

# Phenology and growth of three temperate forest life forms in response to artificial soil warming

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## Summary

**1** Responses of temperate deciduous forest vegetation to artificial soil warming (simulating one component of projected global climate change) were investigated in field plots over two growing seasons, 1992–93. Six replicate plots were established for each of three treatments: heating, disturbance-control, and intact control. Growth and phenology of 26 species of three life forms (12 herbaceous understorey species; six shrub species; eight tree species) were monitored non-destructively in the plots at 20 sampling dates.

**2** Phenology of leaf emergence and flower production in saplings was not affected by soil warming. Mature trees and shrubs leafed out slightly earlier and in larger numbers in heated plots. Trees flowered earlier and in higher proportions in the heated plots in 1993.

**3** Mean area per leaf per plant and leaf expansion rates in 1992 were greatest in control saplings of *Acer pensylvanicum* and *Fagus grandifolia*. *Vaccinium corymbosum*, a shrub, showed reduced leaf sizes under soil heating.

**4** Soil warming significantly enhanced relative diameter growth of woody individuals, especially shrubs, in 1992. This effect was less pronounced in 1993.

**5** Species richness was lower in heated plots than in intact control plots at all sampling dates in both years. Disturbed but unheated control plots exhibited the lowest species richness overall. Species richness declined in all plots in 1993.

**6** Changes in relative abundance of herbaceous species from 1992 to 1993 were highly variable, and not significantly affected by treatment. Rank abundances of species changed more from 1992 to 1993 in intact control plots than in the other two treatments.

**7** Total density (stems m<sup>-2</sup>) of herbaceous species was highest in heated plots during April and May of both years, reflecting accelerated emergence of *Maianthemum canadense* and *Uvularia sessilifolia*. From June through October, however, intact control plots exhibited the highest stem densities, as numbers of the early emergents declined.

**8** Photosynthetic rates of the dominant herbs, *Maianthemum canadense* and *Uvularia sessilifolia*, were not significantly affected by heating.

**9** Of all life forms, herbaceous species were most sensitive to soil warming. Their early appearance could influence carbon and nutrient acquisition dynamics under changed climatic conditions in deciduous forests.

**Keywords:** climate change, species richness, spring ephemerals, temperature, understorey

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## Introduction

Increasing global temperatures are likely to accompany rising atmospheric CO<sub>2</sub> in the coming century (Houghton 1991; Wigley & Raper 1992; Taylor & Penner 1994). General Circulation Models predict that mean annual air temperature may rise by as much as 1–5 °C in the northern temperate zone, with concomitant rises in soil temperature. Existing experimental and correlative evidence from temperate and boreal field sites suggests that temperature rise will significantly modify soil processes, with implications for nutrient availability and plant growth. Predicted and demonstrated outcomes of soil warming include accelerated litter decomposition (Van Cleve *et al.* 1983, 1990; Melillo *et al.* 1990), stimulated nitrogen mineralization (Pastor & Post 1988; Foster 1989; Bonan & Van Cleve 1992; Ellert & Bettany 1992; Caticala *et al.* 1994), increased nitrate release (Joslin & Wolfe 1993), higher CO<sub>2</sub> efflux (Edwards 1975; Hanson *et al.* 1993; Peterjohn *et al.* 1994), stimulated CH<sub>4</sub> uptake (Peterjohn *et al.* 1994), enhanced sulphate and nitrate leaching (Buldgen 1982; Duckworth & Cresser 1991), and increased N<sub>2</sub>O release (Sitaula & Bakken 1993; but see Peterjohn *et al.* 1993). Rising soil temperature may also alter the community composition of litter microfungal communities (Carreiro & Koske 1992), as well as VAM and ectomycorrhizal root colonization dynamics (Parke *et al.* 1983). Warming also modifies physical properties of soils, including cation adsorption, frost-heaving susceptibility, and most importantly, soil water content and availability (Peterjohn *et al.* 1994; Harte *et al.* 1995). Together, these abiotic changes will impinge on plant establishment, nutrient uptake, and growth.

Soil warming may influence plant growth and metabolism directly, potentially accelerating ramet and leaf emergence in the spring, or hastening reproduction. Changes in vegetation profile, productivity, biomass, and turnover in response to warming may feedback on soil dynamics in response to warming, whose further changes will magnify ecosystem-level effects (Raich & Schlesinger 1992; Bridgham *et al.* 1995; Harte *et al.* 1995). However, most of these predicted effects have been inferred from greenhouse, field correlation, and air-warming studies (Anderson & McNaughton 1973; Turner & Jarvis 1975; Lawrence & Oechel 1984; Chapin & Shaver 1985; Van Cleve *et al.* 1990; Parsons *et al.* 1994), and vegetation responses to soil warming have been assessed directly by only a few manipulative studies. Changes in plant metabolism may be manifested in growth increases, but the magnitude of these enhancements are known to vary among species. Lawrence & Oechel (1984) and Chapin & Shaver (1985) have found interspecific disparities in biomass gain and photosynthesis in response to warming. Warmer soil temperatures may be associated with higher root maintenance respiration (Lawrence & Oechel 1984), decreased fine

root longevity (Redmond 1955; Hendrick & Pregitzer 1993) and slowed root growth (Anderson & McNaughton 1973), which may hinder the capacity of plants to assimilate excess mobile nutrients released by warming. However, high foliar nutrient concentrations, possibly reflecting stimulated nutrient uptake by roots, have been detected in *Picea mariana* (Mill.) B.S.P. grown under high soil temperature regimes (Van Cleve *et al.* 1990). Higher soil temperatures could also alleviate photosynthetic limitations following leaf-out early in the growing season (DeLucia & Smith 1987). Soil temperature, moisture and fertility may act synergistically in producing growth effects (Parsons *et al.* 1994).

Much less is known about the effects of soil temperature on plant fitness, demography, and community-level interactions. Germination of five northern tree species (Burton & Bazzaz 1991) and emergence of understory herbs (Rogers 1983) have been shown to be accelerated in increased soil temperatures and aseasonally warm periods. Under soil warming treatments, yield increases of 19–50% have been found for agronomic grasses (Rykbost *et al.* 1975a) and 19–100% for a range of crops (Rykbost *et al.* 1975b), as a consequence of large vegetative growth enhancements in early spring. The experiments of Murray *et al.* (1994) and Beuker (1994) suggest that temperature and elevated CO<sub>2</sub> effects on bud dormancy are synergistic and provenance-specific. Cannell *et al.* (1989) proposed that climatic warming could hinder growth and increase die-back in provenances of trees adapted to cooler regions. They pointed out that reproductive phenology could be disrupted, pollen development and transfer impaired, and masting regimes altered as mean temperature increases rapidly, but to our knowledge reproductive phenology and output in response to soil warming have not been explicitly examined to date.

In this study, we sought to determine whether artificial soil warming measurably alters growth and the temporal dynamics of leaf and fruit production in three contrasting plant growth forms, which effectively grow at three different distances from the substrate. The growth forms examined were: the 'spring ephemerals' and other perennial herbs covering the forest floor; shrubs of < 1.5 m height; and canopy trees. We hypothesized that soil warming would exert differential effects on emergence, phenology, leaf expansion rates, growth, vegetative and sexual reproduction amongst species (within growth forms) and amongst growth forms, with consequences for changing community structure in the plots.

## Methods

### STUDY SITE

The experimental study site is in the Harvard Forest (42°30'N, 72°10'W), Petersham, Massachusetts, USA:

a Transition hardwood/white-pine/hemlock system, at  $\approx 300$  m a.s.l. Gloucester Series sandy-loam and glacial till shallowly overlie gneiss and granite bedrock at a mean depth of 3 m. Mean annual air temperatures are 20 °C in July and -7 °C in January (8.5 °C overall), with evenly distributed mean annual precipitation of  $\approx 105$  cm (Spurr 1957). The research site occupies  $\approx 1300$  m<sup>2</sup> of even-aged mixed deciduous forest < 100 years old. Dominant plant species in the experimental plots appear in Table 1.

#### HEATING METHODS

In summer 1991, eighteen 6-m  $\times$  6-m experimental plots were established in six blocks of three treatments each. A 1 m buffer was left around the edge of each plot, creating a working space of 5 m  $\times$  5 m. Soils in 'heated' plots were heated to 5 °C above ambient using subterranean heating cables spaced 20 cm apart and buried at 10 cm (see Peterjohn *et al.* 1994 for more detailed descriptions of methods). 'Disturbance-control' plots contained buried cables that were not supplied with electricity; thus, disturbance associated with burial was simulated while soil temperature remained at ambient levels. 'Control' plots were left

**Table 1** Dominant herbaceous, shrub and tree species studied in the soil warming plots. Nomenclature follows Gleason & Cronquist (1991). 'Life form' indicates the typical growth form of the species: T = tree, S = shrub, H = herbaceous perennial.

Species and authority	Family	Life form
<i>Acer pensylvanicum</i> L.	Aceraceae	T
<i>Acer rubrum</i> L.	Aceraceae	T
<i>Amelanchier arborea</i> (Michx.f.) Fern.	Rosaceae	S
<i>Aralia nudicaulis</i> L.	Araliaceae	H
<i>Castanea dentata</i> (Marshall) Borkh.	Fagaceae	T
<i>Clintonia borealis</i> (Aiton) Raf.	Liliaceae	H
<i>Crataegus crus-galli</i> L.	Rosaceae	S
<i>Dennstaedtia punctilobula</i> (Michx.) Moore	Polypodiaceae	H
<i>Fagus grandifolia</i> Ehrh.	Fagaceae	T
<i>Gaultheria procumbens</i> L.	Ericaceae	H
<i>Lycopodium annotinum</i> L.	Lycopodiaceae	H
<i>Lycopodium obscurum</i> L.	Lycopodiaceae	H
<i>Maianthemum canadense</i> Desf.	Liliaceae	H
<i>Medeola virginiana</i> L.	Liliaceae	H
<i>Mitchella repens</i> L.	Rubiaceae	H
<i>Prunus serotina</i> Ehrh.	Rosaceae	T
<i>Quercus alba</i> L.	Fagaceae	T
<i>Quercus rubra</i> L.	Fagaceae	T
<i>Sorbus americana</i> Marshall	Rosaceae	T
<i>Trientalis borealis</i> Raf.	Primulaceae	H
<i>Uvularia sessilifolia</i> L.	Liliaceae	H
<i>Vaccinium corymbosum</i> L.	Ericaceae	S
<i>Vaccinium vacillans</i> Torr.	Ericaceae	S
<i>Viburnum acerifolium</i> L.	Caprifoliaceae	S
<i>Viburnum lentago</i> L.	Caprifoliaceae	S

intact. The primary focus of the experiment has been to monitor changes in soil processes with temperature increase, including methane uptake, CO<sub>2</sub> efflux, and N mineralization (Peterjohn *et al.* 1994). Therefore, in order to avoid trampling and disruption of long-term monitoring at the plots, all plant measurements we made were taken from portable wooden pallets, and were necessarily non-destructive. No harvests of tissues or excavation of whole plants for biomass estimates were undertaken. Our protocols and interpretations reflect these methodological restrictions.

#### GROWTH AND PHENOLOGY OF WOODY VEGETATION

Beginning in April 1992, the spring following initiation of soil warming, all woody individuals between 5 mm and 35 mm in basal diameter were identified to species (Table 1) and labelled with numbered plastic tags wrapped around the main stem. A subset of larger trees was also monitored ( $n = 12$  in heated and control plots;  $n = 15$  in disturbance-control plots). Total sample sizes were 109 woody individuals each in control and heated plots, and 115 in disturbance-control plots. In April and September of 1992 and 1993, diameter ( $\pm 0.1$  mm) was measured at two orthogonal locations at the base of the main stem of each plant, as an index of growth over the season. To obtain mean relative diameter increments from April to September 1992 and 1993, the orthogonal diameter measures at each sampling date were first averaged. Relative increments were then calculated for each year separately as

$$[(\text{AvgDiam}_{\text{Sept}} - \text{AvgDiam}_{\text{Apr}}) / \text{AvgDiam}_{\text{Apr}}].$$

Resulting values were arcsine-square root transformed to equalize variances, and investigated with ANOVA using soil treatment as a fixed factor in a randomized block design.

At eight spring-summer sampling dates in 1992 and 13 sampling dates in 1993, the phenological status of each of the marked woody individuals was noted. Individuals were inspected for evidence of leaves and reproductive structures, and placed into one of eight phenological states occurring roughly in chronological order: (1) leaf buds closed; (2) buds opening; (3) new leaves expanding; (4) fully expanded leaves with emerging new leaf pair; (5) reproductive (flowers or fruits present); (6) > 50% of leaves changing colour; (7) > 50% of leaves brown or abscised; (8) all leaves dropped. For statistical analyses, data on the phenology of reproduction and leaf production were considered separately. Percentages of all woody individuals reproducing per quadrat were calculated for each year, in three growth classes: trees (> 25 cm basal diameter), saplings ( $\leq 25$  cm basal diameter), and shrub species. Six values of percentage reproductive individuals were obtained per treatment per growth class per year. In addition, occurrences of

folivory on individuals were recorded. Mortality of labelled individuals was noted.

In order to quantify average area per leaf and leaf expansion rates throughout the 1992 season, we measured the length of the midrib of at least six randomly chosen leaves per plant, in shrubs and saplings in each plot. Leaf area was calculated subsequently from nondestructive leaf length measures, from quadratic regressions of leaf area on leaf length obtained for a sample of 60 leaves collected randomly from each species within the quadrats ( $0.925 \leq r^2 \leq 0.977$ ).

#### COMMUNITY STRUCTURE, PHYSIOLOGY AND POPULATION DYNAMICS OF HERBACEOUS SPECIES

In each plot, a 1-m  $\times$  1-m subplot was randomly designated for monitoring herbaceous flora (< 5 mm basal diameter) and tree seedlings (species appear in Table 1). Each subplot ( $n = 18$ ) was observed from 1992 to 1993. At all sampling dates, all ramets of each species present in the subplot were counted to determine stem density (per  $m^2$ ). Species richness, diversity and evenness values per plot were derived from these censuses. Diversity was calculated as the Shannon-Weiner index  $H' = -\sum p_i \ln(p_i)$  where  $p_i$  is the proportion of the  $i$ th species in each subplot. Evenness was scored as  $J = H' / \ln(S)$  where  $S =$  species richness in each subplot (scale of 0–1 where 0 indicates disproportionate dominance of a few taxa). As an index of vegetative propagation activity and ramet mortality, relative changes in ramet density from 5 June 1992 to 17 May 1993 (dates of density maxima) were computed as  $[(\text{Density}_{1993} - \text{Density}_{1992}) / (\text{Density}_{1992})]$ . The percentage of individuals in vegetative, flowering, fruiting, and fruit dehiscence phases was also recorded for each species in 1993. For the few ramets that actually reproduced, fruit set was quantified as an index of reproductive output.

Because the two dominant forest floor herbs, *Uvularia sessilifolia* L. and *Maianthemum canadense* Desf. showed accelerated appearance in heated plots (see below), their photosynthetic rates were characterized to investigate whether soil warming was influencing plant metabolism. One ramet per species growing naturally in full sun ( $> 600 \mu E m^{-2} s^{-1} PAR$ ) and one growing in shade ( $< 300 \mu E m^{-2} s^{-1}$ ) was selected in each subplot ( $n = 6$  ramets/species/light environment/soil treatment; total = 72). *In situ* photosynthesis and transpiration measurements were made on one fully expanded leaf per ramet between 10.00 and 14.00 hours (cloudless day) on 22 May 1994, using a Li-Cor 6200 photosynthesis system (Li-Cor, Lincoln, NB, USA) fitted with a 0.25-L cuvette. Sun and shade ramets were examined to obtain a range of photosynthesis values for each species, and to ensure that treatment effects were not obscured by light limitation.

Unless otherwise indicated, parametric tests were

performed on untransformed data following inspection for normality and homoscedasticity using the MGLH routine of SYSTAT<sup>®</sup> version 5.03 (Wilkinson *et al.* 1992). Reported  $F$ -values are subscripted with the treatment degrees of freedom, and residual degrees of freedom (reflecting sample sizes).

## Results

### GROWTH AND PHENOLOGY OF WOODY VEGETATION

Woody plants exhibited higher diameter growth rates (Fig. 1) in the heated plots during 1992 ( $F_{2,266} = 3.167$ ;  $P = 0.044$  for treatment effect, all individuals pooled). ANOVA on 1993 data, however, indicated no significant differences amongst treatments ( $F_{2,274} = 2.422$ ;  $P = 0.091$ ). The variance in diameter increment for the heated population was much higher in 1992; 1993 responses were less variable (box plot shows range of values, Fig. 1). Out of the total population of woody plants, shrubs (see Table 1 for designations) were the most responsive life form during 1992 (ANOVA by life form, model as above,  $F_{2,52} = 3.122$ ;  $P = 0.052$  for treatment effect).

Treatment differences in phenological patterns of reproduction, leaf production, and leaf senescence through 1992 and 1993 appear in Fig. 2. Kruskal-Wallis nonparametric ANOVA performed on figures of percentage reproductives per year (see Methods) revealed no significant treatment effects on reproduction ( $n = 18$ ,  $0.133 < P < 0.368$  for separate comparisons by growth form in 1992 & 1993), as reproductive events were rare in all plots. In both years, a higher proportion of trees and saplings flowered in the heated plots than in the other treatment plots

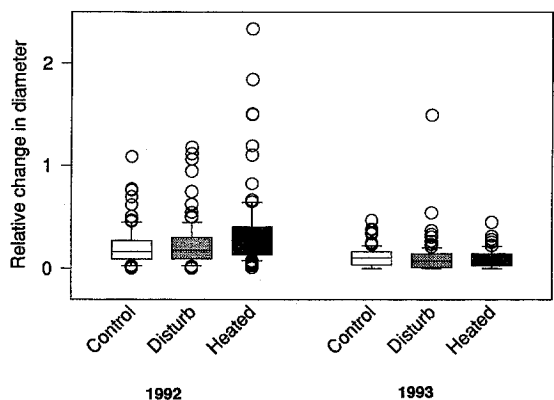
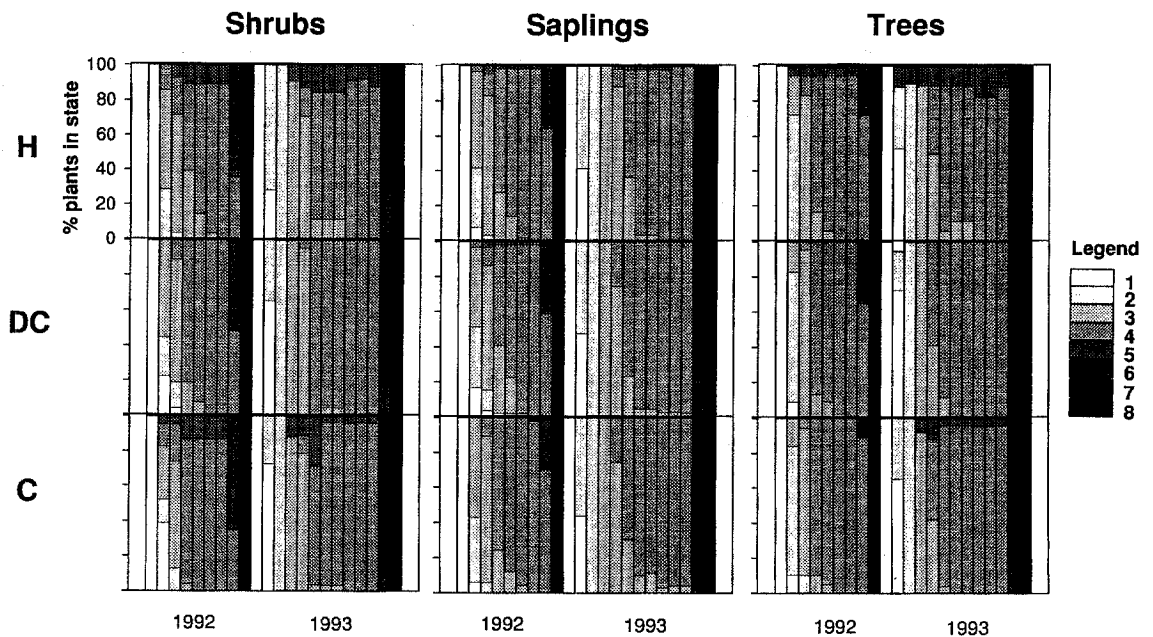


Fig. 1 Mean relative diameter increments of all woody vegetation in control, disturbance-control, and heated plots in 1992 ( $n = 284$ ) and 1993 ( $n = 292$ ). See text for formula for relative diameter growth calculations. Middle line of box plot indicates median; upper and lower box bounds are the upper and lower quartiles; error bars mark the 10th and 90th percentiles of the distributions, with outliers indicated by circles.



**Fig. 2** Stacked bar charts showing the proportion of woody plants in each of eight phenological states: (1) leaf buds present; (2) buds opening; (3) new leaves expanding; (4) fully expanded leaves with emerging new pair; (5) reproductive; (6) > 50% leaves changing colour; (7) > 50% leaves brown or abscised; (8) all leaves dropped. Bar heights represent percentages for all plots summed within a treatment ( $n = 6$ ). Each bar represents a single census date. Trees (individuals with basal diameter > 25 cm), saplings (basal diameter  $\leq 6$  cm) and shrubs (by taxonomic affiliation) are depicted separately. C = Control plots; DC = Disturbance-control plots; H = heated plots.

(1.5–22.2% of all heated individuals vs. 1.5–4.6% all others). Shrubs, however, flowered in higher proportion (12–28%) in the intact control plots. Dates and duration of reproduction could not be compared, due to empty cells within treatment populations. By visual inspection of the data, it was apparent that three striped maples (*Acer pensylvanicum* L.) began flowering between 23 April and 13 May 1993 in the heated plots, whereas flowering ensued later (17 May onward) in the other treatments. However, no other trends were discernible.

To detect timing differences in leaf phenology due to treatment, the proportion of woody individuals attaining fully expanded leaves (phenological status  $\geq 3$  in the above scheme) by 13 May 1992 were determined. Similarly, the proportions of individuals breaking buds (status  $\geq 2$ ) by 27 April 1993 were counted. Percentages of early leafing trees and shrubs were higher in the heated plots (mean<sub>tree</sub>  $\pm$  SD per plot =  $31.3 \pm 18.8\%$ ,  $n = 6$ ; mean<sub>shrub</sub> =  $59.7 \pm 33.9\%$ ) than in other treatments (range<sub>tree</sub> = 18.1–27.4%; range<sub>shrub</sub> = 37.5–45.0%) in 1992. The same trends held for 1993 in the heated plots (mean<sub>tree</sub> per plot  $40.9 \pm 25.7\%$ ; mean<sub>shrub</sub>  $66.1 \pm 9.3\%$ ). Saplings showed no accelerated leaf production due to heating in either year. Kruskal–Wallis one-way analysis of variance conducted separately on saplings, shrubs and trees revealed no significant treatment effects on any growth class ( $n = 18$ ,  $0.204 < P < 0.695$ ).

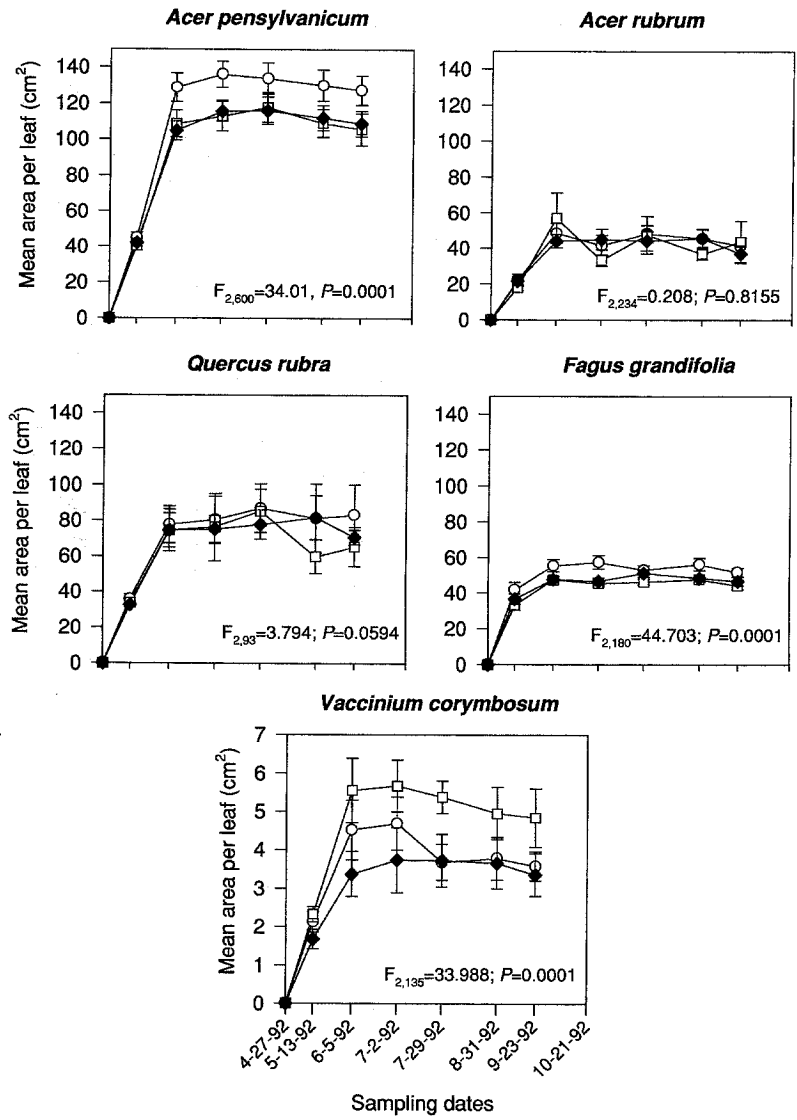
Leaf expansion rates were measured as mean leaf area per leaf per plant over six sampling dates in 1992. Five species with sufficient leaf numbers per treatment to permit statistical analyses were examined by means

of two-factor ANOVA, treating heating regime and date (and interaction) as fixed effects. Leaf growth trajectories and the results of ANOVA are shown in Fig. 3. Treatment exerted no significant effects on leaf expansion in *Acer rubrum* L. and *Quercus rubra* L. saplings ( $F$ -values and probabilities appear in Fig. 3). However, *Acer pensylvanicum* L. and *Fagus grandifolia* Ehrh. saplings from control plots showed significantly higher mean leaf area than saplings in disturbance-control and heated plots (Fig. 3). Leaf expansion rates were depressed in *Vaccinium corymbosum* L. shrubs in heated plots relative to controls, especially during the first 40 days of leaf-out. Disturbance-control individuals of this species showed significantly greater leaf area than shrubs of the other two treatments. No date–treatment interactions were significant, indicating that soil treatment did not modify the phenology of leaf growth through the season, merely the final leaf area attained.

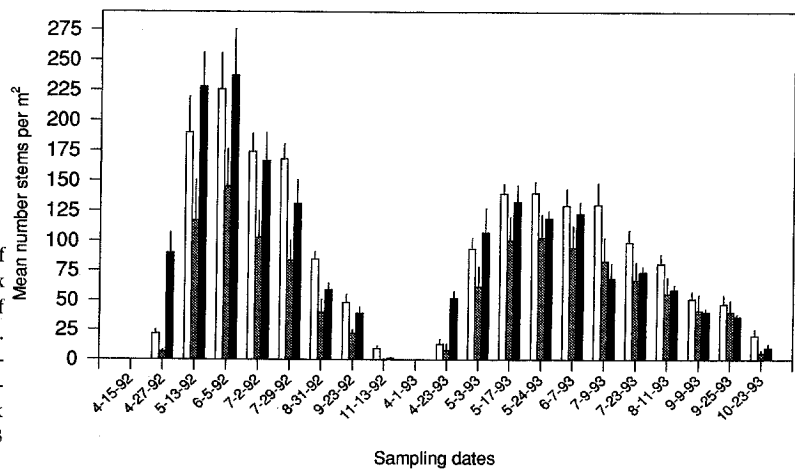
In 1993, herbivores had attacked leaves on > 90% of all woody plants across all plots by August, with no detectable differences amongst treatments. Mortality amongst woody stems was uniformly low across treatments (total<sub>heated</sub> = 4.6%; total<sub>disturb</sub> = 3.5%; total<sub>control</sub> = 3.7%).

#### COMMUNITY STRUCTURE, PHYSIOLOGY AND POPULATION DYNAMICS OF HERBACEOUS SPECIES

Densities of all herbaceous ramets in the subplots (Fig. 4) were significantly higher in the heated plots in the early part of both seasons, largely due to the



**Fig. 3** Leaf expansion dynamics of five common woody species in heated (filled diamonds), disturbance-control (open squares) and control (open circles) treatments. Shown are mean area per leaf ( $\pm 1$  SE), measured on seven sampling dates from 27 April 1992, when leaves began opening, to 21 October, when all leaves were shed. Insets show results of two-way ANOVA, with  $F$ -values (subscripts show treatment degrees of freedom, error term degrees of freedom) and probability values.



**Fig. 4** Mean densities ( $\pm 1$  SE) of all herbaceous species across six plots per treatment. Each cluster of bars represents a single census date. White bars refer to the intact control plots, shaded bars the disturbance-control plots, and black bars the heated plots. 1992 and 1993 data are shown for comparison.

accelerated appearance of *Maianthemum canadense* and *Uvularia sessilifolia* (ANOVA on log-transformed 27 April 1992 densities:  $F_{2,15} = 33.715$ ,  $P < 0.0001$  for treatment effect; ANOVA on log-transformed 23 April 1993 densities:  $F_{2,15} = 8.664$ ,  $P < 0.004$ ). By week two, ramets had emerged in the other plots, and the treatment effect essentially disappeared (ANOVA on 13 May 1992 densities:  $F_{2,15} = 3.403$ ,  $P = 0.060$ ; 3 May 1993:  $F_{2,15} = 2.094$ ;  $P = 0.158$ ). For the remainder of both seasons, stem densities were highest in intact control plots, intermediate in heated plots, and lowest in disturbance-control plots. Differences between treatment means were less pronounced in 1993 than in 1992 (Fig. 4). The maximum density attained and the number of days to achieve maximum density were also tabulated for each plot. Treatment exerted significant effects on maximum stem density in 1992 (ANOVA log-transformed data  $F_{2,15} = 4.713$ ;  $P = 0.026$ ) and marginal effects in 1993 ( $F_{2,15} = 3.390$ ;  $P = 0.061$ ). The number of days required to reach maximum density was unresponsive to treatment in 1992 (Kruskal–Wallis  $H$  with 2 d.f. = 4.528;  $P = 0.104$ ) and 1993 ( $H = 0.023$ ;  $P = 0.988$ ). Stem densities were considerably lower in 1993 than 1992 in all plots (Fig. 4). However, treatment effects on the relative change in maximum stem density from 1992 to 1993 were not significant ( $F_{2,15} = 2.413$ ;  $P = 0.123$ ), indicating stem densities were declining uniformly across all plots.

Species richness was highest in intact control plots at all sampling dates (Fig. 5). Maximum richness values were significantly higher in control plots in both 1992 (ANOVA  $F_{2,15} = 5.535$ ;  $P = 0.016$  for treatment effects) and 1993 (ANOVA  $F_{2,15} = 4.171$ ;  $P = 0.036$ ). Disturbance-control plots contained the fewest species throughout both years. Species diversity ( $H'$ ) ranged from 0.699–1.429 in heated plots; 0.688–1.211 in disturbance-control plots (lowest values); and 0.919–1.542 in intact control plots (highest values). Mean  $\pm$  SD species evenness ( $J$ ), which indicates if the community comprises a balanced mixture of species, ranged from  $0.604 \pm 0.134$  in heated

plots to  $0.635 \pm 0.103$  in control plots, with no significant differences amongst treatments (ANOVA  $F_{2,15} = 0.399$ ,  $P = 0.678$ ).

Many changes in relative abundance occurred amongst herbaceous species in the subplots between 1992 and 1993 (data not shown). *Maianthemum canadense* and *Uvularia sessilifolia* declined in abundance in all plots from 1992 to 1993, while the densities of *Lycopodium annotinum* L. and *Medeola virginiana* L. increased. Due to high variability in density changes, no treatment effects were detected for any of the 10 species tested (ANOVA on arcsine-square root-transformed values of relative change,  $0.451 \leq P \leq 0.987$  for treatment effects). Friedman's two-way non-parametric analysis of variance was used to explore changes in rank abundance of species in the subplots between 1992 and 1993. A marginally higher-than-expected concordance between years was found in heated and disturbance-control plots (Kendall's coefficient of concordance  $W = 0.290$ ; Friedman's test statistic  $\chi^2_1 = 3.769$ ,  $P = 0.052$ ). Control plots showed no systematic variation in rankings amongst years (Kendall's  $W = 0.148$ ;  $\chi^2_1 = 1.923$ ;  $P = 0.166$ ).

Sexual reproduction was rare amongst the herbaceous perennial species monitored in the subplots. Hence, variance in reproductive output swamped any apparent trends due to treatment. During summer 1993, only *Maianthemum canadense*, *Uvularia sessilifolia*, *Trientalis borealis*, and *Medeola virginiana* produced fruits. Despite early appearance of the former two species, no acceleration of flowering or fruit maturation occurred under soil warming; date of reproductive onset was identical amongst treatments and variable amongst species. Three indices of reproductive output followed divergent trends amongst treatments. The mean ( $\pm$  SD) percentage of total individuals reproducing in 1993 was highest in disturbance-control plots ( $4.3 \pm 4.1\%$ ,  $n = 6$  plots per treatment) and lowest in heated plots ( $2.9 \pm 2.1$ ). The mean  $\pm$  SD total number of fruits produced across all individuals per subplot was  $11.5 \pm 13.0$  in control plots;  $4.3 \pm 4.0$  in disturbance-control plots; and

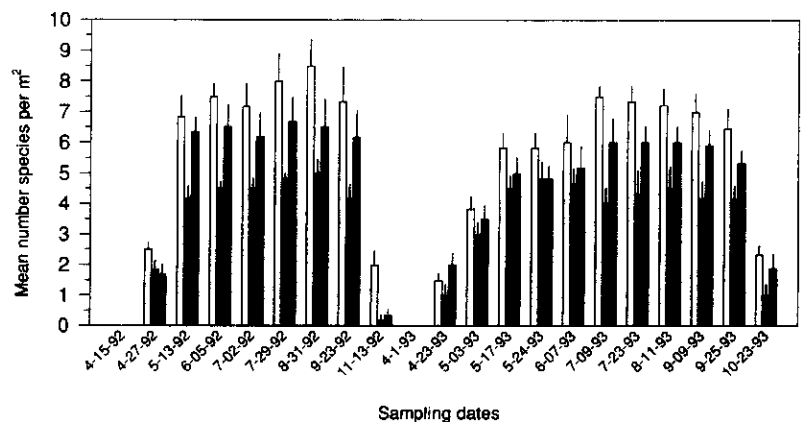


Fig. 5 Mean number of species ( $\pm$  1 SE) occurring in each plot, by treatment, in 1992 and 1993. Sampling dates appear below bar clusters. Bar codings are per Fig. 4.

$4.8 \pm 3.4$  in heated plots. Finally, the mean number of fruits produced per individual was  $2.9 \pm 2.1$  in heated plots;  $2.2 \pm 1.5$  in control plots; and  $1.2 \pm 0.7$  in disturbance-control plots, with no significant treatment effects.

Photosynthetic rates differed between the two predominant species, *Maianthemum canadense* and *Uvularia sessilifolia*, but was not influenced by warming treatments (ANOVA, fixed model with treatment, species and light as effects;  $F_{2,59} = 0.367$ ;  $P = 0.694$  for treatment effect, with no significant treatment interactions). High-light photosynthetic rates varied from a mean of  $2.47 \pm 0.32 \mu\text{mol m}^{-2} \text{s}^{-1}$  in heated plots to  $3.06 \pm 0.24 \mu\text{mol m}^{-2} \text{s}^{-1}$  in *Maianthemum canadense* controls. *Uvularia sessilifolia* high-light photosynthetic rates were somewhat higher, ranging from  $3.82 \pm 0.23 \mu\text{mol m}^{-2} \text{s}^{-1}$  in control plots to  $4.88 \pm 0.39 \mu\text{mol m}^{-2} \text{s}^{-1}$  in disturbance-control plots. Low-light photosynthetic rates hovered uniformly around  $2.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  for both species, and were not affected by treatments, although heated *Maianthemum canadense* ramets showed no disparity between high- and low-light photosynthesis rates. Transpiration rates were significantly higher in the disturbance-control plots (lowest in the control plots), especially for *Uvularia* (ANOVA as above,  $F_{2,59} = 5.412$ ;  $P = 0.007$  for treatment effect;  $P = 0.052$  for treatment-species interaction).

## Discussion

Artificial warming of the soil at the Harvard Forest has thus far resulted in substantially increased soil temperature (by  $\approx 5^\circ\text{C}$  as intended), increased daily average  $\text{CO}_2$  efflux, increased uptake of  $\text{CH}_4$ , and decreased mineral soil moisture (Peterjohn *et al.* 1994), all processes with large potential effects on plant growth. For example,  $\text{CO}_2$  effluxes were enhanced 40% under soil warming in 1991, although the magnitude of this enhancement fluctuated in subsequent years (9% increase in 1992, 19% increase in 1993). The year-to-year variability in response may reflect changes in root or microbial respiration attributable to higher rainfall (and soil moisture) in 1992, vs. hotter and drier weather in the 1993 summer (Catalano *et al.* 1994).  $\text{CO}_2$  efflux also has been higher in the disturbance control plots, but less than in the heated plots. Warming has consistently stimulated net N mineralization throughout, but has had little effect on already low nitrification rates (Peterjohn *et al.* 1994). Higher levels of measurable  $\text{NO}_3^-$  have been observed since spring 1993 in the heated plots relative to the other controls (K. Newkirk, personal communication), but levels of available N remain quite low throughout ( $< 0.1 \text{ mg L}^{-1}$ ). The moisture content of the forest floor layer has been reduced in the heated plots relative to the other two treatments; in the mineral layer, soil moisture has been lower in both heated

and disturbance control plots relative to controls (Newkirk *et al.* 1994; Peterjohn 1994).

The complex direct and indirect effects of soil warming on these plants vary amongst life forms and species, and change over time, complicating our conclusions. Of all life forms studied, the herbaceous understorey layer displayed the most dramatic reaction to soil warming. *Maianthemum canadense* and *Uvularia sessilifolia*, the herbaceous dominants accounting for  $\approx 60\%$  of forest ground cover, emerged 7–10 days earlier in the growing season under soil warming conditions (Fig. 4; cf. Peterjohn *et al.* 1993). It is reasonable to expect that plant species growing at or just above the soil surface will be affected most profoundly by changes in soil structure, chemistry and microbial activity, as leaves, stems and roots all occur within the sphere of influence of soil warming. *Maianthemum canadense* and *Uvularia sessilifolia* emerged much earlier in heated plots in both years, well before canopy leaf-out. Premature emergence of herbaceous species renders them vulnerable to unpredictable frosts and late-winter storms, and hardness or programmed late emergence may afford a long-term selective advantage. However, a longer window of light was available to these early appearing species. Sensitivity to an 'early spring' (*sensu* Rogers 1983) may lend opportunistic ephemerals a possible growth and fitness advantage, as these species accrue most of their photosynthate prior to canopy flush (Bazzaz & Bliss 1971; Brown *et al.* 1985; Masarovicova & Elias 1986). These populations may also capture labile nutrients released by soil warming; indeed, understorey herbaceous species have been observed to assimilate flushes of nutrients made available by spring snow-melt (Muller & Bormann 1976). At the same time, microbial competition for N pools may preclude increased uptake by vegetation (Grossman *et al.* 1993). Because ramets were not analysed for foliar N, it is difficult to say whether precocious herbaceous perennials were absorbing available soil nutrients (even possibly confounding apparent heating effects on *in situ* nitrate or ammonium levels). Likewise, while soil warming increased the local concentrations of  $\text{CO}_2$  available for assimilation by ground-dwelling herbs, elevated  $\text{CO}_2$  effects were not visible in photosynthetic rates or the leaf area attained by ramets (data not shown). In this study, photosynthetic rates were far more sensitive to understorey light levels than to soil temperatures.

Sexual reproduction was rare in the herbaceous species, typical of many understorey taxa (Bierzychudek 1982; Barrett & Helenurm 1987), and treatment effects on fitness thus were difficult to ascertain. Vegetative ramet demography may be a better indicator of growth and fitness in these species. Accelerated emergence did not guarantee greater longevity, fitness, or opportunity for season-long carbon gain in *Maianthemum canadense* or *Uvularia sessilifolia* in this



study. Densities of early appearing herbs in the heated plots declined below that of intact control plots by June of both years. If early appearing genets were accruing more carbon or nutrients, one might expect higher overall rates of ramet proliferation in the heated plots. Both species had decreased in abundance in all treatments from 1992 to 1993 (Fig. 4), while cover of other herbs had expanded. Evenness and diversity scores did not change appreciably between years, however; treatments did not appear to select for certain species in the plots. Both heating and disturbance negatively affected species richness in both years (Fig. 5). The summer of 1993 was drier and warmer than 1992, and the effects of this drying on ramet mortality or production may have been exacerbated in both heated and disturbance control plots, where soil water content was somewhat reduced. The percentage cover and community composition of forest herbs are known to change considerably from year to year, especially as canopy cover changes (Brewer 1980; Davison & Forman 1982). As herb cover itself may in part control tree seedling regeneration patterns (Maguire & Forman 1983), soil warming influences on herbaceous species, as well as biotic feedbacks of canopy cover on soil warming should be investigated carefully.

Shrubs were slightly less sensitive to soil warming than herbaceous species, and showed responses generally intermediate between herbaceous perennials and trees. Shrubs exhibited the highest growth (diameter increment) sensitivity of all woody species to soil warming. Shrubs leafed out earlier than mature trees in both seasons. A higher proportion of shrubs had flushed leaves in early spring in the heating plots (Fig. 2), although treatment effects were obscured by high variance amongst individuals. However, leaf expansion rates and mean area per leaf of *Vaccinium corymbosum* were negatively affected by soil warming relative to controls (Fig. 3). Reduced soil moisture in the shrub rooting zone due to heating could inhibit leaf expansion. Boreal congeners exhibit variable responses of shoot biomass to heating: *Vaccinium vitis-idaea* has shown enhanced biomass growing in artificially warmed air, while other *Vaccinium* species appear unaffected (Parsons *et al.* 1994). Both Chapin & Shaver (1985) and Parsons *et al.* (1994) demonstrated that biomass responses to warming are products of synergistic interactions of air temperature increase with water availability and soil fertility. Air and soil warming effects on shoot growth and leaf expansion may not be strictly comparable, however, as air warming exerts unique influences on leaf size and production.

In considering the impacts of soil warming on ecosystem function, most interest has been focused on trees, the largest biomass contributor in the plant community. Lawrence & Oechel (1984) determined that high soil temperatures stimulated photosynthetic rates in hardwood seedlings, but the effects on mature

trees are largely unknown. Elevated soil temperatures have contributed to increases in net photosynthesis, leaf water potential and stomatal conductance in *Picea sitchensis* (Bong.) Carr. (Turner & Jarvis 1975) and montane herbs (Anderson & McNaughton 1973). Foliar nutrient concentrations have risen in black spruce, *Picea mariana*, in response to *in situ* warming (Van Cleve *et al.* 1990). In the present study, trees and saplings were moderately sensitive to soil warming in terms of diameter growth during the first year of the experiment (Fig. 1), but this effect had diminished in 1993. Leaf expansion rates in saplings behaved similarly: two sapling species exhibited no effects of soil warming, and two others appeared more responsive to disturbance in general than to heating *per se* (Fig. 3). Again, reduced water content of both heated and disturbance control soils may have hindered water uptake of deeper-rooted species. Larger numbers of trees in the heated plots attained full leaf-out by the early 1992 and 1993 sampling dates (Fig. 2), but saplings showed no such trends. Higher percentages of trees and saplings flowered in the heated plots than in the other treatments (Fig. 2), which could be a consequence of earlier leaf-out; however, it is unclear whether heating alone stimulated flowering in these populations.

Our findings should be interpreted with caution, as underground heating cables, excellent for studying soil processes, produce their own effects on plant growth independent of temperature (National Science Foundation 1992). These cables were buried at a depth of 10 cm, optimal for producing even heating throughout the upper 20 cm of soil (Peterjohn *et al.* 1993). Most herbaceous species examined here produce rhizomes in the upper 5 cm of the soil profile (*Maianthemum canadense*, *Uvularia sessilifolia*, *Aralia nudicaulis*, *Medeola virginiana*, *Trientalis borealis*) or proliferate stolons across the soil surface (*Lycopodium* spp., *Mitchella repens*, *Gaultheria procumbens*; Sobey & Barkhouse 1977; L. George, personal communication). Trees and shrubs, however, may send some portion of their roots well below the heating profile. Species with different subterranean morphologies will exhibit differential responses to both soil disturbance and the heating treatment. Moreover, the air is not simultaneously warmed as is expected under global change. Other past studies, on the other hand, have warmed air without warming soil (e.g. Chapin & Shaver 1985; Parsons *et al.* 1994); the two conditions are difficult to achieve in concert in the field (but see Harte *et al.* 1995). Soil disturbance is a necessary consequence of the underground cable method, with its own impacts on plants. Species in the disturbance-control plots exhibited differences in richness, stem density, transpiration and fruit output that may have resulted from physical perturbation of the soil profile with concomitant changes in microbial activity and water availability. On the other hand, intermediate responses of plants in the heated plots

may reflect a mitigating influence of heating on post-disturbance recovery. Aside from this caveat, however, soil warming clearly modified features of seasonal growth amongst the different life forms, and this multispecies study yields hypotheses about the trajectories of forest community structure under climate change.

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