Morning reduction of photosynthetic capacity before midday depression

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Midday depression of photosynthesis has important consequences for ecosystem carbon exchange. Recent studies of forest trees have demonstrated that latent reduction of photosynthetic capacity can begin in the early morning, preceding the midday depression. We investigated whether such early morning reduction also occurs in an herbaceous species, Oenothera biennis. Diurnal changes of the photosynthetic light response curve (measured using a light-emitting diode) and incident sunlight intensity were measured under field conditions. The following results were obtained: (1) the light-saturated photosynthetic rate decreased beginning at sunrise; (2) the incident sunlight intensity on the leaves increased from sunrise; and (3) combining (1) and (2), the net photosynthetic rate under natural sunlight intensity increased from sunrise, reached a maximum at mid-morning, and then showed midday depression. Our results demonstrate that the latent morning reduction of photosynthetic capacity begins at sunrise, preceding the apparent midday depression, in agreement with previous studies of forest trees.

Terrestrial ecosystems in temperate regions can function as carbon sinks, thereby moderating the effects of climate change1,2. Accordingly, the response of terrestrial ecosystems to the changing climate is currently an area of major concern in the field of plant ecophysiology. Recent process-based models have successfully predicted ecosystem carbon and water exchanges and their responses to climate change2–6. For more accurate predictions of these process-based models, the dependence of carbon exchange should be evaluated for each environmental variable independently in leaf-level studies.

The daytime carbon and water exchanges of plant leaves reflect a balance between stimulation from high light exposure and depression from a high vapor pressure deficit7,8. High light exposure during the day stimulates stomata to open, thereby driving gas exchange9. In turn, the stomatal aperture is negatively dependent on the transpiration rate10, and stomata often close during the day when the humidity deficit is high11–15. Consequently, leaf gas exchange may show a midday depression on particularly sunny days16. This midday depression has been reported not only in dry regions16, but also in wet temperate regions14,17,18 and can reduce ecosystem-level carbon uptake19,20. Hence, understanding of midday depression at the scale of the individual leaf is necessary for improving the process-based modeling of ecosystem gas exchange. Considering the processes described above, the midday depression can be considered to result from the combination of the effects of light intensity, which positively drives photosynthesis, and other factors that reduce the photosynthetic rate by means of stomatal closure. Therefore, it is necessary to separately evaluate the effects of diurnally changing light intensity independently from other factors. One means of achieving this objective is to repeatedly measure photosynthetic light response curves independently of the external light intensity over the time course of one day. Recently, two studies of tropical rainforest tree species21,22 and one study of a temperate tree species23 investigated diurnal changes in photosynthetic capacity under saturating light intensity and the in situ photosynthetic rate under natural sunlight intensity conditions. These studies demonstrated that the reduction in photosynthetic capacity could begin as early as dawn, preceding the apparent midday depression. At present, however, the early morning reduction in photosynthetic capacity has been reported only for forest trees; thus, it remains unclear whether such a pattern also applies to herbs that grow in open habitats of wet temperate regions. Hence, we here report the results of a field experiment in which we investigated the effect of changing light intensity and diurnal changes in photosynthetic light capacity on midday depression in the temperate perennial herb Oenothera biennis.
**Results**

The observed patterns of diurnal change in the photosynthetic light response curves were similar among the three investigated plants. The photosynthetic rate at each photosynthetic photon flux density (PPFD) value declined from the first measurement taken just after sunrise toward midday (Fig. 1). Photosynthetic rates and stomatal conductance values were lowest around early afternoon (Fig. 1 and 2), when the leaf temperature and vapor pressure deficit were high (Fig. 3 and 4), and then recovered toward sunset. In contrast, incident PPFD increased after sunrise and reached a maximum around noon (Fig. 5a). Combining these two opposing effects, the in situ net photosynthetic rate of the leaves increased after sunrise, reached a maximum around mid-morning, and then showed midday depression (Fig. 5b). In the afternoon, the experimental leaves, which faced the southeast direction, were shaded by other leaves on the same stem.

The relative photosynthetic rate was positively correlated with relative stomatal conductance during the day (Fig. 6), indicating that at least part of the reduction in photosynthetic rate during the day was related to stomatal closure. The observed daily net photosynthesis rate was 34% lower on average (range 30–38% for the four leaves) compared with that under the hypothetical situation of no midday depression. In turn, the midday depression reduced daily transpiration by 45% (40–52%) compared with the hypothetical

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**Figure 1 | Diurnal course of light response curves of net photosynthetic rate of the leaves.** The same set of symbols is used for all panels to indicate the incident LED light intensity on each leaf.

**Figure 2 | Diurnal course of leaf conductance to H2O.**
situation. Consequently, the midday depression increased daily water-use efficiency by 22% (9–46%) compared with the hypothetical situation without midday depression.

**Discussion**

The reduction in photosynthetic capacity started from as early as sunrise, preceding the apparent midday depression. This reduction was offset by an increase in incident PPFD in the early morning, which explains why the midday depression effect was apparent only at midday. Our result is consistent with reports for two tropical canopy tree species, *Dipterocarpus sublamellatus* and *Neobalanocarpus heimii*[^21][^22], and for one temperate tree species, *Quercus crispula*[^23]. This agreement among experimental results strongly suggests that the latent morning reduction in photosynthetic capacity is a common phenomenon across species. Recent studies have incorporated leaf-level stomatal regulation into process-based models of ecosystem gas exchanges of forest trees[^3][^4]. Our present results indicated the necessity of incorporating stomatal regulation into models for herbaceous communities as well. Our results, together with the previous results on trees[^21][^23], indicate the potential of underestimating photosynthetic capacity even in the morning if the leaves show midday depression at the subsequent midday hours. As the process-based models rely on field measurements of a limited sample of leaves[^24][^26], future studies are needed to further investigate the

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is a pioneer species in open, disturbed habitats, such as roadsides, in Japan. Three monocarpic perennial herbs that was introduced to Japan from North America, and it in August 2006 was 27.6°C during the hottest part of summer. The mean air temperature at the site (data from IPU-1 at Ishikawa Prefectural University). The study was conducted in the dry season (summer) in 2006. The rain days (2002–2008) at the study site were 14.3 days.

Measurement of photosynthesis. We measured the photosynthetic rates of a total of eight leaves from the three plants on August 3 (Plant 1), August 24 (Plant 2), and September 4 (Plant 3), 2006 using a portable photosynthesis system (LI-6400; LI-COR, Lincoln, USA) equipped with an LED light source (LI-6400-02B). For each leaf, photosynthetic light response curves were repeatedly measured (4–6 times) from dawn to dusk. During all but the first (dawn) measurement for each leaf, the incident PPFD on the leaf surface was lowered progressively (2000, 1500, 1000, 750, 500, 250, 125, 63, 32, and 0 µmol m⁻² s⁻¹). Incident PPFD, supplied as natural sunlight to each leaf surface, was determined prior to the dawn measurements using a quantum sensor (IKS-27; KOITO Kogyo, Yokohama, Japan) temporarily placed on the center of each leaf lamina. During the dawn measurements, the highest PPFD supplied by the LED was controlled so that it did not exceed the recorded in situ incident PPFD to avoid artificially stimulating the leaves with excessively high light intensities. During each measurement, the PPFD was kept constant at each decreasing level until equilibration. Leaf conductance to H₂O (gHL; mmol m⁻² s⁻¹), leaf transpiration rate (Trenal; mmol H₂O m⁻² s⁻¹), leaf temperature, and vapor pressure deficit based on leaf temperature were simultaneously calculated using the LI-6400 system. In the following analyses, leaf conductance was regarded as equivalent to leaf stomatal conductance, assuming that the leaf boundary layer resistance was negligible. The CO₂ concentration of the air entering the leaf chamber was controlled at 350 ppm.

Measurement of incident PPFD. We chose two consecutive clear days with very similar weather to conduct measurements (Fig. 7). For Plant 1, a diurnal course of photosynthetic light response curves was measured on the first day (August 3) as described above, and a diurnal course of light intensity on the same leaves was measured on the second day (August 4). Light data from August 4 were used as an estimate for photosynthesis on August 3, assuming that the weather conditions were the same over these two days. For Plants 2 and 3, rainy or cloudy weather prevailed after the photosynthetic measurements, so neither incident light intensity nor the photosynthetic rate under natural sunlight was estimated. We used small, leaf-mounted gallium arsenide photodiodes (150 mg; G1118; Hamamatsu Photonics, Corvallis, OR, USA) to determine the actual and hypothetical photosynthetic rates. The stomatal conductance was controlled so that it did not exceed the recorded in situ incident PPFD to avoid artificially stimulating the leaves with excessively high light intensities. During each measurement, the PPFD was kept constant at each decreasing level until equilibration. Leaf conductance to H₂O (gHL; mmol m⁻² s⁻¹), leaf transpiration rate (Trenal; mmol H₂O m⁻² s⁻¹), leaf temperature, and vapor pressure deficit based on leaf temperature were simultaneously calculated using the LI-6400 system. In the following analyses, leaf conductance was regarded as equivalent to leaf stomatal conductance, assuming that the leaf boundary layer resistance was negligible. The CO₂ concentration of the air entering the leaf chamber was controlled at 350 ppm.

**Methods**

**Study site and materials.** Our study site consisted of an artificially constructed open-sky empty lot on the campus of Ishikawa Prefectural University, Nonoichi, Ishikawa Prefecture, Japan (36°30’N, 136°35’E). The mean annual temperature and precipitation (2002–2008) at the study site were 14.3°C and 2161 mm, respectively (data from IPU-1 at Ishikawa Prefectural University). The study was conducted in August 2006, during the hottest part of the summer. The mean air temperature at the site in August 2006 was 27.6°C. The study species, Oenothera biennis (L. Onagraceae), is a monocarpic perennial herb that was introduced to Japan from North America, and it is a pioneer species in open, disturbed habitats, such as roadsides, in Japan. Three single-stem individual bolting rosettes (i.e., vertical stems, 0.8–1.3 m tall) that were naturally growing at the site were measured in situ. These three plants, hereafter referred to as Plants 1, 2, and 3, were isolated and had no shading from neighbors.
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K.K. performed the experiments and analyzed the data; K.K. and S.T. wrote the paper.

Additional information
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