

HOW THE PROBLEM OF SEXES IS DEALT WITH IN TREE BRANCHING

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ABSTRACT. Reproductive elements in adult woody plants originate from the vegetative shoot sections by different methods of segregation: (1) terminal flowering in competition with the vegetative apex, or (2) lateral inflorescence shoots occupying a vacant shoot section. Reproductive elements increasingly displace vegetative meristems during tree ageing. Several strategies have been invented to overcome this competition. The reference matrix for the restructured system due to reproduction is the unit of extension. Its program undergoes a regressive metamorphosis. As a consequence, the branching pattern changes. Research presented here is based upon the structural analysis and comparison of temperate deciduous species.

Key words: branching dynamics, branching pattern, inflorescence shoot, reproduction, unit of extension

INTRODUCTION

Reproduction biology is a recent topic in Gymnosperm research, while in Angiosperms, it was investigated centuries ago. Reproduction biology concentrates on the working of the reproductive organ or complex itself, in detail on its structure, ontogenesis, ecological and physiological parameters. It has rarely been asked how reproduction originates from the vegetative system. Normally, it establishes a huge crown in woody plants before starting the adult phase. It continues to grow and develops successively when reproduction emerges in the organism.

It is shown from a morphological standpoint that reproduction can transform the vegetative structure drastically. The reconstruction is intrinsic to the developmental program. In addition, environmental triggers can modify the principal body plan. A reliable reference unit within the vegetative system is the 'unit of extension' (UE, FIGURE 1a). Hallé et al. (1978: 30 f.) used it to explain the structure of monopodial species with rhythmic growth. In the present paper, an extended version of it is used to also analyze species having a modular construction (l.c. 4); a module can often differentiate into UEs (FIGURE 2). It is suggested that reproduction establishes from a given position within the UE compared to an UE form in vegetative phase or in non-reproductive state. Whether a reproductive element takes the place of a strong vegetative meristem or a 'vacant' position, is discussed. The main question is: What kind of relationship do reproductive meristems have to the purely vegetative ones — competitiveness or collegiality? The problem is demonstrated by two species and how their vegetative structure changes throughout a tree's life span. A general overview of oth-

er selected species is presented to evaluate the impact of reproduction on the branching.

MATERIAL AND METHODS

Architectural studies of plants are based mainly on the analysis and comparison of plant structure and function.

Structure relates to (1) the organizational construction ('Bauplan') covering the serial (i.e., longitudinal) sequence of organs, and (2) the modification of this sequence due to developmental changes. Hierarchical grades of organization are distinguished to understand the system complexity: (a) phyton (cf. Rutishauser and Sattler 1985), (b) units of extension and their association within a branch (FIGURE 1b), and (c) crown with subsystems due to reiteration.

Function relates to the spatial shoot orientation, plasticity of growth and optimization to light, biomechanical stability, and other questions dealing with ecological triggers and competitiveness. It is suggested to apply to all kinds of adaptation to the above innate program.

The problem is illustrated with two temperate deciduous species. The overall developmental program (vegetative, advanced adult and senescent age) is given by the homonomous series of the unit of extension suggested as key to branch structure and overall crown formation. The final profiles of units or branches are not simply a depiction of the plant form found in nature but the result of the structural analysis, the visualization of the interrelationship of structural and functional parameters. They illustrate the length dimension, branching ratio, distribution of flowers, spatial orientation and shoot longevity over a decade or even longer (FIGURE 1). The process described is feasible in principle for any given species (see Drénou 1994, Gleissner 1998a,

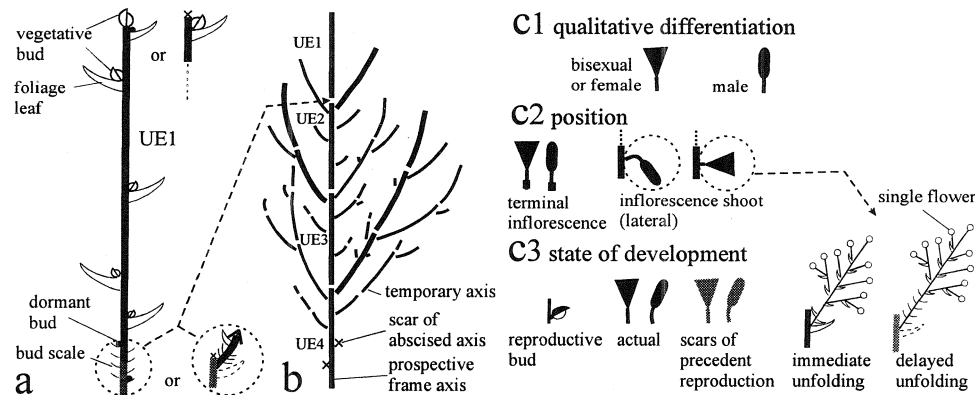


FIGURE 1. Legend and basic shoot elements. **a.** Unit of extension (UE): a set of morphological parameters each showing a serial gradient along the same shoot section: (1) heterophylly: bud scales – foliage leaves, (2) curve of internodes, (3) quantitative meristematic activity in the axils, (4) serial precedence, e.g., acrotomy see (b), (5) differentiation into vegetative or reproductive organs, see FIGURE 2, (6) longevity of vegetative axes, see (b). **b.** Branch in an overall profile, constructed by single UEs, their extension and longevity depend on their origin along their mother unit, thin-lined branchlets will shed. **c.** Symbols of reproductive elements.

1998b for other species). For the arrangement of reproductive elements, 40 other species are also included in TABLE 1. The samples mainly originated from urban or forest trees of the city of Aachen. Sampling was done with the help of an elevator truck or using the double rope technique.

RESULTS

Reproductive Element Construction

There are, in principal, two positions to integrate reproductive elements into the sequence of

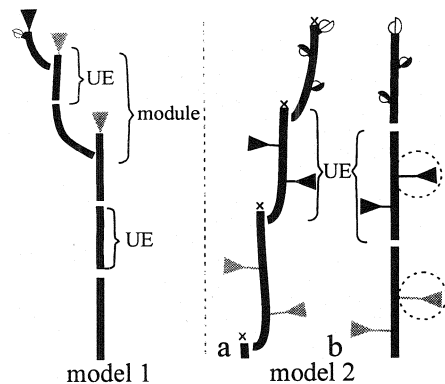


FIGURE 2. Shoot chain models including the position of reproductive elements within the vegetative system. Model 1. Anthetic-sympodial due to a terminal inflorescence. Model 2. Division of labour into vegetative shoots and inflorescence shoots. **a.** Ananthic-sympodial due to innately triggered shoot tip abortion. **b.** Monopodial with prominent terminal renewal bud.

vegetative shoot sections. The rule behind, the shoot chain, is repeated in subsequent growth (FIGURE 2). In Model 1, every shoot generation ends up with a terminal inflorescence. Reproduction itself is the basis for creating a renewing meristem. This is why it is called anthetic-sympodial. In Model 2, there is a division of labor into pure vegetative shoots and lateral 'inflorescence shoots' which do not affect the vegetative pattern essentially. In 2a, a regular shoot tip abortion is included by vegetative innate reasons, i.e., ananthic-sympodial. In 2b, the vegetative apex continues with a vegetative bud, i.e., monopodial.

Most of the temperate deciduous species have bisexual flowers, thus only one type of reproductive element is needed. Some species, however, segregate the sexes within the reproductive element itself (*Alnus glutinosa*, cf. Jäger 1980; *Castanea sativa*). Others produce male and female elements to be placed at different positions within the UE (see below). The latter is the normal case in many Gymnosperms, which are not referred to in the present paper.

Fagus sylvatica (European Beech)

Environmental triggers stimulate the fructification frequency and intensity in mast years. This ecological phenomenon correlates with an alternate UE development. Reproduction separates in male and female inflorescence shoots. They unfold together with their vegetative unit (FIGURE 3B). That is why the vegetative bud is swollen by the pre-formed inflorescence primordia. A non-reproductive UE can be identified by

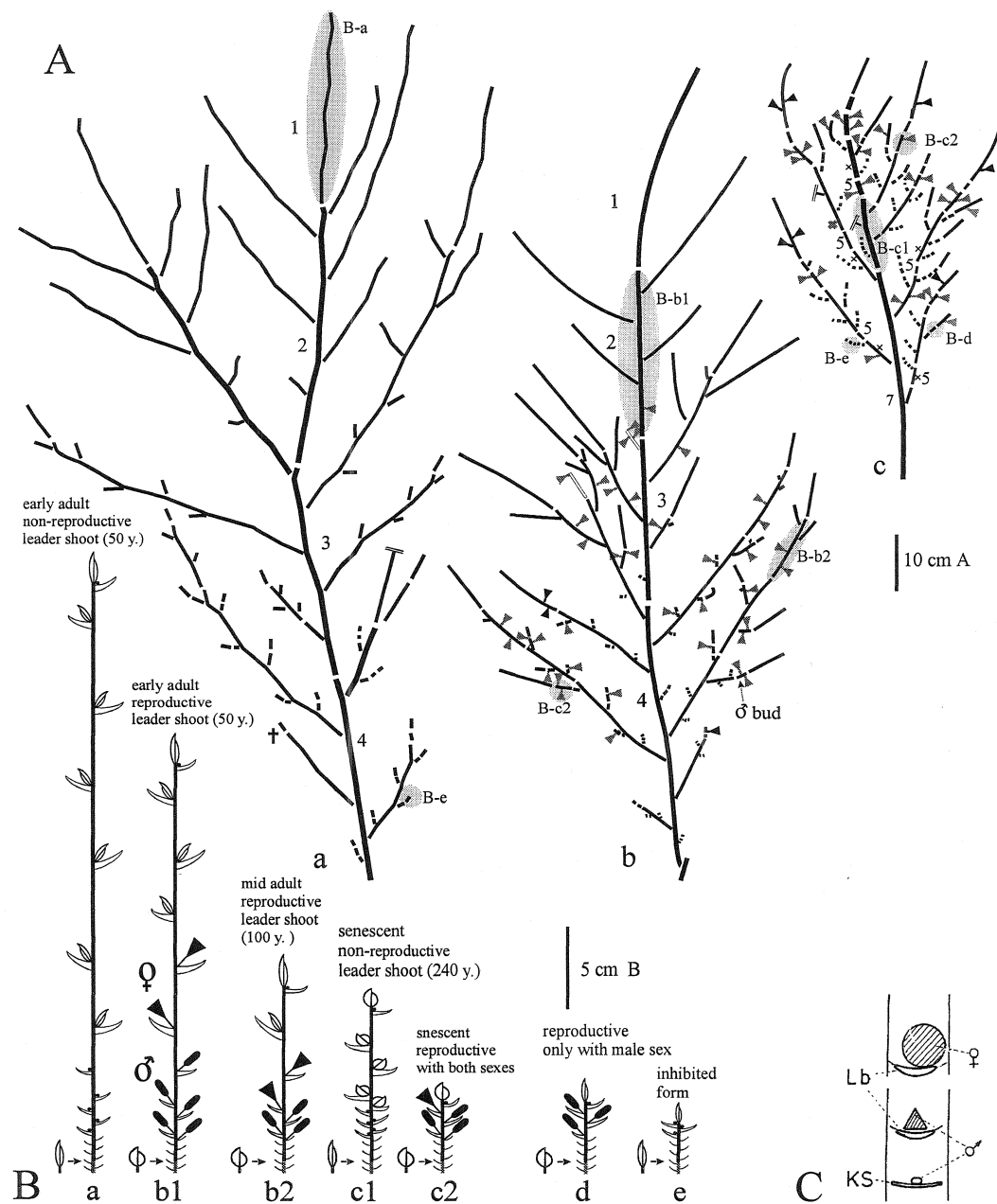


FIGURE 3. *Fagus sylvatica* (European Beech). Alternation between a reproductive and a non-reproductive UE form. **A.** (a-c). Dynamics of canopy leader branches. a. Early adult phase, 42 yr. b. Mid adult phase, 90 yr. c. Senescent phase, 240 yr. (dotted sections refer to B, male reproduction not depicted). **B.** Corresponding dynamics of the unit of extension. **C.** Scars of reproductive elements enable to reconstruct the reproductive frequency and intensity over several seasons.

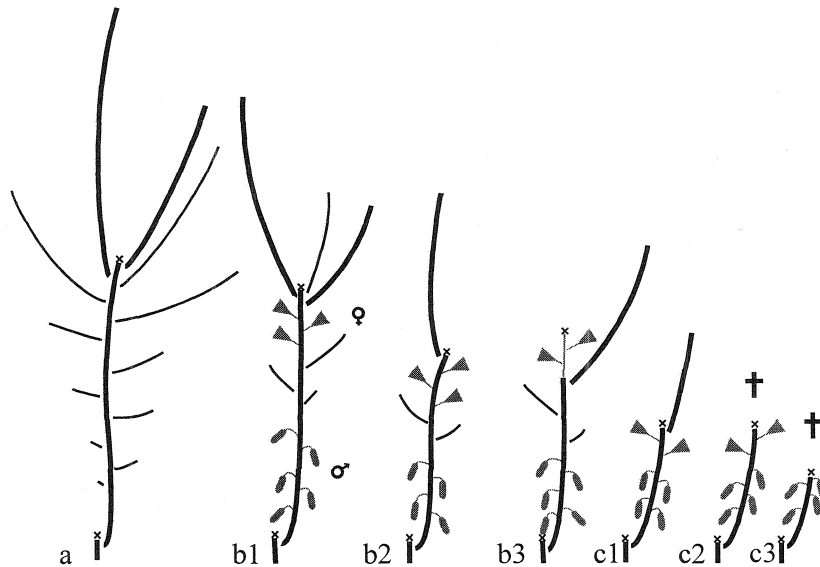


FIGURE 4. *Castanea sativa* (Sweet Chestnut). Series of the canopy UE showing the change of balance between vegetative growth and reproduction. *a*. Vegetative phase. *b*. *b1*: Adult phase: Female (androgynous) inflorescence shoots take the place of vegetative meristems (not depicted at the latest unit). *b2-3*: 'disorderly' separation of vegetative from reproductive sections. *c*. Senescent phase and at branchlets of younger trees: distal UE shortening. *c2-3*: intense reproduction causes a branch dieback.

its thinner and longer bud. The UE differentiates into two alternate manifestations having either reproductive meristems at the base section and less branching, or more lateral shoots and being longer.

In vegetative or non-reproductive state (FIGURE 3A-a) a strong offshoot often competes to its mother axis. Together they form a forking trunk later on. The branching at the UE base is weak, and leads to the development of unbranched short-shoot-chains. These chains persist over 14–20 seasons before branch abscission starts. During the adult state, units grow with shortened length due to reproduction. Also canopy leaders can be affected. Being non-reproductive next season, they again extend in length (FIGURE 3A-b). In senescent trees, the flowering frequency and intensity are higher and seem to be less dependent on environmental triggers. Seasons with a strong unit, as in season 6 or 7, are followed by reproductive units having less or no lateral branching (FIGURE 3A-c). As a result, competition rises between building vegetative shoots and inflorescence shoots as the minimization of the units results in the shortening of the upper UE section. Besides the renewal bud, the place is left only for female and male inflorescence shoots. At weaker branchlets, only the males are expressed. The UE shortening is partially compensated in non-reproductive seasons. The 'best rows' in a branch are re-

served for the female inflorescences which have to guarantee a successful fructification. The males have to be content with the 'back rows'. The side branches of younger trees grow as the senescent leader shoots do to some extent. This trend of anticipation has been found in other species as well, but have a different structure and reproductive arrangement [e.g., *Acer pseudoplatanus* (Gleissner 1998b)].

Castanea sativa (Chestnut)

Sexes are separated in distal female (androgynous) and proximal male inflorescence shoots (FIGURE 4). The vegetative continuation is guaranteed by a lateral meristem in accordance with the ananthic-sympodial shoot chain. The series of the UE perform the ongoing displacement of vegetative elements by reproduction. The more the tree progresses with age, the more the UE is shortened from its distal section. Only a single bud or shoot is left for innovation. In case all UE meristems are used up for reproduction, the concerned shoot section dies back.

DISCUSSION

Other species and other models are included into comparison and discussion to evaluate the impact of reproduction on the branch formation (FIGURE 5, TABLE 1). In Model 1, a terminal in-

TABLE 1. Species list according to a different model of reproductive arrangement. Specimen origin: [AC]—Botanical Garden of Aachen and nearby forest plantations and urban areas, so far no other origin is mentioned. Additional origin: [Ar]—Arnold Arboretum, Boston, USA; [Bay]—Botanical Garden, Bayreuth, Germany; [Da]—Botanical Garden Berlin-Dahlem, Germany; [Sp]—Späth-Arboretum, Berlin, Germany. Annotations with further references: 1, Drénou (1994); 2, Gleissner (1998b); 3, Gleissner (1999); 4, Hauser 1932; 5, Jäger 1980; 6, Lüscher 1990; 7, Pilger 1922; 8, Thiébaud and Puech 1984.

Model (1). Terminal inflorescence. <i>Alnus glutinosa</i> (L.) Gaertn. ⁵ <i>Aesculus hippocastanum</i> L. ³ <i>Cornus alba</i> L. <i>Rhus typhina</i> L. <i>Sambucus nigra</i> L. <i>Viburnum rhytidophyllum</i> Hemsl.	Model (2). Inflorescence shoot at vacant position. <i>Callistemon speciosus</i> (Sims) DC <i>Evonymus europaeus</i> L. <i>Fraxinus excelsior</i> L. <i>Hippophae rhamnoides</i> L. <i>Ilex aquifolium</i> L. <i>Populus × canadensis</i> Moench ³ <i>Prunus avium</i> L., ³ <i>P. spinosa</i> L. <i>Tilia tomentosa</i> Moench ² [Da]	Model (3). 'Mixed'. <i>Betula pendula</i> Roth. ^{2,4,5} <i>Carpinus betulus</i> L. ³ <i>Juglans regia</i> L.	Model (4). Competition to vegetative shoots. (4a). Distal renewal remains: <i>Castanea sativa</i> Mill. (adult age) ^{1,3} <i>Quercus robur</i> L., ^{1,2,4} <i>Q. petraea</i> L. (4b). No distal renewal left <i>Castanea sativa</i> (old age) <i>Salix × smithiana</i> Willd. <i>Syringa vulgaris</i> L.
Strategies to compensate for the competition to vegetative meristems: Model 5. (5a). Double use of axils for both reproduction and vegetative innovation. <i>Forsythia × intermedia</i> Zab. ⁷ <i>Poncirus trifoliata</i> (L.) Raf. [Bay] <i>Robinia pseudacacia</i> L. ³ <i>Zelkova serrata</i> (Thun. ex Murr.) Mak. [Ar] (5b). Long-term reproduction by prophyll or accessory shoots <i>Cercis siliquastrum</i> L. ³ <i>C. canadensis</i> L. [Ar]	Model (6). Seasonal alternation of reproductive and non-reproductive UE (6a). <i>Fagus sylvatica</i> L. ^{6,8} <i>Ulmus carpiniifolia</i> Gled. ^{4,7} <i>U. × hollandica</i> Mill. (6b). <i>Acer platanoides</i> L. <i>A. pseudoplatanus</i> L. ²	Model (7). Additional abbreviated reproductive element per season. (7a). <i>Tilia cordata</i> Mill. <i>T. platyphyllos</i> Scop. ² [Ar, Da, Sp] (other <i>Tilia</i> species ²) (7b). <i>Amelanchier ovalis</i> Med. <i>A. lamarckii</i> F.-G. Schroeder <i>Crataegus laevigata</i> (Poir.) DC <i>Liquidambar styraciflua</i> L. [Ar] <i>Malus pumila</i> Mill. [Bay] <i>Platanus × hybrida</i> Brot. ^{1,3}	

inflorescence competes for the apex where a strong renewal bud is expressed in non-reproductive state. A more or less regular switch of the apical dominance results. In Model 2, the inflorescence shoots place a vacant position at the unit base section, thus there is no considerable competition to vegetative meristems. All other Models, 3–7, are structural modifications of Model 1 and 2. Model 3 represents a structure with both terminal and lateral reproduction due to the differentiation into unisexual flowers (*Carpinus betulus* with terminal female reproduction; *Betula pendula*, with reversed position of sexes). In Model 4, inflorescence shoots displace strong vegetative shoots at the distal UE position (e.g., *Prunus padus*, *Quercus robur*).

Different strategies are invented to overcome to some extent the competition of reproductive and vegetative meristems. In Model 5, the foliage leaf axil provides a meristem complex consisting of accessory and/or prophyll buds which enable to produce inflorescence shoots and vegetative shoots from the same axil next season (*Robinia pseudacacia*). Model 5 with long-term use of axils for reproductive purposes is rare in temperate climates (*Cercis siliquastrum*). It is common for the tropical families of Apocynaceae, Euphorbiaceae, Leguminosae and Sapota-

ceae (Gleissner 1998a). In Model 6, an alternation of reproductive and non-reproductive UE forms takes place as shown for Beech in detail. The analogous trend is found in systems with terminal reproduction, e.g., *Acer pseudoplatanus* with a nearly regular switch every second season. In Model 7, a reproductive shoot section is inserted additionally into the vegetative program as in many *Tilia* species and, analogously, in *Platanus × hybrida*.

CONCLUSION AND FUTURE DIRECTIONS

Reproduction is an important factor to be integrated in the initial vegetative structure. Its emergence and strength is predictable because it is programmed to develop from a distinct UE section. Concerning the competitiveness or collegiality to vegetative meristems, there are two general trends that minimize the vegetative shoot unit:

1. the change of the vegetative program during ageing affects the UE length and leads to less foliage leaves per unit and less vegetative meristems; and
2. reproduction gives another reason for shortening the UE. A subsequent non-reproductive

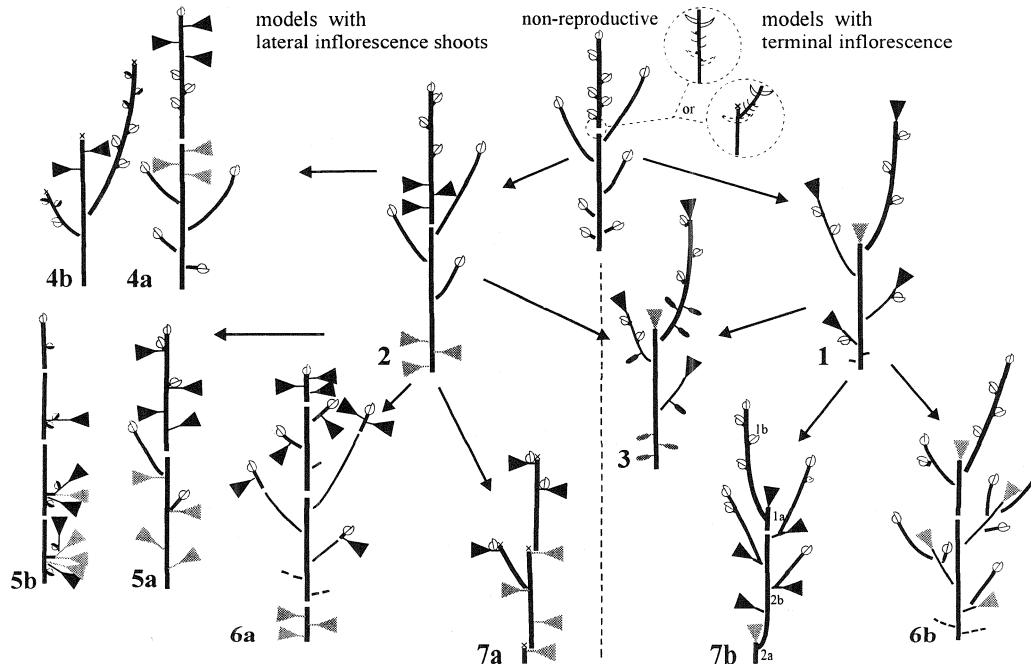


FIGURE 5. Arrangement of reproductive elements in comparing temperate species listed in TABLE 1. (Models 1–7). 1. Competition for the apex. 2. Occupying vacant positions. 3. Mixed Model 1 + 2. 4(a, b). Competition to strong vegetative shoots. (Models 5–7). Strategies to compensate for the competition to vegetative meristems: 5. Double (5a), respectively multiple use (5b) of axils by accessory or prophyll shoots. 6(a, b). Alternation of reproductive and non-reproductive UEs. 7(a, b). Insertion of an additional reproductive shoot section.

UE can again be extended and of higher branching ratio.

Both trends are superimposed, resulting in an ongoing displacement of vegetative meristems by reproductive elements, which are in principal unable of any further vegetative capacity. The subordinate branches of an earlier developmental phase anticipate the pattern of the senescent leader shoots. Although 'intelligent' Models (5–7) are in existence to overcome the competition, as a final result, there is an increase of reproduction at the expense of the vegetative continuation of the system. This problem is innate to the 'Bauplan'. In addition, the spatial branch position and the environment can modify the reproductive intensity and frequency (not referred to here).

The presented approach should be extended to the tropics with its high biodiversity to detect other models of reproductive element arrangement. A detailed problem is that subordinate branches can die off because of intense reproduction (e.g., *Castanea*, *Carpinus*, Gleissner 1999). A challenging question is: Can excessive reproduction cause a partial crown dieback (e.g.,

Eschweilera sagotiana, Lecithydaceae, Gleissner unpubl. data) or death of the system?

The approach can be used for tree assessment with forest dieback and urban trees. Man-made growth stresses may cause a premature senescence (Roloff 1989). The present paper has given evidence that the reproductive ratio becomes higher throughout the tree's life span in healthy trees, whereas the flowering ratio distinctly decreases within stressed trees (Gleissner 1998b, Gleissner and Froebe in press). Up-to-date computer-modelling is based on the vegetative structure. If reproduction is included, it will help to improve the modeling of growth dynamics.

ACKNOWLEDGMENTS

My sincerest thanks are given to Prof. Dr. H. A. Froebe and Prof. Dr. A. Roloff for their support and encouragement on this study, to the German Science Foundation to sponsor the participation in the Second Canopy Conference and to M.-L. Cox-Hammersen for the critical reading and correction of the manuscript.

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