

A Whole Tree Perspective

T M Hinckley, University of Washington, Seattle, WA, USA

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Introduction

Trees are spectacular organisms (Figure 1); they can accumulate an incredible amount of biomass, they can live for long times, they can grow in extraordinarily stressful environments, they are globally important because of their historic roles in providing fuel and fiber and their more recent and emerging roles in providing chemicals including pharmaceuticals, providing habitat for a diverse array of organisms, and sequestering carbon. Although any organism is the sum of its parts, changes in the function of a part (e.g., leaf herbivory as the result of an insect outbreak) are not always reflected in changes in the whole organism (i.e., a scaling issue). As a consequence, knowledge about the growth, development, functioning, and morphology of the parts enables one to understand the mechanisms behind how a tree grows, develops, functions, and, ultimately, appears, but this knowledge alone often fails to predict accurately the response of the whole organism (i.e., issues of scaling and context). Therefore, an article focusing on the integrated whole organism has merit. Other articles in this Encyclo-

pedia have either viewed a part of the whole tree or a particular process or property of the tree. In contrast, this article will take an integrated approach and focus on the entire tree.

Five topics will be developed here. First, the nature and definition of the individual organism will be explored. Second, the current status of understanding at the whole organism level about one of several key physiological processes associated with carbon, water, and nutrient acquisition and their use will be presented. Third, 'perception' of internal and external changes, and then the transmission and 'interpretation' of this 'perception' are critical for tree survival. The whole area of biophysical and biochemical signaling has become a major topic and research area at the tissue and cell levels of biological organization – what is known at higher levels? Fourth, there are a number of scaling issues that need additional discussion; for example, over the last 10 to 15 years, branches have been defined as an appropriate, intermediate scale of biological organization for the study of large, complex trees – there may be significant weaknesses in this assumption. Fifth and finally, major human social and cultural development was set in motion between 8000 and 10000 years ago by the domestication of a few critical crop species and now we are totally dependent upon these. Over this same period of time, comparatively little genetic selection has occurred with forest trees. Because of advances in molecular biology and genetics, opportunities to domesticate trees over vastly shorter time scales are now possible.

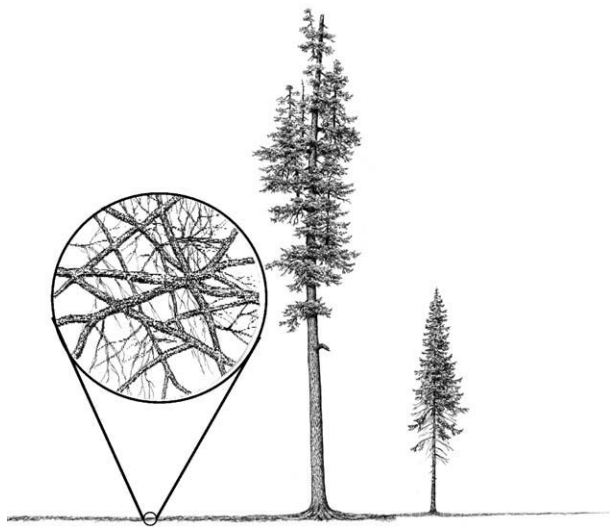


Figure 1 Two *Pseudotsuga menziesii* trees, one an old-growth, the other 80 years old, are shown with their 'root' systems. Emphasized in this drawing is the change in crown complexity, as well as size, with age and the horizontal and interconnected extent of the root systems. Drawn by Dr Robert Van Pelt.

Definition of the Whole Tree

The whole tree (i.e., the organism) might be defined as a system of relatively fine organs (i.e., foliage and fine roots) acquiring resources (i.e., carbon, nutrients, and water) then linked via a coarser system of roots, stems, and branches to create a particular form. Architectural form, trade-offs between structure and function, and optimization of carbon 'investment' in the construction and maintenance of support and transport tissue vs. tissue involved in resource acquisition are widely discussed in the literature. Therefore, the visible form that a tree takes is the result of architectural and process rules (i.e., the hardwired or genetic component) and their interplay over time with the combined abiotic and biotic environment. This interplay has been examined in a number of ways: (1) efforts to seek general rules of form and function, (2) documentation under natural and experimental conditions of changes in form and function with abrupt changes in the environment, (3) common garden studies involving

many different genotypes and at least two very different 'gardens,' and (4), most recently, the use of a wide range of molecular tools. Emerging from these studies are a number of generalizations. First, trees, within a prescribed genetic framework, respond to a set of environmental conditions and this response can be described morphologically (e.g., sun-shade), physiologically (e.g., quantum efficiency), and allometrically (e.g., root:shoot ratio). Second, trees, in contrast to most plants and animals, may harbor tremendous genetic variation (however, it is not certain whether this translates to higher levels of adaptive genetic variation). Third, the individual tree often has a very large capacity to acclimate to new or different environmental conditions. Fourth, large differences in morphology or function between one genotype and another may be due to only a few genes; unfortunately, there is insufficient evidence at present for this to be unequivocal.

Trees are large, sessile organisms capable of long life and capable of living in extraordinarily diverse environments. These attributes place special restrictions on the form and function of trees. The desiccation properties of woody angiosperms and gymnosperms versus other photosynthesizing plants have been compared and a major difference in the two groups' ability to tolerate or function at low water potentials was noted. The inability of woody angiosperms and gymnosperms to tolerate low water potentials means that water loss must be strongly (and rapidly) regulated. How then do stomata 80 m from the root system perceive decreases in soil water potential (or cessation of root growth)? In addition, competition for resources, particularly light, has favored two very different life history traits and these are often found together in the same organism. Height growth, whether to gain competitive advantages for light or reproduction or both, means that transporting resources becomes increasingly difficult and, as trees become taller and bigger, potentially carbon maintenance costs increase. Finally, as a result of increases in tree height, foliage is always being added at the top (i.e., in relatively high light environments) and lost at the bottom (i.e., in low light environments). In sum, a tree's response to competition is carbon-costly and mechanically risky and, therefore, establishes one of the first goals of domestication; that is the elimination of continuous height growth (discussed below).

Although the aboveground portion of one tree can be readily and visually separated from another tree, where one organism stops belowground and another begins is not clear. Root grafts, known for a long time, represent one means by which one organism and another may be connected positively (resources)

and negatively (disease). However, belowground connections may be far more complex and extensive – evidence suggests that mycorrhizal roots of an individual of one species are connected with other individuals of the same species. In fact, mycorrhizal roots of one species may be connected to another species. For example, in 1997, Simard and others found that stable ^{13}C moves from the deciduous hardwood *Betula papyrifera* to the evergreen conifer *Pseudotsuga menziesii* and vice versa via a common, interconnected ecto-mycorrhizal species. These experiments indicated that belowground carbon sharing is of sufficient magnitude that it may help ensure the coexistence of these two species in mixed communities.

More recent work using radioactive ^{14}C demonstrated bidirectional carbon exchange, depending upon phenological state, between the spring ephemeral *Erythronium americanum* and sugar maple (*Acer saccharum*) saplings via the mycelium of arbuscular mycorrhizal (AM) fungi. It was also noted that the exchange via the AM fungi was specific because there was no uptake of ^{14}C in associated yellow birches (*Betula alleghaniensis*) (an ecto-mycorrhizal tree species). Such studies illustrate how, via interconnected AM or ecto-mycorrhizae, individuals of the same species and of different species can positively influence each other. Implied then is that the absence of this connection could negatively affect the remaining organism – this suggests that the individual's performance is more than the combination of its genetic background and the environment or that the definition of either the 'individual' or the 'environment' must be made more comprehensive.

Fungal endophytes are fungi growing asymptotically on stems and leaves. They have been found in every species of plant examined to date, including marine macroalgae, mosses, ferns, 'gymnosperms,' and herbaceous and woody angiosperms. Research more than two decades old on species-specific endophytes and the 'extended phenotype' in grasses has demonstrated the close relatedness of this mutualism where the endophytic fungi lives on the host species and, as a consequence, deters herbivores and enhances the physiology of the host. For several species of grass, the endophytic relationship may be necessary for survival. In a 2002 study of *Dichanthelium lanuginosum* plants from geothermal soils in Lassen Volcanic and Yellowstone National Parks, Redman and others noted that the beneficial effect of a fungal symbiosis increased with soil temperatures. In contrast to grasses, the newly discovered relationship between endophytes and trees is different – many endophytic species coexist on leaves and stems,

they are highly diverse within and among host, they are transmitted horizontally (vs. within the seed or clonally) and they may not defend the host against herbivores. However in spite of the uncertainty about whether tree endophytes provide benefits to the host or not, a number of researchers are beginning to examine both natural and genetically engineered endophytic relationships with host trees (e.g., white pine blister rust and *Pinus monticola* and *P. albicaulis*). If fungal diversity mimics the noted enormous diversity of prokaryotic organisms both above and below ground, then there could be several important consequences to our consideration of the organism (and, therefore, groups of organisms in stands, communities, or ecosystems). First, it may be, except under experimental conditions, difficult to study the individual organism separated from its associated microflora. As a consequence, we have an 'extended phenotype' to consider. Second, because evolutionary change occurs rather slowly in long-lived organisms, evolutionary changes in the associated microflora may play a significant role in 'assisting' the host organism to deal with, for example, historical and projected climate change. Third, any consideration of domestication must also consider opportunities with the associated or introduced microflora. As this section concludes, our definition of the whole organism has been greatly extended. In addition, we have seen how trees, perhaps because of their size and longevity, may have temporally and spatially a vastly more diverse and complex relationship with other organisms.

Key Structural-Functional Relationships

A number of important structural-functional relationships might be presented (e.g., carbon allocation, crown and root architecture, and hydraulic architecture). It is important to note that these can be treated as separate topics; however, they must be ultimately integrated when considering the whole organism. Although all three of these have been extensively covered elsewhere (see *Tree Physiology: Canopy Processes; Nutritional Physiology of Trees; Shoot Growth and Canopy Development*), I have chosen plant hydraulic architecture both because of personal interest, but also because it provides clear evidence of structural-functional integration that spans from fractions of a minute to the lifetime of the tree and because it is a subject that supports and links well with subsequent sections.

Plant Hydraulic Architecture

Hydraulic architecture has been for the last 25 years and is still a dominant theme in plant and tree water

relations. In a recent comparison of leaf-specific hydraulic conductance to transpiration or whole-plant hydraulic conductance to plant leaf area over vastly different life-forms, strong support was found for function-structure integration. Further, it was suggested that there is considerable flexibility in these relationships depending upon the availability of resources. In a very careful analysis of the water conducting system in *Laurus azorica* trees, it was found that there was a strong relationship between petiole hydraulic conductivity and whole tree or stand transpiration; however, it was noted that stem hydraulic capacity exceeded actual water movement by almost a factor of 45. This could perhaps be a safety feature where the stem can transport all the water needed using only a small fraction of its vessels – the remaining vessels may serve in a capacitance role. Somewhat similar results were found when the hydraulic conductances of fine and coarse roots of *Prunus* were compared: coarse root capacity was not the limiting factor.

Hydraulic redistribution of water within the root system is now well documented. Perhaps even more noteworthy have been the recent observations on giant, coastal *Sequoia sempervirens* trees. Unlike work published on large, old-growth *P. menziesii* that demonstrated a considerable lag between xylem water movement at 50 m vs. 2 m, the new observations indicate no lags and even reverse flow where the source of water is either from dew on the foliage or from pools of water in large branch crotches. The presence of roots in these pools means that the hydraulic gradient to the foliage should be thought of in terms of meters vs. tens of meters. Clear, general structural-functional relationships with regard to tree hydraulic properties may exist, but considerable variability appears also to occur. Although the quantitative nature of science tends to focus on means and patterns, variation and outliers may be equally important to understand and document.

Integration also implies that the water system within a tree forms an integrated network; however, a number of investigations of insect activity and herbivory within the crown of trees suggest otherwise. In addition to clear within-plant heterogeneity in growth, morphology, and chemistry, due to differences in tissue age, light availability, or previous damage by herbivores, some of these studies indicated that heterogeneity originated in the soil environment (experimentally demonstrated via split-root studies) and can be modulated or accentuated by the pattern of water transport (e.g., sectoral vs. nonsectoral). Hydraulic architecture provides a wonderful framework to understand tree function and structure; however, large gaps in our understanding of

how the entire system might be integrated (e.g., reconciling the segmentation theory to the limiting role that root xylem hydraulic conductivity plays or cavitation as an early warning system vs. a source of water or refilling as a diurnal vs. seasonal process) still exist.

Signaling

Because of the massive size of trees and the lack of a central nervous system, long-distance communication would seem to be both critical and mechanistically interesting. For example, sudden damage to the root system or rapid changes in soil oxygen, temperature, or moisture could have a profound effect on water supply. Because water loss is only regulated at the stomatal-leaf level, until stomata were to close, a 5-m or 65-m tree would continue to lose water and would soon reach critical leaf and xylem water potentials. During a typical day, leaf water potentials decline to near critical, but rarely less than critical levels. That is, a tree functions near the point of catastrophic xylem failure (i.e., runaway cavitation). Critical leaf water potentials have long been known to cause stomatal closure; however, this might be a case of 'too little – too late.' Without adequate short- and long-distance 'communication,' xylem water potential could easily exceed this critical point.

For a long time, plant growth substances (or regulators or hormones) have been recognized as important controls over plant growth and function, including stomatal control. The timing of the onset and cessation of growth and dormancy, for example, appears to be under a number of different controls. Changes from juvenile to mature, the onset of reproductive activity, and reproductive activity itself are under strong control. Plant form, as manifested by apical dominance and apical control, is controlled by plant growth substances. Watching the initiation and spread of vegetative growth in the crown of a tree would certainly suggest that various chemicals, transported in the xylem or phloem, could be largely responsible. Herbaceous plants, tree seedlings, and tree saplings have all been shown to transport various substances (e.g., K^+ , Ca^{++} , abscisic acid (ABA), and zeatin riboside (i.e., a cytokinin)) from the root to the shoot in response to changes in the rhizosphere. Flooding, root damage, and cessation of root growth due to temperature or compaction have all been shown to elicit a group of growth inhibitors (e.g., increases in ABA) and suppress growth promoters (e.g., cytokinins) – these then result in stomatal closure and cessation of leaf growth. The response of trees to wounding suggests that wound-induced (win) mRNAs are transmitted

in the same manner and direction as currently produced photosynthates (e.g., acropetally in leaves and branches near the apex of the tree, both acropetally and basipetally in leaves and branches found in mid positions, and largely basipetally in lower leaves or branches). Clearly, biochemical messages or signals can be moved in both the phloem and xylem; however, their movement, except in ring-porous species, will be relatively slow (less than 8 m and 1 m h^{-1} for diffuse-porous and gymnosperms, respectively).

Present opinion is that long-distance transport of a biochemical message would be too slow to provide timely stomatal closure in *Pinus sylvestris*. There is limited (controversial and shaky) evidence that small changes in water potential, due to a few cavitation events, may be propagated close to the speed of sound within the microfibrils of the cell wall – this biophysical message then results in the release of Ca^{++} or ABA at the stomata. Even studies of herbaceous plants such as *Ricinus communis* have suggested that initial changes in stomatal conductance were not due to ABA transport from the roots to the foliage, but due to changes in root hydraulic conductivity. Unfortunately for large trees, the transmission of gradual changes in root hydraulic conductivity is likely not fast enough to cause stomatal closure and avoidance of runaway cavitation. Evidence, albeit again controversial, has been provided for very rapid responses in large (35 m plus) *Nothofagus* trees in New Zealand. Therefore, there is limited evidence for a mechanism for rapid signaling within a large tree; however, as attractive as this might be, there is still too little evidence.

Over relatively short distances (i.e., within a cell, between cells, and even within a tissue), there has been a recent explosion in information on signaling. Whether one is reviewing an organ or a whole organism level study of plant growth substances and their role, one is impressed with the difficulty of elucidating mechanism and particular an integrated, *in situ* view of biophysical and biochemical mechanisms responsible for signaling. What is needed is an understanding of rapid, long-distance signaling in very large trees.

Scaling

The ecological and physiological literature is filled with studies from 0.1-ha plots or from chloroplasts or leaves and then extrapolated and discussed at much larger scales. The process of scaling has been discussed, reviewed and used extensively. Because of this article's focus on the organism and the comments under the section on the definition of the organism, it

is worth reviewing an important point and presenting some current aspects of scaling that might be useful to take from this article. For me, what continues to be an important lesson of scaling is the following observation. One should always be concerned with three scales in any study. The scale below that of the study provides an understanding of mechanism and the scale above that of the study provides the context – for our present purpose, the parts of the tree are critical for mechanism and the stand (or population), community, and ecosystem are critical for context.

Scaling in physiological ecology appears to focus on a number of specific issues. First, can one scale one's readings at, for example, the leaf level to the whole tree. Second, scaling from a seedling to a tree involves understanding how morphology and process change with stage of development. Finally, for large, complex organisms, is it possible to use an intermediate scale (i.e., between the leaf and the tree) for study and, therefore, scaling? The branch has become a favorite example of this latter issue. Recent research has highlighted ways in which branch autonomy may fail and, therefore, the reliance on branches as an intermediate step in scaling may also fail.

Of the diversity of different invasive and non-invasive techniques that have emerged over the last two decades, perhaps the use of stable isotopes has proven the most useful for whole plant studies of (1) carbon allocation and movement within an individual, from parent to offspring via seed, between individuals, and within ecosystem(s), and (2) water movement. Techniques to measure water flow, especially those that can be used to develop depth profiles and can detect both zero flow and flow in either direction, have also been invaluable in an understanding of the parts and the whole.

Domestication

Around 10 000 years ago, people living in the Fertile Crescent (in what is now the Middle East) began to rely increasingly on domesticated grains such as rye. Domesticated corn appeared about 9000 years ago in Mexico and rice in China around 8000 years ago. These events had a profound influence on humans. As an increasing number of crops (and animals) became domesticated, there was a transformation from hunting and gathering to agricultural cultivation and associated settlements. In terms of social evolution, this was extraordinary. Today, we recognize the absolute dependence of most human societies (and all developed societies) on domesticated crops and animals. For plants, we also understand the genetic changes linked to domestication.

There appear to have been three features associated with the domestication of most crop plants: (1) there was a radical transformation of the wild plant in terms of structure and function (often the domesticated plant shows little or no resemblance to the original progenitor), (2) this transformation typically involved a few key mutations and these had huge effects, and (3) the initial transformations occurred very soon in the process, that is, they were rapid. It is important to note that the first mutation(s) associated with domestication were likely very rare and were probably noted because of either intensive observation (via gathering) or early cultivation. Since these first large steps, refinements using conventional breeding methods have come much more slowly, have represented much more subtle changes in structure and function, and have involved a greater number of genes.

Over this same period of time, why were trees not domesticated? A number of reasons may exist for this and they include: the relatively long generation cycle in trees, the lack of edible products from most trees, the high inherent genetic and phenotypic variability within populations and between populations of trees, and the difficulty of both observing and capturing useful mutations. Clearly some selection and partial domestication has occurred (e.g., *Olea europea* and *Pinus caribaea*); however, in comparison to say the domestication of corn, trees are still analogous to the original teosinte.

Having this background and now having the platform provided by molecular biology and genetics, it should be possible to domesticate trees. What specific attributes might one seek? The following is a potential list:

1. A high rate of biomass accumulation.
2. Strong apical control (i.e., a single axis).
3. A narrow, confined crown with minimal branching.
4. Maximum light interception by the foliage and high quantum use efficiencies.
5. Apical meristems, buds, or shoots insensitive to the presence of neighboring trees (i.e., competition insensitive).
6. Reduced height growth after some initial, rapid minimal gain in height (i.e., a platform on which biomass is added).
7. Greater carbon allocation to the stem.
8. No reproductive activity (unless elicited).
9. Low cell lignin content.
10. No 'juvenile' stemwood (assumes the stem is the site of biomass accumulation).
11. More efficient resource acquisition especially by roots and associated microflora.

Many of these, as happened with crop domestication, represent dramatic changes in the structure of a tree and how that structure functions. Our ability to visualize this 'new' tree is extraordinarily difficult as we are so used to incremental changes. Modeling, including the use of 'virtual plants,' offers one approach. However, there are large segments of society who, for one reason or another, will find such a transformation of a tree unacceptable. Relying on either conventional silviculture or further increases in a CO₂ fertilizing effect to meet future fiber and fuel needs may not be realistic. Given continued population growth, increased consumption, the relatively low carbon costs of using wood and wood products (vs. other products for construction, for heating, for chemicals), it would seem unwise not to explore this opportunity. Had the same constraints been placed on the original progenitors for our current agricultural crops, I would not be writing and you would not be reading.

Summary and Conclusions

Understanding how the whole organism functions, and that it is not merely the sum of its parts, that it can be represented as an 'extended phenotype,' and that an untapped potential for change in its phenotype exists are the key messages developed within this article. It is also clear that there are very large unknowns: what are the controls on age- and size-related declines in productivity, how is 'information' transmitted through an organism, and how is transport in the phloem and the xylem controlled and integrated? Finally, what changes in structure and function would accompany domestication and how does our current understanding of whole tree physiology aid or impede domestication?

See also: **Ecology:** Forest Canopies. **Environment:** Carbon Cycle. **Hydrology:** Hydrological Cycle. **Soil Biology and Tree Growth:** Tree Roots and their Interaction with Soil. **Tree Physiology:** Canopy Processes; Mycorrhizae; Nutritional Physiology of Trees; Physiology and Silviculture; Root System Physiology; Shoot Growth and Canopy Development; Stress; Tropical Tree Seed Physiology; Xylem Physiology.

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Xylem Physiology

J R Barnett, University of Reading, Reading, UK

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Introduction

Secondary xylem, or wood, is a product of the activity of a secondary meristem, the vascular cambium. Those plants which possess one can be very long-lived, their life span being only limited by catastrophic events such as gales and lightning strikes or disease. More wood is added each season, with the result that it is the most abundant natural product on earth. The cambium and xylem differentiation have been the subjects of a number of monographs and it is not the purpose of this chapter to précis these works. Rather, some important aspects of the way the structure of wood is related to its behavior and