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Research article

Photosynthetic properties of spring geophytes assessed by chlorophyll fluorescence analysis

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ABSTRACT

Since spring ephemerals are credited to be all “sun” species with unusually elevate photosynthesis, in contrast to shade-tolerant trees and understory geophytes with a long aboveground cycle, we examined the photosynthetic efficiency of 6 woody species, 9 long-cycle geophytes, and 8 spring ephemeral geophytes using blue flashes of increasing energy with the Imaging PAM fluorometer. Several parameters were obtained: quantum yield of electron transport (ΦETR) or of PSII (ΦPSII), maximum measured photosynthesis rate (ETR_{hv}), maximum extrapolated rate of photosynthesis (ETR_{em}), half-saturating photon flux density (K_{PAR}), and in some cases photochemical (qP) and non-photochemical quenching (NPQ). Results confirm the ecological consistency of the three plant groups, with internal differences. Woody species have low ETR_{em} and K_{PAR} values with good ΦETR; long-cycle herbs have low ETR_{em} and ΦETR and moderate K_{PAR} values; spring ephemerals have elevate ΦETR, ETR_{em} and K_{PAR} values. The mean ETR_{em} of ephemerals of 91 μmol m^{-2} s^{-1} exceeds that of long-cycle herbs 2.9-fold and woody species 4.8-fold, and corresponds to 19 μmol CO_2 m^{-2} s^{-1} by assuming an ETR/ΦCO_2 ratio of 4.7. Highest photosynthesis rates and K_{PAR} were exhibited by five ephemerals (*Eranthis, Erythronium, Narcissus, Scilla, Tulipa*) with peak ETR_{em} values equivalent to ~40 μmol CO_2 m^{-2} s^{-1} or ~60 μmol CO_2 (g Chl)$^{-1}$ s^{-1} (“sun” species). According to a new, fluorescence based heliophily index, all trees and five long-cycle herbs were definitely “shade” species, while four long-cycle herbs and three ephemerals were intermediate shade-tolerant.

1. Introduction

The photosynthetic performances of higher plants can vary widely according to growth forms, species, organs and stages in relation to diverse ecophysiological demands (Osmond et al., 1982). A large number of perennial herbs with a permanent underground reserve organ are known as geophytes, and have different photosynthetic activities and phenologies according to the length of aboveground persistence and the timing of flushing, flowering, fruit set and senescence (Whigham, 2004).

Within the geophyte assemblage, spring ephemerals represent a group of plants which emerge from soil in late winter and have a short aboveground life span available to accomplish the whole of their productive and reproductive functions (Dafni et al., 1981; Kudo et al., 2008; Taylor and Pearcy, 1976). Soon after emergence, these understory plants are in full bloom and can thus exploit the bright springtime sunlight for fruit maturation and filling of subterranean reserves. They will undergo mass senescence and death about two months later, at the time of tree canopy closure and consequent decline of light availability. This life habit may require strong photosynthetic performances, the more so during climatically unstable early springs. On the other hand, the geophytes with a long aboveground vegetation cycle (long-cycle herbs) are as common as spring ephemerals in many deciduous forest environments. In a study of North-American woodlands, Sparling (1967) on the basis of divergent photosynthesis rates and requirements distinguished between spring ephemerals as highly productive “sun plants”, and slow-growth, summer-green herbs as “shade plants”, with few intermediate forms. This grouping of geophytes on the basis of phenology and life forms has been upheld by recent studies (Gandin et al., 2011; Rothstein and Zak, 2001; Sunmonu and Kudo, 2014), but it obviously needs confirmation and refinement in other environmental contexts. Other plant types adopt

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Abbreviations

CCD	Charge-coupled device
ETR	Electron transport rate
K_{PAR}	Half-saturation PFD for ETR
ETR_{hv}	Highest measured electron transport rate
F_t	Instantaneous Chl fluorescence
F_m	Maximum Chl fluorescence after sample dark adaptation
F_m'	Maximum Chl fluorescence under illumination
ETR_{em}	Maximum extrapolated photosynthetic electron transport rate
F_o	Minimum (dark) Chl fluorescence
NPQ	Non-photochemical quenching
qP	Photochemical quenching
PFD	Photon flux density
PAR	Photosynthetically active radiation
PEBHI	Photosynthetic ETR-based heliophily index
ΦCO_2	Quantum yield of CO_2 assimilation
ΦO_2	Quantum yield of O_2 evolution
ΦPSII	Quantum yield of PSII
ΦETR	Quantum yield of PSII-dependent electron transport
F_v	Variable Chl fluorescence

fundamentally different strategies. Trees for example - both deciduous and evergreen - have an elevate primary production based on large assimilatory surfaces with a high leaf area index, each leaf usually having a low photosynthetic capacity.

It has been maintained that spring ephemerals occur in many parts of the northern hemisphere, but not in western Europe (Lapointe, 2001). However, spring ephemerals as defined above are found in most European countries, although few recent studies have been dedicated to their ecology (with the exception of *Erythronium dens-canis*: Esteban et al., 2008; La Rocca et al., 2014; Mondoni et al., 2012). Hilly areas in the northern Apennines are partially covered by relatively young, mixed stands dominated by hop-hornbeam (*Ostrya carpinifolia*) and downy oak (*Quercus pubescens*). Here the spring ephemerals are represented by a few common species, such as *Anemone* spp. and some Liliaceae (*E. dens-canis*, *Scilla bifolia*), and in addition a number of understory herbs living in particular forest niches (Marconi and Corbetta, 2014). An extreme case is represented by plants in shady, damp sites such as *Leucojum vernum* and *Galanthus nivalis*, whose blossoms are often seen peeping out of melting snow in late winter. Early-flowering species with similar phenology also occur in more open habitats, e.g. the winter-blooming *Eranthis hyemalis*, orchids and other monocots (including *Narcissus* and *Tulipa* species), and may be included in the spring ephemerals assemblage in a wider sense. It can be surmised that the short aboveground growth period of all these plants is supported by an intense photosynthesis, as it is also the case for many C3 perennial herbs of seasonally arid zones, whose exceptional photosynthetic performances are well known (Berry and Björkman, 1980; Levizou et al., 2004; Osmond et al., 1982). On the other hand, many understory geophytes of northern Apennines are characterized by extended aboveground vegetation times (i.e., long-cycle herbs) and may be expected to carry out their primary production at a fairly leisurely pace. However, these aspects remain to be verified with the use of appropriate analytical approaches on adequate plant samples.

The sharp distinction between "shade" and "sun" species has been challenged in recent years with gradual acceptance of a more elaborate concept of plant-light relationships, entailing a number of intermediate situations and an empirical scale of shade tolerance based on plant autoecology (Ellenberg, 1979; Humbert et al., 2007; Niinemets and Valladares, 2006). Among vascular plants, extreme shade tolerators are known to possess, as a rule, enhanced levels of LHCII proteins and Chl *b* (to compensate for paucity of PSII light in the understory) and low dark respiration, besides suitable morphological adaptations. Conversely, authentic "sun" plants are usually enriched in chloroplast electron transport components and photosynthetic enzymes, with higher photosynthesis and strongly reduced amounts of antenna proteins compared to "shade" species (Anderson et al., 1995; Hallik et al., 2012; Hogewoning et al., 2012; Lichtenthaler et al., 2007), not without exceptions (Živčák et al., 2014) often due to manifold, specific and infraspecific adaptations (Murchie and Horton, 1997; Valladares et al., 2016).

In this paper we have addressed a number of plants, mainly geophytes of both life forms (spring ephemeral and long-cycle herbs) and some woody species, by measuring chlorophyll fluorescence *in vivo* with the aid of a pulse-modulated imaging fluorometer (Schreiber et al., 1986). This powerful technique allows a non-invasive assessment of photosynthetic and thermal dissipation parameters and can thus disclose peculiarities and subtle differences in light use and shade tolerance by plant species, as well as comparisons between ecological groupings. A detailed ecophysiological arrangement of understory herbs according to light demands and photosynthetic performances has thus becomes feasible, using a novel "heliophily index" based on parameters of Chl fluorescence.

2. Materials and methods

2.1. Plant materials

Experiments were carried out on 23 plant species, including 6 woody plants of various origins, 9 native long-cycle herbs and 8 native spring ephemerals. Several plants used for the experiments, collected on hills surrounding Bologna, were grown for one to three years in pots in the Botanic Garden of the University of Bologna, in partial shade on enriched soil with watering in summer: *Anemone ranunculoides* L. (Ranunculaceae), *Cyclamen hederifolium* Aiton (Primulaceae), *Erythronium dens-canis* L. (Liliaceae), *Eranthis hyemalis* (L.) Salisb. (Ranunculaceae), *Galanthus nivalis* L. (Amaryllidaceae), *Helleborus viridis* L. (Ranunculaceae), *Leucojum vernum* L. (Amaryllidaceae), *Primula vulgaris* Huds. (Primulaceae), *Pulmonaria apennina* Cristofolini et Puppi (Boraginaceae), *Scilla bifolia* L. (Liliaceae). Single detached leaves or leafy shoots of herbs growing in the Botanic Garden were also used for experiments, care being taken to avoid water stress: *Arum italicum* L. (Araceae), *Helleborus foetidus* L. (Ranunculaceae), *Narcissus tazetta* L. (Amaryllidaceae), *Petasites fragrans* (Vill.) C. Presl. (Asteraceae), *Ranunculus ficaria* L. (Ranunculaceae), *Symphytum officinale* L. (Boraginaceae), *Tulipa praecox* Ten. (Liliaceae). Leaves or ramets of trees were also used: *Eriobotrya japonica* (Thunb.) Lindl. (Rosaceae), *Hedera helix* L. (Araliaceae), *Laurus nobilis* L. (Lauraceae), *Metasequoia glyptostroboides* Hu et Cheng (Taxodiaceae), *Sequoia sempervirens* (D.Don) Endl. (Taxodiaceae), *Taxus baccata* L. (Taxaceae), all evergreens except *Metasequoia*. The experiments were conducted in the Plant Physiology Laboratory at a temperature of 20–21 °C from February to May 2015 and from December 2015 to May 2016 (though not on very chilly days). Prior to an experiment the plant or leaf sample was allowed to acclimate for at least 1 h in darkness, care being taken to avoid water stress.