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Shoot growth processes, assessed by bud development types, reflect Norway spruce vitality and sink prioritization

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Abstract

Crown defoliation, is a product of the tree crown status from the past several years of growth, which can be misleading if used as a stress indicator when assessing current Norway spruce vitality. To evaluate recovery processes in previously damaged trees a newly developed macroscopic indicator based on proportions of bud development types was investigated. In 1998 and 1999, 474 mature Norway spruce trees were sampled for macroscopic measurements, 293 trees for tree-ring increments and 40 trees for study of metabolic markers (concentration of chlorophylls, phenolic compounds and lignin). Study sites were located in the Czech Republic, in the Sumava Mts, a relatively unpolluted and undisturbed area, and in the Krusne hory Mts, which exhibited a whole range of tree damage corresponding to a gradient of increasing air pollution load. Three categories of trees were identified which reflect current levels of intensity of shoot formation and capacity to replace potential needle loss by activation of buds with growth potential: accelerated, stabilized and decreased shoot growth. Relative to sink prioritization, we concluded that the highest vitality occurred in trees with stabilized shoot growth and the lowest vitality in trees with accelerated shoot growth. In conifers, the amount of allocated assimilates to low priority carbon sinks (such as stem growth, production of protective chemical compounds and reproductive organs) depends on what is remaining from the shoot growth processes which are of the highest priority. Significant inverse relationships were found between the intensity of shoot growth, tree-ring increments, production of reproductive organs and concentration of phenolic compounds in the needles. The highest allocation of assimilates to crown recovery occurred in trees with crown defoliation of 50–69% indicating forest recovery was observed in the most heavily damaged areas impacted by air pollution in the past. The present criterion of bud development types has potential for forestry management applications as it is easily applied in the field and, in contrast with standard forestry measurement of crown defoliation, it reflects accurately tree recovery and decline processes under multiple stress impacts.

Keywords: Tree vitality; Buds; Carbon allocation; Sink/source concept; Crown defoliation; Norway spruce (*Picea abies*)

1. Introduction

According to Dobbertin and Brang (2001) tree vitality can be defined as ‘the ability of a tree to assimilate, survive stress, react to changing conditions, and reproduce’. Crown defoliation (needle loss) is a non-specific symptom of Norway spruce (*Picea abies*/L./Karst.) vitality widely used in forest practice. It has been questioned whether defoliation is a valid indicator of tree vitality, since it does not reflect early stages of crown recovery (Salemaa and Jukola-Sulonen, 1990; Cudlín et al., 2001; Dobbertin and Brang, 2001). The processes leading to crown regeneration in mature trees (i.e. to forest recovery) enable replacement of lost assimilative organs caused by the

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impact of multiple stresses and promotes tree resistance to defoliation (Chen et al., 2001). Therefore, the assessment and understanding of crown recovery and decline processes might be an important tool for forestry management practice for taking appropriate measures in time, or for identification of resistant or susceptible individuals to environmental factors.

The term 'tree growth' often refers to stem increments (e.g. Schulz and Härtling, 2003), however, tree growth comprises both shoot and stem increments. In the present study, the production of assimilative organs and wood formation is separated. Therefore, we use the term 'shoot growth' for production of shoots, while 'stem growth' is used for depiction of stem radial increments.

Crown regeneration of Norway spruce trees is accomplished by formation of two types of shoots, which differ in the duration of the dormant period between bud set and bud burst (Kozlowski, 1971). Regular shoots are differentiated following vegetative season after bud set from dormant buds. Secondary shoots, also called adventitious, epicormic or proventitious shoots (Gruber, 1994), are initiated at least two seasons after bud set. The buds giving origin to secondary shoots are called 'buds with growth potential' since they contain healthy meristems and they include dormant and latent buds (Albrechtová, 1997; Polák et al., 2003, 2004). Buds with growth potential resume development and form secondary shoots depending on their development program or in response to environmental cues (Shimizu-Sato and Mori, 2001). They normally do not resume their growth activity unless the trees are stressed as, for example, due to insect infestation (Powell, 1974), damage and defoliation (Halle et al., 1978) or pruning (Ishii et al., 2000).

One of the tools used to identify and quantify intensity of shoot growth and thus intensity of crown regeneration is based on the activity of apical meristems contained in the buds. Any disruption of bud development reduces the biomass and/or quality of foliage produced in the following year (Straw et al., 2000), while bud metabolic status reflects the photosynthetic activity of needles and transport capacity (Lipavská et al., 2000). Therefore, buds and photosynthetically active needles are mutually dependent. On the basis of a detailed anatomical study, Albrechtová (1997) developed a macroscopic criterion for classification of individual vegetative bud development types, allowing fast estimation of current Norway spruce vitality. The method is applicable to 1-year and older shoots and separates three types of vegetative buds according to their activity and regenerative potential: (1) active (regular) buds producing regular shoots; and two inactive bud types developed in two alternative ways depending on a combination of external and internal factors. Inactive bud types may have meristematic regions (2) that are dead or lost (an aborted bud) or (3) those regions that remain viable at least until the following season (a bud with growth potential).

Buds containing apical meristems are considered, among the plant tissues, to be a strong sink for carbon (e.g. Lipavská et al., 2000; Svobodová et al., 2000). The allocation of carbohydrates to individual physiological processes is in accordance with the principles of sink/source concept, proposed to explain how and why resource availability influences the allocation of plant resources to shoot growth and stem growth (Wareing and Patrick, 1975; Honkanen and Haukioja, 1994). It assumes that different physiological processes compete for resources and variations in the strengths of sources (e.g. leaves) and sinks (actively growing meristems) influence resource allocation and quantitative changes in growth. Running and Gower (1991) and Klap et al. (2000) suggested that conifers allocate carbon to different tissues or physiological processes according to the following prioritization: (1) maintenance respiration; (2) shoot growth and storage; (3) root growth and storage; (4) stem growth and storage; (5) synthesis of protective chemical compounds; (6) production of reproductive organs.

4. Conclusions

Crown defoliation allows the classification of past foliar loss in a crown for conifers, but does not reflect current recovery or declining processes. Using the proportion individual bud development types as indicator (assessed on 1-year-old shoots) we separated the following shoot growth categories of Norway spruce associated with multiple impacts of stress factors: accelerated shoot growth, stabilized shoot growth and decreased shoot growth. These categories reflect the current trend of tree recovery or decline processes. This finding has direct implications in forestry practices for forecasting of forest stand dynamics and development. It will facilitate the selection of resistant trees for propagation and stressed susceptible trees for tree logging. Because of the simplicity of this method, it can be easily applied under field conditions and seem to have a practical potential for large-scale monitoring of Norway spruce decline and recovery events.

Our study supports the prioritization of sink/source physiological processes for conifers. The result of the present study points to the importance of the sink/source relationship of Norway spruce trees in recovery from heavy damage. We found that heavily defoliated trees (defoliation 50–69%) exhibited the most intensive crown regeneration, i.e. highest allocation of assimilates to the primary shoot growth processes. In addition to high defoliation, these trees are also weakened by insufficient carbohydrate allocation to low priority carbon sinks (e.g. reproduction, stem increment growth and synthesis of protective chemical compounds), which decreases their chance for sustainable survival.

From the long-term perspective, our data supported the conclusion that the vitality of Norway spruce forests in the Czech Republic previously heavily impacted by air pollution is in agreement with the conclusion of the R.M.A.C.R. (2002). This means that: (1) forests, which have been relatively healthy since the beginning of 1990s, have started to decline as a result of long-term impact of multiple stress factors, and (2) forests, which have been heavily damaged and survived the extreme stress conditions, have started to recover in the central and eastern Krusne hory, likely in response to improved air pollution conditions during the last decade. However, due to changes in soil conditions induced by long-term heavy acidic loads it can be expected, that even after improvement of air quality, the stress conditions are going to persist much longer. The local surviving spruce forests are still on the edge of ecological stability. Large-scale ameliorative measures of forestry management such as liming with crushed dolomite have been applied there since the 1970s and their effects and consequences on the long-term stand dynamics have yet to be evaluated.