directly among tree species, and interspecific comparisons based on published data are difficult because of the variety of methods used.

In this study, we compared nine adult temperate tree species growing on the campus of the University of Paris XI: six deciduous species (European beech (*Fagus sylvatica* L.), common oak (*Quercus robur* L.), small-leaved linden (*Tilia cordata* Mill.), silver birch (*Betula pendula* Roth.), ash (*Fraxinus excelsior* L.) and alder (*Alnus glutinosa* (L.) Gaertn.)); two evergreen species (Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.)); and ginkgo (*Ginkgo biloba* L.), a surviving member of a primitive group of gymnosperms. The experiment was carried out on current-year stems during winter and summer. Gas exchange, chlorophyll and nitrogen concentrations, maximum quantum yield of PSII and location of chlorophyll were examined. Our main objectives were: (1) to characterize the physiological variation in stem photosynthesis among species and between studied seasons; (2) to investigate the relationships between functional (gas exchange, fluorescence parameters) and structural (chlorophyll, nitrogen, stem mass per area) traits and compare these relationships to those commonly observed in leaves. Because the stem is not specialized for photosynthesis, we predicted minimum nitrogen and chlorophyll investment for all species.

## Materials and methods

### *Site description and plant materials*

The experiment was conducted in 2004 on nine tree species grown in a temperate climate on the campus of the University of Paris XI (48°42′ N, 02°10′ E), 25 km south-west of Paris, France (elevation: 65 m). The studied species, European beech, common oak, small-leaved linden tree, silver birch, ash, alder, Norway spruce and Scots pine are commonly observed in European temperate forests or parks. *Ginkgo biloba* was chosen because it is recognized as a "living fossil" that possesses primitive characters. In the gymnosperm phylogeny, it is the unique representative of the Ginkgoales branch. The trees were located on the same type of soil (brown soil in the process of formation on top of colluviums), and were of similar height (15–20 m) and age (35–50 years).

Current-year stems of three trees per species were sampled at the end of June (summer period) and at the end of March (winter period). During the measurement periods, mean diurnal temperatures were, on average, 16.3 °C at the end of June and 7.6 °C at the end of March. For each tree, all parameters were measured in the midsection of 2–3 current-year stems, the diameter of which varied between 2 mm (*Betula pendula*) and 5 mm (*Pinus sylvestris*). We sampled sun-exposed stems from the outer crown at a height of about 2–4 m with a pruning hook. Samples were harvested around 1400 h UT for gas exchange; samples for chlorophyll extraction were immediately immersed in liquid nitrogen and stored at –80 °C until assayed.

### *Gas-exchange measurements*

Gas exchange was measured in the laboratory on detached stems with an LI-6400 portable photosynthesis system (Li-Cor, Lincoln, NE) and a conifer chamber (Li-Cor Model 6400-05) similar to the one described by Damesin (2003). In this chamber, temperature and $CO_2$ are controlled by the LI-6400 portable photosynthesis system. Each stem sample was immediately recut under distilled water in the section of tissue produced the previous year. A part of the current-year stem was immediately placed in the chamber and the cut end kept submerged in water during measurements. Sometimes it was necessary to remove a leaf (or most of the needles for *P. abies* and *P. sylvestris*) on the current-year stem when the internode was not long enough to fill the chamber. Because of the leaf and needle scars and the high $CO_2$ concentration in the stem, "wound respiration" might have occurred but was not taken into account because, for each species, the difference in $CO_2$ efflux between an intact stem and a stem from which a leaf had been removed was negligible.

Measurements were made at 20 °C, a $CO_2$ concentration of 390 ppm, 60% relative humidity and 1400 or 0 μmol $m^{-2}$ $s^{-1}$ of photosynthetically active radiation (PAR) to determine $CO_2$ efflux rates in the light ($R_l$) and in the dark, i.e., dark respiration rate ($R_d$). A mercury light source (2 × 1000 W HQI, OSRAM, Munich, Germany) was placed 1 m above the chamber. Also, a small laboratory-made gallium arsenide phosphide PAR sensor, calibrated with the Li-Cor PAR sensor located in a leaf chamber, was installed in the 6400-05 chamber close to the sample. Under both light conditions, samples were acclimated for 15–20 min before measurements were made. Efflux of $CO_2$ was measured five to 10 times at 30-s intervals. The system was checked for leaks by blowing around the chamber for each measured sample. To express $CO_2$ efflux in terms of mass and area units, stem areas were measured and the tissues were dried at 60 °C for 48 h. A relationship between the observed decrease in $CO_2$ efflux from stem tissue in the light has been linked to photosynthesis by $^{14}CO_2$ labeling studies (Langenfeld-Heyser 1989) and by experiments with a Clark-type $O_2$ electrode (Pfanz and Aschan 2001) and possibly also to light inhibition of respiration (this was shown in leaves (Atkin et al. 2000) but has never been investigated in stems); however, we were unable to distinguish between these effects. In our study, the value obtained by subtracting $R_d$ from $R_l$ is referred to as the apparent gross photosynthetic rate ($P_g$).

### *Nitrogen concentration*

Dry mass (DW) of each sample used for gas-exchange measurements was determined. Subsequently, the samples were cut into small pieces and ground to a powder (MM200, RETSCH, Haan, Germany). The nitrogen concentration of the powder was determined with an elemental analyzer at the "Service Central d'Analyse du CNRS" (Vernaison, France).

### *Chlorophyll concentration*

The proximal half of the second internode of the stem was sampled. Each stem sample was cut finely with a pair of pruning shears, and placed in a tube with 4 ml of *N,N*-dimethyl-