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CO_2 assimilation of primary and regrowth foliage of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.): response to defoliation

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Summary. The CO_2 assimilation of primary foliage of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.), and of regrowth foliage produced in response to simulated insect defoliation, was measured throughout the season by infrared gas analysis: parallel measurements of leaf conductance were obtained by ventilated diffusion porometry. The rate of net photosynthesis, measured at a quantum flux density of 1,150 μmol $m^{-2}s^{-1}$, of primary foliage of both species increased from slightly negative values to about 5 μmol $m^{-2}s^{-1}$ by early June. Thereafter the rate of photosynthesis of maple slowly declined to about 4 μmol $m^{-2}s^{-1}$ before onset of a senescent decline in early September, while that of oak slowly increased to about 8 μmol $m^{-2}s^{-1}$ before onset of senescence. Manual defoliation to simulate insect attack in mid-June elicited refoliation proportional to the severity of defoliation in early July. After 100% defoliation, fully expanded regrowth foliage of maple, but not of oak, had a rate of net photosynthesis from mid-July through September that was about 50% higher than in the primary foliage of undefoliated trees. A 30 to 60% enhancement of photosynthesis of residual primary foliage remaining on 50 and 75% defoliated trees during July was also observed. The seasonal patterns of CO_2 exchange of primary and regrowth foliage, and the enhancement of CO_2 assimilation in residual foliage, was paralleled by similar changes in leaf conductance to water vapour.

Carbon budgets of leaf canopies of each species showed that the net assimilation of the leaf canopy of both species ranged from 19 to 67% more than what would have been expected solely from replacement of leaf area. This response was greater in maple than in oak, presumably a reflection of the high rate of CO_2 assimilation of regrowth maple foliage compared with that of the undefoliated control in maple.

The increased CO_2 assimilation of regrowth maple foliage and the increases in CO_2 assimilation of residual primary foliage after defoliation offer evidence that heretofore unanticipated physiological mechanisms may be important to perennial species coping with herbivory.

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Introduction

Periodic defoliation of deciduous hardwood forests by phytophagous insects may have important consequences to species composition of the forest (Stephens 1971; Campbell and Sloan 1977), and may cause death of species intolerant of leaf loss (Kulman 1971; Campbell and Sloan 1977). Insect defoliation of trees can alter the light environment (Collins 1969) and the nutrient and water relations (Stephens et al. 1972; Kitchell et al. 1979; Swank et al. 1979) within the forest ecosystem. Thus, defoliating insects can play an important role in regulating competition, succession, death, nutrient cycling and long term productivity in forest ecosystems (Mattson and Addy 1975).

In the northeastern U.S.A., the climax vegetation is red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.) (Stephens and Waggoner 1980). The primary defoliators of this vegetation are gypsy moth (*Lymantria dispar* L.) and elm spanworm (*Ennomos subsignarius* Hbn.). Defoliation usually occurs in mid-June with little subsequent leaf loss, and whole sections of the forest are usually totally defoliated. The lepidopterous larvae preferentially defoliate red oak compared with red maple (Campbell and Sloan 1977; Stephens 1981).

Compared to knowledge of the impact of the herbivore, little is known of how deciduous trees adapt to the stress of insect defoliation. Our previous research on the response of red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.) to simulated insect defoliation (Heichel and Turner 1976) showed that severe defoliation hastened refoliation in the same season and budbreak in successive seasons compared with zero or mild defoliation. Species differences in the numbers of regrowth leaves formed, areas of individual regrowth leaves, and canopy growth in successive years of defoliation were also evident. The resistance to water vapour of regrowth foliage of red maple was much less than that of primary foliage on undefoliated trees, while no such difference was evident in red oak (Turner and Heichel 1977). This latter result suggested that leaf properties associated with CO_2 assimilation may have consequences in the growth and survival of deciduous trees when defoliated. Therefore, we examined the CO_2 assimilation characteristics of foliage from defoliated and undefoliated trees and developed simple carbon budgets of leaf canopies to demonstrate the importance of photosynthetic rates and replacement of leaf area in response to defoliation in both maple and oak.

Materials and methods

The physiological responses of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.) to insect feeding were investigated by controlled defoliations in the field. Insect attack was simulated by manually defoliating 9 to 11 yr old trees of red oak and 13 to 15 yr old trees of red maple that were about 8 m tall, had stem diameters of 5 to 9 cm, and were growing in monospecific, open stands in 0.001 ha plots at Lockwood Farm, Mt. Carmel, Connecticut. Scaffolding allowed access to the tree crowns. Leaf emergence began on 30 April in maple and 6 May in oak; the mean date of 50% budbreak was 2 May in maple and 9 May in oak. Three trees of each species were subjected to either 50, 75, or 100% manual defoliation between 13 and 16 June by removing every other leaf, three of every four leaves, or all leaves on every branch of each tree. Defoliation was effected by removal of leaf blades, but without removal of the petiole or damage to dormant buds. Three undefoliated trees of each species served as controls. The fully defoliated trees began to refoliate on 2 and 3 July in maple and oak, respectively, and the 75% defoliated trees a few days later. The mean date of refoliation for both species was 7 July (Heichel and Turner 1976). The leaves began to change colour on 28 September and the mean date of 50% senescence, i.e. when 50% of the leaves per tree were no longer green, was 14 and 17 October in maple and oak, respectively.

Leaf conductance, net photosynthesis, and dark respiration of primary (original) foliage and regrowth foliage produced in response to controlled defoliation were measured at frequent intervals from emergence to senescence to establish seasonal patterns. Leaves at a range of quantum flux densities were randomly sampled in the upper half of the canopy from the three replicate trees of each treatment. The abaxial conductance of small leaves for the 3 weeks encompassing emergence was measured with a small-aperture diffusion porometer (Byrne et al. 1970). During the rest of the season a porometer exposing 2.85 cm^2 of the abaxial surface was used (Turner and Parlange 1970). Neither species had stomata on the adaxial surface. Both porometers were initially cross-calibrated and the calibrations remained unchanged during use. Measurements of leaf conductance were confined to periods of bright sunshine or uniform cloud cover between 0900 and 1300. Between observations the porometers were shaded and for 15 s before each measurement the leaf was shaded to equilibrate leaf and porometer temperatures (Morrow and Slatyer 1971). This brief shading is insufficient to induce stomatal closure in maple and oak (Woods and Turner 1971). Immediately after measurements of conductance, the quantum flux density incident on the adaxial epidermis was measured.

Measurements of photosynthesis and respiration of primary foliage between 3 May and 7 June were made on twigs excised in the field beneath air-free distilled water and transported to the laboratory. All CO_2 exchange measurements were completed within 45 min of excision. Use of excised twigs was necessary because frequent precipitation early in the season precluded the use of gas analysis equipment in the field. Meteorological conditions during the experiments were previously reported (Turner and Heichel 1977). After 7 June nondestructive measurements of CO_2 assimilation were made on attached foliage from a field-based portable laboratory. Entire leaves, groups of leaves, or sections of leaves were enclosed in a 150 cm^3 acrylic plastic chamber for CO_2-exchange measurements that was described previously (Heichel and Turner 1972). The rates of photosynthesis and respiration were computed from the CO_2 concentrations in the input and exit gas streams, net flow through the chamber, and leaf area. To ensure a fast response of the infrared analyzer to CO_2 exchange, the air in the chamber was recirculated at the rate of 9 litre min^{-1} or one chamber volume per s. Net flow through the chamber ranged from 0.67 to 2.3 litre min^{-1}, depending upon leaf activity.

All CO_2 exchange measurements were made at 310 ± 3 µl CO_2 $litre^{-1}$ at 0, 160, 320, 640, and 1,150 µmol $m^{-2}s^{-1}$ photosynthetically active radiation provided by an incandescent lamp attenuated by neutral density screens and an infrared reflecting filter. Respiration was measured on darkened leaves before measuring net photosynthesis. Leaf temperature was maintained at 27° C, and was monitored by a fine-wire thermocouple appressed to the abaxial surface and connected to a recording potentiometer. Vapour pressure in the chamber was not measured or controlled. Leaf areas were measured by tracing the outline of the foliage in the chamber on thin cardboard, followed by area determinations of foliage cutouts with a Hayashi Denko AAM-5[1] automatic area meter.

Results

Response of CO_2 assimilation to light

One-day-old leaves of both red maple and red oak had insufficient photosynthesis activity to maintain a positive net carbon balance at any quantum flux density (Fig. 1A, B). However, the net CO_2 assimilation of these emerging leaves varied with quantum flux density, indicating that some photosynthetic activity occurred. On day 5

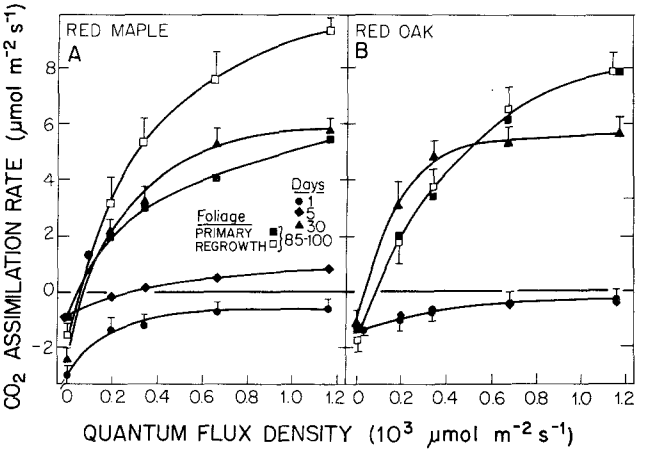

Fig. 1 A, B. Response to quantum flux density of CO_2 assimilation of primary foliage of **A** red maple and **B** red oak at various days after leaf emergence and for regrowth foliage measured 85 to 100 days after the primary foliage emerged (i.e. 25 to 40 days after emergence of regrowth foliage). Stomata of maple and oak 1 and 5 days after emergence are nonresponsive to light; mean leaf conductance was 0.06 cm s^{-1} for foliage on each species on each of these dates

[1] Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by the USDA and does not imply its approval to the exclusion of other products or vendors that may also be suitable

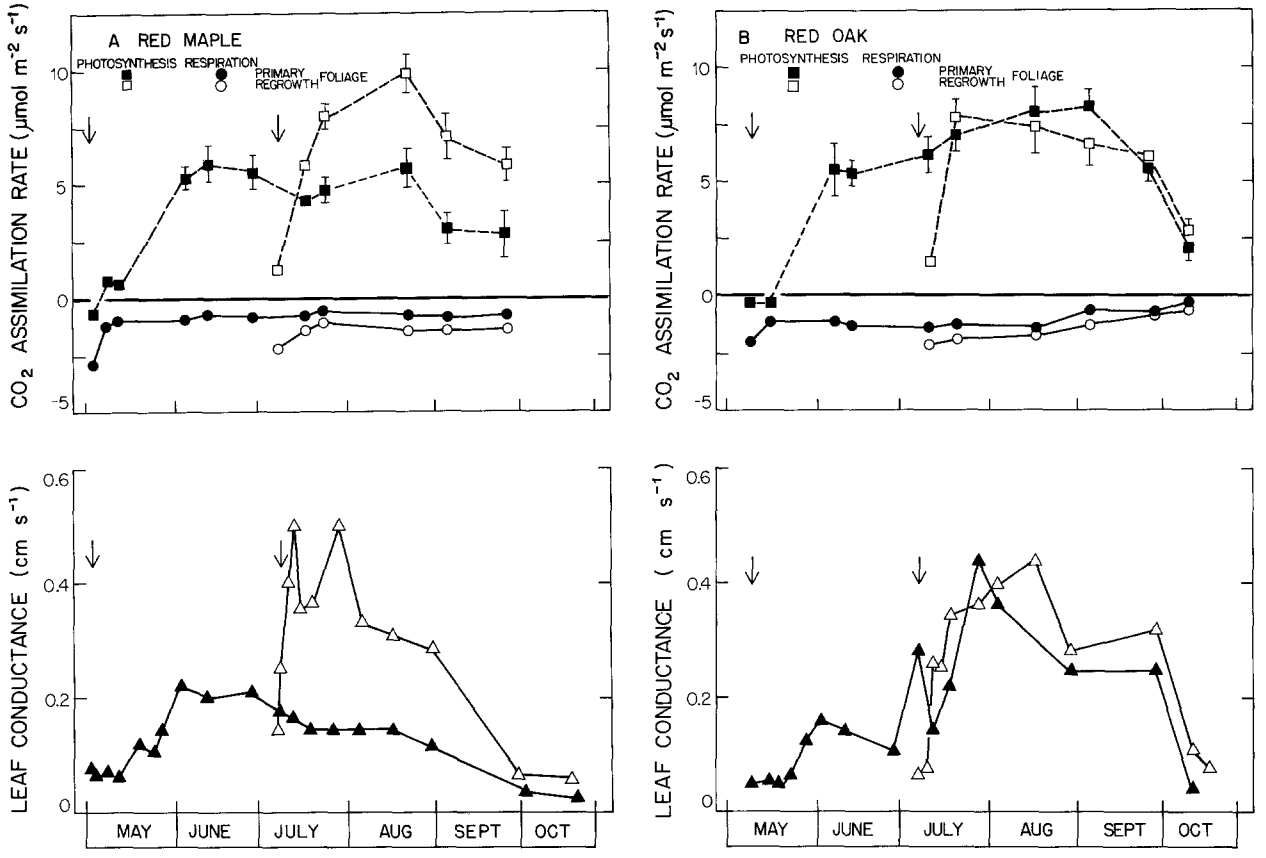

Fig. 2A, B. Seasonal patterns of CO_2 assimilation (upper panel) and leaf conductance (lower panel) of primary and regrowth foliage of **A** red maple and **B** red oak. CO_2 assimilation was measured at 310 μl CO_2 $litre^{-1}$, 27° C, and 1,150 μmol $m^{-2}s^{-1}$. Values of leaf conductance at ambient temperature and CO_2, and at 1,150 μmol $m^{-2}s^{-1}$ were incorporated from measurements obtained at a range of quantum flux densities (see Turner and Heichel 1977). Vertical bars signify ± standard error of the mean of three replicates; standard errors for dark respiration (<0.05 μmol $m^{-2}s^{-1}$) are omitted. Vertical arrows signify dates of 50% budbreak for primary and regrowth foliage

after emergence maple leaves had positive CO_2 assimilation rates at intermediate light whereas CO_2 assimilation of oak was negative at all quantum flux densities as on day 1. Thirty days after emergence maple and oak leaves responded similarly to quantum flux density except that light saturation occurred at lower quantum flux densities in oak than in maple. Eighty five to 100 days after leaf emergence, the maple foliage had a similar response to light as at 30 days after emergence (Fig. 1A), but the primary foliage of oak had a greater CO_2 assimilation rate than that of maple at the highest quantum flux density measured (Fig. 1A, B).

Regrowth foliage was fully developed on 100% defoliated maple and oak by 70 to 80 days after emergence of the primary leaves. This enabled comparisons of CO_2 assimilation of the two foliage types at similar times of the growing season. Twenty-five to 40 days after the leaves emerged, CO_2 assimilation rates of regrowth maple foliage were higher than those of primary foliage at all quantum flux densities above zero (Fig. 1A). In contrast, the light responses of CO_2 assimilation in regrowth and primary oak foliage were similar at all quantum flux densities (Fig. 1B).

Seasonal patterns of CO_2 assimilation

It is clear from the light response curves for photosynthesis that the CO_2 assimilation of red maple at 1,150 μmol $m^{-2}s^{-1}$ was negative or low in emerging primary leaves, but rates of 5 μmol $m^{-2}s^{-1}$ were attained in early June and maintained for nearly 80 days before a decline of about 50% in September and October (Fig. 2A). Net photosynthesis of regrowth foliage at 50% budbreak was initially only 20% that of primary foliage from undefoliated trees. However, CO_2 assimilation rates of regrowth foliage significantly ($P<0.05$) exceeded those of primary foliage within 10 days and remained significantly greater for the rest of the season (Fig. 2A). Dark respiration of emerging primary and regrowth leaves at 50% budbreak was double that of expanded leaves later in the season. Respiration rates of regrowth foliage were significantly ($P<0.05$) higher than those of primary foliage by about 20% throughout the season. The patterns of net photosynthesis of primary and of regrowth foliage mirrored those of leaf conductance throughout the growing season.

The seasonal pattern of CO_2 assimilation by primary and regrowth foliage of red oak at 1,150 μmol $m^{-2}s^{-1}$ (Fig. 2B) is very similar to that of red maple. However, photosynthetic rates of oak tended to increase from mid-June through mid-September, while those of red maple gradually declined. Thus, photosynthetic CO_2 assimilation of primary foliage of oak was significantly ($P<0.05$) greater than that of maple throughout much of the season. However, the photosynthetic rates of the regrowth foliage of red oak were less than that of red maple during August

Table 1. CO_2 assimilation (μmol $m^{-2}s^{-1}$) and leaf conductance (cm s^{-1}) in light (1,150 and 800 μmol $m^{-2}s^{-1}$, respectively) and CO_2 efflux in darkness of foliage of undefoliated trees compared with that of primary foliage remaining on partly defoliated trees. Measurements were made between 10 and 24 July for red oak and on 26 and 27 July for red maple. Defoliation treatments were imposed between 13 and 16 June. Values are mean ± standard error of eight replicates

	Red maple				Red oak			
	light	% of control	dark	% of control	light	% of control	dark	% of control
CO_2assimilation								
Undefoliated	4.8 ±0.6	100	0.6±0.06	100	5.7 ±0.6	100	1.3±0.1	100
75% defoliation	6.5 ±0.8	135	0.9±0.06	150	7.1 ±0.7	125	1.6±0.1	123
50% defoliation	8.4 ±0.8	175	1.6±0.1	266	8.8 ±0.8	154	2.1±0.2	162
Leaf conductance								
Undefoliated	0.14±0.01	100	–	–	0.24±0.02	100	–	–
75% defoliation	0.15±0.01	107	–	–	0.22±0.03	97	–	–
50% defoliation	0.18±0.01	136	–	–	0.35±0.03	146	–	–

and September. Rates of dark respiration of regrowth oak foliage were greater than those of primary foliage, in conformity with the results on maple. As in maple, the similarity in CO_2 assimilation rates of the two foliage types on red oak was associated with the similarities in leaf conductance between the foliage types (Fig. 2B).

The stimulation of photosynthetic CO_2 assimilation by defoliation (Fig. 1, 2) is not limited solely to regrowth foliage on completely defoliated maple. It also occurred in residual primary foliage of partly defoliated oak and maple (Table 1). Compared to CO_2 assimilation by primary foliage of undefoliated trees, photosynthesis of primary foliage was significantly ($P<0.05$) enhanced about 130% in 75% defoliated maple and oak and about 165% in 50% defoliated trees. Dark respiration of primary foliage was significantly ($P<0.05$) increased by 23 to 50% in 75% defoliated trees and by 62 to 166% in 50% defoliated trees. Leaf conductance of primary foliage remaining after defoliation was also enhanced (Table 1); the enhancement was significant in the 50% but not for the 75% defoliated trees of each species.,

Discussion

The responses of CO_2 assimilation to light (Fig. 1) and the seasonal patterns of CO_2 assimilation (Fig. 2) clearly show the importance of increased photosynthesis of primary and regrowth foliage in reducing the adverse effects of defoliation. The patterns of CO_2 assimilation of primary and regrowth foliage closely mirrored leaf conductance (Fig. 2) and confirm conclusions drawn previously from stomatal resistance measurements (Turner and Heichel 1977). Enhanced photosynthetic assimilation in regrowth foliage of perennial grasses (Caldwell et al. 1981) and in remnant primary foliage of a perennial legume (Hodgkinson 1974) following defoliation has also been observed. This suggests that such a photosynthetic enhancement may be a common response in perennial species subject to leaf loss.

Dark respiration of emerging primary and regrowth leaves of maple and oak was frequently greater than that of fully expanded primary and regrowth foliage (Fig. 1, 2). This clearly reflects the greater synthetic activity in young compared with more mature organs. Respiration rates of expanded foliage, which largely reflect maintenance costs, were greater for regrowth than for primary foliage of both species (Fig. 2). This is consistent with our observation that expanded regrowth foliage had about a 25% greater nitrogen concentration than comparable primary foliage (data not shown), and the dependence of maintenance respiration on protein concentration (Penning de Vries 1975).

The impact of changes in CO_2 assimilation rates and quantity of leaf area renewed resulting from defoliation can be illustrated by using previous (Heichel and Turner 1976) and present results to develop carbon budgets for leaf canopies of control and defoliated trees (Tables 2, 3). These budgets were calculated to exemplify days 85 through 100 after emergence, the part of the season when differences in CO_2 assimilation between primary and regrowth foliage were the greatest (Fig. 2). The budgets presume that all leaves in the canopy were equally exposed to light, but do not consider branch or trunk respiration rates or the cost of new foliage. These are necessary oversimplifications that should not affect the general concepts arising from the calculations. Furthermore our calculations are based on the assumption that all leaves are on average at a quantum flux density of half full sunlight. Since the differences in photosynthesis between primary and regrowth foliage were similar at all quantum flux densities in both species, variation in mean canopy light will not alter the conclusions.

Net assimilation after refoliation clearly decreased with severity of defoliation, and no treatment approached the levels observed in the undefoliated trees. However, both species were consistent in showing a greater net assimilation capability after refoliation than would be anticipated solely from knowledge of leaf removal (Tables 2, 3). It is instructive to consider the roles of leaf area regeneration and leaf CO_2 assimilation in this response.

Fifty percent defoliated trees replaced little leaf area, ended the season with about 48% of control leaf area, but because of the increased assimilation rate of the remaining foliage, had about 77% of control assimilation capacity. Seventy-five percent defoliated trees averaged about 39%, and 100% defoliated trees about 32%, of control leaf area after refoliation, but again because of the enhanced assimilation of the regrowth or remaining foliage, both treatments retained about 48% of control assimilation capacity. Net assimilation capacity of the canopy over all treatments after refoliation ranged from 19 to 67% greater than what would be expected solely on the basis of leaf area replacement.

Table 2. Daily carbon budgets for leaf canopies of red maple for days 85 to 110 in July and August. Leaf area data (mean ± standard error of 3 replicates) are taken from Heichel and Turner (1976). Gas exchange data are taken from Fig. 2 and Table 1, and adjusted to a 14 h photoperiod. For ease of calculation we assume that photosynthesis and respiration rates of regrowth foliage on 50 and 75% defoliated trees are similar to those of 100% defoliated trees shown in Fig. 2

Foliage type	Variable	Units	Defoliation treatment			
			0	50	75	100
Primary	Leaf area	(dm^2/tree)	753 ±70	327 ±39	179 ±28	0
	Photosynthesis	(g CO_2/day)	79.8± 7.0	60.2± 7.0	25.2± 4.2	–
	Respiration	(g CO_2/day)	8.0± 1.0	8.0± 1.0	3.0± 0.4	–
	Daily carbon fixed	(g CO_2/day)	71.8	52.2	22.2	0
Regrowth	Leaf area	(dm^2/tree)	0	14 ±11	57 ±41	251 ±36
	Photosynthesis	(g CO_2/day)	–	2.8± 1.4	9.8± 7.0	44.8± 7.0
	Respiration	(g CO_2/day)	–	0.2± 0.1	1.0± 0.6	4.0± 0.6
	Daily carbon fixed	(g CO_2/day)	0	2.6	8.8	40.8
	Net assimilation	(g CO_2/day)	71.8	54.8	31.0	40.8
	% of control		100	76	43	57
	% from regrowth foliage		0	5	40	100
	Leaf area after refoliation	(dm^2/tree)	753 ±70	341 ±39	236 ±35	251 ±36
	% as regrowth		0	4	24	100
	% of control		100	45	31	33

Table 3. Daily carbon budgets for leaf canopies of red oak for days 85 to 110 in July and August. Leaf area data (mean ± standard error of 3 replicates) are taken from Heichel and Turner (1976). Gas exchange data are taken from Fig. 2 and Table 1, and adjusted to a 14 h photoperiod. For ease of calculation we assume that photosynthesis and respiration rates of regrowth foliage on 50 and 75% defoliated trees are similar to those of 100% defoliated trees shown in Fig. 2

Foliage type	Variable	Units	Defoliation treatment			
			0	50	75	100
Primary	Leaf area	(dm^2/tree)	659 ±30	330 ±88	178 ±71	0
	Photosynthesis	(g CO_2/day)	86.6± 4.2	64.4 ±16.8	28.0±11.2	–
	Respiration	(g CO_2/day)	18.0± 1.0	11.0 ± 3.0	4.0± 2.0	–
	Daily carbon fixed	(g CO_2/day)	68.6	53.4	24.0	0
Regrowth	Leaf area	(dm^2/tree)	0	4 ± 4	132 ±51	182 ±96
	Photosynthesis	(g CO_2/day)	–	0.7 ± 0.7	22.4± 8.4	32.2±15.4
	Respiration	(g CO_2/day)	–	0.14±0.14	8.0± 1.0	7.0± 2.8
	Daily carbon fixed	(g CO_2/day)	0	0.56	14.4	25.2
	Net assimilation	(g CO_2/day)	68.6	54.0	38.4	25.2
	% of control		100	79	56	37
	% from regrowth foliage		0	1	60	100
	Leaf area after refoliation	(dm^2/tree)	659 ±30	334 ±88	310 ±70	182 ±86
	% as regrowth		0	1	43	100
	% of control		100	51	47	28

This response was greater in maple than in oak, apparently because of the large differences in CO_2 assimilation observed between control and regrowth maple foliage (Fig. 2A). Clearly the changes of CO_2 assimilation in residual primary foliage (Table 1) and in regrowth foliage (Fig. 2) can significantly contribute to amelioration of defoliation-induced reductions in canopy assimilation.

The contribution of the regrowth foliage to the daily assimilation varied with the extent of refoliation. For 50% defoliated maple and oak the proportion of the daily carbon budget attributable to regrowth foliage ranged from 1 to 5% and very closely resembled the proportion of leaf canopy comprised of regrowth foliage. At this level of defoliation, the alteration of leaf photosynthesis and respiration of regrowth and residual primary foliage apparently had little net impact on the canopy carbon budget. The proportion of the carbon budget of 75% defoliated maple and oak attributable to regrowth foliage ranged from 40% for maple to 60% for oak. These amounts are about 50% greater than the proportional contribution of regrowth foliage to the maple or oak canopies. Apart from the enhancement of CO_2 assimilation in residual primary foliage (Table 1), the greater benefit of regrowth foliage to the carbon budget of oak is due to its relatively greater amount of refoliation compared to maple (Table 2). Altered photosynthetic capacity of regrowth compared to control foliage (Fig. 2B) was not involved. For maple, which replaced comparatively less of its removed leaf area than did oak, increased CO_2 assimilation by regrowth compared to control foliage was more important.

The increase in CO_2 assimilation rates caused by defoliation is absent from current hypotheses of the responses

of plants to herbivory (Mattson and Addy 1975; Mooney and Gulman 1982). This, as well as the extent of replacement of removed by regrowth foliage, may be important in understanding the growth and survival of species such as maple and oak which are unequally attractive food sources to defoliators (Stephens 1971; Campbell and Sloan 1977; Morrow and LaMarche 1978), especially when the species experience equally severe or even catastrophic (either total or successive) defoliations.

References

Byrne GF, Rose CW, Slatyer RO (1970) An aspirated diffusion porometer. Agr Meteorol 7:39–44

Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS (1981) Coping with herbivory: Photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. Oecologia (Berlin) 50:14–24

Campbell RW, Sloan RJ (1977) Forest stand responses to defoliation by the gypsy moth. Forest Sci Monograph 19, p 34

Collins S (1961) Benefits to understory from canopy defoliation by gypsy moth larvae. Ecology 42:836–838

Heichel GH, Turner NC (1972) Carbon dioxide and water vapour exchange of bean leaves responding to fusicoccin. Physiol Plant Pathol 2:375–381

Heichel GH, Turner NC (1976) Phenology and leaf growth of defoliated hardwood trees. In: Anderson J, Kaya H (eds) Perspectives in forest entomology. Academic Press, New York, pp 31–40

Hodgkinson KC (1974) Influence of partial defoliation on photosynthesis, photorespiration, and transpiration by lucerne leaves of different ages. Aust J Plant Physiol 1:561–578

Kitchell JF, O'Neill RV, Webb D, Gallepp GA, Bartell SM, Koonce JF, Ausmus BS (1979) Consumer regulation of nutrient cycling. Bioscience 29:34–38

Kulman JH (1971) Effects of insect defoliation on growth and mortality of trees. Ann Rev Entomol 16:289–324

Mattson WJ, Addy ND (1975) Phytophagous insects as regulators of forest primary production. Science 190:515–522

Mooney HA, Gulmon SL (1982) Constraints on leaf structure and function in reference to herbivory. Bioscience 32:198–206

Morrow PA, LaMarche VC Jr. (1978) Tree ring evidence for chronic insect suppression of productivity in subalpine *Eucalyptus*. Science 201:1244–1246

Morrow PA, and Slatyer RO (1971) Leaf temperature effects on measurements of diffusive resistance to water vapour transfer. Plant Physiol 47:559–561

Penning de Vries FWT (1975) The cost of maintenance processes in plant cells. Ann Bot 39:77–92

Stephens GR (1971) The relation of insect defoliation to mortality in Connecticut forests. Conn Agric Exp Stn Bull 723, p 16

Stephens GR (1981) Defoliation and mortality in Connecticut forests. Conn Agric Exp Stn Bull 796, p 13

Stephens GR, Turner NC, DeRoo HC (1972) Some effects of defoliation by gypsy moth (*Porthetria dispar* L.) and elm spanworm (*Ennomos subsignarius* Hbn.) on water balance and growth of deciduous forest trees. Forest Sci 18:326–330

Stephens GR, Waggoner PE (1980) A half century of natural transitions in mixed hardwood forests. Conn Agric Exp Stn Bull 783, p 43

Swank WT, Warde JB, Drossley DA Jr, Todd RL (1981) Insect defoliation enhances nutrient export from forest ecosystems. Oecologia (Berlin) 51:297–299

Turner NC, Heichel GH (1977) Stomatal development and seasonal changes in diffusive resistance of primary and regrowth foliage of red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.). New Phytol 78:71–81

Turner NC, Parlange J-Y (1970) Analysis of operation and calibration of a ventilated diffusion porometer. Plant Physiol 46:175–177

Woods DB, Turner NC (1971) Stomatal response to changing light by four tree species of varying shade tolerance. New Phytol 70:77–84

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