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Original article

Beech (*Fagus sylvatica* L.) branches show acclimation of xylem anatomy and hydraulic properties to increased light after thinning

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Abstract – Hydraulic acclimation of *Fagus sylvatica* L. was analysed in response to forest thinning. Several months after thinning, leaf and xylem water potential and stomatal conductance of thinned branches were compared to sun-exposed and shade branches. We characterised vulnerability to cavitation for branches taken from these three treatments. We compared effect of thinning on xylem anatomy (mean vessel diameter, vessel density). Thinned branches exhibited higher stomatal conductance and lower leaf water potential. These results were well correlated with vulnerability to cavitation. Thinned branches were less vulnerable than shade branches and mean vessel diameter and vessel density increased in thinned branches. These differences showed a partial hydraulic acclimation to climate changes. We confirmed that vulnerability to cavitation and xylem anatomy in *Fagus sylvatica* acclimate to changing light conditions, and we concluded that hydraulic architecture acclimates sufficiently fast after environmental changes to protect xylem from dysfunction while maintaining open stomata.

***Fagus sylvatica* L. / thinning / xylem embolism / xylem anatomy / light acclimation**

Résumé – Acclimatation anatomique et hydraulique du xylème après une éclaircie chez le hêtre (*Fagus sylvatica* L.). Nous avons analysé l'acclimatation hydraulique de hêtre *Fagus sylvatica* L. suite à une éclaircie forestière. Quelques mois après l'éclaircie, nous avons mesuré le potentiel hydrique des feuilles et du xylème et la conductance stomatique de branches « éclaircies » et comparé ces résultats à des branches de lumière et d'ombre. Nous avons déterminé la vulnérabilité à la cavitation de ces branches et caractérisé leurs différences morphologiques et anatomiques. Les branches « éclaircies » ont présenté des conductances stomatiques plus fortes et des potentiels hydriques foliaires plus négatifs que les autres branches. Ces branches présentaient une vulnérabilité à la cavitation plus faible que les branches d'ombre et des vaisseaux plus gros et plus nombreux. Ces résultats montrent une acclimatation hydraulique partielle mais suffisamment rapide pour protéger le xylème de dysfonctionnement et confirment que la vulnérabilité à la cavitation chez le hêtre dépend fortement des conditions lumineuses.

***Fagus sylvatica* L. / éclaircie / embolie / anatomie / acclimatation**

1. INTRODUCTION

Many species need canopy gaps to have enough light to achieve growth and reproduction [1]. The formation of canopy gaps is important in the dynamics of old growth beech forests [22]. However, gap formation represents a potentially stressful event to understorey saplings and shade branches [7, 21, 27]. Light intensity in the understorey is often less than 5% of that on the canopy [31] and can increase very strongly when a gap is formed or after thinning [2]. Solar radiation, temperature and VPD (vapour deficit pressure) are considerably higher in gaps than in the understorey [8, 10, 18, 23]. The greater input of energy can cause increases in leaf transpiration and a larger water potential gradient [21]. Therefore, xylem embolism may increase, reducing water transfer to the leaves, and limiting branch growth and productivity. Branches exposed to canopy gaps may increase transpiration without a rise in the water potential gradient by increasing hydraulic conductivity. The hydraulic conductivity of a stem increases with the fourth power of the radius of the conducting elements as described by the Hagen-Poiseuille law [32]. Changes in xylem anatomy, with increases in vessel diameter, are expected to have a strong impact on hydraulic conductivity; xylem acclimation is

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needed to avoid xylem dysfunction and branch death. Within the highly competitive environment of a recent thinning, the capacity to acclimate to a higher level of irradiance is beneficial. Acclimation in this case is a process by which physiological and morphological changes increase the ability for water transfer and growth in a new environmental regime [19].

In a temperate forest, thinnings are conducted during winter. When the growing season starts, branches are subjected to a new microclimate. We were interested in how branches acclimate soon after these changes (the first year after thinning). Beech presents strong differences in branch morphology depending on light regime [16]. In the upper parts of the crown, branches are characterised by long internodes in contrast to shade branches where shoots are very short with very short internodes. Long and short beech shoots show large differences in their hydraulic structure with higher hydraulic resistances in the short shoots that modify water relations at the branch level [16, 20]. Thus, for the same transpiration level, short shoots have a larger water potential gradient. Changes in light regime (with temperature and VPD changing) should interact with branch morphology [10, 11, 20, 26] and should modify water relations in trees [16]. After stand opening, beech trees are subjected to drastic changes of light condition that require acclimation to sustain the higher evaporative demand [23]. We studied the effects of changed light conditions due to thinning on branch morphology, xylem anatomy and hydraulic properties that control water transfer in trees to learn how beech acclimates to thinning in the year after treatment.

2. MATERIALS AND METHODS

2.1. Plant Material

Five dominant 30-year-old *Fagus sylvatica* L. trees were chosen in a recently thinned stand in the State Forest of Hesse, in the eastern part of France (48° 40' N, 7° 05' E, elevation: 300 m). Two scaffolding towers were installed in the stand to access the crowns. During winter 1998–1999, the stand was thinned; almost 25% of the basal area was removed. Trees were growing in a closed stand. There were three types of branches: (i) upper branches exposed to full sunlight (= sun-exposed branches), (ii) lower branches were heavily shaded in 1998 by upper crown branches and surrounding trees (= shade branches) and (iii) branches exposed directly to full sun after thinning in 1999 (= thinned branches). More details about the stand structure are published elsewhere [7, 12, 14–16] and microclimate is characterised in *table I* for each treatment. Branch morphology, xylem anatomy and water relations were measured on the five trees accessible from towers. In addition, 11 surrounding trees were measured for xylem hydraulic properties and branch morphology.

2.2. Branch morphology

We analysed branch morphology by measuring the length of the shoots from the three types of branches on the 16 study trees (two to three branches per branch type per tree). We calculated the percentage of long and short lateral branches on the three kinds of branches and determined whether the terminal shoot was a long or short shoot [20, 26]. To avoid differences due to the age of the branch, we analysed branches less than six years old. We classified long shoots as shoots with internodes longer than 5 mm. The branch apices and all the lateral shoots were counted and measured to be classified as long or short shoots.

Table I. Mean values of vapour deficit pressure (VPD) and photosyntheticaly active radiation (PAR) during the experiment near the sun-exposed, thinned and shade branches (n = 30 measures × 5 sunny days).

	VPD, hPa	PAR, $\mu mol\ s^{-1}\ m^{-2}$
Sun branches	2.130 ± 0.312	1850 ± 50
Thinned branches	1.790 ± 0.155	1550 ± 150
Shade branches	1.393 ± 0.337	255 ± 55

2.3. Xylem anatomy

Vessel diameters and densities were measured in one-year-old twigs of the three branch types from five trees (40 twigs per branch type per tree). Sun-exposed and shade branches were harvested in November 1998 just before thinning and thinned branches were harvested in July 1999. Thin cross sections were made by hand with a new razor blade and observed with a light microscope (magnification: 200×). On each cross section we delimited four sectors bounded by rays and measured all the vessels in the early wood with a eyepiece micrometer (resolution one µm). For each vessel we measured the minimum and maximum lumen diameters and computed the mean. Vessel densities were measured on 10 twigs per branch type and tree by counting all the vessels in the early wood delimited by two rays.

In July 1999, we collected 15 samples from shade branches from the five trees to check possible modification in the xylem anatomy of branches remaining in the shade from 1998 and 1999. The measurements described above were conducted on these branches.

2.4. Water potential and stomatal conductance

Leaf water potentials (Ψ_{leaf}) were assessed with a portable pressure chamber (PMS, Corvalis, Oregon, USA) during summer 1999. Access to the crown was made from the scaffolding. Predawn leaf water potential was measured at 3:00 (solar time) i.e. one hour before sunrise. Measurements were made every 90 min from 7:30 (i.e. after dew evaporation) to 19:00 (sunset). Xylem water potential (Ψ_{xylem}) was estimated by measuring the water potential of leaves that had been enclosed in an aluminium foil early in the morning [7, 28]. Stomatal conductance (g_s) was measured with a portable porometer (Li-Cor 1600, Lincoln, Nebraska, USA). Six leaves were measured for g_s and three for Ψ measurements for each of five trees.

2.5. Vulnerability curves

Vulnerability curves (VCs) are plots of percent loss of conductivity (PLC) versus Ψ_{xylem}. They were constructed by dehydrating excised branches in the laboratory and measuring loss of hydraulic conductance caused by air blockages in xylem conduits of short (2–3 cm) shoot internodes [24]. We established VCs for

current-year twigs during July and August 1998 for sun-exposed and shade branches (11 trees, three branches per tree) and July 1999 for thinned branches (10 branches, three branches per tree) [16]. Branches were harvested with a 6-meter-long pruning pole in the morning. We enclosed them in a black airtight plastic bag to reduce water loss through transpiration and brought them rapidly to the laboratory for hydraulic analysis. In the laboratory, the samples were dehydrated by pressurisation [3–5] for 30 to 45 min until sap exudation ceased, then enclosed for at least one hour in a black airtight plastic bag to stop transpiration and remove water potential gradients between leaves and xylem tissues. Ψ_{xylem} was assumed to be the negative of the air pressurisation value. Ψ_{xylem} was then returned to zero by immersing the branches 30 min in tap water before hydraulic analysis. The initial hydraulic conductivity $K_{init.}$ (mmol m s^{-1} MPa^{-1}) was measured by forcing distilled water with 6 kPa pressure difference through each sample which comprised 15 internodes. We measured the resulting flow rate (mmol s^{-1}) with an analytical balance connected to a computer. The dehydration by pressurisation and measurement of conductivity was conducted at increasing pressures until conductivity became negligible. Air embolism was then removed by forcing water through the segment at 100 kPa until the conductivity no longer increased. This usually required two cycles of flushing. The final conductivity was defined as the maximum ($K_{max.}$). PLC was then calculated as: PLC = 100 (1 – $K_{init.}$ / $K_{max.}$).

Vulnerability curves were determined for five shade branches in summer 1999 to learn whether there changes since thinning.

2.6. LSC measurement

K_{max} values are an indicator of xylem efficiency. Along with xylem anatomy it provides a means to evaluate efficiency for water transport. The efficiency of branch xylem in conducting water was estimated by measuring the leaf specific conductivity (LSC, mmol s^{-1} MPa^{-1} m^{-1}). This parameter links water potential gradient across a branch ($d\Psi$, MPa m^{-1}) to water flow (F, mmol s^{-1}) through the branch: $d\Psi = F / (LSC \times \text{leaf area})$.

LSC was calculated as the ratio between $K_{max.}$ measured during VC establishment and the leaf area supported by the sample. LSC was measured for the three branch types on 11 trees (8–9 twigs per tree).

2.7. Native PLC in the trees at the end of summer

In late August 1999, we measured PLC on 9 current year branches taken from shade, sun-exposed and thinned positions in the study trees. We determined whether native embolism was higher in thinned branches than in the sun-exposed and shade branches.

To avoid artificial embolism induced by cutting the branch and transporting it to the laboratory, we cut 2 meter-long branches, longer than the longest vessel measured in the beech branches (63 cm, [33]), and enclosed them in a black airtight plastic bag which protected them from heat and dehydration. Branches were recut under water in the lab and PLC measurements were made rapidly as above.

2.8. Statistical analysis

The significance of treatment effects was determined by analysis of variance (ANOVA). Differences between means were considered significant if $P < 0.01$ (Fisher's exact test). The tree was the experimental unit and sample size was 5 for xylem anatomy and water relations, 11 for hydraulic properties and 16 for branch morphology. The experimental layout was a completely randomised design.

3. RESULTS

3.1. Branch morphology

Morphology of branches grown at different light intensities showed large differences (*table II*). The shortest internode measured for a long shoot was 11 mm and the longest internode for a short shoot was 2.5 mm. Sun-exposed branch apices always developed long shoots while shade branches produced 45% short apical shoots with very small internodes. The thinned branches produced a smaller percentage of short shoots (35%). These branches had longer apical shoots than shade branches and 22% of the short apical shoots were transformed into long apical shoots (compared with the previous years growth units). The result was increased elongation of the thinned branches.

The morphology of the lateral axis depended very much on light regime. Sun-exposed branches exhibited very few short shoots as compared to shade ones (15% versus 60%, *table II*). Thinning induced changes in the lateral twig morphology with a strong tendency to twig elongation, 33% of the short shoots developed into long shoots. Thinning induced very quickly strong changes in the branch morphology with a high tendency in twig elongation.

3.2. Xylem anatomy

Sun-exposed branches had larger-diameter vessel than shade branches (*table III*). We found that long shoots had larger-diameter vessels than short shoots sun-exposed and

Table II. Percent long apical shoot and lateral shoots on sun-exposed, thinned and shade branches (n = 16, letters indicate significant differences, $P < 0.01$).

	Percent long apical shoot	Percent long lateral shoots
Sun branches	100% ± 0% (a)	85% ± 3% (a')
Thinned branches	65% ± 5% (b)	60% ± 5% (b')
Shade branches	55% ± 2% (c)	40% ± 6% (c')

Table III. Thinning impact on xylem anatomy: vessel diameter and vessel density for long and short shoots from sun-exposed, shade and thinned branches. Measurements were made on the current year shoots (n = 5, letters indicate significant differences, $P < 0.01$).

	Mean vessel diameter (μm)	Vessel density (vessel mm^{-2})
Long sun-exposed	30.1 ± 4.1 (a)	1350 ± 35 (a)
Long thinned	27.2 ± 5.3 (b)	1009 ± 30 (b)
Long shade	24.0 ± 6.6 (c)	946 ± 36 (c)
Short sun-exposed	26.2 ± 4.8 (b)	730 ± 34 (d)
Short thinned	26.5 ± 5.2 (b)	748 ± 37 (d)
Short shade	21.7 ± 6.0 (d)	698 ± 38 (d)

shade branches. After thinning, vessels of shade branches exposed to full sunlight greatly increased in diameter. Short and long shoots had vessel diameters similar to sun-exposed vessels. Vessels from short shoots showed the greatest increase in diameter.

These changes in conduit diameter were correlated with an increase of vessel density. Long thinned shoots increased in vessel density. We could not detect a significant relation between vessel density and irradiance in the short shoots.

No anatomical differences were found between 1998 and 1999 shade [7].

3.3. Stomatal conductance and leaf water potential

Results represent mean values of three sunny days. From sunrise to 15:30, thinned branches had higher g_s than sun-exposed and shade branches (*figure 1*). The g_s values for sun-exposed and shade branches were not different during the morning and the beginning of the afternoon. Stomatal conductance remained stable during the first part of the afternoon until 15:30 when crown shade induced stomatal closure of the shade and thinned leaves. Sun-exposed branches kept higher g_s values until sunset.

Leaf water potential dropped after sunrise to reach minimal values at midday. Sun-exposed and thinned branches were not different until 15:30 when shade occurred, then Ψ of thinned branches increased slowly to reach "shade" Ψ values in the evening. Shade branches had high Ψ values over the entire day.

3.4. Xylem water potential

Xylem water potential values were higher than leaf water potential (*table IV*). This means there are strong hydraulic resistances limiting water transfer from xylem vessels to evaporative zones. The xylem water potential of thinned branches was intermediate to the values for sun-exposed and shade branches and very close to the shade (–0.8 vs. –0.7 MPa). In contrast, thinned branches had leaf water potentials close to sun-exposed branches (–2.7 vs. –2.8 MPa). Thus, thinned branches had the greatest water potential drop (–1.9 MPa). There were no significant differences in water potential drop between leaves and xylem for sun-exposed and shade branches (–1.3 MPa).

3.5. Vulnerability curves

Thinned branches showed vulnerability intermediate between sun-exposed and shade branches (*figure 2*). One year after thinning, the lower parts of the crown exposed to full light showed a decrease in vulnerability to cavitation. We found differences in the Ψ inducing 50% embolism (Ψ_{50}): –2.25 MPa,

Table IV. Differences between xylem and leaf water potential for sun-exposed, shade and thinned beech branches during a sunny day (n = 5, letters indicate significant differences, $P < 0.01$).

	Sun-exposed branches	Thinned branches	Shade branches
Ψ xylem – Ψleaf (MPa)	1.30 ± 0.25 (a)	1.90 ± 0.25 (b)	1.30 ± 0.30 (a)

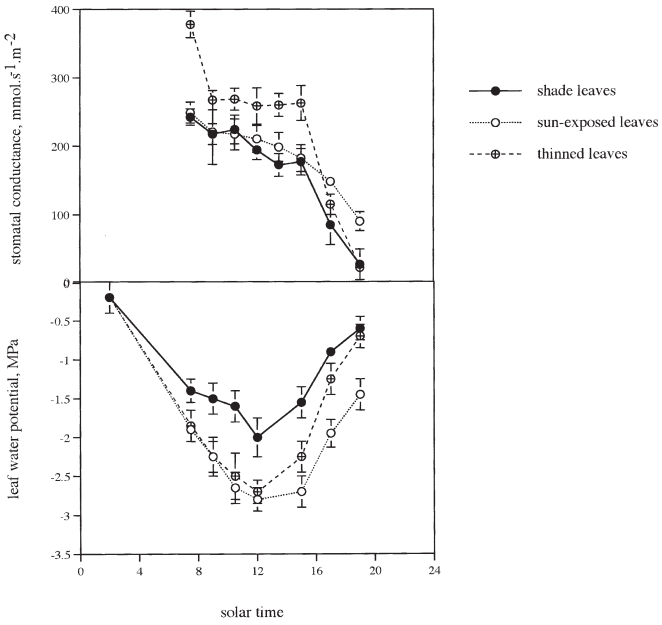

Figure 1. Mean stomatal conductance and leaf water potential values for sun-exposed, shade and thinned branches during sunny days. Error bars indicate standard error (n = 5).

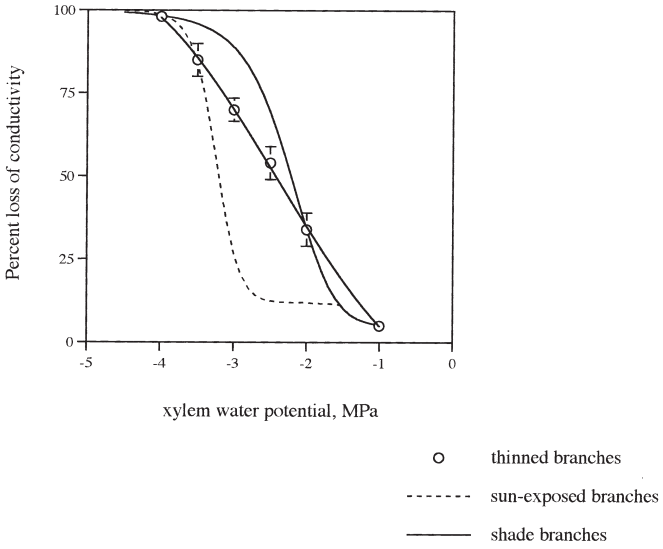

Figure 2. Vulnerability curve of *Fagus sylvatica* twigs from current year shoots of thinned, shaded and sun-exposed branches. Error bars represent standard error (n = 11).

Table V. Native embolism in late August 1999 (native PLC) and mean values of leaf specific hydraulic conductivity (LSC) for one-year-old beech shoots cut from sun-exposed, shade or thinned branches (n = 16, letters indicate significant differences, $P < 0.01$).

	Sun-exposed branches	Thinned branches	Shade branches
Native PLC (%)	9.00 ± 0.50 (b)	18.50 ± 2.50(a)	5.50 ± 2.00 (c)
LSC (mmol s^{-1} m^{-1} MPa^{-1})	12.36 ± 1.52 (a)	9.56 ± 1.07 (b)	5.43 ± 2.46 (c)

–3.1 MPa and –2.5 MPa for shade, sun-exposed and thinned branches respectively. Differences in PLC between shade and thinned branches were greatest for low Ψ values (i.e. Ψ values below –2 MPa).

We found differences in native PLC (see *table V*), thinned branches had the greatest PLC (18% of conductivity loss).

3.6. Hydraulic conductivity

The anatomical modifications induced changes in hydraulic conductivity. Thinned branches increased vessel diameter, which induced a rise in leaf specific conductivity (see *table V*). Values increased from 5.43 in shade branches to 9.56 mmol s^{-1} m MPa^{-1} after thinning. These changes were not correlated with changes in leaf area.

4. DISCUSSION

We observed changes in xylem anatomy and water relations of beech soon after thinning. Our results showed that thinned branches were different from shade branches both from a physiological and anatomical point of view. Thinned branches were different from sun-exposed branches, but they were not totally acclimated to the new light level. Leaf water potential of thinned branches reached values close to sun-exposed branches (*table II*). Light intensity increased and higher transpiration induced a strong decrease in leaf water potential. To estimate water transfer efficiency between xylem and evaporative zones, we measured the water potential gradient between leaves and xylem. For the three kinds of branches water potential in the leaf was 1.3–1.9 MPa lower than in the xylem (*table IV*). This result occurred because the leaf is a zone with high hydraulic resistances that limit water transfer. Indeed, in a branch most of the hydraulic resistance to the sap pathway is extra-vascular and located in the leaf blades [6, 7, 29, 30] and petioles presented a strong constriction to water flow [16]. This hydraulic characteristic limits cavitation events to peripheral parts of the trees during water stress if the peripheral parts are vulnerable. When tensions increase during drought, water potential drops to lower values in the leaf blades and petioles than in the stem. Petioles may embolise while water potential is still not critical in the shoots. The leaves dry and abcise strongly limiting transpiration and water potential stops dropping in the branch and in the trunk [32]. The water potential difference between xylem and leaves was equal in shade and sun-exposed branches (1.3 MPa). For thinned branches the difference was higher (1.9 MPa), indicating greater limitation to water transfer from xylem to the (see *table I*). Hydraulic acclimation was not total, however higher g_s values in thinned branches showed that leaves were able to support high tensions (Ψ_{min} < 2.9 MPa) and to conserve high g_s. Lemoine et al. [16] showed in beech that stomatal closure occurs just before Ψ_{xylem} drops to the Ψ inducing cavitation. Leaves acclimate rapidly to the new growth conditions after thinning whereas xylem needed more time. These differences between leaf and xylem acclimation could explain why native PLC in thinned branches is higher than the other ones (18%, *table V*). To estimate xylem acclimation state, we measured vessel diameter and density. Our results showed that vessel diameter and density increased after thinning both for long and short shoots. Vessel diameter increases had to have a strong impact on hydraulic resistances (Hagen-Poiseuille law). We observed for thinned branches an increased LSC (see *table V*), but values did not reach those of sun-exposed branches. This increase in xylem conductivity limited the water potential gradient between xylem and leaves but not totally as describe above (*table IV*).

Figure 2 shows that thinned branches were less vulnerable to cavitation than shade branches but more than sun-exposed ones. Our results confirmed that vulnerability to cavitation is correlated with light intensity. Cochard et al. [7] found that for adult beech trees and potted saplings the higher the light intensity the lower was the vulnerability to cavitation. Thus, growth and microclimatic conditions strongly influence hydraulic characteristics and xylem safety. In beech, shade branches with smaller vessel diameter (see *table III*) had greater vulnerability to cavitation (*figure 2*). In beech, and in these experimental conditions, vulnerability to cavitation seemed to be correlated inversely with vessel diameter. Larger diameter vessels had lower xylem vulnerability to cavitation. However, it has been demonstrated that xylem vulnerability is not directly correlated with conduit diameter but dependent on pit pore diameter [3, 4, 13, 17]. Wider vessels had a higher probability to have big pit pores and so be more vulnerable to cavitation. Our results confirm those of Cochard et al. [7], suggesting that vulnerability depends on climatic conditions during growth. Vapour pressure deficit, temperature, irradiance during vessel differentiation may play an important part in pit pore formation. Sun-exposed branches are subjected to high xylem tensions over much of the day, so pit pore may acclimate to these conditions. Whereas a shade branch develops in a less stressful environment (for water demand, temperature, etc.) pit pore differentiation will acclimate to this growth condition and could be larger, and less resistant to water tensions (Jurin's law, [32]). Branches integrate climatic parameters during growth, and develop structure suitable to the environment. Hydraulic modifications observed for beech in this study may have

important ecological implication for branch growth in canopy gaps. The increase in hydraulic conductivity and in xylem safety (decrease in vulnerability to cavitation) for beech in gaps may accelerate growth rate (*table II*) by reducing hydraulic limitation to carbon assimilation [17]. These benefits may contribute to the greater success of branches (or seedlings) when a gap occurs.

Plants can respond to their environments through developmental plasticity in many ways [9, 25]. Studies of anatomical plasticity shed light on the subtle ways that plants can adjust their phenotypes to maintain function in contrasting conditions. Plant architecture can also vary in response to the environment. In herbaceous plants, shading can alter the plant architecture as a result of effects on cell division and differentiation as well as organ size and structure [25]. Studies of architectural plasticity provide useful insight into the specific developmental components of plastic responses. Plasticity might also contribute to the ability of a species to withstand sudden environmental changes, such as those caused by human disturbance, because such changes generally occur too rapidly for an evolutionary response and can create conditions not previously experienced during the organism's life history.

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