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Seasonal variation in the gas exchange characteristics of *Primula* species

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Summary. Seasonal dynamics of CO_2 uptake are presented for three species of *Primula* native to the British Isles. Leaf photosynthetic rates were estimated in the field from the assimilation of $^{14}CO_2$. Maximum photosynthetic rates showed a steady decline as the year passed in all three species but *P. vulgaris* displayed a peak in photosynthetic rate prior to canopy expansion which was not observed in the other species.

Overwintered leaves of *P. vulgaris* photosynthesised at comparable rates to those of leaves at the end of the previous growing season. The carbon gain due to these overwintered leaves together with that from utilization of the high, spring light phase by the first formed leaves could result in a greater allocation of resources to flowering.

Information from a comparison of light response curves measured at a similar developmental stage, in the field and the laboratory, allowed the species to be ranked according to their degree of shade tolerance; *P. vulgaris* greater than *P. elatior* greater than *P. veris*.

Introduction

Primula veris L., *P. vulgaris* Huds. and *P. elatior* (L) Hill are spring flowering geophytes. In the British Isles *P. veris* is generally associated with open grassy places, and *P. vulgaris* and *P. elatior* with woodlands. The occurrence of the latter species in shaded situations is a consequence of their poorly developed drought tolerance (Whale 1983). Within woodlands differences in waterlogging-tolerance influence distribution, with *P. vulgaris* absent or less frequent in waterlogged places. *P. veris* is waterlogging-intolerant but relatively drought-tolerant. The association of this species with open habitat types may be a consequence of its poor shade tolerance (e.g. Keith-Lucas 1968). Measurements of photosynthetic CO_2 uptake in the three species, growing in their characteristic habitats were carried out throughout one growing season in order to determine the seasonal dynamics of photosynthesis. Photosynthetic parameters of plants at a similar developmental stage, were used to contrast the shade tolerance of the species.

P. vulgaris produces its leaves before, and *P. elatior* almost contemporaneously with tree canopy expansion. Leaves of both *P. veris* and *P. elatior* senesce in the autumn, whereas *P. vulgaris* maintains some leaves throughout the winter in shady situations. The seasonal course of photosynthesis could provide information on the significance of the early spring, high light phase and of overwintering leaves to the carbon economy of *P. vulgaris*.

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Materials and methods

CO_2 uptake of leaves in the field was assessed from the assimilation of $^{14}CO_2$ from a labelled air supply. An aluminium handpiece, incorporating an assimilation chamber (volume 3.6 cm^3), could be clamped onto individual leaves (Fig. 1). Aliquots of labelled gas were delivered to the assimilation chamber using an apparatus similar to that described by Incoll (1977, single gas system). Leaves were exposed to labelled gas for 30 s at a flow rate of 2 $ml \cdot s^{-1}$. Discs of 15 mm diameter were then punched from exposed areas directly into scintillation vials, containing 1 ml of tissue solubilizer ('lumosolve'), using a modified parallel action paper punch (Maun Industries, Notts.). Discs were solubilized for a minimum of 12 h and then bleached with 1 ml saturated benzoyl peroxide at 50° C for 1 h. After cooling 0.1 ml glacial acetic acid and 8 ml 'lipoluma' were added and the mixture allowed to stand in the dark for 12 h prior to counting. Both 'lumasolve' and 'lipoluma' are trademarks of Lumac systems, Basel, Switzerland.

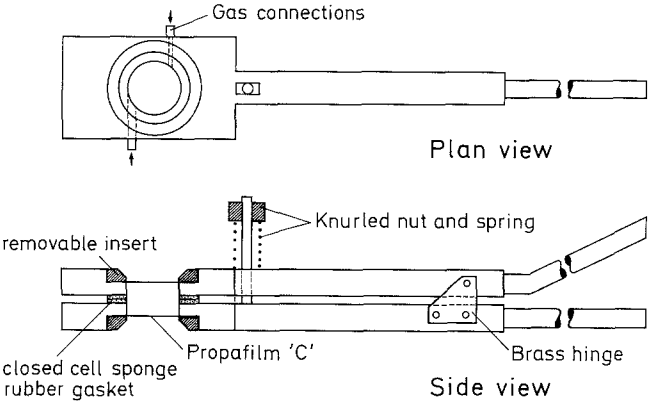

Fig. 1. Major features of the handpiece design. The body of the handpiece was constructed from aluminium, the handles from mild steel and the hinge from brass. The insert allowed replacement of the propafilm '*C*' windows (28 μm ICI Ltd.). The gas flow to the handpiece was equally divided between the upper and lower halves of the assimilation chamber and the flow then united after the handpiece

The magnitude of the flow rate used was determined by clamping the handpiece onto leaves of the different species and varying flow rate until there was no change in CO_2 uptake, at light saturation, as determined with an infra red gas analyser. Under these conditions boundary layer resistances would be negligible in comparison with other resistances to CO_2 assimilation.

By measuring photosynthetic rate within 30 s from clamping the handpiece onto the leaf it was hoped that the rates observed would be similar to those existing before the leaf was clamped, i.e. that the leaf would have had insufficient time to respond to the altered environmental conditions imposed by the handpiece. Provided that the light climate is not appreciably altered and that the CO_2 concentration used is similar to ambient, rates measured are probably similar to those of the leaf immediately before measurement.

Leaf temperature was measured using a 0.0132 cm copper/constantan thermocouple closely appressed to the abaxial surface of the leaf, and photosynthetically active radiation using a quantum sensor (constructed as described in Bell and Incoll 1981), calibrated with a Wotan HQI-E 400 W Power Stars lamp. The formula;

$$g\ (\text{mmol}\cdot\text{m}^{-2}\text{s}^{-1}) = \frac{1}{\text{rs}} \cdot \frac{273}{(273+\text{T})} \cdot \frac{10^4}{22.4} \tag{1}$$

where T is in °C and rs in $\text{s}\cdot\text{cm}^{-1}$; was used to convert measurements of stomatal resistance, made with an automatic porometer (Delta-T devices, mk·II), to conductance values. Measurements were made on the abaxial (lower) surface of the leaf, a little before an adjacent area of the lamina was exposed to $^{14}CO_2$.

Photosynthetic rates were calculated from the relationship; (Long and Incoll 1979)

$$\text{Fc} = \frac{\text{assay}\cdot f\cdot \text{Ca}}{A\cdot\varepsilon\cdot\text{Ral}} \quad \mu\text{mol CO}_2\cdot\text{m}^{-2}\text{s}^{-1} \tag{2}$$

where assay = number of disintegrations counted ($\text{c}\cdot\text{s}^{-1}$), f = flow rate of the air stream ($\text{ml}\cdot\text{s}^{-1}$), Ca = CO_2 concentration in the air stream ($\text{mol}\cdot\text{m}^{-3}$), A = sampled area of leaf (m^2), ε = efficiency of counting ($\text{c}\cdot\text{d}^{-1}$), Ral = radioactivity in an aliquot of labelled gas ($\text{d}\cdot\text{s}^{-1}$ = Bq).

'Ca' was 0.66 $\text{g}\cdot\text{m}^{-3}$ as determined using an infra-red gas analyser and a calibration gas supplied by the British Oxygen Company (Special Gases Division). The total activity of the labelled gas was determined on each occasion that gas exchange measurements were made, by diverting the gas flow to the handpiece through a train of scintillation vials each containing 3 ml of a CO_2 trap (ethanolamine: methoxyethanol, 1:2 v/v). Subsequently 15 ml of a cocktail containing toluene:methoxyethanol, 2:1 v/v, and $5\ \text{g}\cdot\text{l}^{-1}$ PPO (2,5-diphenyloxazole) were added to the CO_2 trap and the mixture counted (Jeffrey and Alvarez 1961). The second vial in the train rarely had as much as 1% of the total counts present. When initially prepared cylinders contained 4.88×10^6 $\text{Bq}\cdot\text{mol}^{-1}$.

The empirical relation used to describe the light response curve was;

$$y = A + B\exp(-Cx) \tag{3}$$

where y = photosynthetic rate ($\mu\text{mol}\cdot\text{m}^{-2}\text{s}^{-1}$) and x = incident photon flux density, IPFD ($\mu\text{mol}\cdot\text{m}^{-2}\text{s}^{-1}$). Equation (3) was derived from the monomolecular growth equation used by a number of authors to describe light response curves, e.g. Rawson and Constable (1980). Parameter estimates were determined by least squares iteration (BMD-P statistical package, University of California).

As $x\to\infty$, $\exp(-Cx)\to 0$ and the asymptote is A, the maximum photosynthetic rate. Differentiating Eq. (3) yields;

$$\frac{\partial y}{\partial x} = -BC\cdot\exp(-Cx) \tag{4}$$

When x is small, then $\exp(-Cx)\to 1$, so that

$$\frac{\partial y}{\partial x} = -BC = q, \tag{5}$$

where q is the calculated quantum use efficiency, henceforward referred to simply as quantum efficiency. Equation (5) is a linear approximation holding only for small values of x; however the parameter estimates (B, C) are based on the entire dataset. The standard deviation for the estimated quantum efficiency was determined from;

$$\begin{aligned} SD(q) &= \text{var}(q) \\ &= C^2\text{var}(B) + 2\text{cov}(BC)BC + B^2\text{var}(C). \end{aligned} \tag{6}$$

Values for quantum efficiency calculated in this manner were of the same order as estimates from linear regressions for small subsets of the dataset. For example the dataset for *P. vulgaris* obtained during week 19 yielded a value for quantum efficiency of 14 ± 1 nmol $CO_2\cdot\mu$mol photons^{-1}, which compares well with 16 ± 1.4 nmol $CO_2\cdot\mu$mol photons^{-1} obtained by linear regression for values of $x\leqq 50\ \mu\text{mol}\cdot\text{m}^{-2}\text{s}^{-1}$ ($n=16$, $r^2=0.89$). If however values for $x\leqq 100\ \mu\text{mol}\cdot\text{m}^{-2}\text{s}^{-1}$ had been used in the linear regression the quantum efficiency would then have been only 11 nmol $CO_2\cdot\mu$mol photons^{-1} and this illustrates the advantage of using the parameter estimates B, C in deriving quantum efficiency.

It follows from Eq. (2) that $A+B$ gives the intercept on the y-axis when $x=0$. Both the y intercept given from the parameters of the fitted curve ($0.06\ \mu\text{mol}\cdot\text{m}^2\text{s}^{-1}$) and that from the linear regression ($0.02\ \mu\text{mol}\cdot\text{m}^2\text{s}^{-1}$) are similar (data for week 19, *P. vulgaris*). Negative values would be expected for this quantity but inspection of table 1 indicates that positive values are not infrequent. Experiments in which the incorporation of $^{14}CO_2$ was assessed in the dark indicated 'apparent photosynthetic rates' of the order $0.06\ \mu\text{mol}\cdot\text{m}^2\text{s}^{-1}$, in all species, as a result of the 'trapping' of $^{14}CO_2$ in the boundary layer and intercellular spaces. *P. veris* had the greatest mean 'apparent dark fixation' of $^{14}CO_2$ (0.02, 0.21, −0.02 for *P. vulgaris, P. veris* and *P. elatior* respectively). Caalculated photosynthetic rates were not corrected for this error as it was small in comparison to the rates usually measured. Dark respiration rates, however, could not be extrapolated from the fitted curve and as a corollary to this the monomolecular model, $y = A(1-\exp(-Bx))$, could have been fitted to the data directly and, although constrained to pass through the origin, would have given similar results for maximum photosynthetic rates, quantum efficiency and light saturation.

Generally from 50–80 leaf exposures were made under a variety of light conditions to allow an accurate estimate of the parameters in equation 2. Early in the year, when daylength was short, natural variations in light intensity were used to collect data over a range of values. When

daylength was longer artificial shading was used to provide the variation in light quantity. When such shading was used plants were allowed 1 hr to adjust to the altered light conditions.

Individuals of the three species were sampled at random from three populations at Waterperry wood, Oxfordshire (GR SP/6009), Blewbury, Oxfordshire (GR SU/5284) and Waresley wood, Cambridgeshire (GR TL/2654) for *P. vulgaris, P. veris* and *P. elatior* respectively. Only leaves of similar external appearance and position within a rosette were sampled on any one occasion because of the ontogenetic variation in photosynthetic characteristics between leaves in differeent layers of a rosette (Whale 1982). The woodlands were both 'coppice with standards', a type of woodland management where, amongst an understory of fast growing trees, cutover at intervals of 7–11 years (the 'coppice'), a few more valuable timber trees, are allowed to grow for longer periods of, from 60–100 years, before being felled and the cycle repeated. The coppice at Waterperry wood had been cut within the last three years to leave standards of oak and invasive white poplar (*Quercus robur* L, *Populus alba* L), but there had been little coppice regrowth because of grazing by deer. Standards were of ash (*Fraxinus excelsior* L) with a well developed coppice of hazel (Corylus avellana L) at Waresley wood. Blewbury Down was a grassland slope (SE aspect) dominated by *Brachypodium pinnatum* L., with some scrub.

Results

The results from field studies of photosynthesis, where there is no control over environmental variables, may be difficult to interpret because photosynthesis is dependent on more than one independent variable. However the species of *Primula* studied have a broad temperature optimum (Whale 1982) and if one assumes that water stress was unlikely then photosynthetic rate was largely a function of IPFD. Parameters from fitted light response curves can therefore be used to compare plant performance at different sampling dates. The empirical relationship of photosynthetic rate to IPFD given in equation 2 fits the data well. Figure 2 presents data from two days of measurements on *P. vulgaris* to illustrate the best and worst fits for this species. Table 1 summarizes the photosynthetic characteristics of the species. Maximum photosynthetic rate declined with time in all three species, and was not correlated with quantum efficiency in *P. elatior* or *P. veris,* although there was some correlation in *P. vulgaris* (Table 1). Maximum photosynthetic rates were considerably greater in *P. veris* than in the other species. The reduced number of sample dates for *P. veris* was a consequence of disturbance at the experimental site, which rendered it impossible to continue measurements. *P. vulgaris* and *P. elatior* had similar maximum photosynthetic rates throughout the year, but the former displayed a peak in maximum photosynthetic rate prior to canopy expansion (week 12). This may have been a consequence of the developmental stage at which leaves were sampled, since the leaves of *P. vulgaris* were usually larger than those of the other species and it was possible to clamp the handpiece onto leaves just emerging from the overwintering rhizome and which were still held perpendicular to the soil surface. At this first sampling date leaf expansion was very incomplete. In comparison the leaves of the other species were more completely expanded before the first

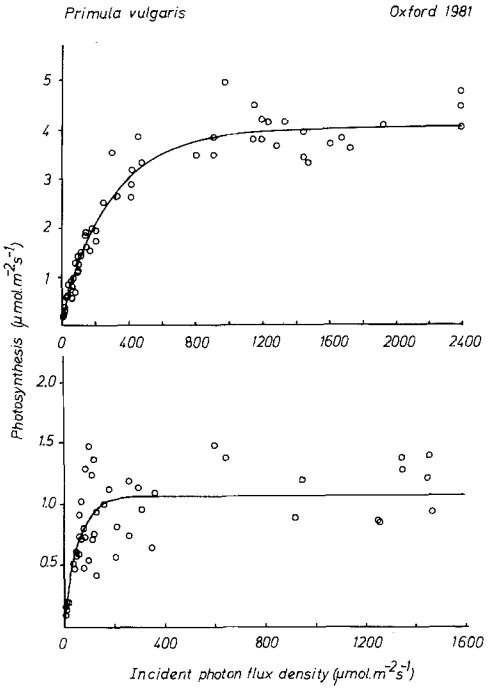

Fig. 2. The equation $y = A + B\exp(-Cx)$ fitted to two datasets for *P. vulgaris* obtained during week 19 and week 36 (upper and lower graphs respectively) to illustrate the best and worst fits of the model to the data for this species. The positive CO_2 uptake on week 19 at zero IPFD probably represents the inclusion of non-assimilated $^{14}CO_2$ trapped in intercellular air spaces and amongst the hairs on the leaf in the estimate of $^{14}CO_2$ assimilated

measurements were possible. It is not known whether the other species would have shown a similar peak in photosynthetic rate if measurements earlier in the year had been possible.

The data in Table 1 provides some indication that photosynthetic rate may light saturate earlier in *P. vulgaris* under shade. For instance leaves at the end of the growing season (wk. 36), which were shaded, light saturated much earlier than the overwintered leaves, which were unshaded (Wk. 8), although maximum photosynthetic rate did not differ. However the number of occasions on which measurements were made were too few to allow a rigorous comparison of light saturation in shaded and unshaded plants. Indeed studies of the gas exchange of plants grown under different shading regimes indicated little photochemical adaptation within species (Whale 1982), and *P. elatior* showed no correlation of light saturation with canopy expansion, rather photosynthetic rate tended to light saturate earlier as the season progressed. This was consistent with the observation that throughout most of its range this species is a plant of more open habitats and its restriction to woodlands in the British Isles atypical of the species as a whole.

Quantum efficiencies in *P. veris* remained relatively constant throughout the year, declining only towards the end of the season. The peak in quantum efficiency for *P. elatior* at week 23 was not associated with any increase in maximum photosynthetic rate and, apart from this value, trends in quantum efficiency were very similar to those of *P. veris*. Quantum efficiency was broadly correlated with maximum photosynthetic rate in *P. vulgaris*.

Table 1. The seasonal change in gas exchange characteristics determined in the field. Maximum photosynthetic rates ($\mu mol \cdot m^{-2}s^{-1}$) and quantum efficiency ($nmol \cdot CO_2 \cdot \mu mol\ photon^{-1}$) were derived from the parameters of the fitted curve [Eq. (2)]. Week 0 commenced 29/12/80. Light saturation was estimated as the incident photon flux density at which 90% of the maximum photosynthetic rate was achieved. 'r^2' is the proportion of the total variation explained by the fitted function. Values are ± their standard errors. 'F' indicates flowering and 'S' senescing plants. Light saturation point has units of $\mu mol \cdot m^{-2}s^{-1}$

	Week No	Temperature range (°C)	Maximum photosynthetic rate	y-intecept	Light saturation point	Calculated quantum efficienty	r^2	Observations
P. vulgaris	8[a]	5– 3	1.1±0.1	0.13	330	5±1	0.69	70
	7	8– 3	5.1±0.3	0.19	295	39±8	0.71	80
	F 12	18–12	9.3±0.6	−0.25	430	52±6	0.87	76
	F 19	19–12	4.0±0.06	0.06	645	14±1	0.96	70
	25	19–17	4.0±0.1	−0.06	340	27±3	0.91	60
	31	20–18	3.8±0.1	0.06	250	30±5	0.84	60
	S 36	24–20	1.1±0.06	0.006	120	20±6	0.59	50
P. elatior	F 12	18–15	6.1±0.2	−0.32	645	23±3	0.88	78
	F 16	24–19	4.8±0.2	0.25	550	19±2	0.82	70
	20	25–20	4.3±0.1	−0.13	550	18±3	0.88	70
	23	18–16	4.7±0.3	−0.25	300	38±4	0.94	70
	31	25–21	3.9±0.1	0.13	430	20±4	0.80	50
	S 35	23–19	1.5±0.1	0.19	320	9±3	0.65	52
P. veris	*F* 15	17–14	10.5±0.4	0.32	1160	20±3	0.91	79
	20	23–20	9.2±0.4	0.19	1140	20±3	0.92	72
	23	24–16	7.3±0.3	0.13	740	23±3	0.90	71
	28	24–22	4.9±0.3	0.19	800	12±2	0.80	60

[a] This value is for overwintered leaves that were green and turgid but damaged to varying degrees by fallen branches, deer, etc.

Table 2. A comparison of the species' photosynthetic characteristics from light response curves obtained at a similar developmental stage in the laboratory and the field. Field photosynthetic data is that given for week 12 (*P. vulgaris* and *P. elatior*) and week 15 (*P. veris*) in Table 1. *P. veris* developes its leaf area latter in the year than the first named species. Laboratory studies considered 5 leaves, from the same whorl of a single rosette, for each species, at the same time as the field measurements were made. The conditions under which these measurements were made were; 20° C, 0.6 $mg \cdot m^{-3}$ CO_2, 8.6 $mg \cdot m^{-3}$ H_2O and illuminated with a Wotan HQI-E 250 W metal halide lamp with dysprosium additive. Plants for laboratory studies were grown on John Innes potting compost at 84% of natural daylight in unheated glass structures. Maximum photosynthetic and dark respiration rates, light compensation and saturation points have units of $\mu mol \cdot m^{-2}s^{-1}$

	Field studies			Laboratory studies		
Primula spp.	*vulgaris*	*veris*	*elatior*	*vulgaris*	*veris*	*elatior*
Maximum photosynthetic rate	9.3±0.6	10.5±0.4	6.1±0.2	12.8±3.2	12.0±0.6	11.4±0.6
Dark respiration rate		unassessed		1.6±0.3	2.7±0.2	0.8±0.2
Calculated quantum efficiency	52 ±6	20±3	23 ±3	18 ±0.4	18 ±0.6	15 ±0.4
Light compensation point		unassessed		100 ±20	160 ±10	80 ±10
Light saturation point	430	1160	645	>1400	>1400	>1400

Comparison of maximum photosynthetic rate, quantum efficiency and light saturation requirement for leaves measured at a similar developmental stage (cf. Benecke et al. 1981) contrasts the differential shade tolerance of the species (Table 2). Data are also presented for measurements made in the laboratory under controlled conditions and, taken together with the field data, indicate that *P. veris* was the least, and *P. vulgaris* the most shade tolerant of the species with *P. elatior* intermediate between the two. Maximum photosynthetic rates obtained in the laboratory were greater than those obtained in the field, despite the latter being 'gross' measurements. This was almost certainly due to the different conditions under which the measurements were made and to the situations in which the plants were growing.

Discussion

The peak in maximum photosynthetic rate shown by *P. vulgaris*, prior to leaf canopy expansion (weeks 16 and 19 for shrub and tree canopy expansion respectively), resembled the situation in other woodland herbs, characterized by leaf production before canopy expansion. Such plants have high maximum photosynthetic rates and a high light requirement for saturation (e.g. Mahall and Bormann 1978). However, leaf production was not confined to the spring, high light phase in *P. vulgaris* (Whale 1982). It was probable, although difficult to be absolutely certain, that the leaves sampled in the field at week 12 were part of the leaf population sampled at week 7. The peak in photosynthetic maxima before canopy expansion would then be

a result of ontogenetic trends within a population of leaves of the same physiological age. There is ample evidence for a quadratic response in photosynthetic maxima during leaf development (e.g. Constable and Rawson 1980). A very real difficulty exists in separating ontogenetic trends within a population of even aged leaves from seasonal trends between leaves produced at different times of the year, especially when destructive methods are used in estimating photosynthesis. By considering only those leaves contributing most to the assimilatory potential of the plants it was possible to make repeatable measurements of seasonal changes in the photosynthetic characteristics for this leaf type, and hence for the plant. It is of note that the trends observed in photosynthetic characteristics are similar to those occurring during the ontogeny of individual leaves.

The datasets of Fig. 2 display considerable scatter about the fitted curve. Neglecting errors in the functioning of the gas supply apparatus, leading to variation in Ral (Eq. (2)) and the non-photosynthetic 'apparent assimilation of $^{14}CO_2$, which are small, other sources of error are chiefly the result of;

i) variation in the photosynthetic characteristics of individual leaves.

ii) differences in the pre-exposure history of individual leaves, e.g. leaves may have been buffeted by winds more on one plant than another as a result of differences in elevation.

iii) photosynthetic rate is dependent on factors other than IPFD. The most significant of these are probably temperature and water stress.

Except for early in the year temperature was not correlated with IPFD as shading screens were used to produce variation in flux density. The temperature variation for data points around the asymptote was usually 2–3° C. In view of the broad temperature optimum of these plants multiple regressions of photosynthetic rate on temperature and IPFD were not carried out, especially as r^2's were high for the photosynthetic rate, IPFD relations.

Differences in vapour pressure deficit from day to day may have affected photosynthetic rate. On occasions when water stress was deemed likely measurements of stomatal conductance were made. It is suggested that Figs. 3a, 4b, c indicate periods when conductance *per se* did not limit photosynthetic rate. Conductance increased but maximum photosynthetic rate remained relatively constant. A different situation is apparent in Fig. 3b. At high light intensities (● points) increasing stomatal conductance was correlated with increasing photosynthetic rate. However, photosynthetic rate was never limited by stomatal conductance as calculated internal CO_2 concentrations were greater in Fig. 3b than a. Thus at a conductance of 100 mmol·m^{2}s^{-1} the internal CO_2 concentration was 263 ppm and 205 ppm respectively. Figure 4b does not display the same relation of photosynthetic rate to stomatal conductance as in Figs. 4a and c at light saturation. Indeed the leaves measured in week 23 (Fig. 4b) had a greater water use efficiency than in week 20 (Fig. 4a) at light saturation. However, differences in estimated maximum photosynthetic rate were not significantly different on these two occasions and, although the range of conductances measured was less in week 23 (Fig. 4b), there is little evidence that they limited maximum photosynthetic rate. Examination of Fig. 4 indicates that the range of stomatal conductance falls as the season passes. This is consistent with similar observations

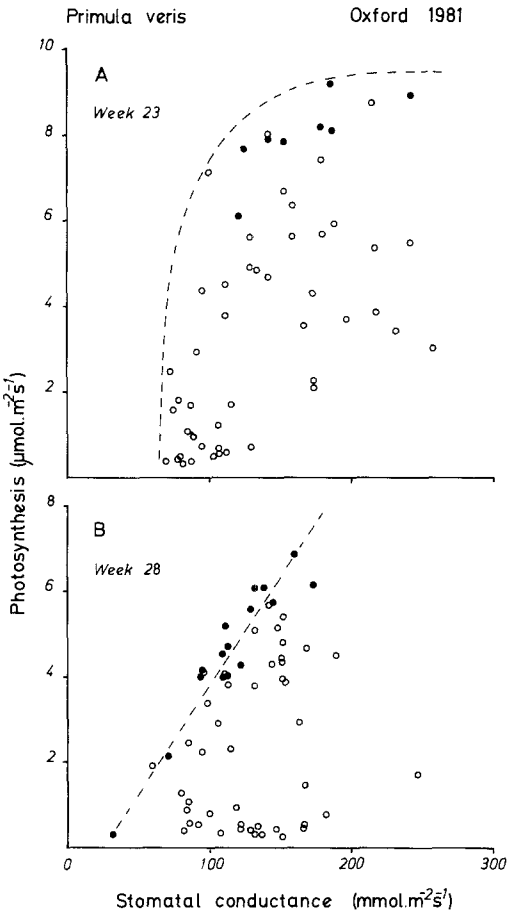

Fig. 3A, B. Stomatal conductance and photosynthetic rate, obtained under conditions of varying IPFD, VPD (not measured) and temperature (see Table 1 for range), for two days of separate measurements on *P. veris*. ● indicates values obtained at light saturation. The broken lines in the Figures emphasise the trends in photosynthesis and conductance values. The broken line in **B** is the linear regression through the points obtained at light saturation

where the range of observed values declines with increasing leaf age (see Schulze and Hall 1982 for examples).

On only one occasion were measurements of stomatal conductance much less than 400 mmol·m^{-2}s^{-1} for *P. vulgaris*, which probably reflects the nature of the habitat in which the population was situated (a sheltered area of low lying ground, crossed by small streams). On this occasion there was no suggestion that conductance limited photosynthetic rate. It was therefore unlikely that measured photosynthetic rates were affected by water stress in any of the species.

Bjorkman and Holmgren (1963) maintained that higher quantum efficiencies were associated with shade adapted plants and higher maximum photosynthetic rates with plants adapted to high light environments. On this basis *P. veris* was the least shade tolerant of the three species and *P. vulgaris* the most (Table 2). In many ways *P. elatior* was intermediate between these two species having quantum efficiencies similar to those in *P. veris* but maximum photosynthetic rates and light requirements for saturation similar to *P. vulgaris*. The relative shade tolerance of the species suggested here was in agreement with that from work with artificial shade (Whale 1982). Differences between the spe-

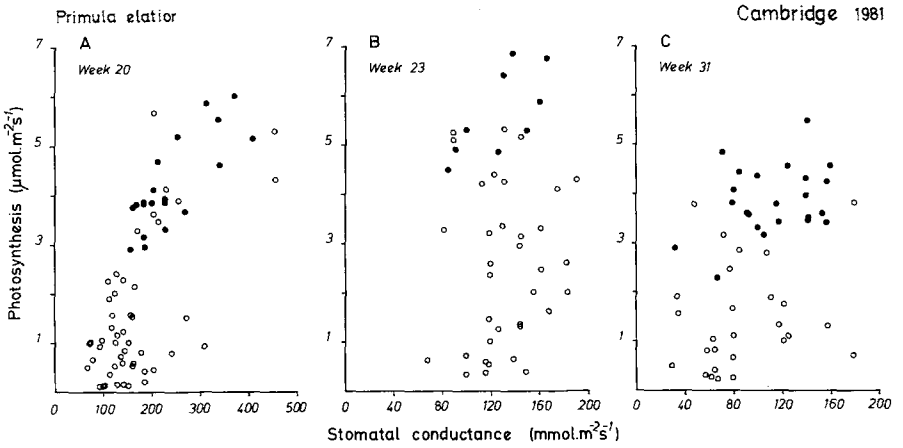

Fig. 4A–C. Stomatal conductance and photosynthetic rate, obtained under conditions of varying IPFD, VPD (not measured) and temperature (see Table 1 for range) for three days of separate measurements on *P. elatior*. Symbols as in Fig. 3

cies, with respect to their shade tolerance, were most clearly shown in the field data (Table 1), whereas results from the laboratory studies were more difficult to interpret (Table 2). Differences between species are more likely to be displayed under field conditions where there is considerable interaction of factors; especially in situations where no single factor can be said to controll the species' distribution (Whale 1983). Field experiments should therefore, as far as possible, be complementary to those in the laboratory, and *vice versa*.

The presence of overwintering leaves in *P. vulgaris*, which were capable of a positive contribution to the carbon balance of the plant (Table 1, week 8), and the species' ability to utilize the high spring light phase before canopy expansion could both be thought to constitute a significant contribution to the carbon economy of the plant. However, Helliwell (1980) found that it was the light climate experienced from May to November that most affected biomass production. High light earlier in the year lead only to increased flower production. This suggested that the carbon gain in the early spring, high light phase was largely used in the reproductive effort. Poshkurlat (1962) states that flower primordia are present in *P. veris* in late autumn and it is likely that a similar situation exists in the other two species. An increased carbon gain in the spring could initiate new flower primordia and/or increase the proportion of dormant flower buds developing, which would otherwise abort or remain dormant. There is, however, no information on this question.

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