Petiole hyponasty: an ethylene-driven, adaptive response to changes in the environment

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Abstract

Background

Many plant species can actively reorient their organs in response to dynamic environmental conditions. Organ movement can be an integral part of plant development or can occur in response to unfavourable external circumstances. These active reactions take place with or without a directional stimulus and can be driven either by changes in turgor pressure or by asymmetric growth. Petiole hyponasty is upward movement driven by a higher rate of cell expansion on the lower (abaxial) compared with the upper (adaxial) side. Hyponasty is common among rosette species facing environmental stresses such as flooding, proximity of neighbours or elevated ambient temperature. The complex regulatory mechanism of hyponasty involves activation of pathways at molecular and developmental levels, with ethylene playing a crucial role.

Scope

We present current knowledge on the mechanisms that promote hyponasty in the context of other organ movements, including tropic and nastic reactions together with circumnutation. We describe major environmental cues resulting in hyponasty and briefly discuss their perception and signal transduction. Since ethylene is a central agent triggering hyponasty, we focus on ethylene in controlling different stages during plant development and summarize current knowledge on the relationship between ethylene and cell growth.

Introduction

All living organisms are challenged to cope with environmental heterogeneity. For the past century, the phenomenon of phenotypic plasticity, which allows individual genotypes to adjust to multiple environments, has been a focus of much interest. Due to lack of short-term migration ability, plants have evolved a range of traits and processes which allow them to maintain their functions in dynamic environments (Bradshaw 1965; Schlichting 1986; Sultan 2000). Ultimately, these processes lead to morphological and physiological modifications, some of which appear to have an adaptive role (Van Kleunen and Fischer 2005; Ghalambor et al. 2007).

Plant organ movements play a special role in coping with ambient changes and have been given much

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attention since the birth of modern plant biology. According to the commonly accepted classification, they are divided into three arbitrary categories: tropisms, nutations and nastic movements. Tropic reactions are triggered by an exogenous directional stimulus to which a plant can react either with asymmetric axial (differential) growth or with changes in turgor status (Shropshire 1979). Although the vast majority of studies have been carried out on photo- and gravitropism (Shropshire 1979; Hart 1990), which are induced by light and gravity, respectively (Firn and Digby 1980; Morita and Tasaka 2004; Iino 2006), the classification of tropisms extends far beyond that. There are other tropic reactions such as heliotropism (sun tracking) (Jaffe 1970; Ehleringer and Forseth 1980), thigmotropism (reaction to touch or physical contact with an object) (Shropshire 1979), chemotropism (response to a chemical substance) (Tsao 1949; Kim 1989) hydro- and chemotropism (Jaffe et al. 1985; Takahashi 1997) or even traumatotropism (response to wounding and injuries) (Hart 1990). Some tropic movements, however, might be induced by non-directional stimuli, e.g. ethylene application or oxygen withdrawal from the roots can cause negative shoot gravitropism in a diageotropic Solanum lycopersicum mutant (Jackson 1979).

Circumnutations are autonomous, helical movements that require a circadian oscillator (Johnsson 1979; Stolarz 2009). They occur usually in young organs of a wide range of plant species, e.g. Pisum sativum tendrils (Jaffe 1972), Helianthus annuus hypocotyls (Brown et al. 1990) or coleoptiles of Avena sp. (Anker 1972). Alongside the numerous, rather descriptive studies on circumnutations, molecular tools for studying the regulatory mechanism have now become available. Recent studies, for example, demonstrated the importance of endodermal development and gravitropism in circumnutational movements (Kitazawa et al. 2005; Johnsson et al. 2009).

Nastic movements occur without a strong directional component (Brauner 1954; Romberger et al. 1993). The most extensively studied rapid nastic movements, such as closing of the Aldrovanda or Dionaea trap to catch insects (Iijima and Sibaoa 1985; Hodick and Sievers 1989) and seismo- and thigmonomic movements of Mimosa leaves (Sibaoa 1962, 1991), are based on changes in the osmotic status of specific cells. Some species, belonging to the Fabaceae family in particular, possess specialized structures, pulvini, which consist of motor cells with elastic cell walls and a large, quickly contractable vacuole (Satter et al. 1990; Romberger et al. 1993). Although initially classified as movements driven by reversible turgor reactions, many nastic responses depend on unequal growth rates between two anatomically different sides of the organ (differential growth) (Romberger et al. 1993). Thermonastic opening of Tulipa and Crocus tepals is one of the most elegant examples of differential growth triggered by differences in tissue sensitivity to ambient temperature, where the outer epidermis of the perianth has a growth optimum \(\sim 10^\circ C\) lower than that of the inner one (Wood 1953).

Epinasty is usually described for leaves and floral organs and takes place when, as a result of differential growth, an organ bends outward and downward (Kang 1979). It is usually triggered by unfavourable ambient conditions such as waterlogging (Kawase 1974; Jackson and Campbell 1976), salinity stress (Jones and Elabd 1989), drought (Ruiz-Sanchez et al. 2000) or pathogen attack (Evidente et al. 1996; Michielse and Rep 2009). The complex regulation of epinastic movements consists of many factors, among which gravity, ethylene and auxin play a central role (Stewart and Freebairn 1969; Lin et al. 2008; Perez-Perez et al. 2010). The opposite type of asymmetric growth, when abaxial tissue exhibits higher growth rates in comparison to adaxial cells, is called hyponasty (Kang 1979) (Fig. 1). Hyponasty has been mostly reported for leaf blades of monocots and dicots (Lippincott and Lippincott 1968; Street et al. 1992) as well as leaf petioles (Voesenek and Blom 1989; Cox et al. 2003; Pierik et al. 2003). Hyponastic responses are of high functional significance in coping with a wide range of abiotic types of stress such as flooding, shade or elevated temperatures (reviewed in Van Zanten et al. 2010).

**Hyponasty in response to abiotic stress**

**Flooding**

Various types of environmental stress can cause plant organs to grow hyponastically. Studies on semi-aquatic species led to the identification of a suite of submergence escape characteristics which include hyponasty (reviewed in Voesenek et al. 2006). Waterlogging, partial submergence and total submergence have a significant effect on the leaf angle of Rumex palustris (Voesenek and Blom 1989), Leontodon taraxoides (Grimoldi et al. 1999), Paspalum dilatatum (Insauti et al. 2001) or Rorippa sylvestris (Stift et al. 2008). Although initial studies on submergence-induced differential growth focused mostly on species naturally occurring in occasionally flooded habitats, recent experiments revealed that hyponasty in Arabidopsis thaliana (arabidopsis) can be used to unravel mechanisms explaining flooding-induced hyponasty (Peeters et al. 2002; Millenaar et al. 2005; Pierik et al. 2005; Vashisht et al. 2011). Hyponasty in flood-tolerant species is a prerequisite for non-differential...
petiole/leaf blade elongation (Cox et al. 2003). The combined action of hyponasty followed by accelerated linear elongation helps the plant to re-establish contact with air and, in turn, restore successful gas exchange (Voese- nek and Blom 1989) and aerial photosynthesis (Mommer et al. 2005). The significance of hyponasty preceding petiole elongation has been demonstrated with experiments where submerged *R. palustris* petioles were fixed at certain angles. If the angle was set $\angle 40^\circ$ relative to the horizontal plane, rates of underwater elongation were much lower than in control plants, whereas fixing the angle closer to the vertical ($\sim 80^\circ$) permitted petiole elongation rates to increase. In the first instance, faster elongation rates were restored when the $\angle 40^\circ$ fixation angle was released (Cox et al. 2003). The volatile phytohormone ethylene plays a central role in this complex regulatory mechanism of hyponastic response. Its diffusion from submerged tissues is severely reduced when submerged and as a result its endogenous concentrations significantly increase (Jackson 1985; Voese- nek et al. 1993; Banga et al. 1996). This physical entrapment is crucial for both hyponasty and non-differential linear petiole or internode elongation (Voese- nek and Blom 1989; Banga et al. 1997; Kende et al. 1998). Ethylene involvement is indicated by the strong inhibition of petiole angles in submerged *R. palustris* plants by application of the ethylene perception inhibitor 1-methylocyclopropene (1-MCP) (Cox et al. 2004). Moreover, it has been demonstrated that ethylene regulates two crucial events during the first phase of submergence response: rapid acidification of the apoplast (Vreeburg et al. 2005) and up-regulation of expansin transcript levels (Vriezen et al. 2000; Vreeburg et al. 2005). Different stages of submergence-induced hyponasty can be positively regulated by auxin (indole-3-acetic acid; IAA) and gibberellins (GAs) as downstream targets for ethylene, whereas the growth-inhibitory hormone, abscisic acid (ABA), negatively influences the response. Since deblading experiments resulted in a dramatic delay in the hyponastic response to submergence, it has been concluded that the onset of petiole hyponasty depends on auxin transport from the leaf lamina (Cox et al. 2006). Furthermore, the stage when hyponastic growth is fastest coincides with a lateral redistribution of IAA (Cox et al. 2004). Importantly, the stimulating effect of auxin and ethylene on hyponasty is independent of the effect of these hormones on the subsequent non-differential linear petiole elongation. Submergence depresses the endogenous levels of ABA within 2 h of submergence. This decrease is an outcome of an inhibition of ABA biosynthesis and has a stimulatory effect on all stages of submergence-induced hyponasty (initiation, speed and maintenance). In contrast, following the reduction of ABA levels, increased concentrations of GAs serve a promoting function during the speeding-up phase of differential growth (Benschop et al. 2006). Recently, it has been discovered that the increase in expression of *SNORKEL* genes, which belong to the ethylene response factor (ERF) family, is required for submergence-induced internode elongation in deepwater rice (Hattori et al. 2009) and that it might act through the GA signalling pathway. Since the hyponastic response in dicot species is also GA dependent, ERFs could be crucial components of the mechanism in this case also.

**Fig. 1** Ethylene-induced hyponasty in *R. palustris* (A and B) and *A. thaliana* (C and D). (A and C) Plants after 6 h in control conditions and (B and D) after 6 h of ethylene exposure.
Shade

Many plants, particularly angiosperms, display the so-called shade avoidance syndrome (SAS) when growing in dense communities. Shade avoidance syndrome consists of various phenotypic adjustments which affect all stages in a plant’s life cycle, influencing their germination, chloroplast development, extension growth, apical dominance, distribution of assimilates and flowering time (Smith and Whitelam 1997; Smith 2000). Depending on the overall plant morphology, extension growth applies to different organs. It can stimulate elongation of internodes, as in Sorghum bicolor (Finlayson et al. 1998), Urtica dioica, Senecio vulgaris (Morgan and Smith 1979), prairie ecotype of Stellaria longipes (Sasidharan et al. 2008) or Datura ferox (Ballaré et al. 1990), or in the case of the rosette species, such as arabidopsis or R. palustris, causes hyponastic growth and elongation of petioles (Pierik et al. 2005). When the proximity of other plants reduces photosynthetic performance, petiole hyponasty is a successful escape strategy (Hutchings and de Kroon 1994; Ballaré et al. 1995; Schmitt 1997; Pierik et al. 2003, 2004). Experiments on two Potentilla species demonstrated that, despite the lack of homology between petioles and internodes, they show a similar response to shade. This is in accordance with the hypothesis that analogous organs which share ecological function can show similar plasticity in response to environmental changes (Huber 1996). Discovery of the red:far-red (R:FR) ratio as the primary signal triggering SAS prior to actual physical shading (Morgan and Smith 1976; Ballaré et al. 1987, 1990) has generated wide interest in this area and contributed to our current understanding of the molecular sensory mechanism for detecting the threat of shade. Photoreceptors involved in the perception of light changes include a set of phytochromes responding to altered R:FR ratios (Quail et al. 1995; Neff et al. 2000; Smith 2000) together with blue light-induced cryptochromes and phototropins (Christie et al. 1998; Briggs and Huala 1999; Cashmore et al. 1999). Molecular aspects of signal transduction and transcriptional regulation upon shade have been rigorously reviewed by Franklin (2008). Studies on dense canopies of Nicotiana tabacum demonstrated that the perception of ethylene plays a crucial role in competition for light. In canopies, ethylene concentrations are elevated by almost 4-fold compared with the ambient atmosphere and ethylene-insensitive plants display delayed shade avoidance responses in comparison to the wild type (Pierik et al. 2003, 2004). Not surprisingly, auxin and its transport, which play an important role in most of the differential growth processes, are key players in the regulation of growth responses upon shade (Morelli and Ruberti 2000; Keuskamp et al. 2010, 2011; Kozuka et al. 2010). Detailed studies by Tao et al. (2008) have confirmed that activation of the tryptophan-dependent pathway of auxin synthesis is absolutely necessary for SAS. Additionally, the blockage of auxin receptor TIR1 as well as impairment of a transporting protein, PIN3, lessens the auxin gradient, thereby reducing shade avoidance symptoms, including hyponasty (Keuskamp et al. 2010). Auxin acts synergistically with brassinosteroids (BRs) since the inhibition of both hormones almost entirely blocks elongation of the hypocotyl (Keuskamp et al. 2011). Although these experiments were carried out on hypocotyls, it is likely that such contributory function of BRs applies to hyponasty since the exclusive role of auxin in ethylene-induced hyponasty is still under debate (Van Zanten et al. 2009a). Notably, a set of BR-responsive genes is essential for petiole elongation in shade (Kozuka et al. 2010). Gibberellins and GA-mediated DELLA degradation have been demonstrated to contribute to SAS (Djakovic-Petrovic et al. 2007); however, there is evidence that the GA pathway acts in an ethylene- and auxin-independent manner (Pierik et al. 2009). At a cellular level, low R:FR ratios and green shade lead to the apoplastic acidification and increase in the levels of certain cell wall-modifying enzymes—expansins and xylloglucan endotransglucosylases/hydrolases (Sasidharan et al. 2008, 2010).

Studies from the past decade have demonstrated that light perception interacts tightly with temperature signalling and that phytohormones and transcriptional regulators probably serve as nodes in this crosstalk (Franklin 2009; Koini et al. 2009). Common responses to these stresses include clear morphological changes such as hypocotyl elongation (Gray et al. 1998) or early flowering (Balasubramanian et al. 2006). Interestingly, elevated temperatures lead also to hyponastic responses (Koini et al. 2009; Van Zanten et al. 2009b), and ethylene has been shown to regulate heat-induced hyponasty negatively (Van Zanten et al. 2009b). Previous experiments have revealed that leaf inclination is tightly associated with leaf temperature and that elevated angles influence cooling properties (Medina et al. 1978). According to King (1997), vertical leaf orientation in Eucalyptus sp. is highly beneficial when dealing with low temperatures.

As mentioned above, ethylene is one of several key regulators of hyponastic responses to various environmental changes. As shown by Pierik et al. (2005), application of ethylene alone can mimic the response of plants to flooding or shaded conditions in both arabidopsis and R. palustris. Therefore, ethylene-induced
hyponasty is a suitable study system to help identify the regulatory network and developmental switches in differential petiole growth.

**Ethylene and plant development**

A number of observations that illuminating gas leaking from pipes in orchards had a dramatic effect on plants growing in the vicinity (Girardin 1864) led to the discovery of ethylene as a plant hormone. The analysis of active compounds in illuminating gas performed by Neljubow (1901) identified ethylene as a component responsible for its strong morphogenetic effects at high dilution. Subsequently, a number of descriptive reports, such as ethylene’s influence on the development of flowers in carnations (Crocker and Knight 1908) or epinasty and leaf abscission (Doubt 1917), promoted much subsequent interest in ethylene biology.

The mosaic effect of ethylene on plant growth concerns alterations of fundamental processes at all developmental stages. Due to technical challenges, little is known about the role of ethylene during zygotic embryogenesis. The peak of ethylene concentration in *Brassica napus* embryos has been detected at the torpedo stage (Johnson-Flanagan and Spencer 1994) and, as shown by studies on microspore-derived embryos, ethylene is necessary for the lateral expansion of cotyledons (Hays et al. 2000), whereas antagonistic interaction between ethylene and ABA leads to breaking of dormancy (Koornneef et al. 2002; Gniazdowska et al. 2010). At the post-embryonic stage, the best recognized effect of ethylene during skotomorphogenesis is the so-called triple response. It consists of inhibition of hypocotyl and root elongation, exaggeration of the apical hook and hypocotyl thickening (Knight and Crocker 1913; Pratt and Biale 1944), and has been used as an efficient bioassay in identifying ethylene-related mutations (Bleecker et al. 1988; Guzman and Ecker 1990). During formation of the apical hook, ethylene causes differential cell elongation (Lehman et al. 1996; Raz and Ecker 1999) and, as revealed by detailed study on the kinetics of the response, prevents it from opening (Lehman et al. 1996; Gallego-Bartolome et al. 2011). Smalle and Van Der Straeten (1997) showed that ethylene has a stimulatory effect on hypocotyl expansion in light. In below-ground tissues, ethylene stimulates roots to expand radially (Dolan 1997; Smalle and Van Der Straeten 1997), regulates adventitious root formation (Jusaitis 1986; Liu et al. 1990), affects the differentiation pattern of atrichoblasts and trichoblasts (Schneider et al. 1997) and, through crosstalk with auxin, inhibits lateral root formation (Ruzicka et al. 2007; Ivanchenko et al. 2008; Negi et al. 2008; Lewis et al. 2011). Its role in reproductive development includes flowering induction, e.g. in *Ananas sativus* (Burg and Burg 1966), and promoting female sex determination in *Cucumis sativus* and *Cucumis melo* (McMurray and Miller 1968; Boualem et al. 2008; Wang et al. 2010). Other thoroughly studied properties of ethylene concern the final events in plant development such as fruit ripening (Burg and Burg 1962; Barry and Giovannoni 2007), onset of leaf senescence (Zacorias and Reid 1990; Thomas et al. 2003) and leaf abscission (Abeles and Rubinstein 1964). Interestingly, as shown by Summers et al. (1996), the complete absence of ethylene biosynthesis does not cause a disturbed overall development in *Potamogeton pectinatus*. Accordingly, ethylene-insensitive mutant and transgenic genotypes under optimal growth chamber conditions do not display disturbed growth (Tholen et al. 2004).

**Ethylene and organ growth**

**Cell expansion**

Early observations of cell growth in the presence of ethylene provided data about its inhibitory function on various types of tissues (Hayashi and Maclachlan 1984). A number of experiments on arabidopsis roots have shown that ethylene treatment leads to isodiametric cell growth which is dependent on both auxin biosynthesis in the root tip (Stepanova et al. 2005; Swarup et al. 2007) and rootward auxin transport (Ruzicka et al. 2007). Often, ethylene-treated cells do not cease their growth entirely but, instead, start to expand in a radial dimension, e.g. in epicotyl cells of *P. sativum* (Apelbaum and Burg 1971). It is not clear, though, if this effect is a result of cell wall metabolism and matrix composition changes due to ethylene treatment (Eisinger et al. 1983). On the other hand, studies on *Picea abies* show that ethylene can negatively affect the incorporation of wall carbohydrates (Ingemanson et al. 1991). Naturally, this lateral expansion requires a different orientation of cortical cytoskeleton and, therefore, ethylene has also been associated with longitudinal organization of cortical microtubules (CMTs) (Steen and Chadwick 1981; Lang et al. 1982; Roberts et al. 1985; Yuan et al. 1994; Soga et al. 2010).

Although obviously legitimate, this classical concept of ethylene’s inhibitory effect on cell elongation has been complemented with reports of its stimulatory properties (reviewed in Pierik et al. 2006). These include stem elongation in *Callitriche platycarpa* (Musgrave et al. 1972), previously mentioned cell expansion-driven petiole elongation in submerged *R. palustris* plants (Cox et al. 2004), internode elongation in submerged deep-water rice (Kende et al. 1998) or arabidopsis hypocotyl...
elongation in light (Smalle and Van Der Straeten 1997; Le et al. 2005). Moreover, it has been demonstrated that low-nutrient-grown arabidopsis seedlings exhibit transverse (elongation-stimulating) CMT orientation upon treatment with the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (Le et al. 2005). Recently, a study of cell sizes on two sides of ethylene-treated arabidopsis petioles provided evidence that ethylene and ad- and abaxial identity defines whether the orientation of the cytoskeleton is transverse or longitudinal (Polko et al. 2012). The two contrasting ideas on the effect of ethylene on the direction of cell expansion can be species as well as concentration dependent. In some plants, e.g. Triticum aestivum, low ethylene concentrations stimulate growth whereas high concentrations have an inhibitory effect. Almost four decades ago, Konings and Jackson (1979) already highlighted this dual role of ethylene, which was coined the Janus face of ethylene by Pierik et al. (2006) in their review of a biphasic model for growth control by ethylene.

Cell division and endocycle

Apelbaum and Burg (1972) showed that ethylene dramatically reduces cell division frequencies in meristematic tissues of P. sativum and that it is likely due to lower rates of DNA synthesis. A similar decrease was observed in prothallia of a fern, Onoclea sensibilis (Edwards and Miller 1972), which suggests that this inhibitory effect on cell proliferation might be conserved within the plant kingdom. On the other hand, studies on the early petiole ontogeny in Nymphoides peltata revealed that ethylene stimulates cell proliferation in a dose-dependent manner (Ridge and Amarasinghe 1984). More recent analysis of growth responses in the vascular cambium of Populus showed that ethylene can have a positive effect on cell divisions in this meristem, leading to stimulation of xylem growth (Love et al. 2009). As shown by Kazama et al. (2004) in C. sativus, ethylene not only affects cell divisions per se, which results in increased stomata and trichome abundance, but also alters cell polarity and division planes. Another well-known response of cells to ethylene is enhanced ploidy, which results from an increased number of DNA replication rounds without mitosis. This endoreduplication is, in turn, often coupled with increased cell sizes, e.g. in hypocotyls of Cucumis (Gendreau et al. 1999; Dan et al. 2003) or in arabidopsis petal tissue (Roeder et al. 2010). The possibility of ethylene directly affecting the cell cycle has generated a wide interest in unravelling its targets in the cell cycle machinery. A study by Skirycz et al. (2011) demonstrated that ethylene acts on cell cycle progression by reducing the activity of CDKA1, possibly by post-transcriptional regulation. The exact mechanism of this interaction, though, has yet to be elucidated.

Conclusions and forward look

For the last decade, hyponasty has been given considerable attention as part of a general escape mechanism from unfavourable ambient conditions. Despite the broad knowledge on the functionality and hormonal regulation of ethylene-induced hyponasty (reviewed in Van Zanten et al. 2010) and growing insights into the developmental alterations leading to upward petiole movement, there are still many important questions to be answered. Since hyponasty involves asymmetric cell expansion, a process that often coincides with enhanced endoreduplication, one might expect differential regulation of cell cycle-related components. Our current knowledge on the coordination of cell expansion during organogenesis allows the assumption that specific gradients of the growth-regulating factors might play a role in the regulation of hyponasty. Although auxins are major regulators of hyponasty in response to light, their role in ethylene-induced hyponasty might be marginal (Van Zanten et al. 2009a). Another group of growth-stimulating hormones, BRs, could serve as potential players. Experiments have demonstrated that BR perception and signal transduction are crucial for the occurrence of shade avoidance-related traits (Kazuka et al. 2010; Keuskamp et al. 2011) and that, under certain conditions, BR–ethylene crosstalk is crucial for elongation responses in hypocotyls (De Grauwe et al. 2005). Moreover, as shown by Gonzalez-Garcia et al. (2011), the progression in cell cycle in the arabidopsis root meristem is BR dependent, which suggests a hypothetical role for both in the regulation of hyponasty. Integration of multidisciplinary approaches such as plant physiology, developmental biology, biophysics and modelling not only could help in understanding the complex mechanism of hyponasty, but also any other alterations of plant architecture resulting from diverse external stresses.

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All authors wrote the review.

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Conflicts of interest statement

None declared.

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