

REVIEW PAPERS

Growth Vigor in Wych Elm (*Ulmus glabra* Huds.)

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Abstract

The objective of the review is to identify morphogenetic phenomena related to growth vigor in Wych elm (*Ulmus glabra* Huds.). It may provide guidance for the improved initial selection of the plants and planting sites, as well as strict adherence to correct planting techniques – the primary considerations in preventing dieback condition in Wych elm. An approach and framework to the research of growth vigor in Wych elm are presented relating to the concepts of apical dominance, branching architecture, branch shedding, dormancy, etc., as reported in the scientific literature on temperate and boreal woody angiosperms. Clear, healthy bark and perfect natural pruning seems to be the background for the presence of growth vigor in Wych elm. Growth vigor, i.e. resistance to biotic and abiotic stress and the ability to repair and recover from damage, is a phenomenon; hypothetically, all the factors, phenological and architectural, contributing to this phenomenon, comply with the axiom of uniform stress. Finally, it must be checked in the future research of Wych elm, whether or not the adaptive stress is a consequence of highly determinate growth pattern.

Key words: apical dominance, branch shedding, branching architecture, dormancy, growth pattern, growth vigor, Wych elm.

Introduction

Trees are limited by their adaptive strategies to certain “allowable” combinations of attributes (Huxley and Wood 1984). In the checklist of multipurpose tree attributes (in relation to possible production and service functions) provided by Carlowitz (1986) the attribute of vigor is described as a major need irrespective of purpose. Study objective was to conduct and summarize a literature overview on trait relationships from the perspective of growth vigor that may provide guidance for the improved initial selection of trees. Proper initial selection of trees and planting sites, as well as strict adherence to correct planting techniques, are primary considerations in preventing dieback condition. Extensive dieback and death can occur rapidly in the case of Dutch elm disease, wilt infections and others. The overall objective of the suggested research is to identify relationships, and to develop a hypothesis on the basic “mechanisms” between tree characters on the one hand, and the occurrence of morphogenetic phenomena related to growth vigor in Wych elm on the other hand. The material used in this review comprises articles extracted from the literature as well as web-reports and other free web-records focused on the woody angiosperms of temperate and boreal zones and related to the various aspects of growth

vigor in Wych elm. Web-site addresses are listed in the “References” section. The literature overview is presented referring to the concepts of growth pattern, growth habit and growth rhythm.

Wych elm

Wych elm (*Ulmus glabra* Huds. = *U. montana* With. = *U. scabra* Mill.) is a tree (Elwes and Henry 1913), which sometimes attains 40 m in height and 6 m or more in girth. Typically it has a spreading, broadly rounded or ovate crown supported by a short bole. The bark is grey and smooth and becomes furrowed with age (Hempel and Wilhelm 1889, Sherman-Broyles 2007). The branches spread to pendulous, glabrous, branchlets that lack corky wings. Twigs are ash-grey to red-brown, villous when young. The tree is notable for its very tough, supple young shoots. Buds are conical, obtuse, with reddish brown to dark brown scales, which are ciliate in margin and glabrous to densely pubescent on the surface with yellowish brown hair. The leaves are readily distinguishable from the other species by their short stout densely villous petioles, exceeding 2-7 mm in length; equally rough on the upper surface, though rather downy beneath; the leaf blade is elliptic to obovate, (4-)7-14(-16) × (3-) 4.5-8(-10) cm, with the base being strongly oblique with

the lowermost lobe strongly overlapping, covering the petiole. The leaf margins are doubly serrate, apex long-acuminate to cuspidate, sometimes with three acuminate lobes at a broad apex. The leaves have fifteen to eighteen pairs of lateral nerves, which are often forked. The upper surface of the leaves are strigose to scabrous with scattered short hair while the lower surface have a soft white pubescence, dense on the midrib and lateral nerves, forming axil-tufts at their junctions, and scattered on the surface between the nerves. In *Ulmus scabra* the short shoots have mostly three to five leaves, with the largest one at the top of the shoot (Jentys-Szaferowa 1970). One of the two stipules is intrapetiolar (Stevens 2006).

Wych elm has a more northerly distribution than the other European elms, occurring as far north as latitude 67°N at Beiarn in Norway. The common name Wych comes from Anglo Saxon meaning, "with pliant branches" or from Gaelic meaning "drooping". The name *glabra* means smooth, a probable reference to the fact that the bark of this tree is smoother than that of *Ulmus minor* Mill. Wych elm shows little variation in the wild state (Elwes and Henry 1913). Interesting taxonomic variants of *U. glabra* with a corky rhytidom were described in Romania (Borlea 1995) and a distinctive form with long leaf stalks occurs in northern Spain (Richens 1983). The following geographical form has been described by Elwes and Henry (1913) - *U. montana*, var. *laciniata* Maximowicz. It has young glabrous branchlets or with scattered hair. Leaves that occur at the end of the branchlets, are large, 15 to 17.5 cm long and 7.5 to 10 cm wide; usually with three, occasionally five, large cuspidate-acuminate lobes; their upper surface is scabrous, with minute tubercles, each of which bears a short bristle; the lower surface is covered with a dense soft pubescence. Var. *laciniata* is a common form of *U. montana* in eastern Asia. Trees attain 30 m in height in the broad-leaved forests of central Yezo (Japan). Both normal and tricuspidate leaves occur occasionally on the same individual tree. In eastern Asia the peculiar tricuspidate leaves occur normally on adult trees; and young trees raised in the Arnold Arboretum from Japanese seed preserve the remarkable character of the foliage (Elwes and Henry 1913).

Uotila (1997), Myking and Yakovlev (2006) divide the species into two subspecies: *U. glabra* subsp. *glabra* (in the south of the species' range) has leaves that are relatively broad, short tapering, with acute lobes present, trees often have a short, forked trunk and a low, broad crown; *U. glabra* subsp. *montana* (Stokes) Lindqvist. (in the north of the species' range) has leaves that are relatively long, long tapering, without acute lobes, the upper surface of which are strigose (Sherman-Broyles 2007), trees commonly have a

long single trunk and a tall, narrow crown. However, there is much overlap between populations with these characteristics and the distinction may be due to environmental influence, rather than genetic variation; the subspecies are not accepted by Flora Europaea.

Growth pattern

All meristems are derived from apical meristems, so all of the tissues within the plant organs (*i.e.* leaves, stems, and roots) trace their origin back to the apical meristems. Apical meristems are the completely undifferentiated (indeterminate) meristems in a plant. Morphological organization of apical meristems of a shoot (from the tip downwards) after Sachs (1965): apical region, where differentiation/organogenesis occurs, and sub-apical region, where elongation occurs. Apical meristems may differentiate into three kinds of primary meristem: protoderm, procambium (which also produces the vascular cambium, a secondary meristem) and ground meristem (which also produces the cork cambium, another secondary meristem). Four processes have been considered in topology research (de Reffye 1981a, b, c) performed on coffee trees by introducing stochastic modelling of meristem activity: (1) primary growth, *i.e.*, the dynamics of metamers emergence; (2) branching, *i.e.*, the probability of a given axillary meristem to elongate into a shoot; (3) flowering, *i.e.*, the probability of a given terminal or axillary meristem to develop into a flower; and (4) the probability of meristem mortality. Primary growth initiated by apical meristems near tips of shoots (by buds) and roots (by meristematic points) results in the elongation of a tree body. Additional units of tree phenotypes – metamers – are normally 'added on' by the process of indeterminate growth from the shoot apical meristem. Metamers are distinct units that contain nodes (meristematic regions) and single internodes with an associated leaf and lateral bud. The meristem emergence rate is an important aspect for quantifying plant structure and development. Genetically programmed changes among successive metamers can include such traits as shoot orientation, phyllotaxy, leaf size, shape, anatomy and biochemistry, internode length and width, the fates of lateral meristems, and the capacity to flower (Goebel 1900, Arber 1919, Allsopp 1965, 1967). These changes occur as a normal expression of whole-plant ontogeny (Ashby 1948, Jones 1999). There can also be a trade-off between different repeating components of plant structure (modules), such as flowers, leaves, and internodes, or groupings of these components, such as metamers or shoot units and branches (Harper and Bell 1979, Waller and Steingraeber 1985, Porter 1989, Bell 1991). For

example, Richens (Jeffers 1999) suggested that the leaves on long shoots show far less sharp differentiation (in leaf length and breadth, petiole length, leaf base asymmetry, teeth number, teeth breadth, length and depth) between different kinds of elm (*Ulmus* L.) than those on short shoots. Leaves from proleptic shoots of elms, produced after the main emergence of leaves in spring, are also less sharply differentiated.

In this review growth vigor refers to the resistance to biotic and abiotic stress and the ability to repair and recover from damage. A tree is a self-optimising mechanical structure, a generating system which reacts to mechanical and physiological stresses by growing more vigorously to re-enforce weak areas, while depriving less stressed parts. The same mechanism enables the branches to be connected to the stem without notch stresses in the transitional zone (Mattheck 1998). This precept is described as the axiom of uniform stress. The highest notch stresses apply at the margin of the fresh branch hole (Mattheck 1998), and consequently this is where the greatest deviation from the optimum state of uniform stress occurs. Hence an implied condition of growth vigor in Wych elm is rapid, even growth.

Tree crown is in a state of dynamic equilibrium: the addition of new branches and internodes at the apices is compensated by the loss of oldest branches further down (Prusinkiewicz *et al.* 1997). Normal shedding at the branch base occurs after death of branch symplast. The decay-causing fungi usually move down towards the branch protection zone within the branch collar. The branch is not really tied into the trunk but is held by a series of trunk collars. As a branch begins to die, within the base of the branch, a protection zone that contains antimicrobial substances begins to form. Decayed wood at the base of branches facilitates shedding. The branch fractures on the outer side of the protection zone, and falls or sheds out of the socket. The tree closes the wound, and smoothes out any unevenness remaining on the surface. Although it seems that only the trunk is growing higher, the crown is continually changing: new internodes and branches replace shed branches.

In the course of shedding of younger branches, hardwoods form in the branch basis a protection zone of tyloses and inclusions (Mayer-Wegelin 1929, Trendelenburg and Mayer-Wegelin 1955). The formation of such protection zone seems similar to heartwood formation and requires vital parenchyma cells; in older and larger branches the protection zone is incomplete and limited to the sapwood (von Aufsess 1975, 1984). For this reason, larger branches may have been found more susceptible to rot (in *Fagus sylvatica* L.: Mayer-Wegelin 1929, Erteld and Achterberg 1954). Further-

more, larger branches are exposed for a longer time to exterior influences, as the duration between branch necrosis and occlusion approximately increases with branch diameter (in *Fagus sylvatica* L.: Volkert 1953). If fungi gain entry, the large stub will become a rotten knot and may even channel rot into the heartwood of the tree. If fungi do not infect the branch stub, the dead knot becomes very hard because of drying, but may become infected by stain causing bacteria and cause stain zones to develop within the tree stem rather than rot columns. Many dead knots in the hard hardwood species react this way. Similar to larger branches, more inclined branches are reported to be more susceptible to rot in *Fagus sylvatica* L. (Mayer-Wegelin 1929, Erteld and Achterberg 1954, Wernsdörfer *et al.* 2005).

A limb is a branch or subdivision of the stem or an outgrowth from the stem (Pickens and Orr 2006). It may have been a primary branch from the pith of the main stem or have entered later from a latent or dormant bud. In standing trees, limbs and other knot indicators are the largest group of log grade defects. Limb failure has been reported on tree species of 19 genera, including *Ulmus*, *Pyrus*, *Quercus*, *etc.* (Rushforth 1979, Harris 1983). Often, limbs break off in the lower and middle crown. Most commonly, breakage occurs 1 to 4 m from the branch attachment on long limbs that extend to or beyond the tree canopy. Fractures usually occur where the branch bends from an upright position to the horizontal position (Keslick and Keslick 2004). Breaks are short and at right angles to the axis of the branch. Most of the summer limb failures are reported as occurring on long horizontal limbs - large symplastless branches that are in a horizontal position. Seemingly healthy limbs up to a meter in diameter occasionally break out of mature trees during calm weather following a heavy summer rain which terminates a period of increasing soil dryness (England; Rushforth 1979).

In forestry it is good practice and important that the dead branch/knot dimensions and height, diameter at breast height (hd-ratio), relative height of the crown base are controlled (to a certain extent) by silvicultural treatment: for any given site conditions, natural pruning and the crown base height at a given stage of tree growth will depend on how the concurrence by neighbouring trees is managed by tending and thinning (Wernsdörfer 2005). The related live crown size controls diameter growth, and thus the height-diameter ratio and the duration of knot occlusion/knot depth. In this respect, for example, beech trees growing with a very wide spacing are reported to contain relatively small red hearts up to target diameters (Klädtker 2002, Seeling and Becker 2002).

Growth habit

Plant shape is defined by its branching architecture (Ustin *et al.* 1991), which is a major aspect of the architectural approach to the study of trees (Guédon *et al.* 2001). The architectural analysis is based on three major architectural concepts: the architectural model, the architectural unit and reiteration (Barthélémy *et al.* 1991). The architectural model of a tree is the growth pattern that determines its successive architectural phases (Hallé and Oldeman 1970) and developmental sequence of branching (Bell 1991). According to Hallé and Oldeman (1970), who described 24 different models for tropical trees, the architectural model is an inherent growth strategy that defines both the manner in which the form of the plant is expressed and the resulting architecture. The identification of the architectural model is based on four major groups of simple morphological features: type of growth, branching pattern, morphological differentiation of axes and the position of the sex organs (Hallé and Oldeman 1970, Hallé *et al.* 1978).

The architectural unit of a species represents its fundamental architectural and functional structural component. It is composed of all categories of axes (Barthélémy *et al.* 1991). Axis polymorphism represents a true morphological differentiation related to meristem expression and activity (Hallé and Oldeman 1970). For any tree species, there are a finite number of axis categories, the nature and relative position of which define the architectural unit (Bell 1991). The architecture of a plant can be seen as a hierarchical branched system in which the axes can be grouped into categories according to their morphological, anatomical or functional distinctive features (Barthélémy and Caraglio 2007). Depending on the determinate or indeterminate growth pattern of an axis, each category of axis results from the succession of shoots in a monopodial system (*Acer* sp.: Troll 1937) or the succession of modules in sympodial trees (*Ulmus* sp.: Troll 1937; Figure 1). As a result of branching, sibling axes succeed topologically from a parent axis (Figure 2; Hallé *et al.* 1978, Barthélémy *et al.* 1989, 1991). This spatial succession is referred to as 'branching order'. It is composed of all categories of sympodial units presenting the same 'physiological age of a meristem' (Barthélémy *et al.* 1997). When successive sympodial units, even though not strictly edified by a single meristem, are more or less in a rectilinear disposition, it can be considered that the general spatial direction of such a succession constitutes an axis. The relative arrangement of the categories of sympodial units may depend on the degree of differentiation among them, which, in turn, may be related to particular morphological processes such

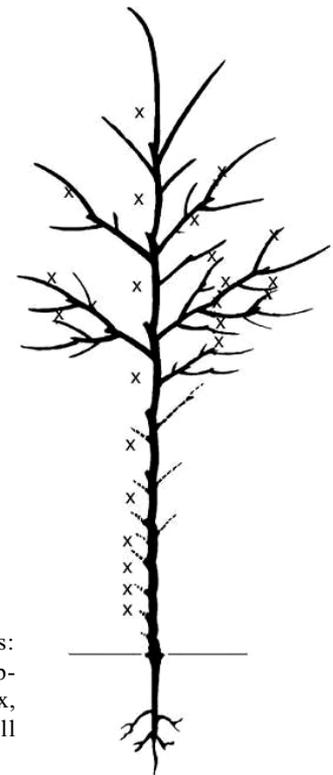


Figure 1. Sympodial trees: *Ulmus* sp.; dotted lines represent self shed branches; x, apical mortality. From Troll (1937)

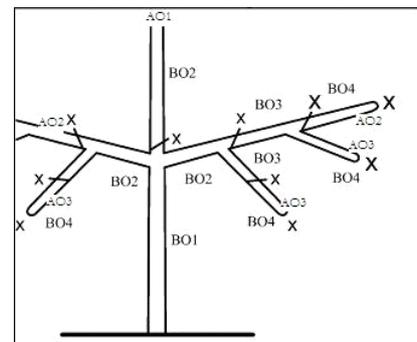


Figure 2. Branching orders (BO1, BO2, BO3, BO4) and axis orders (AO1, AO2, AO3) for a sympodial branching system; x, apical mortality. From Hallé *et al.* (1978), Barthélémy *et al.* (1989, 1991)

as acrotony. In general terms, there are the higher the branching order and the higher the degree of differentiation. In a sympodial branching system (pseudomonopodium *sensu* Troll 1937), the branching order may increase rapidly. The number of branching orders seems to depend upon leaf size, with lower numbers in large-leaved species such as horse chestnut and maple (Buck-Sorlin and Bell 2000). The number of identifiable branching orders in *Quercus petraea* and *Q. robur* is limited to seven, while only five orders have been found in *Acer rubrum* (Wilson 1966).

The morphological characteristics incorporated into an architectural unit can be directly observed or estimated without an extensive use of measuring instruments. They include, among others (Prusinkiewicz 1998): the orientation of branches (*e.g.* orthotropic or plagiotropic), type of branching (monopodial or sympodial), persistence of branches (indefinite, long or short), degree of lateral shoot development as a function of their position on a mother branch (acrotony, mesotony or basitony), type of meristematic activity (rhythmic or continuous), number of internodes per growth unit, leaf arrangement (phyllotaxis), and position of reproductive organs on the branches (terminal or lateral). The terms acrotony, basitony and mesotony to be used only in reference to the privileged localization of sibling shoots on a parent shoot (respectively distal part, proximal part and median position) without reference to their relative vigor or length, which can be given in precise terms in addition (Barthélémy and Caraglio 2007). These terms should be used only at the growth unit, annual shoot or axis levels or, at least, the plant level of organization under consideration must be specified when using these terms. The privileged repartition of sibling shoots on the upper, lateral or basal position of a slanted or horizontal parent shoot or axis is referred to, respectively, as epitony, amphitony or hypotony (Troll 1937). Amphitony is a frequent feature in rectilinear branches whereas epitony and hypotony are characterized by the predominant development of lateral axes on the convex side of the curved, downwardly or upwardly orientated branches (Caraglio and Barthélémy 1997). Schulze *et al.* (1986) concluded that generally only acrotony coupled with hypotonic branching is capable of developing a permanent and dominating canopy. In oak (*Quercus petraea* and *Q. robur*: Buck-Sorlin and Bell 2000) the strongest branches are recruited from the subapical zone, *i.e.* the branching pattern acrotonic. Subapical buds in oak are all buds, crowded in a pseudo whorl just below the terminal bud (with a subtending leaf); basal buds - small dormant buds at the shoot base without a subtending leaf; median buds - all remaining later buds (see also Harmer 1989). A lower number of basal buds visible with the naked eye can be regarded as a fairly good measure for shoot vigor in oak (*Quercus petraea* and *Q. robur*: Buck-Sorlin and Bell 2000).

The complete or partial repetition of the architectural unit during ontogenesis is a common phenomenon in trees (Barthélémy *et al.* 1991) and is defined as reiteration (Oldeman 1974). The result of this process is termed a 'reiterated complex'. An adult tree is a stack of reiterations, each of which represents a repetition of an architectural unit (Jaeger and de Reffye 1992). Sequential reiteration is a very common and a major morphogenetic process underlying crown con-

struction in most forest trees. It must not be interpreted as a move backwards within the developmental sequence of the original organism, but rather as part of this sequence as presented by the continuous and gradual trends in morphological and/or anatomical parameters observed during the whole sequence of tree development (Nicolini and Chanson 1999).

Apical dominance is the phenomenon whereby the main central stem of the plant is dominant over (*i.e.*, grows more strongly than) other side stems, and on a branch, the main stem of the branch is further dominant over its own side branchlets. In trees the apex of the main trunk bears the dominant meristem. Therefore the apex of the trunk grows fast and is not shadowed by branches. Growing away from the stem, the branches also receive more light than would a bundle of branches lying close to the stem and pointing upwards (Mattheck 1998). The death, abscission, abortion or transformation of the apex, and the resulting sympodial branching pattern is very common in nature and may be due to a variety of causes including severe competition by lateral shoots for water and nutrients (Brown *et al.* 1967), accidental injury (in *Fraxinus pennsylvanica*: Remphrey and Davidson 1992), genetic programming (in *Ulmus americana*: Millington 1963) or determinate growth. In Wych elm determinate growth corresponds to an irreversible transformation of the apical meristem - apical mortality (Figure 1 and 2; Troll 1937; Hallé *et al.* 1978, Barthélémy *et al.* 1989, 1991, Barthélémy and Caraglio 2007).

The concept of excurrent versus decurrent trees has been introduced, in relation to apical dominance, in forest trees (Brown *et al.* 1967). These terms, which refer to a definitive main stem producing lateral branches (excurrent) or a main stem that spreads and becomes indistinguishable from the uppermost branches (decurrent), have probably been among the most commonly used in classifications of forest and fruit trees. Trees with an excurrent growth habit develop with a central leader (stem) to the top. Poplars, the wild cherry and few other broad-leaved trees grow in this way for many years: the side-buds extend branches and the central bud usually continues the axis of the branch or tree. Trees with a decurrent growth habit develop a more rounded form, as multiple scaffold (primary) branches originate from the trunk. Scaffold branches are the first level of branches arising from the trunk and become the main structural system of the tree. In decurrent trees, the ability to maintain the strong central leader is lost and rounded form develops as in elms and flowering crabs.

Dominance of parent axes of a tree depends on several factors related to its growth habit. The first factor is the primary direction of elongation of the

apex, which can be modified by subsequent re-orientations of the stem. The relative dynamics of loading and diameter growth plays an important role in the final shoot form (Fournier *et al.* 1994). Another effect of diameter growth is active re-orientation of the stem, due to the maturation of new wood layers and more specifically to the action of tension wood (Archer 1986). A righting mechanism which allows the broad-leaved tree to grow vertically against gravity by forming tension wood is called negative geotropism (Mattheck 1998). This mechanism, just like phototropism, is dominant over geotropic branch growth.

In training trees, arborists do not tolerate the development of co-dominant trunks (compression fork: Mattheck 1998). Co-dominant trunks (Whiting *et al.* 2007) - a branch union with two trunks (or branches) of similar size is structurally weak and prone to damage: swaying of the stems under wind may cause the trunks to spread out. Included (or hidden) bark between the trunks prevents the wood from growing together. With co-dominant trunks, no branch collar develops knitting the two trunks together. A secondary effect of such a fork is double pith and, usually, a large bark pocket where the forked stems join. The branch union is structurally weak and prone to breakage as the trunks reach a size greater than 8 to 10 cm diameter.

Growth rhythm

In this review growth rhythm refers mainly to the timing of ontogenetic changes and the conception of dormancy. The timing of ontogenetic changes is subject to environmental influence (Allsopp 1967, Lee and Richards 1991, Jones 1995, and examples given by Alpert and Simms 2002). The initiation of determinate structures (*e.g.*, leaves, inflorescences, flowers) one or more growing seasons prior to their complete maturation and function (Hallé *et al.* 1978, Diggle 1997a) is common among temperate trees, shrubs and herbaceous perennials and is nearly ubiquitous among taxa of the arctic and alpine tundra (reviewed by Sørensen 1941). Predictive dormancy which appears as a survival mechanism is a process that is built into the growth cycle of the majority of temperate woody plants as a forced cessation caused by environments outside the affected structure. It is usually accompanied by the development of resting buds (embryonic shoots) which involve the bud scales – modified leaves that are sometimes represented only by stipules. Induction of dormancy is defined as the change of the primordia that cease growing and production of shoots for a while or that form special organs (bud scales instead of leaf and flower primordia). Bud scale development

in trees is an evolutionary adaptation as they spread from the tropics to temperate regions (Okubo 2000). Within the same genus, the number of scales in the leaf bud is less in southern regions than in northern regions (in *Camellia* sp.: Uemoto *et al.* 1990). In addition, the number of bud scales in one tree is greater when they are formed on spring shoots than on summer shoots. As demonstrated in several species by Barthélémy *et al.* (1997) buds in terminal positions on long shoots possess more organs than those on spurs at the same age, themselves possessing more organs than axillary buds. These results are consistent with those of other studies conducted in different species and demonstrating a decrease in the number of pre-formed leaves with branching order (Remphrey and Davidson 1994).

Dormancy is assured by special adaptations (Okubo 2000). As described by Hallé *et al.* (1978, Chapter 4) and Bell (1991, page 298), during the normal development of a tree many buds remain dormant and do not produce new branches. In many trees a proportion of the lateral buds along the length of a shoot remains unopened in the following and succeeding years (Mitchell 1994). They become covered by the bark, but move out with the cambium so that they are always near the surface and retain connection back to the pith by means of a stele - a bundle of water-conducting tissues also known as a bud trace. They are an insurance against the old age or premature death of the main shoot. These buds may be subsequently activated by the removal of leading buds from the branch system, which results in an environmentally-adjusted tree architecture: dormant buds may develop into an epicormic sprouts and proceed by annual growth to become an epicormic limbs. Epicormic limbs are identified by their tendency to grow nearly parallel to the main tree stem and by an abrupt increase in diameter at the base. The bark of these limbs retains a smooth or juvenile appearance to a much larger size than primary branches. An epicormic sprouts are known as water sprouts that form on stems and branches, and suckers (basal shoots), which grow from a bud at the base or roots of a tree. Wych elm rarely produces suckers differing in this respect from all the other British elms (Elwes and Henry 1913). Water sprouts are a result of a disturbance to a tree or to the tree's surroundings (Mercker 2005/2006). Most commonly, water sprouts follow sudden exposure to increased light levels, for instance, after a forest has been released via thinning or selective harvesting. Water sprouts show very strong apical dominance. They can have a profound effect on the quality of lumber produced in a forest. Newly formed water sprouts do not penetrate deeply into the interior wood,

but if allowed to grow, can become sizable branches, significantly lowering lumber grade and value.

Indeterminate growth (episodic growth; Deppong and Cline 2000) in response to environmental conditions, characterized by intermittent periods of shoot elongation (flushes) interrupted by period of dormancy, is a common phenomenon in woody species in temperate and particularly in tropical environments. In temperate regions with unfavourable conditions, climatic factors affect growth (Okubo 2000) and irregular or erratic growth traits of plants are normal and a natural plant response to irregular or erratic external factors such as cold summer, warm winter, etc. Consequential dormancy occurs when organisms enter a dormant phase after adverse conditions have arisen. This is commonly found in areas with an unpredictable climate. Under favourable environmental conditions, plants continue growing, and the growth of their buds is not synchronized because no factors force the buds to do so except for the apical dominance. As Okubo (2000) commented, 'trees can continue growing at any time, in nearly constant conditions'. But, during their evolution from tropical regions, a mechanism to modify development was inserted in the developmental sequence at various stages, due to unfavourable conditions. A temperate climate plant will automatically go dormant, no matter what environmental conditions it experiences. Deciduous plants will lose their leaves; evergreens will curtail all new growth. Going through an "eternal summer" and the resultant automatic dormancy is stressful to the plant and usually fatal. The fatality rate increases to 100% if the plant does not receive the necessary period of cold temperatures required to break the dormancy. Most plants will require a certain number of hours of "chilling" at temperatures between about 0 °C and 10 °C to be able to break dormancy.

Conclusions

Poor architecture of a tree is a growth pattern that indicates its weakness or structural imbalance. Poor architecture often arises after many years of damage from storms, unusual growing conditions, improper pruning, topping, and other damage that weakens trees and makes them more susceptible disease caused by pest organisms. In arid and windy sites bark beetles, the carrier of the Dutch elm disease fungus, may prefer to feed on branches of smaller, understory trees rather than the larger, more exposed elms (Stack *et al.* 1996). When this happens, such smaller trees may become infected while the larger, overstory trees are not. Thereby an implicit evidence of growth vigor in

Wych elm is open-grown habit of a tree (Evans 1984) together with long, single, unforked trunk and a tall, narrow crown (Uotila 1997). However, despite the fact that successive sympodial units or modules of trunk in sympodial trees like Wych elm are more or less in a rectilinear disposition owing to strong vigor of lateral growth, they are not really tied up into the strong and uniform axis (not strictly edified by a single meristem). Furthermore, amphitony is a common feature in rectilinear branches of Wych elm, but generally only acrotony coupled with hypotonic branching is capable of developing a permanent and dominating canopy (Schulze *et al.* 1986). In Wych elm the terms acrotony, basitony and mesotony should be used only to specify the degree of annual shoot development as a function of their position on a mother branch, because in Wych elm terminal growth succeeds topologically from a lateral branching (see Figure 1).

The two distinct, but co-ordinated morphogenetic events in the life of a tree, organogenesis and extension (Champagnat *et al.* 1986), are the results of the interaction between its genetic potential and the surrounding environmental conditions. In analyses of phenotypic variation in plants genetically programmed ontogenetic changes in form and function (*e.g.*, metamorphosis) can be similar in pattern to environmentally induced changes (plasticity). The metamorphosis is subject to plasticity (Diggle 2002). Experiments that controlled for both leaf position (architecture, *sensu* Diggle 1995) and environment, demonstrated that although environment (temperature), leaf position, and their interaction all contribute to variation in leaf traits, position has by far the greatest effect. Although the observed pattern of intra-individual variation in leaf traits is consistent with plastic responses to a changing thermal environment, this variation is primarily the result of a fixed ontogenetic progression of leaf types.

The internal environment of the plant - a critical determinant of developmental response (Diggle 2002) - provides the context in which a metamer/meristem develops and will play a large role in determining the morphological and/or anatomical response of that metamer to external environmental variables. The internal environment in which a meristem develops is influenced, in turn, by the past history of the individual on which it is borne, including ontogenetic stage and previous plastic responses, by the position of the meristem within the architectural ground plan, and by other competing sinks (ontogenetic contingency; Diggle 1994, Watson *et al.* 1995, Pigliucci 1998). The dependency of the phenotypic variation on the previous developmental history of the organism was termed ontogenetic contingency. It may provide a mechanism

of apparent morphological integration of developmental responses among plant parts. "The idea of a form implicitly contains also the history of such a form" (Hallé *et al.* 1978). Correspondingly, the architectural unit may be viewed as a sequence of branch types, rather than merely a set of branch types. "In this sequence, leading from axis 1 to the ultimate axis category, following the specific branching pattern, each branch is the expression of a particular state of meristematic activity and the branch series as a whole can be considered to be tracking the overall activity" (Barthélémy *et al.* 1991). Diggle (1995, 1997b, 2002) termed the inherent variation within axes 'architectural effects' in recognition of the association of this variation with the position of the plant structures within the overall architecture of a plant. It was the basis for phenotypic characterisation protocol establishment in the assessment of Wych elm trees. Trait values of interest (Collin *et al.* 2002, Black-Samuelsson *et al.* 2003, Myking and Skruppa 2007, Petrokas 2008) to the research of growth vigor in Wych elm are presented here relating to the concept of shoot differentiation and bud fate, which are controlled by a whole plant network of correlations (Champagnat 1961, Nozeran *et al.* 1984, Greenwood 1987). Some of the tree condition traits, which are to be used in the research of growth vigor in Wych elm, are the following:

Bark condition of stem axis. The parent axis of order 1 - across the perimeter of cross section at the basal zone of stem: 1...3- 1- no ribbing, no fissures, 3- ribbing and fissures are present.

Bark condition of branch axes. The strongest parent axes from order 2 to the ultimate orders - across the perimeter of cross section at the basal zone of branch: see above.

Natural pruning of stem axis. At the crown base of stem (= order 1 parent axis): 1- decomposed limb knotholes, 2- limb failure (stubs), 3- branch occlusion (knots), 4- branch shedding (scars), 5- no knotholes, stubs, knots, scars.

Natural pruning of branch axes. At the crown base of strongest branches (= parent axes from order 2 to the ultimate orders): see above.

Branching trend of parent axes. The strongest branches from order 2 to the ultimate orders: 1...5- 1- epitony (privileged repartition of sibling axes on the upside of parent axes), 3- amphitony (privileged repartition of sibling axes on the sides of parent axes), 5- hypotony (privileged repartition of sibling axes on the underside of parent axes).

Basal bud variability of tree axes. The number of small dormant buds (at the end of vegetation period) without a subtending leaf at the base of sterile annual shoots of order 1 or 2 strongest axes.

Some of the growth rate traits, which are to be used in the research, are the following:

Height and diameter increment of tree axes. The height of stem (= tree axis of order 1) at the end of vegetation period (measured on standing tree by device) or the length of strongest branch/shoot (= tree axis of order X); the diameter of stem/branch or shoot at root neck/close to the previous order axis and in its tangential direction at the end of vegetation period (over bark; crosswise calliper measurement).

Increase in order number of tree axes. It is the number of sequencing strongest axes from order 1 (= stem) to the ultimate orders (= shoots) per time unit.

Increase in leaf length. Limiting lengths (mm) of leaves between annual shoots of strongest axes of sequencing orders at once.

The suggested values of interest for the evaluation of growth habit traits are as follows:

Dominance of stem axis. The strongest parent axis of order 1: 1- multi-dominant axes: the union of several stems/branches at the root neck/branch base, 2- co-dominant axes: at the basal zone of stem/branch - the diameter of any side axis is about the half the diameter at the base of union, 3- decurrent axis: the axis is bifurcated or trifurcated; lower offshoot of supposed axis is prevailing, 4- apparent axis: some offshoot of supposed axis is prevailing at the furcations, 5- excurrent axis: there are no furcations of axis - rectilinear axis is prevailing at full height/length.

Dominance of branch axes. The strongest parent axes from order 2 to the ultimate orders: see above.

Branching type of parent axes. The penultimate strongest woody axes: 1...5- 1- acrotonic (strongest sibling axis is recruited from the subapical zone of parent axis), 3- mesotonic (strongest sibling axis is recruited from the median zone of parent axis), 5- basitonic (strongest sibling axis is recruited from the basal zone of parent axis).

Branch inclination pattern of parent axes. The inclination of strongest sibling axes on parent axis: the angle α ($^{\circ}$) between the parent axis and the sibling axis estimated using a protractor or visually (1- right, 2- oblique, 3- steep).

Leaf shape variability. Ultimate shape of leaves between annual shoots of strongest axes of sequencing orders: 1- absent acute lobes - (leaves relatively long, narrow, long tapering), 2- 1 acute lobe (3 apparent tips), 3- 3-tipped leaf with 2 acute lobes, 4- 2-3 acute lobes (5 apparent tips), 5- 5-tipped leaf with 4 acute lobes, 6- 7 apparent tips, 7- 7-tipped leaf with 6 acute lobes or over (leaves relatively broad, short tapering); 1...3- 1- lop-sided base, lowermost lobe with 1 lateral nerve, 2- lop-sided base, lowermost lobe with 2 lateral nerves, 3- lop-sided base, lowermost lobe with 3 lateral nerves.

The suggested values of interest for the evaluation of growth rhythm traits are as follows:

Bud burst asynchronization. Defined at the first occurrence of last stage taking into consideration the limiting stages of burst progress between annual shoots of strongest axes of sequencing orders: 1- leaf buds are swollen, the apex of the buds is brownish, 2- buds are still closed, the apex of the buds is pea-green, 3- buds start opening and extremities of the first leaves are visible at the apex of the buds, 4- extremities of some leaves are out but laminae are cuddled together, 5- laminae are separate, but not yet spread, 6- laminae are spreading, 7- first leaves are fully extended.

Bud set asynchronization. Defined at the first occurrence of the last stage taking into consideration the limiting stages of set progress between annual shoots of strongest axes of sequencing orders: 1- beginning of bud development, 2- green bud, 3- dark brown bud.

Leaf colouring asynchronization. Defined at the first occurrence of the last stage taking into consideration the limiting stages of colouring progress between annual shoots of strongest axes of sequencing orders: 1...5- 1- leaves are dark green, 3- extended laminae of leaves are yellow, 5- shrivelled laminae are brown.

The complexity of traits that indicate growth vigor in Wych elm leads to problems in analysing data and drawing conclusions. Different methods of investigation are proposed that allow the problem to be approached from different angles. Deductions made from the different approaches should result in a convergence of inferences. The method of multiple hypotheses (Chamberlain 1897) and the use of various approaches of enquiry are most likely to bring about an agreement between the different pieces of evidence that reinforce same underlying picture (Pigliucci 2003). So it is important to determine phenological and architectural effects specific to the growth vigor of Wych elm. The phenological effect of tree condition differences on growth rate variation have been determined by recent study of trait correlation in Wych elm (Petrokas 2008): the response of stem increment variation to the differentiation of stem natural pruning was significant and negative. The analysis of genetic correlation in Wych elm (Petrokas and Pliūra 2007) showed that adaptiveness of half-sibs is better when genotypes are of late leaf fall and early bud flushing.

Growth vigor of a tree reflects the structural integrity of that tree, as well as its state of health. The quality of a tree structure is determined by processes that conform to the axiom of uniform stress realized as an average over time in two ways - by natural selection and by adaptive growth (Mattheck 1998). Therefore, clear, healthy bark (no ribbing, even slight,

no unusual fissures, which generally indicate internal shake or split; Evans 1984) and perfect natural pruning (no stubs, no knots or evidence of pruning scars; Evans 1984) seems to be the background for the presence of growth vigor in Wych elm. Finally, it must be checked in the future research of Wych elm, whether or not the adaptive stress is a consequence of highly determinate growth pattern.

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ЭНЕРГИЯ РОСТА ИЛЬМА: ОБЗОР

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Резюме

Целью обзора является идентификация морфогенетических феноменов связанных с энергией роста ильма (*Ulmus glabra* Huds.). Это должно послужить направлением для усовершенствованной исходной селекции растений, мест произрастания, а также правильных способов посадки, что является первым шагом к предотвращению голландской болезни ильмовых. Предпосылки и протокол оценки признаков для исследования ростовой корреляции ильма представляются в соответствии с концепцией апикального доминирования, архитектоники ветвления, самоочищения от сучьев, состояния покоя и т.п., древесных видов покрытосеменных средней и северной лесной полосы. Чистая, здоровая кора и безупречное самоочищение от сучьев – проявления энергии роста у ильма. Энергия роста, т. е. устойчивость к действию неблагоприятных биотических и абиотических факторов и способность к восстановлению, является феноменом; гипотетически, все факторы (в том числе фенологические и архитектурные) имеют причастие к этому феномену, так как рост подчиняется аксиоме равномерного распределения стрессовых нагрузок. В будущих исследованиях ильма целесообразно проверить предположение насчет того, что адаптивный стресс является одним из возможных последствий высокодетерминированности характера роста.

Ключевые слова: апикальное доминирование, архитектоника ветвления, ильм, самоочищение от сучьев, состояние покоя, характер роста, энергия роста.