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Spring patterns of freezing resistance and photosynthesis of two leaf phenotypes of *Hedera helix*

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Abstract

Subdominant evergreen broad-leaved plants occurring in deciduous forests throughout temperate zones have only a short window of optimum photoassimilation in spring before canopy closure. Yet increasing photosynthetic and metabolic activity occurs concurrently with reductions in freezing resistance, resulting in vulnerability of plant tissues to late spring freezing events. Our goal was to document the temporal patterns of photosynthesis *versus* freezing resistance during spring in adult and juvenile leaf phenotypes of *Hedera helix* in Switzerland. Freezing resistances in all leaves were well below long-term minimum temperatures experienced at the study site, with adult leaf phenotypes in the forest canopy being more freezing resistant than juvenile leaves occurring closer to the ground. Reductions in freezing resistance were followed by increases in leaf photosynthetic capacities, which appeared synchronized among leaf phenotypes. Adult canopy leaves maintained a higher freezing resistance but lower photosynthetic capacity than juvenile leaves through the end of winter and into early spring. However, shortly after the cessation of freezing temperatures, adult leaves greatly increased their photosynthetic capacity relative to juvenile leaves, yet maintained freezing resistances sufficient to resist late spring freezing events. These patterns highlight the importance of the tradeoff in *H. helix* between exposure to potentially damaging cold temperatures in late spring and the need for high photosynthetic carbon gains before full canopy closure.

Zusammenfassung

Immergrüne Pflanzen im Unterwuchs temperater Laubwäldern verfügen über ein kurzes Zeitfenster im Frühjahr, während dem sie optimal Photoassimilation betreiben können bevor sich das Kronendach schliesst. Ein Anstieg der Photosyntheseleistung im Frühjahr ist allerdings mit einem Rückgang der Frosthärte verknüpft. Das könnte bei diesen Pflanzen zu Beginn der Saison zu einer erhöhten Anfälligkeit für Frostschäden führen. Das Ziel dieser Studie war es, den zeitlichen Verlauf von Photosynthese und Frostresistenz während des Frühjahres in adulten und juvenilen Blatt-Phänotypen von *Hedera helix* in der Schweiz zu dokumentieren. Die Frostresistenz aller Blätter lag deutlich unterhalb der gemessenen Minimum-Temperaturen auf der Studienfläche, wobei adulte Blätter im Kronenraum eine höhere Resistenz aufwiesen als junge Blätter am Waldboden. Der Anstieg der Photosyntheseleistung erfolgte in beiden Blatt-Phänotypen im Frühjahr erst nach dem Enthärten der Frostresistenz. Adulte Blätter zeigten am Winterende und zu Beginn des Frühjahres eine höhere Frostresistenz und entsprechend eine niedrigere Photosyntheseleistung als juvenile Blätter. Allerdings stieg die Photosyntheseleistung adulter Blätter nach den letzten

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stärkeren Frosttagen im Frühjahr stark an und überholte jene juveniler Blättern. Die Frostresistenz blieb aber auch hierbei immer unterhalb der gemessenen minimalen Lufttemperaturen. Das beschriebene zeitliche Muster von Frostresistenz und Photosynthese in *Hedera helix* Blättern verdeutlicht den Konflikt zwischen der Vermeidung von Spätfrostschäden und der Maximierung der Photosyntheseleistung in der kurzen Periode zwischen Winterende und dem Laubaustrieb der kronenbildenden Bäume.

Keywords: Frost resistance; Dehardening; Spring frost; Photosynthetic capacity; Physiological tradeoff

Introduction

Temperate zone deciduous species avoid leaf freezing damage during winter by dropping their foliage and entering into a state of dormancy. Conversely, broad-leaved evergreen species maintain their foliage throughout the year. However, leaves are one of the most freezing sensitive plant tissues and are physiologically costly to maintain, especially during the unfavorable winters of the northern temperate zone (Öquist & Huner, 2003; Sakai & Larcher, 1987). This suggests that the elevational and latitudinal range limits of many broad-leaved evergreen species may be determined by their cold temperature tolerance. Indeed, broad-leaved evergreen distributions in Europe are mostly restricted to the Mediterranean climatic zone, which has relatively mild winters (Sakai, 1980).

The two broad-leaved evergreen species that do exhibit relatively high freezing resistance and thus, inhabit central parts of northern Europe are *Hedera helix* and *Ilex aquifolium* (Iverson, 1944; Sakai, 1980). *H. helix* (common ivy) is unique in that it maintains two phenotypically distinct leaf types on the same plant, adult and juvenile leaves. Adult and juvenile leaf phenotypes may also be referred to as sun and shade leaves. However the terms sun and shade leaves are misleading as leaves are ontogeny-related morphotypes and not a leaf modification in response to light conditions during leaf formation. Therefore we maintain the usage of the terms adult and juvenile leaves, which is consistent with previous similar works (*e.g.* Metcalfe, 2005; Bauer & Bauer, 1980). The names adult and juvenile leaves can be confusing and do not reflect the age of the leaves themselves but rather the life stage of the stem from which the leaves were grown. Adult reproductive stems in *H. helix* are those that are most distant from the basal, non-reproducing juvenile stems (Hoflacher & Bauer, 1982). Both phenotypes may be found in the sun or in the shade but most often *H. helix* changes its leaf phenotype from juvenile to adult with increasing height in the forest, which is due to the change in whole shoot morphology as shoots grow higher in the canopy. As such, in most European forests, *H. helix* leaf phenotypes are strongly stratified within a forest vertical profile. Adult leaves occur in the canopy and juvenile leaves occur on the forest floor or at the base of trees. There is often a transition zone located somewhere in the mid-canopy where leaf phenotypes co-occur but this transition zone is usually relatively small.

Andergassen and Bauer (2002) found that maximum freezing resistance did not vary between the two leaf types but that different temporal patterns of hardening and de-hardening led to higher freezing mortality in juvenile leaves during early or late growing season freezing events. While this study highlighted the similar freezing resistance capacities between the two leaf phenotypes, sampling of leaves occurred at only one height within a botanical garden, which does not reflect the stratified distribution of leaves in a natural forest. Temperature changes significantly within a forest's vertical profile, especially in winter. For example, the canopy may be colder relative to the ground when night-time radiative cooling lowers canopy temperature and the ground vegetation is under snow (Sakai & Larcher, 1987). Conversely, ground cooling may exceed canopy cooling when snow is lacking (Groffman, Hadry, Driscoll, & Fahey, 2006). As the maximum freezing tolerance of leaves is highly correlated with minimum temperatures (Pisek & Schiessl, 1946; Sakai & Weiser, 1973), freezing tolerances of leaves at different heights may vary.

Along with temperature, solar radiation changes considerably with height within a forest (Oberhuber & Bauer, 1991; Poorter et al., 2006). This is particularly relevant for broad-leaved evergreen species in deciduous forests during the early spring and late fall when the canopy remains open and solar radiance is high, even at ground level. During these times most evergreens have large carbon gains relative to other times of the year (Leuzinger, Hartmann, & Körner, 2011; Öquist & Huner, 2003). However, remaining physiologically active when sub-zero temperatures may occur also increases a plant's risk to freezing damage, as active plants tend to be less freezing tolerant than inactive plants (Bauer & Bauer, 1980; Bauer & Kofler, 1987; Weiser, 1970).

Among the many metabolic and physiological changes that occur during the hardening and dehardening process, of particular importance are the alterations to membrane composition and Rubiso activity, which occur simultaneously and often have opposite effects on levels of freezing resistance and photosynthetic activity (Sakai & Larcher, 1987; Sung, Kaplan, Lee, & Guy, 2003). This relationship between photosynthesis and freezing resistance can be readily seen in the fall in *H. helix* plants entering dormancy. As photosynthesis and metabolic activity begin to slow there is a concurrent increase in freezing resistance, which reaches a maximum several weeks after photosynthetic activity has ceased (Steponkus,