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Dark Leaf Respiration in Light and Darkness of an Evergreen and a Deciduous Plant Species[1]

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Dark respiration in light as well as in dark was estimated for attached leaves of an evergreen (*Heteromeles arbutifolia* Ait.) and a deciduous (*Lepechinia fragans* Greene) shrub species using an open gas-exchange system. Dark respiration in light was estimated by the Laisk method. Respiration rates in the dark were always higher than in the light, indicating that light inhibited respiration in both species. The rates of respiration in the dark were higher in the leaves of the deciduous species than in the evergreen species. However, there were no significant differences in respiration rates in light between the species. Thus, the degree of inhibition of respiration by light was greater in the deciduous species (62%) than in the evergreen species (51%). Respiration in both the light and darkness decreased with increasing leaf age. However, because respiration in the light decreased faster with leaf age than respiration in darkness, the degree of inhibition of respiration by light increased with leaf age (from 36% in the youngest leaves to 81% in the mature leaves). This suggests that the rate of dark respiration in the light is related to the rate of biosynthetic processes. Dark respiration in the light decreased with increasing light intensity. Respiration both in the light and in the dark was dependent on leaf temperature. We concluded that respiration in light and respiration in darkness are tightly coupled, with variation in respiration in darkness accounting for more than 60% of the variation in respiration in light. Care must be taken when the relation between respiration in light and respiration in darkness is studied, because the relation varies with species, leaf age, and light intensity.

Previous studies of the relationship between carbon balance and respiration have focused on R_n, assuming that it equals R_d. However, investigations using crop species suggest that respiration is partly inhibited in the light (Sharp et al., 1984; Brooks and Farquhar, 1985).

There is considerable debate about the level of respiration in photosynthetic tissue that occurs in the light (Graham, 1980; Turpin and Weger, 1990). The contrasting estimates of R_d may, in part, be due simply to the different measuring techniques used in the studies. The methods available measure R_d as either O_2 consumption or CO_2 production, measuring in fact two different processes: ETC or TCA, respectively. Although these processes are considered to be interdependent, they can operate in isolation of one another (Turpin and Weger, 1990). For example, Weger et al. (1988) reported that ETC activity is the same in light and dark, but TCA activity decreases in the light. These results are in agreement with both the results of Kromer and Heldt (1991), who showed that ETC activity is necessary in the light for optimal photosynthetic rate, and those of Gemel and Randall (1992), who found that TCA activity is restricted in the light.

The contrasting estimates of R_d may also partly be the result of the different environmental conditions presented in the different studies and/or the different developmental states of the tissues used (Turpin and Weger, 1990; Villar et al., 1994). Thus, comparison of R_d data from previous studies is difficult and necessitates that the effect of environmental and metabolic states on R_d be determined. The dependence of R_d on leaf characteristics (leaf age, leaf N, and leaf carbohydrate concentration) and environmental factors (light intensity and temperature) has not been studied extensively, and the limited results are controversial. Brooks and Farquhar (1985) reported that R_d varies with factors that also affect R_n (e.g. temperature and carbohydrate concentration). However, Harley et al. (1992) found that R_n and R_d are affected differently, with R_n varying with leaf N concentration and temperature, whereas no relationship between these two factors and R_d was observed. Also, the information concerning the extent to which R_d and the inhibition of respiration by light vary among different plant species is very scarce and limited to the data of Brooks and Farquhar (1985), who found a similar degree of inhibition of respiration by light (about 77%) between two crop species (wheat and spinach).

To determine whether the degree of inhibition of respiration by light differs between species, we selected two shrub species differing in many traits, an evergreen species (*Heteromeles arbutifolia*) and a deciduous species (*Lepechinia fragans*). Evergreen species tend to exhibit low rates of

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Abbreviations: **A**, net CO_2 assimilation rate; c_i, internal CO_2 concentration; ETC, mitochondrial electron transport chain; R_d, rate of non-photorespiratory evolution in the light or rate of dark respiration in light; R_n, rate of respiration in darkness; TCA, tricarboxylic acid cycle; Γ^*, CO_2 compensation point in the absence of dark respiration.

photosynthetic carbon gain (due to lower leaf N concentrations) relative to deciduous species (Field and Mooney, 1986; Evans, 1989; Reich et al., 1992). Also, R_n per unit dry weight is generally lower in evergreen species relative to deciduous species (Merino et al., 1982; Larcher, 1983). The lower leaf N concentrations that occur in evergreen species also suggest that R_n will be lower, because R_n is normally positively correlated with N concentration (Amthor, 1989; Ryan, 1991). It seems likely that evergreen species will show a lower R_d and a higher degree of inhibition of respiration by light than deciduous ones, since Mediterranean evergreens have to endure extended periods in which photosynthetic carbon gain is very low.

In the study reported here R_d, R_n, and the degree to which respiration is inhibited by light were investigated, and the relation between R_d and R_n and their dependence on leaf N concentration, leaf age, temperature, and light intensity in two plant species differing in photosynthetic rates and leaf longevity were assessed.

MATERIALS AND METHODS

Plant Material

Two woody species typical of the Californian chaparral were chosen for this study: *Heteromeles arbutifolia* (Ait.), an evergreen shrub whose leaves persist for 2 or 3 years, and *Lepechinia fragans* (Greene), a deciduous shrub whose leaves last 5 or 6 months. Plants were grown in pots in an experimental garden, partially shaded, for 2 years and were watered daily. During the 2 months preceding the experiments, temperatures ranged from 20 to 30°C during the day and 10 to 20°C at night, and at midday the PPFD was close to 600 μmol m^{-2} s^{-1}.

The long life of *H. arbutifolia* leaves allowed their classification as young (rapidly growing leaves, from 15–30 d), medium aged (leaves of approximately 3 months that had ended the phase of expansion of the lamina), and mature (leaves of approximately 2 years of age that had largely finished their growth, both in terms of lamina expansion and thickness).

Gas-Exchange System

Gas exchange in leaves was measured with an open gas-exchange system described by Held et al. (1991). Before the experiments, the IRGA (Analytical Development Co., Hoddesdon, UK; model 225 MK3) was calibrated at the low CO_2 concentrations used in the present study, as recommended by Bloom et al. (1980). No changes in IRGA sensitivity were detected within the CO_2 concentration range used. The O_2 pressure during the experiments was 210 mbar.

The light source was a metal halide lamp (Sylvania, GTE, Danvers, MA) suspended above the leaf chamber. Different PPFDs (measured inside the chamber) were obtained by covering the chamber with nylon mesh filters.

Gas-exchange calculations were made according to Ball (1987), and cuticular conductances were assumed to be zero because of the thick cuticle of leaves of the Mediterranean woody species (Lillis, 1991). Unless specified, all measurements were made at a leaf temperature of 20°C on individual leaves attached to the plant. Unless specified, all experiments were started early in the morning to avoid variation in the respiration rate due to diurnal changes in carbohydrate concentration (Azcón-Bieto et al., 1983). Respiration rates were expressed per unit of leaf dry weight.

Measurement of R_d and R_n

The method of Laisk (1977) (extended by Brooks and Farquhar, 1985) was used to measure R_d. This method determines the c_i at which the rate of photosynthesis equals that of photorespiration. At this c_i (Γ^*), the rate of CO_2 evolution represents R_d. This method analyzes the **A** at low c_i values and varying light intensities. For each leaf, the experiments were repeated at three different PPFDs (40, 75, and 145 μmol m^{-2} s^{-1}). At each photon flux density, photosynthetic rates were measured at decreasing c_i values (usually in the range 90–30 μL L^{-1}). For each PPFD, the linear regression of **A** versus c_i was calculated. In most leaves, all three linear regressions intersected at one point. The y and x coordinates of this point of **A** and c_i represent R_d and Γ^*, respectively, and were determined graphically. A representative example of this method for a leaf of *H. arbutifolia* is shown in Figure 1.

The main disadvantage of the Laisk method is that the experiments must be performed at very low CO_2 concentrations and are, therefore, far below normal ambient CO_2 concentrations. Several studies have reported that decreases in CO_2 concentration result in increases of respiration rates (Amthor et al., 1992; Thomas and Griffin, 1994; Villar et al., 1994). As a result, R_d at ambient CO_2 will be overestimated by the Laisk method. To overcome such potential overestimates and assuming that R_d and R_n are affected similarly by CO_2, we corrected R_d by determining the relationship between R_n measured at 350 and 35 μL L^{-1}

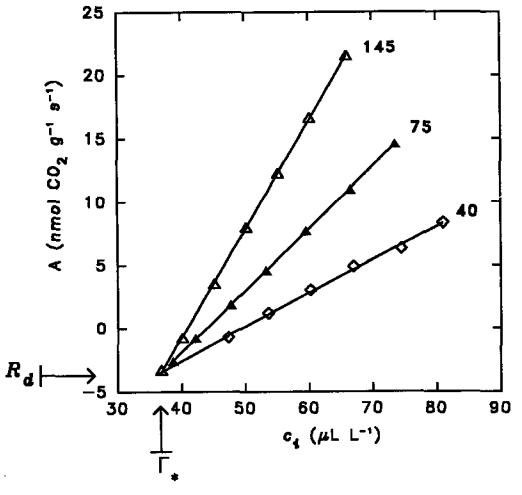

Figure 1. **A** as a function of c_i (μL L^{-1}) for a leaf of *H. arbutifolia* (method of Laisk). Numbers (145, 75, 40) indicate the incident PPFDs under which measurements were made (μmol photons m^{-2} s^{-1}). Lines represent linear regressions at these PPFDs. The arrows indicate the values of R_d and Γ^* for that particular leaf.

for these species (Villar et al., 1994). A zero intercept was assumed for the regression. The relationship between R_n measured at 350 and 35 μL L^{-1} was:

$$R_n = R_{n35} \times 0.6854 \quad (1)$$

where R_n and R_{n35} are the respiration rates in darkness measured at 350 and 35 μL L^{-1}, respectively.

The R_n was measured by covering the chamber with a black cloth at an ambient CO_2 concentration of 350 μL L^{-1}. In most cases the R_n values stabilized within 45 min.

The degree of inhibition of dark respiration by the light was estimated as:

$$\text{Degree of inhibition} = (1 - R_d/R_n) \times 100 \quad (2)$$

The specific leaf area and total Kjeldahl N were measured for all leaves used for gas exchange. Finely ground dry tissue was digested in an aluminum block using the method of Issac and Johnson (1976) and analyzed colorimetrically with a Technicon (Tarrytown, NY) Autoanalizer II using a Berthelot reaction (Technicon industrial method No. 146–171).

Effect of Extended Dark and Light Periods

R_n and R_d in medium-aged leaves of the two species were measured just before sunrise. At this time of the day, because of the long dark period (approximately 9 h), the carbohydrate level of the leaf was likely to have been at its minimum (Azcón-Bieto et al., 1983). Measurements of R_n and R_d at sunrise should, therefore, reflect their values under low carbohydrate concentration. Therefore, we measured R_n, R_d, and $\Gamma*$ for the same leaf at sunrise according to the method described above.

To measure R_d at potentially high leaf carbohydrate concentrations, the procedure described by Brooks and Farquhar (1985) was used: immediately following the measurement of R_d at sunrise, each leaf was subjected to a PPFD of 600 μmol m^{-2} s^{-1} and 500 μL L^{-1} of ambient CO_2 concentration for 5 h. Previous studies (Hrubec et al., 1985) have demonstrated that these conditions are sufficient to significantly increase leaf carbohydrate levels. Following this illumination period, each leaf was subjected to a PPFD of 150 μmol m^{-2} s^{-1} and to an ambient CO_2 concentration such that the intercellular concentration of CO_2 was equal to $\Gamma*$. The CO_2 efflux obtained at these conditions represented R_d under potentially high carbohydrate conditions. Finally, R_n was determined for the same leaf, yielding R_n under potentially high carbohydrate conditions.

Effect of Temperature and Light Intensity

To analyze the effect of temperature on R_d and R_n, two medium-aged leaves were selected from each species. In three successive experiments, R_d and $\Gamma*$ were estimated according to the method of Laisk at leaf temperatures of 10, 20, and 30°C. In the same leaves, R_n was measured at the same three temperatures.

The effect of light intensity on R_d was studied in one leaf of each species. R_d and $\Gamma*$ of each leaf were measured following the method of Laisk. R_d was then measured at different PPFDs from near 0 to 800 μmol m^{-2} s^{-1}, keeping c_i always equal to $\Gamma*$ of the leaf by selecting appropriate ambient CO_2 concentrations. The rate of CO_2 evolution at each selected light intensity (measured after a stabilization period of approximately 30 min) was taken as the R_d at that light intensity. The sequence of different PPFD values was random to avoid the effect of the time on R_d. The R_n of each leaf was measured at the end of the experiment.

RESULTS

Rates of Respiration (R_d and R_n)

There were no significant differences ($P > 0.05$) between the mean values of R_d in the leaves of medium age for the two species (2.6 ± 0.3 and 2.1 ± 0.2 nmol CO_2 g^{-1} s^{-1} for *L. fragans* and *H. arbutifolia*, respectively; Table I). However, the mean value of R_n for leaves of the deciduous species, *L. fragans*, was higher ($P < 0.05$) than that for leaves of the evergreen species, *H. arbutifolia* (7.3 ± 1.1 versus 4.5 ± 0.5 nmol CO_2 g^{-1} s^{-1}, respectively; Table I).

Within each species, R_n was significantly higher ($P < 0.05$) than R_d, demonstrating that dark respiration is partially inhibited in light. The degree of inhibition of dark respiration by the light for the medium-aged leaves was significantly higher ($P < 0.05$) for the deciduous species, *L. fragans* (61.8%), than for the evergreen one, *H. arbutifolia* (51.0%, Table I). R_d and R_n were positively correlated in each species (Fig. 2). However, the regression line of *L. fragans* had a significantly ($P < 0.05$) lower slope than *H. arbutifolia*, again demonstrating that the inhibition of respiration by light was greater in *L. fragans*. In both species, more than 60% of the variation of R_d was explained by the variation in R_n.

There was no difference ($P < 0.05$) in $\Gamma*$ between the two species (35.8 ± 0.4 μL L^{-1} for *H. arbutifolia* and 35.6 ± 0.6 μL L^{-1} for *L. fragans*).

Table I. *R_d and R_n, $\Gamma*$, organic N concentration, and degree of inhibition of dark respiration by light of medium-aged leaves of H. arbutifolia (n = 8) and L. fragans (n = 7)*

Values represent the means ± SE. The degree of inhibition of dark respiration by the light was estimated as $(1 - R_d/R_n) \times 100$.

Species	R_d	R_n	$\Gamma*$	N	Inhibition
	nmol CO_2 g^{-1} s^{-1}	nmol CO_2 g^{-1} s^{-1}	μL L^{-1}	%	%
H. arbutifolia	2.1 ± 0.2	4.5 ± 0.5	35.8 ± 0.4	2.0 ± 0.1	51.0 ± 2.1
L. fragans	2.6 ± 0.3	7.3 ± 1.1	35.6 ± 0.6	3.4 ± 0.2	61.8 ± 4.7

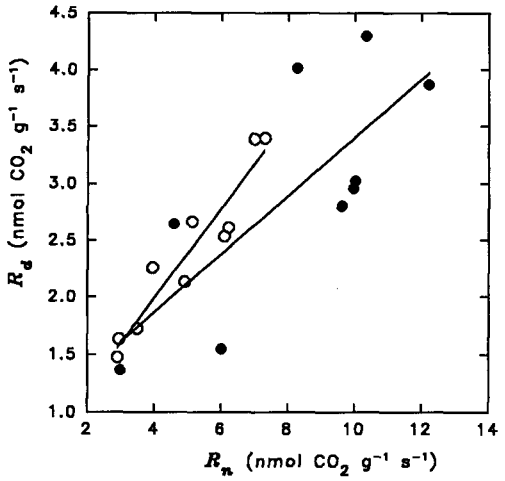

Figure 2. Relationship between R_d and R_n in medium-aged leaves of *H. arbutifolia* (○) and *L. fragans* (●). The lines represent the linear regression for each species: *H. arbutifolia*, $y = 0.4206 + 0.3934x$ ($r^2 = 0.90$, $n = 10$); *L. fragans*, $y = 0.8433 + 0.2562x$ ($r^2 = 0.58$, $n = 9$).

Effect of Leaf Age

Figure 3 shows the mean values of R_d, R_n, and the degree of inhibition of respiration by light with respect to leaf age in *H. arbutifolia*. Both R_d and R_n decreased significantly with increasing leaf age. However, because R_d decreased faster with leaf age than R_n, the degree of inhibition of respiration by light increased with age, from 36% in the youngest leaves to 81% in the mature leaves.

Effect of Leaf N and Extended Periods of Light and Darkness

The leaves of the deciduous species (*L. fragans*) showed a significantly higher ($P < 0.05$) N concentration (3.4 ± 0.2%) than the evergreen species (*H. arbutifolia*, 2.0 ± 0.1%; Table I). However, there was no correlation between the rate of respiration (R_d or R_n) and N concentration within each species.

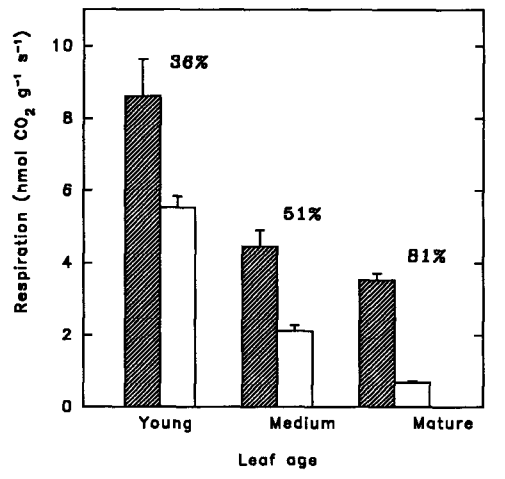

Figure 3. R_d (white bars) and R_n (hatched bars) of leaves of *H. arbutifolia* of different ages. The numbers above the bars indicate the percentages of inhibition of dark respiration in the light, calculated as $(1 - R_d/R_n) \times 100$. The vertical lines above the bars indicate the SE (young and mature leaves, $n = 2$; medium-aged leaves, $n = 8$).

Table II shows R_d and R_n of medium-aged leaves of the two species exposed to extended periods of darkness or light (potentially low and high leaf carbohydrate concentration, respectively). Extended light treatment and high ambient CO_2 concentration, which was expected to increase the carbohydrate concentration, resulted in a significant ($P < 0.05$) increase in R_d for both species and in R_n for *H. arbutifolia*. However, the degree of inhibition was not affected ($P > 0.05$) by presumed carbohydrate levels in either species.

Effect of Temperature and Light Intensity

Table III shows R_d, R_n, and $\Gamma*$ measured at 10, 20, and 30°C. Not surprisingly, R_d and R_n increased with increasing temperature in both species. The degree of inhibition of respiration by light in both species was not affected significantly ($P > 0.05$) by temperature.

For both species, $\Gamma*$ increased with increasing temperature, being identical for the two species at each temperature.

Figure 4 shows the effect of PPFD on R_d and includes the value of R_n (light intensity = zero). In the leaves of both species studied, R_d decreased with increasing PPFD until approximately 200 to 400 μmol m^{-2} s^{-1}, after which it stabilized. The degree of inhibition of respiration by the light was again higher in the leaf of the deciduous species, *L. fragans*, being close to 100% at approximately 300 μmol m^{-2} s^{-1}. The maximum degree of inhibition was approximately 80% in the evergreen species *H. arbutifolia*.

DISCUSSION

In both species R_d was always lower than R_n, indicating that respiration is inhibited in light. These results are in agreement with biochemical studies of TCA activity in light (Gemel and Randall, 1992; Hanning and Heldt, 1993) and R_d studies in whole tissues based on CO_2 production (Sharp et al., 1984; Brooks and Farquhar, 1985; Weger et al., 1988).

Despite major differences in leaf longevity, leaf N concentration (Table I), and specific leaf area (data not shown) between the deciduous and evergreen species, R_d did not differ. In contrast, R_n was higher in the leaves of the deciduous species, *L. fragans*, than in the leaves of the evergreen species, *H. arbutifolia* (Table I). As a result, there was more light-induced inhibition of respiration in the leaves of the deciduous species. Thus, contrary to our original hypothesis, the inhibitory effect of light on respiration is not stronger in leaves of the evergreen species.

The fact that the degree of inhibition of respiration depends on leaf age (Fig. 2) and light intensity (Fig. 4) suggests that it is difficult to compare R_d data from previous studies even if they used the same method. Only the data of Brooks and Farquhar (1985) on wheat and spinach are comparable with ours, because they used the Laisk

Table II. *Effect of extended dark and light periods on the values of R_d and R_n in medium-aged leaves of H. arbutifolia and L. fragans*

Measurements under extended dark and light periods were considered after 9 h of darkness (beginning of the day) and after 5 h at a PPFD of 600 μmol m^{-2} s^{-1} and an ambient CO_2 concentration of 500 μL L^{-1} (prolonged illumination), respectively. Values represent means ± SE of two measurements.

Species	Treatment	R_d	R_n	Inhibition
		nmol CO_2 g^{-1} s^{-1}	nmol CO_2 g^{-1} s^{-1}	%
H. arbutifolia	Beginning of the day	2.4 ± 0.2	5.6 ± 0.7	57.3 ± 0.7
	Prolonged illumination	3.4 ± 0.1	7.1 ± 0.2	52.4 ± 1.0
L. fragans	Beginning of the day	3.0 ± 0.1	7.8 ± 2.3	57.9 ± 11.9
	Prolonged illumination	4.1 ± 0.2	11.3 ± 0.9	63.4 ± 5.0

method, fully expanded leaves, and a light intensity similar to that in our experiments. However, they did not correct R_d for the effect of low CO_2 concentration, which results in an overestimation of R_d (Villar et al., 1994). A correction of the R_d data of Brooks and Farquhar (1985) can be made if we assume that the relationship between respiration rate measured at 350 and 35 μL L^{-1} in wheat and spinach is the same as in our species (Eq. 1). In fact, Amthor et al. (1992) found in a different species, *Rumex crispus*, an effect of decreasing CO_2 concentration from 350 to 35 μL L^{-1} similar to that in this study. The degree of inhibition in wheat and spinach (77%), using corrected data of Brooks and Farquhar (1985), is higher than that in the two species investigated by us.

The lower values of the degree of inhibition estimated in *L. fragans* and *H. arbutifolia*, relative to spinach and wheat, could be due to errors in determining R_d. However, we are confident that our estimates of R_d did not have significant errors, since $\Gamma*$ (an index of CO_2/O_2 specificity of Rubisco) was practically identical for the leaves of both species (Table I and III) and very similar to those published for other C_3 species (Laisk, 1977; Brooks and Farquhar, 1985). Also, we have recently demonstrated the accuracy of the Laisk method in determining R_d (Villar et al., 1994).

Therefore, we conclude that the degree of inhibition of dark respiration in light is species dependent. The causes of the inhibition of respiration by light seem to be related to the photosynthetic processes (Graham, 1980; Turpin and Weger, 1990). A higher photosynthetic rate should result in a greater availability of ATP and NADPH (Turpin and Weger, 1990), thus decreasing the demand for respiratory energy. Therefore, it seems likely that there will be a positive relationship between the degree of inhibition and photosynthetic rate.

Does the degree of inhibition of respiration by light correlate with the rate of photosynthesis? A comparison of photosynthetic rates in wheat (700 nmol CO_2 g^{-1} s^{-1}, Dunstone et al., 1973) with those of *L. fragans* (356 nmol CO_2 g^{-1} s^{-1}) and *H. arbutifolia* (120 nmol CO_2 g^{-1} s^{-1}) suggest that such a correlation may exist. In addition, we found that R_d decreased with increasing photosynthetic activity at the higher light intensities (Fig. 4). Other investigators have also reported a decrease in R_d with an increase in light intensity (Brooks and Farquhar, 1985; Villar et al., 1994). The degree of inhibition of respiration by light does, therefore, appears to be related to the rate of photosynthesis. More detailed experiments are needed to address this hypothesis.

Respiration rate is normally related to N concentration (Amthor, 1989; Ryan, 1991), because of the relationship between respiration and the turnover of proteins. However, in some species there is no correlation between R_n and N concentration (Byrd et al., 1992), suggesting that in such cases respiration rate is related more to the amount of carbohydrate than to growth or maintenance requirements. However, the lack of correlation of respiration rates (R_d or R_n) with N concentration in the two species studied by us seems to be due more to the small coefficient of variation in N concentration in each species (<7%, taking out one leaf of *L. fragans*). Merino et al. (1982) found a positive correlation between R_n and N concentration in *H. arbutifolia* leaves, which have a higher coefficient of variation in N

Table III. *Effect of leaf temperature on R_d, R_n, $\Gamma*$, and degree of inhibition of respiration by light in medium-aged leaves of H. arbutifolia and L. fragans*

Values represent the means of two measurements, except for *H. arbutifolia* at 10°C, which is one measurement.

Species	Leaf Temperature	R_d	R_n	$\Gamma*$	Inhibition
	°C	nmol CO_2 g^{-1} s^{-1}	nmol CO_2 g^{-1} s^{-1}	μL L^{-1}	%
H. arbutifolia	10	0.6	1.4	27.2	60.1
	20	1.4	3.5	37.6	63.0
	30	2.5	7.6	56.2	66.8
L. fragans	10	0.2	2.9	27.0	95.5
	20	2.3	10.3	36.9	77.6
	30	4.5	16.3	58.2	72.2

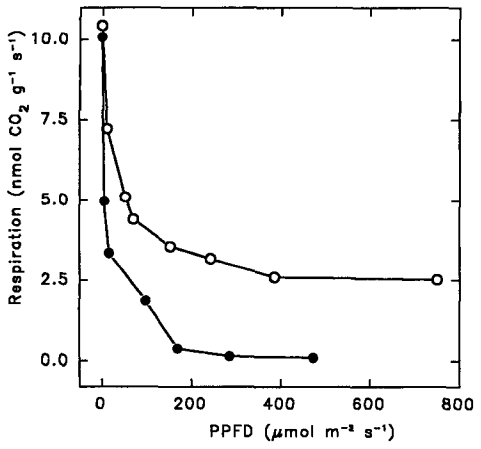

Figure 4. Effect of light intensity on R_d in the leaves of *H. arbutifolia* (○) and *L. fragans* (●). The value of R_n (light intensity = zero) for each species is also included.

concentration (23%). Therefore, we suspect that a relationship can exist between the N concentration and R_d and R_n.

The degree of inhibition also depends on leaf development (Fig. 3). Young leaves had low inhibition of respiration by light (36%), whereas such inhibition reached 81% in mature leaves. These results support the hypothesis of Graham (1980) that young leaves should have less inhibition of respiration by light because of their active growth. In fact, using the data of Merino et al. (1982) for young and mature leaves of *H. arbutifolia* with similar characteristics to those in this study, we found that the young leaves that have a lower inhibition of respiration also have a faster growth (0.086 g g^{-1} d^{-1}) and the mature leaves with higher inhibition of respiration have a slower growth (0.008 g g^{-1} d^{-1}). Growth requires a supply of carbon skeletons for the synthesis of new tissues, which are generated only by respiration. As a result, there would be less inhibition of respiration by light in rapidly growing young leaves, in which the demand for TCA respiratory products is high. This is in agreement with the results of Weger et al. (1988) and Thomas et al. (1993).

The degree of inhibition of respiration by light appears not to be affected by changes in temperature or extended periods of dark and light, since R_d and R_n responded similarly to changes in these factors (Tables II and III). A similar result was reported by Brooks and Farquhar (1985) in spinach leaves. However, Harley et al. (1992) found no effect of temperature on R_d but a significant effect of temperature on R_n. The degree of inhibition of respiration by light, therefore, increased with temperature in the study by Harley et al. (1992). One explanation for the lack of relationship between temperature and R_d in the results of Harley et al. (1992) is that the data in the low c_i portions used to estimate R_d were imprecise and not suitable for rigorous determination of Γ^* and R_d.

The positive relationship between R_d and R_n (Fig. 2) and the similar responses of both to some of the factors considered (temperature and extended periods of dark and light) when other factors that affect R_d remain constant (leaf age and light intensity) suggested that the dark respiratory processes in the light, even if they are not the same, are rather similar to those taking place in darkness. This idea is also supported by the fact that more than 60% of the variation in R_d can be explained by variation in R_n in both species studied in this work and in wheat and spinach (Brooks and Farquhar, 1985).

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