

When branch autonomy fails: Milton's Law of resource availability and allocation

DOUGLAS G. SPRUGEL

College of Forest Resources, University of Washington, Seattle, WA 98195, USA (sprugel@u.washington.edu)

Received December 3, 2001; accepted May 11, 2002; published online October 1, 2002

Summary The branch autonomy principle states that the critical characteristics of a branch's carbohydrate economy (photosynthesis, respiration, growth, etc.) are largely independent of the tree to which the branch is attached, as long as light is the primary factor limiting photosynthesis and growth. However, this may not be generally true because in the spring, photosynthates are translocated from a tree stem into branches, and the amount of photosynthate available for translocation should be a function of the tree's canopy status. And the correlative inhibition principle states that a branch's priority for allocation of carbon and other resources is controlled not only by its own environment, but also by its position relative to other branches on the same tree. A study of the lower limit of branch growth and survival in trees of different sizes shows that the latter principle is more important: even though dominant trees have more resources to allocate, branches on suppressed trees are able to grow and produce new foliage at solar irradiances where branches on dominant trees die. Thus branches are sufficiently interdependent that a positive carbon budget by itself does not ensure branch survival; branch position relative to other branches on the same tree is also important. Other findings indicate that this result is quite general: regardless of the stress involved, a stressed branch on a tree where all other branches are also stressed does better than a similarly stressed branch on a tree where some branches are relatively unstressed. Although branch autonomy is an important and useful principle, it is not an absolute rule governing branch growth.

Keywords: *Abies amabilis*, *correlative inhibition*, *resource allocation*.

Introduction

The branch autonomy principle (Van der Wal 1985, Sprugel and Hinckley 1988, Sprugel et al. 1991) has become a popular and widely used model over the past decade. It is a common component of tree functional models (e.g., Kull and Kruijt 1999, Bosc 2000, Kull and Tulva 2000) and has been used extensively to justify the use of branch bags as a technique for studying air pollution effects on trees (Barton and Jarvis 1999, Lovelock et al. 1999). Its appeal is that it is simple and easily understood, and appears to make clear and understandable predictions about carbohydrate allocation within canopies of

forest trees. Its main drawback is that, in many of the situations where it is applied, it is false.

The branch autonomy hypothesis was originally stated as two premises and a logical inference from them: *if* (1) no branch imports carbohydrate from its parent tree after its first year, and (2) within the morphological constraints imposed by apical control, each branch satisfies its own material and energy requirements before exporting any carbohydrate to the rest of the tree, *then* where light is the primary limiting factor, the critical characteristics of a branch's carbohydrate economy (photosynthesis, respiration, growth, etc.) are largely independent of the tree to which it is attached. One can predict many important growth and physiological characteristics of a branch from its morphology and position in the canopy alone, without reference to the characteristics of the tree as a whole (Sprugel and Hinckley 1988, p 2).

This statement has a variety of weaknesses. Perhaps the most obvious is that it considers only carbon fluxes, although carbon uptake and export are inextricably tied to water and nutrient fluxes, and branches are clearly not autonomous with respect to materials that are harvested by the roots and transported by the stem. This was demonstrated by Whitehead et al. (1996), who shaded the lower part of the canopy of a *Pinus radiata* D. Don tree and observed an almost immediate increase in photosynthesis and stomatal conductance of the remaining leaves. As long as photosynthesis is linked to water supply and nutrient content, the carbon economy of a branch cannot be truly autonomous. (See Sprugel et al. 1991 for a review of branch autonomy as it relates to water and nutrients.)

Another weakness is that the first premise is false, at least at some times of the year. It is probably true that photosynthate does not move from one branch to another during the main part of the growing season (Sprugel et al. 1991), so a branch that becomes so shaded or stressed that it does not fix enough carbon to cover its own maintenance respiration costs dies once it has exhausted its own reserves (cf. Witowski 1997). However, at the beginning of the growing season, when new shoots are rapidly expanding and growing, carbohydrate stored in the stem as starch is mobilized to feed the strong sinks of growing tissues, and there is substantial movement of stored carbohydrate from the stem and roots into branches (Dickmann and Kozlowski 1970, Gordon and Larson 1970). At this time, branches import carbohydrate, and carbon that

was fixed in one branch may easily end up in a different branch (Sprugel et al. 1991).

The second premise is also flawed in that the term “requirements” is dangerously vague. The only energy-using process that is unambiguously required for short-term branch survival is maintenance respiration. However, in the long run, a branch must grow to survive. Branches that have stopped producing new leaves may live on for some time, at least on evergreen trees with long-lived foliage, but after a few years they must die unless new growing points are initiated by epicormic sprouting (e.g., Ishii and Ford 2001). And if growth is considered a requirement, the second premise is also false, because the growth of lower branches is certainly influenced by the rest of the tree, through apical dominance (Wilson 2000), apical control (Cline 1997) or sink/source dynamics (Honkanen et al. 1999).

These weaknesses in the derivation of the branch autonomy principle lead to significant violations of the principle as a whole. Although there can be little question that the single most important control on branch growth is the branch's own environment (Haukioja 1991), it is now clear (and probably should have been in 1988) that in many situations, branch survival and growth are influenced, perhaps substantially, by the condition of the tree to which they are attached. However, it is unclear from theoretical considerations alone what the consequences of these influences will be. For example, in a closed forest stand, a branch's growth is determined mainly by its light environment. But if two branches in a stand are in similar light environments, but one is on a dominant tree whereas the other is on a suppressed tree, which branch will grow faster?

Two conflicting trends may influence the answer to this question. The first is a consequence of a dominant tree having more resources to allocate. With more leaf area and a more favorable position in the canopy, a dominant tree should have a much larger pool of carbohydrates to allocate throughout its canopy, and its larger root system should also give it greater access to water and nutrients. The possibility that a stressed branch might obtain some “relief” by being attached to a healthy tree was one of the greatest concerns in early studies where branch bags were used to treat individual branches with pollutants (McLaughlin 1988, Reich 1988, Sprugel and Hinckley 1988), and it remains a concern today (K. Mooney, University of Colorado, personal communication) because branches are an ideal size for manipulative experiments where treatment of a whole tree may be impossible. Considering only resource availability, one might assume that, in the above example, the branch attached to a dominant tree grows faster and photosynthesizes more than the branch attached to the suppressed tree.

Counteracting this is the tendency for carbon and other resources needed for growth to be allocated preferentially to those branches that are in the best environments (the principle of correlative inhibition; Snow 1931, Novoplansky et al. 1989, Sachs et al. 1993, Sachs and Novoplansky 1995). This concentrates available resources (i.e., new growth) in the parts of the environment most suitable for future development, where the return on investment (light harvested per unit of biomass con-

structed) is likely to be greatest (Novoplansky et al. 1989). Thus, in spring when carbohydrates are temporarily stored in the stem and later reallocated to fuel shoot elongation, there is a strong net movement of carbon fixed in large but shaded branches at the bottom of the canopy upward into smaller but better-lit branches at the top of the canopy (Sprugel et al. 1991). But again, what is important is not the absolute amount of light a branch receives, but how that light compares to that received by the rest of the tree. “Differential conditions... are most effective. Branches in relative shade are inhibited when other branches are exposed to stronger light” (Sachs and Novoplansky 1995). If a dominant tree and a suppressed tree both have branches at the same height in the canopy, the branches on the dominant tree are likely to be its lower branches, near the bottom of its crown, whereas the branches attached to the suppressed tree are likely to be its upper branches, near the top of its crown. The high branches on the suppressed tree, which are in a favored position relative to other branches on the same tree, should receive a high proportion of the resources that that tree has to allocate. Conversely, low branches on a dominant tree, in a relatively unfavorable position, will be discriminated against when resources are allocated.

So considering only resource allocation, a high branch on a suppressed tree should do better than a low branch on a dominant tree, because it is in a better position relative to other branches on the same tree. But considering only resource availability, any branch on a dominant tree might be expected to grow more than any branch on a suppressed tree, because the tree has more resources (water, nutrients and carbohydrates) to allocate. Which is more important in fact? The following small study provides a clue. Additional examples from the literature show that the results from this exercise are quite general.

Materials and methods

The measurements described in this paper were made in a 37-year-old *Abies amabilis* (Dougl.) Forbes stand at 1200 m elevation in the Findley Lake research area, about 65 km southeast of Seattle, Washington (47°20' N, 121°35' W), on the Cedar River watershed. This stand regenerated naturally after a clear-cut in 1955, but most trees are still < 10 m tall because of low site quality and poor growing conditions. The stand is dense, due to a high initial stocking and slow self-thinning; *A. amabilis* is shade-tolerant and able to survive for decades in low light. This stand has been studied extensively and described in many publications (e.g., Grier et al. 1981, Sprugel et al. 1996, Stenberg et al. 1998, Hinckley et al. 1999), which provide more information about the trees and the environment.

In 1992, as part of a larger study of stand structure and physiological scaling (Sprugel et al. 1992, Hinckley et al. 1998, 1999, Martin et al. 1999), I measured the total height and the height of the lowest live branch (base of live crown) of all the trees and saplings on a 2 × 2 m plot. The plot was in one of the denser parts of the stand, with a maximum height of 5.3 m in 1992, a projected leaf area index (LAI) of 13 and a density of

17 trees m^{-2} . I harvested eight trees from the stand, representing the range of heights in the stand but emphasizing the larger trees, and measured the height of the lowest branch with current growth. I also took hemispherical photographs at 0.5 m vertical intervals from 1 to 5 m at the center of the plot, and from 1 to 4.5 m at points halfway from the plot center to the NW, NE, SW and SE corners, to measure the vertical light profile. All photos were taken using a Nikon 8 mm lens and Kodachrome 200 film. These photographs were later analyzed with the CANOPY hemispherical photo analysis program (Rich 1989) to determine total canopy openness (indirect site factor sensu Anderson 1964 and Rich 1989).

Two additional plots in the same area, but with somewhat different stand characteristics, were also analyzed. Plot 2, also 2×2 m, had a maximum height of 5.0 m, LAI of 7.7 and a density of 15 trees m^{-2} . Plot 3, which was 3×3 m, had a maximum height of 7.4 m, LAI of 8.8 and a density of 9.3 trees m^{-2} . Tree characteristics and light profiles were measured as in Plot 1.

Results

The lower limit of current growth (the point below which branches cease to grow) and the height of the base of the live crown (the point below which branches no longer survive) are both lower in smaller trees (Figure 1a). This answers the question posed above: resource availability is outweighed by resource allocation, so despite greater resource availability in dominant trees, branches on suppressed trees continue to grow and produce new foliage at solar irradiances (Figure 1b) where branches on dominant trees die. The same pattern was seen in the other two plots studied (Figure 2).

Although the three tallest sample trees in Plot 1 ranged in height from 3.75 to 5.23 m, they all had the same lower limit of current growth, approximately 2.5 m. Canopy openness at this height in this stand is about 12% (Figure 1b). Again, the same pattern was seen in the other two plots; although the plots dif-

fered substantially in density, dominant height and LAI, within each plot the tallest trees had the same lower limit of current growth, and this limit fell at 12–14% canopy openness (Figure 2).

Discussion

As enumerated below, several recent studies using different research designs support the primary result above and make it more general.

(1) Stoll and Schmid (1998) examined branch growth on the sunlit and shaded sides of Scots pine (*Pinus sylvestris* L.) trees at the edge of a tree patch (created by logging) and compared them with growth of branches on trees in the middle of a forest. Sunlit branches on edge trees grew most, followed by branches on trees in the middle of the forest, followed by shaded branches on edge trees. Shaded branches on edge trees grew less than shaded branches on forest trees even though—or perhaps because—the edge trees as a whole received more light than trees in the forest.

(2) Takenaka (2000) measured growth and mortality of *Litsea acuminata* (Bl.) Kurata shoots, and related them to (i) the light microenvironment of the shoot and (ii) the light microenvironment of the best-lit shoot on the sapling the shoot was attached to. The best growth and lowest mortality occurred on shoots that received the most light (> 10% of full sun). However, shaded shoots (< 5% of full sun) grew more and had less mortality if they were attached to a completely shaded sapling (no shoots > 5% of full sun) than if they were attached to a sapling that had some well-lit branches (at least one shoot > 10% of full sun).

(3) Henriksson (2001) artificially shaded individual branches or whole trees of mountain birch (*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti). Growth was lower and mortality was higher on shaded branches on unshaded trees than on shaded branches on shaded trees. After 2 years,

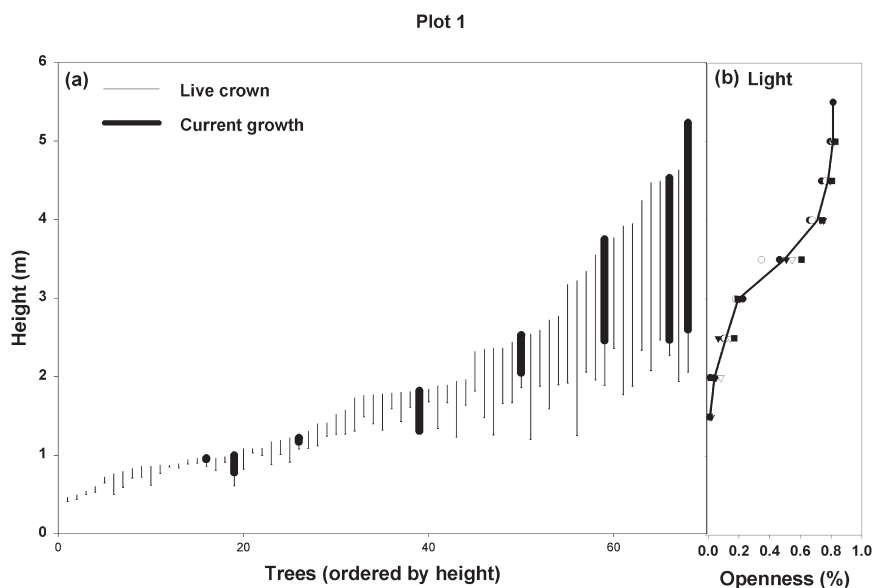


Figure 1. (a) Distribution of live crown (all trees) and current growth (sample trees only) on 68 trees in a 2×2 m plot. (b) Light profile in the same plot. Symbols represent five different vertical transects; heavy line is the mean. Stem density = 17 trees m^{-2} ; projected LAI = 13; maximum height = 5.25 m.

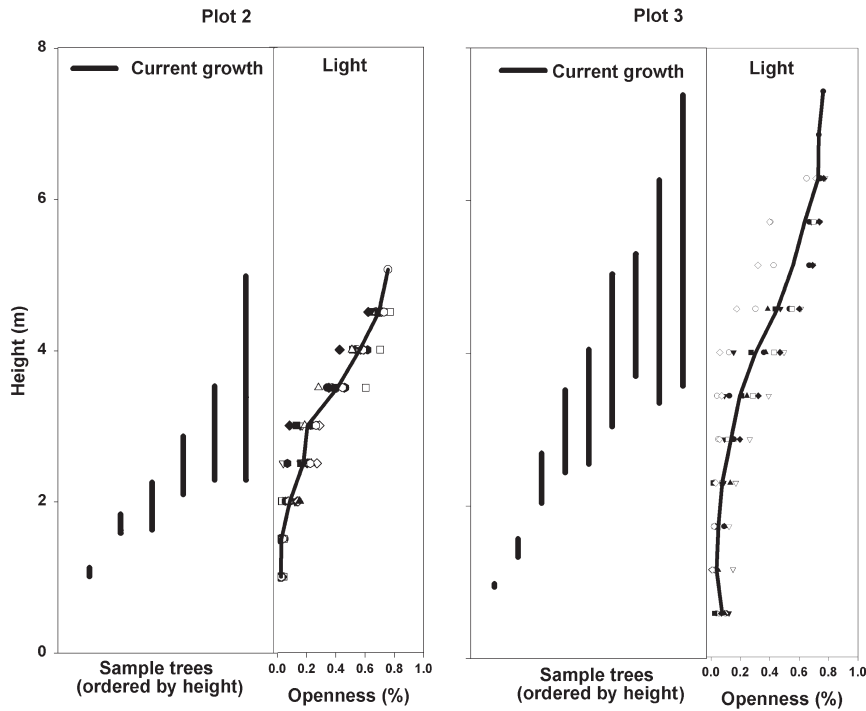


Figure 2. Distribution of current growth on sample trees and light profiles for two additional plots. Symbols represent different vertical transects (12 in Plot 2, 9 in Plot 3); heavy line is the mean. Plot 2 stem density = 15 trees m^{-2} ; LAI = 7.7; maximum height = 5.0 m. Plot 3 stem density = 9.3 trees m^{-2} ; LAI = 8.8; maximum height = 7.4 m.

90% of the shaded branches on unshaded trees had died; no dead branches were observed in any of the other treatments.

All these studies produced the same result: shaded branches in general grow less than sunlit branches, but a shaded branch on a tree in which other branches that are exposed to the sun grows even less and is more likely to die than a shaded branch on a tree where all the other branches are shaded too. Two studies cited below show that stresses other than shading produce the same result.

(1) Honkanen and Haukioja (1994) defoliated individual branches or whole trees of Scots pine in several different experiments. Growth was consistently reduced more on a defoliated branch attached to an undefoliated tree than on a defoliated branch attached to a defoliated tree.

(2) Schaap (1992) used a combination of branch bags and whole-tree chambers to expose whole Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees and individual branches on those trees to either charcoal-filtered (CF) air or 250–300 ppb ozone. Photosynthesis was consistently greater in branches exposed to CF air than on branches exposed to ozone, but branches exposed to CF air on ozone-exposed trees had greater photosynthesis than branches exposed to CF air on trees exposed to CF air, and ozone-exposed branches on ozone-exposed trees had greater photosynthesis than ozone-exposed branches on trees exposed to CF air (Hinckley et al. 1998).

The same pattern is seen in all these studies: stressed branches grow less than unstressed branches, but regardless of the stress involved, a stressed branch on a stressed tree does better than a similarly stressed branch on an unstressed tree. (Note that “stressed” is used here in absolute terms; a branch is

considered “stressed” if it is heavily shaded, browsed or exposed to polluted air, regardless of the condition of other branches on the same tree.) This pattern is particularly clear when the stressed branch on the stressed tree is in a superior position relative to other (even more stressed) branches on that tree, whereas the stressed branch on the unstressed tree is in a relatively inferior position. This may be called Milton’s Law, since it is a specific case of John Milton’s (1667) more general statement: “Better to reign in hell than serve in heaven.”

Milton’s Law will come as no surprise to most forest ecologists, but it is inconsistent with the branch autonomy principle, which states that branch growth and survival are independent of the condition of the tree to which a branch is attached. If that were true, then the base of the live crown, and the lower limit of current growth, would be constant throughout the stand. That this is not true suggests that a branch’s carbon budget alone cannot predict branch growth and survival. An upper branch on a suppressed tree almost certainly has a positive carbon balance, otherwise the tree would quickly die. But there is no reason to expect that a low branch on a dominant tree should cost more to support than a branch at a comparable height on a suppressed tree, especially since sapwood in excess of that needed to supply leaves with water can be converted to heartwood to reduce maintenance respiration costs. Lower branches on dominant trees almost certainly stop producing foliage and die long before they reach a negative carbon balance (in either the broad or narrow senses of Witowski 1997), reflecting an adaptive response to the fact that there are other parts of the tree where photosynthate can be more profitably invested. Thus, although a positive carbon balance is a necessary condition for survival, it is not sufficient.

Bloom et al. (1985) stated that “a plant continues to produce new leaves until the increment in gross photosynthesis equals the increase in respiration.” In other words, plants should invest carbon to produce new leaves wherever the leaves can be expected to fix enough carbon to repay their construction costs (including support tissues). However, this predicts that the lower limit of the crown should be the same in all trees in a stand, and again, this is contradicted by the data in Figures 1 and 2. Plants invest carbon in the locations where there is likely to be the best return on investment (i.e., the maximum carbon fixed per unit of biomass or nitrogen invested), not simply in places where the return on investment will be greater than zero.

This last observation may explain why current growth on dominant trees in all three stands stopped at 12–14% of full sunlight. Optimization theories developed by Field (1983) and Farquhar (1989), among others, suggest that limiting resources should be allocated within a plant in such a way that photosynthetic capacity is proportional to intercepted light. Numerous authors have shown that this can be partly achieved if leaves produced at the top of the canopy are thick and those at the bottom are thin, and if shoots at the top of the canopy are bushy and those at the bottom are flat, so that light interception per unit of newly produced biomass or nitrogen is relatively constant (e.g., Ellsworth and Reich 1993, Sprugel et al. 1996, Stenberg et al. 1998). However, there is a limit to such acclimation; needles must have some thickness to function effectively, and shoots cannot be flatter than flat. The 12–14% openness value may represent the lowest solar irradiance at which *A. amabilis* trees can produce new foliage and shoots that have a lifetime light interception potential per unit biomass equal to that at the top of the canopy.

Finally, that branches on dominant trees die when they may still have a positive carbon economy raises the question of what they die from. There has been little work directly addressing this question, but several possibilities suggest themselves.

(1) Photosynthesis in shaded foliage on dominant trees becomes water-limited because sunlit leaves elsewhere on the tree are stronger sinks for water (e.g., by the mechanism observed by Zwieniecki et al. (2001)). This decreases photosynthesis to the point where the branch cannot fix enough carbon to cover maintenance respiration.

(2) Shaded branches on dominant trees stop producing new leaves, either because leaf production is suppressed by hormones produced by meristems in more favorable positions (Cline 1997, Wilson 2000) or because the meristems in relatively shaded branches are too small and weak to draw resources from the rest of the tree (Honkanen et al. 1999). In deciduous trees, branches that do not produce new leaves soon die. Branches on evergreens can survive for a while without producing new leaves but eventually die as the remaining foliage ages and becomes less efficient, and eventually cannot fix enough carbon to cover maintenance respiration.

(3) Shaded branches on dominant trees are killed through the action of hormones produced by stronger meristems elsewhere, perhaps by mechanisms similar to those causing ab-

scission of leaves in the fall in deciduous trees.

Note that in the first two proposed mechanisms the carbon balance of a shaded branch on a dominant tree actually becomes negative, but this occurs not because there is too little light, but because other resources become limiting so that light is not used as efficiently as it would be by shaded branches on suppressed trees. In the third mechanism, shaded branches die while their carbon balance is still positive. Distinguishing among these possible mechanisms could be a fruitful area for continued research on the mechanisms and exceptions to branch autonomy.

Acknowledgments

The ideas presented here were developed over several years as a result of discussions with Tom Hinckley, Renée Brooks, Wieger Schaap, and others. Renée Brooks and Erkki Haukioja provided helpful suggestions on the manuscript that were greatly appreciated.

References

- Anderson, M.C. 1964. Studies of the woodland light climate. I. The photographic computation of light conditions. *J. Ecol.* 52:27–41.
- Barton, C.V.M. and P.G. Jarvis. 1999. Growth response of branches of *Picea sitchensis* to four years exposure to elevated atmospheric carbon dioxide concentration. *New Phytol.* 44:233–243.
- Bloom, A.J., F.S. Chapin, III and H.A. Mooney. 1985. Resource limitation in plants: an economic analogy. *Annu. Rev. Ecol. Syst.* 16: 363–392.
- Bosc, A. 2000. EMILION, a tree functional–structural model: presentation and first application to the analysis of branch carbon balance. *Ann. For. Sci.* 57:555–569.
- Cline, M.G. 1997. Concepts and terminology of apical dominance. *Am. J. Bot.* 84:1064–1069.
- Dickmann, D.I. and T.T. Kozlowski. 1970. Mobilization and incorporation of photoassimilated ^{14}C by growing vegetative and reproductive tissues of adult *Pinus resinosa* Ait. trees. *Plant Physiol.* 45:284–288.
- Ellsworth, D.S. and P.B. Reich. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* 96:169–178.
- Farquhar, G.D. 1989. Models of integrated photosynthesis of cells and leaves. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 323:357–367.
- Field, C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* 56:341–347.
- Gordon, J.C. and P.R. Larson. 1970. Redistribution of ^{14}C -labeled reserve food in young red pines during shoot elongation. *For. Sci.* 16:14–20.
- Grier, C.C., K.A. Vogt, M.R. Keyes and R.L. Edmonds. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Can. J. For. Res.* 11:155–167.
- Haukioja, E. 1991. The influence of grazing on the evolution, morphology and physiology of plants as modular organisms. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 333:241–247.
- Henriksson, J. 2001. Differential shading of branches or whole trees: survival, growth, and reproduction. *Oecologia* 126:482–486.
- Hinckley, T.M., D.G. Sprugel, J.R. Brooks, K.J. Brown, T.A. Martin, D.A. Roberts, G. Segura, W. Schaap and D. Wang. 1998. Scaling and integration in trees. *In Ecological Scale: Theory and Applications.* Eds. D.L. Peterson and V.T. Parker. Columbia University Press, New York, pp 309–337.

- Hinckley, T.M., M.R. Keyes, T.A. Martin and D.G. Sprugel. 1999. Lessons from montane forests of the Pacific Northwest. *Phyton* 39: 73–84.
- Honkanen, T. and E. Haukioja. 1994. Why does a branch suffer more after branch-wide than after tree-wide defoliation? *Oikos* 71: 441–450.
- Honkanen, T., E. Haukioja and V. Kitunen. 1999. Responses of *Pinus sylvestris* branches to simulated herbivory are modified by tree sink/source dynamics and by external resources. *Funct. Ecol.* 13: 126–140.
- Ishii, H. and E.D. Ford. 2001. The role of epicormic shoot production in maintaining foliage in old *Pseudotsuga menziesii* (Douglas-fir) trees. *Can. J. Bot.* 79:251–264.
- Kull, O. and B. Kruijt. 1999. Acclimation of photosynthesis to light: a mechanistic approach. *Funct. Ecol.* 13:24–36.
- Kull, O. and I. Tulva. 2000. Modeling canopy growth and steady-state leaf area index in an aspen stand. *Ann. For. Sci.* 57:611–621.
- Lovelock, C.E., A. Virgo, M. Popp and K. Winter. 1999. Effects of elevated CO₂ concentrations on photosynthesis, growth and reproduction of branches of the tropical canopy tree species, *Luehea seemannii* Tr. & Planch. *Plant Cell Environ.* 22:49–59.
- Martin, T.A., T.M. Hinckley, F.C. Meinzer and D.G. Sprugel. 1999. The effect of boundary layer conductance on leaf temperature and transpiration of *Abies amabilis* branches. *Tree Physiol.* 19: 435–443.
- McLaughlin, S.B. 1988. The use of branch level measurements in evaluating whole plant responses to air pollutants. *In* Response of Trees to Air Pollution: the Role of Branch Studies. Eds. W.E. Winner and L.B. Phelps. Proc. Workshop, November 5–6, 1987, Boulder, CO, pp 165–185.
- Milton, J. 1667. *Paradise Lost*. Peter Parker, London, 368 p.
- Novoplansky, A., D. Cohen and T. Sachs. 1989. Ecological implications of correlative inhibition between plant shoots. *Physiol. Plant.* 77:136–140.
- Reich, P.B. 1988. Temporal and related considerations for branch studies designed to assess the response of trees to air pollution. *In* Response of Trees to Air Pollution: the Role of Branch Studies. Eds. W.E. Winner and L.B. Phelps. Proc. Workshop, November 5–6, 1987, Boulder, CO, pp 211–230.
- Rich, P.M. 1989. *A manual for analysis of hemispherical canopy photography*. Los Alamos National Laboratory, LA-11733-M, Los Alamos, New Mexico, 80 p.
- Sachs, T. and A. Novoplansky. 1995. Tree form—architectural models do not suffice. *Isr. J. Plant Sci.* 43:203–212.
- Sachs, T., A. Novoplansky and D. Cohen. 1993. Plants as competing populations of redundant organs. *Plant Cell Environ.* 16:765–770.
- Schaap, W. 1992. Use of branch and whole tree exposure systems to evaluate ozone impacts on forest trees. Ph.D. Diss., Univ. Washington, 154 p.
- Snow, G.R.S. 1931. Experiments on growth and inhibition. II. New phenomena of inhibition. *Proc. R. Soc. Lond. Ser. B* 108: 305–316.
- Sprugel, D.G. and T.M. Hinckley. 1988. The branch autonomy theory. *In* Response of Trees to Air Pollution: the Role of Branch Studies. Eds. W.E. Winner and L.B. Phelps. Proc. Workshop, November 5–6, 1987, Boulder, CO, pp 1–19.
- Sprugel, D.G., T.M. Hinckley and W. Schaap. 1991. The theory and practice of branch autonomy. *Annu. Rev. Ecol. Syst.* 22:309–334.
- Sprugel, D.G., J.R. Brooks and T.M. Hinckley. 1992. Distribution of foliar sun/shade morphology and age within an *Abies amabilis* canopy. *Ecol. Soc. Am., August 1992, Bull. E. S. A.* 73(2s): 352–353.
- Sprugel, D.G., J.R. Brooks and T.M. Hinckley. 1996. Effect of light on shoot geometry and needle morphology in *Abies amabilis*. *Tree Physiol.* 16:91–98.
- Stenberg, P., H. Smolander, D.G. Sprugel and S. Smolander. 1998. Shoot structure, light interception, and distribution of nitrogen in a Pacific silver fir canopy. *Tree Physiol.* 18:759–768.
- Stoll, P. and B. Schmid. 1998. Plant foraging and dynamic competition between branches of *Pinus sylvestris* in contrasting light environments. *J. Ecol.* 86:934–945.
- Takenaka, A. 2000. Shoot growth responses to light microenvironment and correlative inhibition in tree seedlings under a forest canopy. *Tree Physiol.* 20:987–991.
- Van der Wal, D.W. 1985. A proposed concept of branch autonomy and non-ring production in branches of Douglas-fir and grand fir. M.Sc. thesis, Univ. Washington, 96 p.
- Whitehead, D., N.J. Livingston, F.M. Kelliher, K.P. Hogan, S. Pepin, T.M. McSeveny and J.N. Byers. 1996. Response of transpiration and photosynthesis to a transient change in illuminated foliage area for a *Pinus radiata* D. Don tree. *Plant Cell Environ.* 18:949–957.
- Wilson, B.F. 2000. Apical control of branch growth and angle in woody plants. *Am. J. Bot.* 87:601–607.
- Witowski, J. 1997. Gas exchange of the lowest branches of young Scots pine: a cost-benefit analysis of seasonal branch carbon budget. *Tree Physiol.* 17:757–765.
- Zwieniecki, M.A., P.J. Melcher and N.M. Holbrook. 2001. Hydrogel control of xylem hydraulic resistance in plants. *Science* 291: 1059–1062.