount of precipitation.

3.2. Soil disturbance and dead wood

For the study of the role of uprooted trees in an ecosystem functioning, no Flemish examples can be considered. Observations of Van der Werf (1983) mostly concern old growth forests in the North-Western part of Germany (Neuenburger Urwald, Hasbruch, Baumweg), Poland (Bialowieza), Austria (Rothwald), France (Fontainebleau) and Slovenia (Kocevje). One of the best documented forest reserves is Neuenburger Urwald. Elaborate studies are available by Nitzschke (1932), Barkman & Groenhuijzen (1965), Londo (1977) and Koop (1981). These studies enable a comparison in time, though quantitative data are mostly lacking.

3.2.1. Vegetation and regeneration on logs

The probably best known example of vegetation growing on fallen logs is the linear regeneration of Picea abies in Scharzwald (Dieterich et al. 1970), Austria (Zukrigl et al. 1963, Mayer et al. 1972), Bialowieza (Fallinski 1976, Van der Werf 1983), Slovenia and Engadin (Van der Werf 1983), although in literature the absence of natural regeneration in old growth stands is often mentioned.

In Neuwald Mayer et al. (1972) found 1.5 to 4 times more seedlings of respectively *Picea abies* and *Abies alba* than on the surrounding soil. Van der Werf (1983) even suggests that the absence of logs in forests is one of the main reasons for the decline of Abies. For beech seedlings a ratio of 0.4 was found. According to Van der Werf, logs are not very stable substrates as at a height of 1 to 2 meter fall down of the seedlings is generally observed.

The occurrence of vegetation on logs depends highly on the roughness of the bark (Koop 1981) and on the degree of decay. On the rough bark of oak, herbs will grow as long as the bark is present. Once the bark has disappeared, only moss species will remain. On the smooth bark of *Fagus sylvatica* and *Carpinus betulus* no herbs species can grow (Koop 1981).

Mayer et al. (1972) describe the succession of fallen trees over three phases. During the first 10 to 30 years the log is covered with acidophyl moss species. Middle-aged logs are less acid and as a consequence less acidophyl species will occur. In a third and more advanced stadium of decay, the difference with the surrounding forest vegetation becomes less clear. Barkman and Groenhuijzen (1965) describe the succession in five gradations. After the occurrence of moss species, higher species of herbs will settle. On mouldered logs, the vegetation is dominated by taller herbs. After a complete decay of the trees, even after 5 to 10 years some species are not able to settle down although they occur in the direct neighbourhood of the tree.
The high amounts of nitrofyl herbal species on logs is suprising because of the low concentrations of nitrogen in bark and wood. Maser and Trappe (1984) ascribe this phenomenon to the fact that these nitrofyl species are fast colonists and can survive because in the first phase of decay there still is a reserve of nutrients present, especially in the phloem.
Ripe wood contains 0.03 to 0.10 % nitrogen and C/N-ratios mostly range between 350 and 500, in the case of *Picea sitchensis* even 1250 (Kaarik 1979). The role of bacteria fixating N from the air is less known. Van der Werf (1983) states that wood decaying fungi, are extremely economic in the use of N in their metabolism.

3.2.2. Vegetation and regeneration on mounds and pits

Mound- and pit-systems result in aberrations from the vegetation of the forest without gaps. The higher pits are colonised by species of dryer forest types, in the mounds species of wetter types occur (Van der Werf 1991). This can cause a pattern of three sub-associations on a micro-scale (Koop 1981). The "middle" plant community is normally dominating and the name of this community is given to the entire forest.

For woody vegetation, the pit is often as important as the dead log (Van der Werf 1983). The competition with the herbal layer is a lot lower and the mineral soil is easier to reach. Mounds can mostly be considered as much less favourable sites. In most forests the pits are holding water in winter and early spring, with often also the formation of ice (Stone 1975).

Rode (1955) found a lot of trees on pits but none in mounds. In Bled (Slovenia), at a height of 1400 meters, regeneration of Picea abies was exclusively found on pits (Van der Werf 1968, personal observations). Less extreme differences were measured by Lyford & MacLean (1966) in Eastern Canada: the number of trees in the mounds was negligible and of small dimensions, on the pits this number was tree times higher than in the undisturbed zones.

Fallinski (1976) considers mounds as "strange elements" in the forest ecosystem. Just after uprooting there is only few vegetation because of the damage by water and burrowing animals. By consequence the succession starts with species not typical for forests like water and marsh plants. Because of uprooting, plants of humid and nutrient rich forest types can occur in nutrient poor and dry forest types.

Nitzschke (1932) and Londo (1977) draw attention to the vegetation composition after leveling of the soil disturbances in the Neuenburger Urwald. These old disturbances have a vegetation that is clearly different from the surrounding zones. Specific species are found on the remains of the pit (Londo 1977, Koop 1981). A more detailed study proved these differences to be most pronounced in the tree phase and in small gaps with a certain degree of shading (Koop 1981). In larger gaps, these micro-gradients hardly occur in the vegetation composition because species favoured by shading are suppressed by ruderal species and ferns.

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