Physiological and Abiotic Determinants of Competitive Ability and Herbivore Resistance

By

D. A. HERMS[1]

K e y   w o r d s : Carbon allocation, secondary metabolism, source/sink interactions, plant defense, stress, herbivory, competition, trade-offs, life history strategy, phenotypic platicity.

S u m m a r y

HERMS D.A. 1999. Physiological and abiotic determinants of competitive ability and herbivore resistance. - Phyton (Horn, Austria) 39 (4): (53) - (64).

A model is outlined in which environmental effects on the phenotypic expression of constitutive secondary metabolism are examined within the theory of source/sink interactions. The quadratic response of secondary metabolism to resource availability predicted by the model is proposed to be an adaptive response to physiological constraints and abiotic stress. The key premise is that a trade-off occurs between growth and defense (including environmental tolerance) because (1) developmental constraints limit secondary metabolism in dividing cells, and (2) substrate competition between primary and secondary metabolic pathways limits chemical defense in rapidly growing plants. This trade-off creates an ecological dilemma: plants must grow fast enough to compete, yet maintain the defenses necessary to resist biotic and abiotic stress. The response of plants to this dilemma has been the evolution of life history specialization and/or adaptive phenotypic plasticity.

I n t r o d u c t i o n

The dichotomy between plant strategies that confer ecological success in resource-rich vs. resource-limited environments is rooted in a trade-off between traits that maximize resource acquisition and those that maximize resource retention (TILMAN 1990, CHAPIN 1993, LAMBERS & POORTER 1992). HERMS &

[1] Department of Entomology, The Ohio State University, Ohio Agricultural Research and Development Center, 1680 Madison Ave., Wooster, Ohio 44691 USA, phone: +330.202.3506; fax: +330.263.3686; email: herms.2@osu.edu

(54)

MATTSON 1992 proposed that this dichotomy exists because (1) developmental constraints limit secondary metabolism and structural reinforcement in dividing cells, and (2) resource demands of growth limit secondary metabolism at the whole plant level. This trade-off creates an ecological dilemma for plants: they must grow fast enough to compete, yet maintain the adaptations (defenses) necessary to resist abiotic and biotic stresses. The evolutionary response has been selection for life history strategies conferring ecological specialization, including adaptive phenotypic plasticity. The objective of this paper is to outline a testable model of the physiological basis underlying these patterns of resource allocation in different environments.

Competitive success in resource-rich environments is dependent on traits which maximize the acquisition of resources necessary to drive rapid growth, preventing usurpation of resources and space by faster growing competitors. Associated traits include high intrinsic rates of nutrient uptake, photosynthesis, respiration, transpiration, and allocation to leaf area (HUSTON & SMITH 1987, TILMAN 1990). However, the production of new leaf area diverts resources from production of anti-herbivore chemicals and structures (GULMON & MOONEY 1986, LAMBERS & POORTER 1992). Consequently, inherently fast growing plants generally have lower levels of defenses and experience higher rates of herbivory than inherently slow growing plants (BRYANT & al. 1983, COLEY & al. 1985). Consequences of this trade-off can be mitigated, however, by adaptations that optimize the benefits of a minimal defensive investment, including inducible resistance, toxins that are effective in low concentrations, qualitative variation in secondary metabolism, defensive mutualisms, and compensatory growth (HERMS & MATTSON 1992).

In resource-limited environments, slow growing plants are not faced with immediate exclusion by competitors, and ecological success places a premium on retention of previously acquired resources. Growth rate has been sacrificed for traits such as long-lived, sclerophyllous leaves, high root:shoot ratios, and strong chemical defenses (HUSTON & SMITH 1987, LAMBERS & POORTER 1992). In resource-limited environments, traits which limit herbivory may also enhance environmental tolerance and competitive ability (HERMS & MATTSON 1992). For example, sclerophyllous leaves may enhance tolerance to drought stress and nutrient limitation as well as represent a significant barrier to herbivory (GRUBB 1986). In arid environments, high concentrations of foliar tannins (BUSSOTTI & al. 1998) and surface resins may protect leaves from desiccation (MEINZER & al. 1990), while flavonoids and other phenolic compounds may protect plants from UV-B radiation and photooxidation damage (LANDRY & al. 1995, LARSON 1995). Secondary metabolites may also increase competitive ability through allelopathic effects on neighbors (FOWLER 1986).

Phenotypic patterns of constitutive secondary metabolism may also represent adaptive uses of limited resources (HERMS & MATTSON 1992). Phenotypic plasticity may enable plants to assume the most adaptive phenotype in a particular environment, buffering the effects of spatial and temporal variation in resource availability (SCHEINER 1993). Plants generally increase their growth in

response to resource enrichment such as fertilization (BAZZAZ & al. 1987). This response may be adaptive, selected for by competitors that would otherwise usurp the plant's space and resources. However, rapid growth in resource-rich environments constrains secondary metabolism and compromises plant defense. Increased secondary metabolism has been frequently observed in response to drought or nutrient limitation (HERMS & MATTSON 1992). This also may be an adaptive response, enhancing survival by increasing stress tolerance and defense in harsh environments when the plant has limited ability to compensate (via growth) for herbivory.

The rest of the paper will outline the physiological basis underlying the trade-off between growth and defense, and how this trade-off interacts with source/sink interactions to impose restrictions on patterns of growth and secondary metabolism in response to variation in resource availability. Observed patterns of resource allocation are consistent with the model, and may represent adaptive patterns of growth and defense within these physiological and abiotic constraints.

Ontogenetic Constraints on Plant Defense at the Cellular Level

At the cellular level, the trade-off between growth and defense results because developmental constraints limit secondary metabolism in dividing cells (LUCKNER & NOVER 1977, LUCKNER 1980). Plant growth occurs at the cellular level through the processes of cell division and cell enlargement (DALE 1988). Secondary metabolism is constrained in meristematic (dividing) cells by the lack of organized enzymatic machinery necessary for their synthesis, and the lack of the specialized structures required for their compartmentation (LUCKNER & NOVER 1977, LUCKNER 1980, WIERMANN 1981). After cell division has ceased, differentiation of cells leads to secondary metabolism, cell wall reinforcement, and formation of resin ducts, secretory glands, trichomes, spines, and other specialized tissues that are critical for limiting herbivory and enhancing stress tolerance (HERMS & MATTSON 1992).

Since the value of a leaf is highest when it is young because of the future return on carbon reinvested into new leaf area (HARPER 1989), it would be adaptive to defend young leaves if possible, especially since immature leaves frequently experience higher levels of herbivory than mature leaves (COLEY 1980, KURSAR & COLEY 1991). Indeed, plants may overcome ontogenetic constraints on secondary metabolism in a number of ways (HERMS & MATTSON 1992). In a seeming paradox, concentrations of some secondary metabolites are often highest in young leaves. This occurs because of secondary metabolism in mature cells within immature leaves. Secondary metabolites are frequently concentrated in epidermal cells (NEUMANN & al. 1991), which are among the first cells in leaves to mature (DALE 1988). In some plants, epithelial ducts, glandular trichomes, and other cells specialized for the synthesis and accumulation of secondary metabolites are also differentiated during early stages of leaf and seedling development. For example,

(56)

in peppermint (*Mentha* x *piperita*), concentrations of monoterpenes are highest in extremely young leaves where they accumulate in specialized, fully differentiated cells (GERSHENZON 1994).

However, defending young leaves may be costly. Precocious cell differentiation may ultimately result in decreased growth. Variation in the growth rate and final size of leaves generally results from variation in the number of cells per leaf rather than cell size, which in turn is determined by the proportion of cells undergoing active division in early primordial stages (KÖRNER & PELAEZ MENENDEZ-RIEDL 1989, FRANCIS 1998). Early stages of leaf growth consist almost entirely of cell division with cell numbers increasing exponentially (DALE 1988). Hence, early differentiation of cells may decrease growth by removing cells from the population of dividing cells at an early stage, thereby decreasing the exponential rate of increase in the cell population, and the ultimate size of the cell population. This would ultimately result in smaller leaves and lower total leaf area, and thereby contribute to the trade-off between growth and defense.

Resource-Based Tradeoffs Between Growth and Defense at the Whole Plant Level

At the whole-plant level, the trade-off between growth and defense can result from competition for carbon among primary and secondary metabolic pathways. Plants have limited resources to support their physiological processes and trade-offs occur among growth, maintenance, storage, reproduction, and defense (BAZZAZ & al. 1987, LAMBERS & POORTER 1992). The trade-off between growth and reproduction is perhaps the one best documented (e.g. NEWELL 1991, MUIR 1995). However, evidence increasingly supports the existence of a trade-off between growth and chemical and structural defense (e.g. HAN & LINCOLN 1994, HWANG & LINDROTH 1997, ELLE & al. 1999). The production of new biomass requires particularly high levels of plant resources (CHUNG & BARNES 1977, MARGOLIS & al. 1991). Consequently, rapidly growing plants may have decreased availability of resources to support other processes, including secondary metabolism (BRYANT & al. 1983, HERMS & MATTSON 1992).

The differential investment of photoassimilates into new leaf area is largely responsible for both genotypic and phenotypic differences in growth rates (KÖRNER 1991, LAMBERS & POORTER 1992). Hence, there may be a very substantial "opportunity cost" of plant defense. The opportunity cost of allocating resources to defense refers to the value those resources would have provided the plant had they been invested in an alternative process such as growth or storage. Secondary metabolism and the elaboration of structural defenses decrease growth by diverting resources from the production of new leaf area (GULMON & MOONEY 1986). Conversely, secondary metabolism may be substrate and/or energy limited during periods of intense growth (e.g. MARGNA & al. 1989). Many intra- and interspecific comparisons document tradeoffs between growth rate and secondary metabolism (HERMS & MATTSON 1992). HAN & LINCOLN 1994, in perhaps the most rigorous

analysis of this trade-off, quantified a substantial genetic and phenotypic trade-off between vegetative growth and secondary metabolism in *Diplacus aurantiacus*.

Trade-offs are inevitable because the resource requirements of secondary metabolism are also substantial (GERSHENZON 1994), and because primary and secondary metabolic pathways compete for common substrate. For example, phenylalanine is the limiting precursor for phenylpropanoid synthesis (lignin, flavonoids, condensed tannins, etc.), and is an essential amino acid for protein synthesis, and thus growth (DA CUNHA 1987, MARGNA & al. 1989). Recent evidence that phenylalanine is continuously regenerated during phenolic biosynthesis indicates that the supply of phenylalanine *per se* does not limit phenolic biosynthesis (RAZAL & al. 1996), but is consistent with a more general carbon-based trade-off between growth and secondary metabolism.

Source / Sink Interactions Regulate Carbon Allocation Among Modules

Allocation and partitioning of carbon within the plant, and thus the availability of substrate to support growth and secondary metabolism, is regulated by source/sink relationships (HERMS & MATTSON 1992). Carbon moves via phloem transport from sources such as chloroplasts and storage organs to sinks such as vegetative meristems and resin ducts (KOZLOWSKI 1992). Source strength is a function of the availability of carbon for export and varies with photosynthetic rate and magnitude of storage reserves (WAREING & PATRICK 1975). Photosynthetic sinks can also vary in their relative ability to attract carbon. Sink strength is a product of sink size and activity, as well as vascular connections to sources (WARDLAW 1990, DICKSON 1991). Actively growing meristems are especially strong photosynthetic sinks (DICKSON 1991, MARCELIS 1996).

The pressure flow hypothesis is the most widely accepted mechanism of phloem transport (KOZLOWSKI 1992). According to this model, photosynthates move through the phloem along concentration and osmotic gradients from regions of high to low. These gradients occur because phloem loading at photosynthetic sources increases the solute concentration in the adjacent phloem, while phloem unloading at photosynthetic sinks where carbon is utilized lowers the concentration. The rate of phloem transport is regulated by sink strength (WOLSWINKEL 1985, MARCELIS 1996). A sharp gradient is maintained in the phloem when strong sinks utilize large quantities of photosynthate, which stimulates rapid phloem unloading, thereby decreasing solute concentration in the adjacent phloem. Weak sink activity, however, limits phloem unloading which results in carbon accumulation in the phloem, decreasing the concentration gradient between source and sink, and thus the rate of phloem transport.

The growth of modules can be sink or source limited (WAREING & PATRICK 1975, PATRICK 1988). Modules are considered to be sink-limited when their growth is constrained by the ability of the sink to utilize carbon and results when resource limitation inhibits cell division and expansion (sink activity) but not

(58)

photosynthesis. Modules are considered to be source-limited when their growth is constrained by available carbon, and results from limited photosynthesis, inadequate storage reserves, and/or competition from other sinks (e.g. vegetative growth limited by reproductive effort).

Source/Sink Interactions Regulate Carbon Partitioning to Secondary Metabolism

Quantitative variation in the constitutive secondary metabolism of plants may be a function of variation in the rate and duration of growth of individual modules, as well as the proportion of modules undergoing growth at any one time (HERMS & MATTSON 1992). Higher plants consist of an integrated population of morphological subunits (modules), each originating from a single meristem (HARPER & WHITE 1974). If a large proportion of modules within a plant is undergoing growth simultaneously, secondary metabolism will be substrate-limited as available carbon is exported to strong sinks to support growth. On the other hand, when the growth of a high proportion of a plant's modules are sink-limited, decreased rate of phloem transport will result in carbon accumulation in source leaves, which increases the availability of substrate to support secondary metabolism. In plants in which the majority of modules are strongly source-limited, both growth and secondary metabolism are predicted to be carbon limited (HERMS & MATTSON 1992).

Abiotic Effects on Secondary Metabolism are Mediated by Source/Sink Interactions

Although source and sink activity is regulated hormonally, both source and sink strength is strongly dependent on resource availability (LUXMORE 1991, KÖRNER 1991). Meristematic activity is limited by even moderate shortages of nutrients and water. Hence, sink-strength is especially sensitive to resource limitation. Any factor that decreases net photosynthesis weakens source strength, including shade, severe drought, and severe nutrient stress. HERMS & MATTSON 1992 proposed that physiological constraints on secondary metabolism interact with effects of resource availability on source and sink strength to result in a non-linear relationship between photosynthesis growth rate, and secondary metabolism (Fig. 1). Resource availability is predicted to have a parabolic effect on constitutive secondary metabolism, with concentrations highest in moderately stressed plants, and lower in plants that are rapidly growing or severely carbon-stressed.

When environmental conditions are favorable, vegetative growth generally receives resource priority over secondary metabolism and storage (BAZZAZ & al. 1987). Indeed, the accelerated growth regimes sometimes used in commercial nursery production demonstrate that woody plants can grow exceedingly fast when

optimal resource levels are provided. However, substrate limitation limits secondary metabolism in fast growing plants (HERMS & MATTSON 1992). Growth is more sensitive to stress than is photosynthesis, being slowed considerably by even moderate shortages of nutrients or water. Photosynthesis, however, is not affected until stress becomes more severe (KÖRNER 1991, LUXMORE 1991). Hence, moderate nutrient deficiency or drought can decrease growth (and thus sink strength) without affecting photosynthesis. Decreased utilization of carbon by photosynthetic sinks slows phloem unloading and consequently, phloem transport. This results in an accumulation of carbohydrates in source leaves, which can increase the pool of substrate available for secondary metabolite biosynthesis. Hence, when moderate nutrient and drought stress impose sink-limitations upon growth, secondary metabolite concentrations are predicted to increase (BRYANT & al. 1983, LORIO 1986, HERMS & MATTSON 1992). At very low resource levels (severe light, water, and/or nutrient deficiency), both growth and photosynthesis are highly constrained (BRYANT & al. 1983, WARING & al. 1985). Because of energy and substrate limitation, carbon-based secondary metabolism and herbivore resistance may also decline. The hypothesis has been supported in the case of nutrient availability (e.g. LARSSON & al. 1986, MIHALIAK & al. 1987, BRYANT & al. 1987a,b, WAINHOUSE & al. 1998), moisture availability (ROSS & BERISFORD 1990, DUNN & LORIO 1993, ROTH & al. 1997), low temperature (LINCOLN & LANGENHEIM 1978, APPLETON & VAN STADEN 1989), and shade (LARSSON & al. 1986, BRYANT 1987, WAINHOUSE & al. 1998).
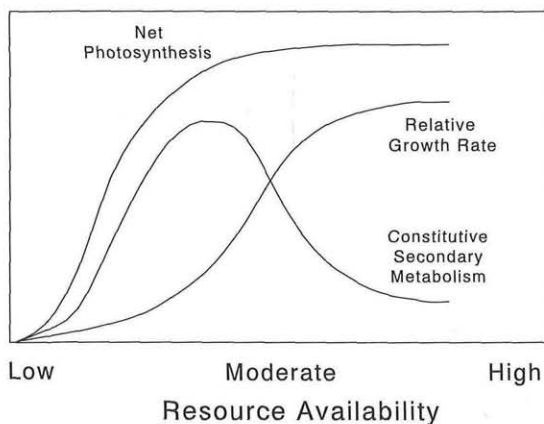

Fig. 1. Postulated nonlinear effects of resource availability on photosynthesis, growth, and constitutive carbon-based secondary metabolism. A positive correlation between growth and secondary metabolism is predicted at low to moderate levels of resource availability. At higher levels of resource availability photosynthesis is not affected, and a negative correlation between growth and secondary metabolism is predicted.

(60)

Studies that found fertilization to increase growth and secondary metabolism (e.g. MCCULLOUGH & KULMAN 1991, BJÖRKMAN & al. 1991,1998) have been deemed inconsistent with the growth/differentiation balance hypothesis because they report a positive correlation between growth and secondary metabolism (HAUKIOJA & al. 1998). However, the parabolic response of secondary metabolism to resource availability predicts explicitly that the trade-off between growth and secondary metabolism will not always result in a negative correlation when the rate of carbon acquisition varies. As resource availability (light, water, and nutrients) increases from low to moderate, photosynthesis also increases. Hence, a positive correlation can occur between growth and secondary metabolism when the plant's carbon budget increases, despite competition for a common resource base. At moderate to high resource levels, where net photosynthesis is close to maximum, the physiological tradeoff becomes evident as a negative correlation between growth and secondary metabolism.

The studies with pine in which fertilization increased growth and foliar terpene concentrations (BJÖRKMAN & al. 1991, 1998, MCCULLOUGH & KULMAN 1991), were conducted on extremely nutrient deficient sites in which tree growth was quite slow. The photosynthetic rates of conifers on nutrient poor sites can increase in response to fertilization (BRIX 1981, LINDER & ROOK 1984). If photosynthesis increased in response to fertilization, the increased carbon budget would result in both increased growth and defense. However, neither study measured photosynthesis, so it is not possible to judge if these studies are truly consistent with the model. LERDAU & al. 1995 did find that fertilization did increase photosynthesis and monoterpene concentration of Douglas-fir (*Pseudotsuga menziesii*). Lorio and his colleagues have studied the relationship between growth, photosynthesis, and terpene biosynthesis in loblolly pine (*Pinus taeda*). They found that when fertilization increased growth without affecting photosynthesis, resin flow declined (WILKENS & al. 1997). On the other hand, when moderate drought stress decreased growth without affecting photosynthesis, resin flow increased (REEVE & al. 1995). But when severe drought stress decreased both growth and photosynthesis, resin flow declined (DUNN & LORIO 1993). Two studies provide direct evidence of quadratic responses of secondary metabolism to stress. LEWINSOHN & al. 1993 and WILKENS & al. 1996 found that water stress and fertilization had quadratic effects on terpene accumulation in grand fir stems (*Abies grandis*), and foliar phenolic concentrations in tomato, respectively. In both cases, secondary metabolite concentrations were highest at the moderate stress level, and low in rapidly growing and severely stressed plants. All of these studies provide indirect evidence for the model depicted in Fig. 1. The best test, however, will quantify growth, photosynthesis, and secondary metabolism in response to at least three levels of water or nutrient availability. I am currently unaware of any published studies that meet these criteria.

Conclusion

Physiological constraints impose limitations on constitutive secondary metabolism and structural reinforcement in rapidly growing plants, resulting in a trade-off between growth and defense. Plants have responded to this dilemma through the evolution of specialized life history strategies and/or adaptive phenotypic plasticity. Intense competition selects for rapid growth in favorable environments, thereby prohibiting the expression of high quantitative levels of defense. Adaptive strategies, however, can maximize the effectiveness of a minimal defensive investment. Increased secondary metabolism is favored when that investment enhances plant fitness to a degree greater than would the same resource investment in an alternative process such as storage or growth. In resource-limited environments, correlated selection by the abiotic environment, competition, and herbivory has selected for traits that maximize the retention of acquired resources, including high levels of carbon-based secondary metabolites which enhance herbivore resistance and stress tolerance in harsh environments (HERMS & MATTSON 1992).

References

APPLETON M.R. & VAN STADEN J. 1989. The relationship between season, growth and isoprenoid biosynthesis in *Parthenium argentatum*. - J. Plant Physiol. 134:524-532.

BAZZAZ F.A., CHIARIELLO N.R., COLEY P.D. & PITELKA L.F. 1987. Allocating resources to reproduction and defense. - BioScience 37:58-67.

BJÖRKMAN C., LARSSON S. & GREF R. 1991. Effects of nitrogen fertilization on pine needle chemistry and sawfly performance. - Oecologia 86:202-209.

— , KYTÖ M, LARRSON S. & NIEMELÄ P. 1998. Different responses of two carbon-based defences in Scots pine needles to nitrogen fertilization. – Ecoscience 5:502-507.

BRIX H. 1981. Effects of nitrogen fertilizer source and application rates on foliar nitrogen concentration, photosynthesis, and growth of Douglas-fir. - Can. J. For. Res. 11:755-780.

BRYANT J.P., CHAPIN F.S. III & KLEIN D.R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. - Oikos 40:357-368.

— 1987. Feltleaf willow-snowshoe hare interactions: Plant carbon/nutrient balance and floodplain succession. - Ecology 68:1319-1327.

— , CHAPIN F.S. III, REICHARDT P. & CLAUSEN T. 1987a. Response of winter chemical defense in Alaska paper birch and green alder to manipulation of plant carbon/nutrient balance. - Oecologia 72:510-514.

— , CLAUSEN T.P., REICHARDT P.B., McCARTHY M.C. & WERNER R.A. 1987b. Effect of nitrogen fertilization upon the secondary chemistry and nutritional value of quaking aspen (*Populus tremuloides* Michx.) leaves for the large aspen tortrix (*Choristoneura conflictana* (Walker)). - Oecologia 73:513-517.

BUSSOTTI F., GRAVANO E., GROSSONI P. & TANI C. 1998. Occurrence of tannins in leaves of beech trees (*Fagus sylvatica*) along an ecological gradient, detected by histochemical and ultrastructural analyses. - New Phytol. 138:469-479.

CHAPIN F.S. III, AUTUMN K. & PUGNAIRE F. 1993. Evolution of suites of traits in response to environmental stress. – Am. Nat. 142:78-92.

CHUNG H.-H. & BARNES R.L. 1977. Photosynthate allocation in *Pinus taeda*. I. Substrate requirements for synthesis of shoot biomass. - Can. J. For. Res. 7:106-111.

(62)

COLEY P.D. 1980. Effects of leaf age and plant life history patterns on herbivory. - Nature 284:545-546.

— , BRYANT J.P. & CHAPIN F.S. III. 1985. Resource availability and plant antiherbivore defense. - Science 230:895-899.

DA CUNHA A. 1987. The estimation of L-phenylalanine ammonia-lyase shows phenylpropanoid biosynthesis to be regulated by L-phenylalanine supply and availability. - Phytochemistry 26:2723-2727.

DALE J.E. 1988. The control of leaf expansion. - Annu. Rev. Plant Physiol. Plant Mol. Biol. 39:267-295.

DICKSON R.E. 1991. Assimilate distribution and storage. – In: RAGHAVENDRA A.S. (Ed.), Physiology of trees, pp. 51-85. – John Wiley & Sons, Inc. New York.

DUNN J.P. & LORIO P.L. JR. 1993. Modified water regimes affect photosynthesis, xylem water potential, cambial growth, and resistance of juvenile *Pinus taeda* L. to *Dedroctonus frontalis* (Coleoptera: Scolytidae). - Environ. Entomol. 22:948-957.

ELLE E., VAN DAM N.M. & HARE J.D. 1999. Cost of glandular trichomes, a "resistance" character in *Datura wrightii* Regel (Solonaceae). – Evolution 53:22-35.

FOWLER N. 1986. The role of competition in plant communities in arid and semiarid regions. - Annu. Rev. Ecol. Syst. 17:89-110.

FRANCIS D. 1998. The cell cycle and plant growth. – In: LAMBERS H, POORTER H. & VAN VUUREN M.M.I. (Eds.), Inherent variation in plant growth. Physiological mechanisms and ecological consequences, pp. 5-20. – Backhuys Publishers. Leiden, The Netherlands.

GERSHENZON J. 1994. Metabolic costs of terpenoid accumulation in higher plants. - J. Chem. Ecol. 20:1281-1328.

GRUBB P.J. 1986. Sclerophylls, pachyphylls and pyncophylls: The nature and significance of hard leaf surfaces. - In: JUNIPER B. & SOUTHWOOD R. (Eds.), Insects and the plant surface, pp. 137-150. - Edward Arnold. London.

GULMON S.L. & MOONEY H.A. 1986. Costs of defense and their effects on plant productivity. - In GIVNISH T.J. (Ed.), On the economy of plant form and function, pp. 681-698. - Cambridge Univ. Press. Cambridge.

HAN K. & LINCOLN D.E. 1994. The evolution of carbon allocation to plant secondary metabolites: a genetic analysis of cost in *Diplacus aurantiacus*. - Evolution 48:1550-1563.

HARPER J.L. & WHITE J. 1974. The demography of plants. - Annu. Rev. Ecol. Syst. 5:419-463.

— 1989. The value of a leaf. - Oecologia 80:53-58.

HAUKIOJA E., OSSIPOV V., KORICHEVA J., HONKANEN T., LARSSON S. & LEMPA K. 1998. Biosynthetic origin of carbon-based secondary compounds: Cause of variable responses of woody plants to fertilization? – Chemoecology 8:133-139.

HERMS D.A. & MATTSON W.J. 1992. The dilemma of plants: To grow or defend. - Quart. Rev. Biol. 67:283-335.

HUSTON M. & SMITH T. 1987. Plant succession: Life history and competition. - Am. Nat. 130:168-198.

HWANG S.Y. & LINDROTH R.L.1997. Clonal variation in foliar chemistry of aspen: Effects on gypsy moth and forest tent caterpillar. - Oecologia 111:99-108.

KÖRNER CH. & PELAEZ MENENDEZ-RIEDL S. 1989. The significance of developmental aspects in plant growth analysis. – In: LAMBERS H, CAMBRIDGE M.L., KONINGS H. & PONS T.L. (Eds.), Causes and consequences of variation and productivity of higher plants, pp. 141-157. – SPB Academic Publishing bv. The Hague, The Netherlands.

— 1991. Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. - Funct. Ecol. 5:162-173.

KOZLOWSKI T.T. 1992. Carbohydrate sources and sinks in woody plants. - Bot. Rev. 58:107-222.

KURSAR T.A. & COLEY P.D. 1991. Nitrogen content and expansion rate of young leaves of rain forest species: Implications for herbivory. - Biotropica 23:141-150.

LAMBERS H. & POORTER H. 1992. Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. – Adv. Ecol. Res. 23:187-261.

LANDRY L.G., CHAPPLE C.C.S. & LAST R.L. 1995. Arabidopsis mutants lacking phenolic sunscreens exhibit enhanced ultraviolet-B injury and oxidative damage. – Plant Physiol. 109:1159-1166.

LARSON R.A. 1995. Plant defenses against oxidative stress. – Arch. Insect Biochem. Physiol. 29:175-186.

LARSSON S., WIREN A., LUNDGREN L. & ERICSSON T. 1986. Effects of light and nutrient stress on leaf phenolic chemistry in *Salix dasyclados* and susceptibility to *Galerucella lineola* (Coleoptera). - Oikos 47:205-210.

LERDAU M., MATSON P., FALL R. & MONSON R. 1995. Ecological controls over monoterpene emissions from douglas-fir (*Pseudotsuga menziesii*). - Ecology 76:2640-2647.

LEWINSOHN E., GIJZEN M., MUZIKA R.M., BARTON K. & CROTEAU R. 1993. Oleoresinosis in grand fir (*Abies grandis*) saplings and mature trees. Modulation of this wound response by light and water stresses. - Plant Physiol. 101:1021-1028.

LINCOLN D.E. & LANGENHEIM J.H. 1978. Effect of light and temperature on monoterpenoid yield and composition in *Satureja douglasii*. - Biochem. Syst. Ecol. 6:21-32.

LINDER S. & ROOK D.A. 1984. Effects of mineral nutrition on carbon dioxide exchange and partitioning of carbon in trees. - In: BOWEN G.D. & NAMBIAR E.K.S. (Eds.), Nutrition of plantation trees, pp. 211-236. - Academic Press. London.

LORIO P.L. JR. 1986. Growth-differentiation balance: A basis for understanding southern pine beetle-tree interactions. - For. Ecol. Manage. 14:259-273.

LUCKNER M. & NOVER L. 1977. Expression of secondary metabolism: An aspect of cell specialization of microorganisms, higher plants, and animals. - In: LUCKNER M., NOVER L. & BÖHM H. (Eds.), Secondary metabolism and cell differentiation, pp. 2-102. - Springer-Verlag. Berlin.

—— 1980. Expression and control of secondary metabolism. - In: BELL E.A. & CHARLWOOD B.V. (Eds.), Secondary plant products. Encyclopedia of plant physiology, New Series. Vol. 8, pp. 23-63. - Springer-Verlag. Berlin.

LUXMORE R.J. 1991. A source-sink framework for coupling water, carbon, and nutrient dynamics of vegetation. - Tree Physiol. 9:267-280.

MARCELIS L.F.M. 1996. Sink strength as a determinant of dry matter partitioning in the whole plant. - J. Exp. Bot. 47:1281-1291.

MARGNA U., MARGNA E. & VAINJARV T. 1989. Influence of nitrogen nutrition on the utilization of L-phenylalanine for building flavonoids in buckwheat seedling tissues. - J. Plant Physiol. 134:697-702.

MARGOLIS H.A., DELANEY S., VEZINA L.-P. & BELLEFLEUR P. 1991. The partitioning of ^{14}C between growth and differentiation within stem-deformed and healthy black spruce seedlings. - Can. J. Bot. 69:1225-1231.

MCCULLOUGH D.G. & KULMAN H.M. 1991. Effects of nitrogen fertilization on young jack pine (*Pinus banksiana*) and on its suitability as a host for jack pine budworm (*Choristoneura pinus*) (Lepidoptera: Tortricidae). - Can. J. For. Res. 21:1447-1458.

MEINZER F.C., WISDOM C.S., GONZALEZ-COLOMA A., RUNDEL P.W. & SCHULTZ L.M. 1990. Effects of leaf resin on stomatal behaviour and gas exchange of *Larrea tridentata* (DC.) Cov. - Funct. Ecol. 4:579-584.

MIHALIAK C.A., COUVET D. & LINCOLN D.E. 1987. Inhibition of feeding by a generalist insect due to increased volatile leaf terpenes under nitrate-limiting conditions. - J. Chem. Ecol. 13:2059-2067.

MUIR M. 1995. The cost of reproduction to the clonal herb *Asarum canadense* (wild ginger). – Can. J. Bot. 73:1683-1686.

NEUMANN G., EL-ASCHKER A. & SCHWEMMLE B. 1991. L-phenylalanine ammonia-lyase and chalcone synthase in seedlings of *Oenothera*: Plasmotype dependent regulation and tissue specific distribution. - J. Plant Physiol. 138:263-269.

NEWELL E.A. 1991. Direct and delayed costs of reproduction in *Aesculus californica*. – J. Ecol. 79:365-378.

PATRICK J.W. 1988. Assimilate partitioning in relation to crop productivity. - HortScience 23:33-40.

(64)

RAZAL R.A., ELLIS S., SINGH S., LEWIS N.G. & TOWERS G.H. N. 1996. Nitrogen recycling in phenylpropanoid metabolism. - Phytochemistry 41:31-35.

REEVE J.D., AYRES M.P. & LORIO P.L. JR. 1995. Host suitability, predation, and bark beetle population dynamics. - In: CAPPUCCINO N. & PRICE P.W. (Eds.), Population dynamics: New approaches and synthesis, pp. 339-357. - Academic Press. San Diego, Ca.

ROSS D.W. & BERISFORD C.W. 1990. Nantucket pine tip moth (Lepidoptera: Tortricidae): Response to water and nutrient status of loblolly pine. - For. Sci. 36:719-733.

ROTH S., MCDONALD E.P. & LINDROTH R.L. 1997. Atmospheric CO_2 and soil water availability: Consequences for tree-insect interactions. - Can. J. For. Res. 27:1281-1290.

SCHEINER S.M. 1993. Genetics and evolution of phenotypic plasticity. – Annu. Rev. Ecol. Syst. 24:35-68.

TILMAN D. 1990. Constraints and tradeoffs: Toward a predictive theory of competition and succession. - Oikos 58:3-15.

WAINHOUSE D., ASHBURNER R., WARD E., & ROSE J. 1998. The effect of variation in light and nitrogen on growth and defence in young Sitka spruce. – Funct. Ecol. 12:561-572.

WARDLAW I.F. 1990. The control of carbon partitioning in plants. - New Phytol. 116:341-381.

WAREING P.F. & PATRICK J. 1975. Source-sink relations and the partition of assimilates in the plant. - In: COOPER J.P. (Ed.), Photosynthesis and productivity in different environments. - Cambridge Univ. Press. Cambridge.

WARING R.H., MCDONALD A.J.S., LARSSON S., ERICSSON T., WIREN A., ARWIDSSON E., ERICSSON A. & LOHAMMAR T. 1985. Differences in chemical composition of plants grown at constant relative growth rates with stable mineral nutrition. - Oecologia 66:157-160.

WIERMANN R. 1981. Secondary plant products and cell and tissue differentiation. -In: CONN E.E. (Ed.), The biochemistry of plants, Volume 7: Secondary plant products, pp. 85-116. - Academic Press. New York.

WILKENS R.T., SPOERKE J.M. & STAMP N.E. 1996. Differential responses of growth and two soluble phenolics of tomato to resource availability. - Ecology 77:247-258.

— , AYRES M.P., LORIO P.L. JR. & HODGES J.D. 1997. Environmental effects on pine tree carbon budgets and resistance to bark beetles. – In: MICKLER R.A. & FOX S. (Eds.), The productivity and sustainability of southern forest ecosystems in a changing environment, pp. 591-616. – Springer-Verlag. New York.

WOLSWINKEL P. 1985. Phloem unloading and turgor-sensitive transport: factors involved in sink control of assimilate partitioning. - Physiol. Plant. 65:331-339.