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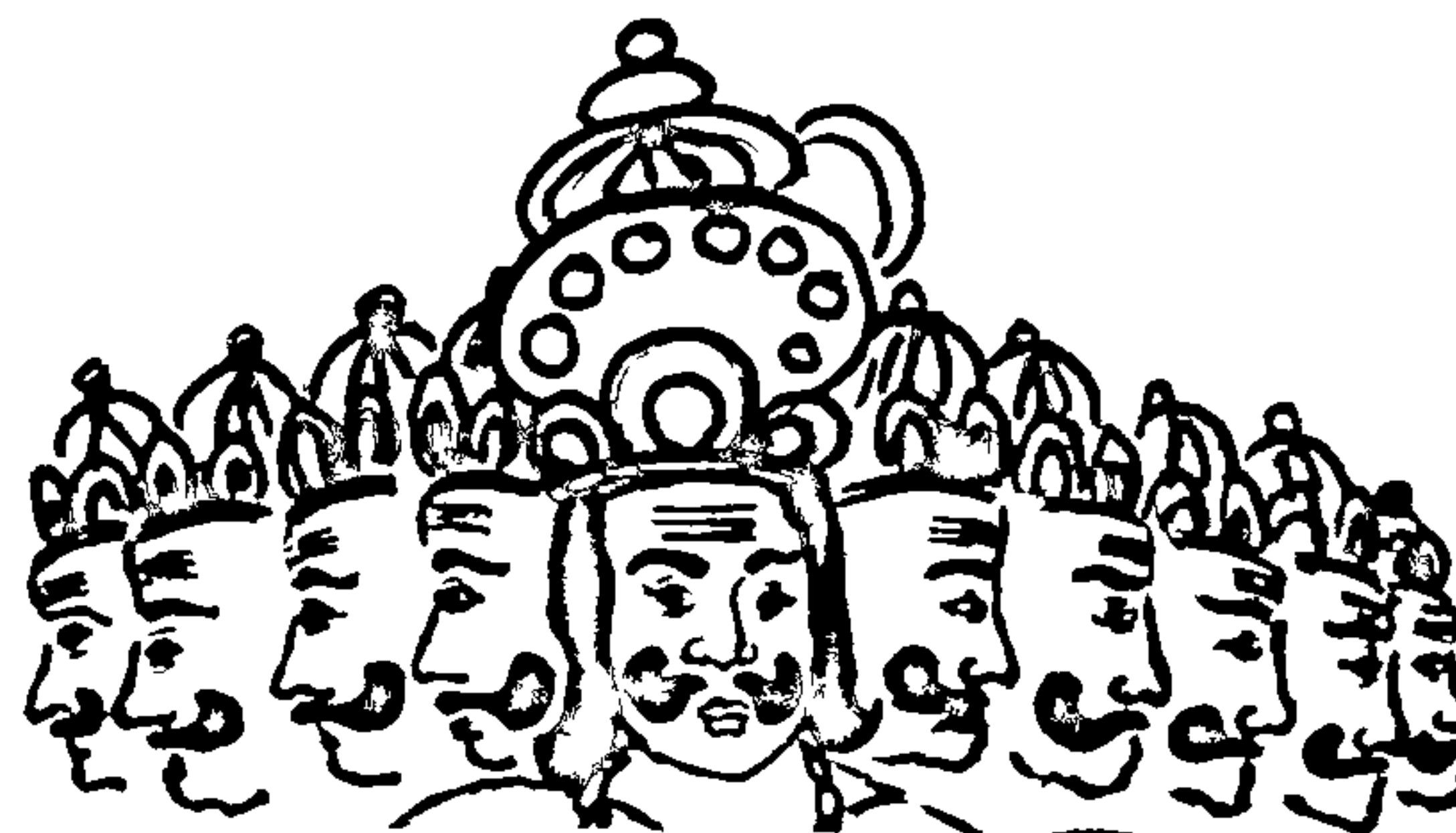
In the epic *Ramayana*, the king of Lanka, Ravana, depicted to have ten faces, is a great warrior, a scholar of scriptures and an accomplished veena player—a multifaceted personality! (idea conceived by V. V. Vaidyanathan and drawn by M. Anil Kumar).

Leaf gas exchange in lightflecks of plants of different successional range in the understorey of a Central European beech forest

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Young seedlings of two vines, in particular *Clematis vitalba* L. and *Rubus fructicosus* agg, and of seven other plants all co-occurring in a European beech forest, were subjected to lightflecks. We study their induction dynamics in particular, since induction state controls light use efficiency, light quantum yield and carbon gain. Distinct differences have been observed in the velocity of photosynthetic induction increase and loss. Pioneer species take a longer time to reach half induction in continuous saturating light as compared to late successional representatives. Despite the identical growth conditions, photosynthesis is induced faster in the pioneer species and the induction is lost slower. This is important for seedling establishment in the understorey.

THE light environment in forest understoreys typically consists of long periods of low PFD[1] separated by periods of short but frequent sunflecks lasting from less than a second up to a few seconds, and rarely sunflecks lasting up to several minutes[1-4]. In a variety of forests it has been shown that sunflecks contribute between 35% and 75% to total daily photon flux[1,3,5]. Current evidence suggests that a large portion of carbon gain is attributable to these higher light phases in the understorey.

For the first lightflecks after darkness or a prolonged dim light phase, photosynthetic carbon gain by a leaf is likely to be limited by low photosynthetic induction. This limitation, however, is gradually removed during subsequent lightflecks[6-8]. Understorey plant species accomplish a considerable portion of their daily carbon

gain during and immediately after sunflecks. The carbon gain during these high light phases depends on the length of the phases and the induction state of the leaf[1,6,8-10]. A shade leaf is quickly induced during a series of sunflecks so that those flecks which occur later are utilized more efficiently than those occurring earlier[9,11]. The capacity of a leaf to assimilate carbon during sunflecks is therefore partly determined by the rate at which this induction occurs. Furthermore, the rate at which this induction is lost following the end of a sunfleck will affect the capacity of the plant to respond to any subsequent high light pulses.

Studies specifically on ecophysiology of leaf gas exchange in lightflecks have been carried out so far on a very limited range of native species, either from north Australian rainforest[6,10-12] from north American[4,13] and from Hawaiian[14] forests. Although several investigations deal with gas exchange of understorey plants from central Europe[15-19] none of them analyse the dynamics of it under the predominantly transient light conditions. Küppers and Schneider[8] presented a first detailed study on the European beech, *Fagus sylvatica* L. In the present study we have chosen nine understorey species, all co-occurring in a European beech forest but of different successional ranges. We wish to further fill the gap of missing data from central Europe and to address the question of whether dynamic responses of photosynthesis are related to successional position of species. If so, this might have an important impact on seedlings after the early establishment phase and in saplings during their survival in the understorey. At that stage of the life cycle the plants often have limited leaf area due to relatively high costs of support in shady environments. Since total plant carbon gain is a function of the total leaf area times mean leaf photosynthetic activity, it is very important to keep leaf activity as high as possible which demands for optimal photosynthetic dynamics in a highly dynamic light environment.

Materials and methods

The experimental species and growth conditions

Eight native species and the introduced *Robinia* (Table 1 *a*), all co-occurring in the seedling or sapling stage at the same site in the shade of the understorey in a central European beech forest near the Botany Institute, were dug out in late summer 1991, potted in their original soil and transferred to a green house. They were cultivated at 12 h day/night cycles of 24/14°C air temperature and 20/10°C dew point at 4% day light. They were watered to field capacity every second day. Under these identical conditions they grew a couple of new leaves completely acclimatized to deep shade. Only these newly grown leaves were taken for measurements.

Although the species co-occur at the same site at identical microclimatic and soil conditions, they represent different successional stages ranging from early pioneers invading fallow land (e.g. *Rubus*) or wall and rock faces (*Hedera*) to late successional species like *Fagus* only establishing in the shade of mid- to late-successional plants. The species are (Table 1 *a*): *Rubus fruticosus* agg. (Rosaceae), a blackberry species, growing as a woody vine and migrating with biennial runners into fallow land (early pioneer, protected by spines), the pioneer *Sorbus aucuparia* L. ssp. aucuparia (= European Mountain Ash, Rosaceae), establishing from seed spread by birds and growing as a tree up to 15 m high, the pioneer *Cornus mas* L. (a dogwood species, Cornaceae), a shrub up to 5 m tall spreading by seeds and suckers, the pioneer *Clematis vitalba* L. (Ranunculaceae), a woody vine depending on open sites but on other plants to grow a veil-like cover, the pioneer Fabaceae *Robinia pseudo-acacia* L. introduced from north America growing as a tree (up to 25 m) with resprouting shoots near the ground protected by thorns, *Prunus avium* L. ssp. *avium* (Rosaceae), a mid- to early late successional tree species (up to 20 m) establishing from seed spread by birds, *Viola reichenbachiana* Jord. (Violaceae), a mid- to late-successional understorey herb depending on shade, the generalist *Hedera helix* L. (Araliaceae), growing both, as an extreme pioneer and sometimes even dominating in the understorey; this plant changes its growth form from a woody vine in the juvenile phase to a true tree in the adult phase, reaching a height of 15 m. The dominating late-successional *Fagus sylvatica* L. depends on shade in the establishment phase and may grow slowly for 20 to 40 years finally reaching a height of 40 m once sufficient light becomes available.

Experimental procedures

For measurements of leaf gas exchange we used the system described in detail by Küppers et al.[20] as modified for monitoring changes in carbon dioxide partial pressure under transient conditions[21]. Experimental procedures, especially the determination of the state of photosynthetic induction independent of stomatal movements, is described by Küppers and Schneider[8] so only a brief outline is given here. However, induction is always expressed relative to full induction.
(i) Following a 2-h dim light phase at 7 µmol photon $m^{-2} s^{-1}$ the course of photosynthetic induction is followed in light just saturating photosynthesis (200 µmol $m^{-2} s^{-1}$) but not causing photoinhibition. Light saturation is determined in the steady state prior to the experiment.
(ii) The state of induction is varied by applying dim light phases of 30 s, 1, 2, 3, 5, 15, 30 min, 1, 2 h after reaching full photosynthetic induction. Induction state is determined at the end of a 30 s lightfleck.

Table 1 a. Successional ranges of the selected species from the same site in the understorey of a central European beech forest. For details see the Materials section

State of succession	Early pioneer	Pioneer	Mid-successional	Mid- to late successional	Late successional
	Rubus	*Rubus*			
	Sorbus	*Sorbus*	*Sorbus*		
		Cornus	*Cornus*		
		Clematis	*Clematis*		
Species		*Robinia**	*Robinia**	*Robinia**	
			Prunus	*Prunus*	
			Viola	*Viola*	*Viola*
	Hedera	*Hedera*	*Hedera*	*Hedera*	*Hedera*
				Fagus	*Fagus*

*Introduced from North America, now an alien plant.

(iii) At identical (almost full) induction saturating light pulses of 1, 3, 5, 10, 20, 30, 40, 60 and 80 s have been applied to determine lightfleck utilization efficiency (LUE), lightfleck quantum yield (LQY)[8], total carbon gained attributable to a lightfleck and the fraction of carbon gained during postillumination. Here, LQY is the total amount of carbon fixed attributable to a certain amount of saturating light. Since light saturation of photosynthesis may vary slightly among species this may affect LQY e.g. at the same amount of carbon fixed in the fleck. We take this into account by expressing carbon fixation per unit of saturating light, thus LQY (μmol CO_2/unit saturating light). Secondly, lightfleck utilization efficiency, LUE, is determined according to Chazdon and Pearcy[11]. The total amount of carbon fixed is expressed relative to an idealized amount assuming the photosynthetic response is instantaneous with the rate taken from steady-state light response at the same photon irradiance. In all cases leaf temperature was 22°C at a leaf-to-air water vapour pressure gradient of 10 MPa Pa^{-1}.

In the following we use the term 'sunfleck' for a short, single phase of photon irradiance in the natural understorey of a forest being distinctly above a general background of diffuse light, whereas a 'lightfleck' is a short, single light pulse in an artificial leaf environment.

Results

Increases and losses of photosynthetic induction in high light and dim light phases

When a leaf has been in darkness or in dim light for several hours its photosynthetic induction is initially low (Figure 1) although dim light may already induce some stomatal opening (not shown). A sudden step to continuous saturating light, strongly induces photosynthesis. Although relative induction is initially the same in both, the early pioneer *Rubus* and the mid-successional *Clematis* (Figure 1), it increases much faster in *Clematis* than in the other species, being 50% of maximum after

4 min or 6.5 min respectively.

On the other hand, the state of induction decreases very quickly in dim light or darkness following a high light phase, thereafter only gradually levelling-off (Figure 2). After two hours induction may still decline though little. Again we observe distinct differences among species: *Rubus* loses half of its induction within 5 min in dim light, whereas 14 min are necessary to drop to the same level in *Clematis*. Whether this has an impact on actual carbon gain, is studied in the following section. However, induction is never completely lost even after many hours in the dark (e.g. Küppers and Schneider[8]).

Postillumination and total carbon gain attributable to lightflecks

Figure 3 a shows that with increasing photosynthetic induction total carbon gain attributable to a lightfleck increases, although the rate of increase may be species-dependent. Similar results have been published for the tropical, monocotyledonal understorey species *Allocasia macrorrhiza*[6] and the winter-deciduous dicotyledonal *Fagus sylvatica*[8]. So it is very likely that
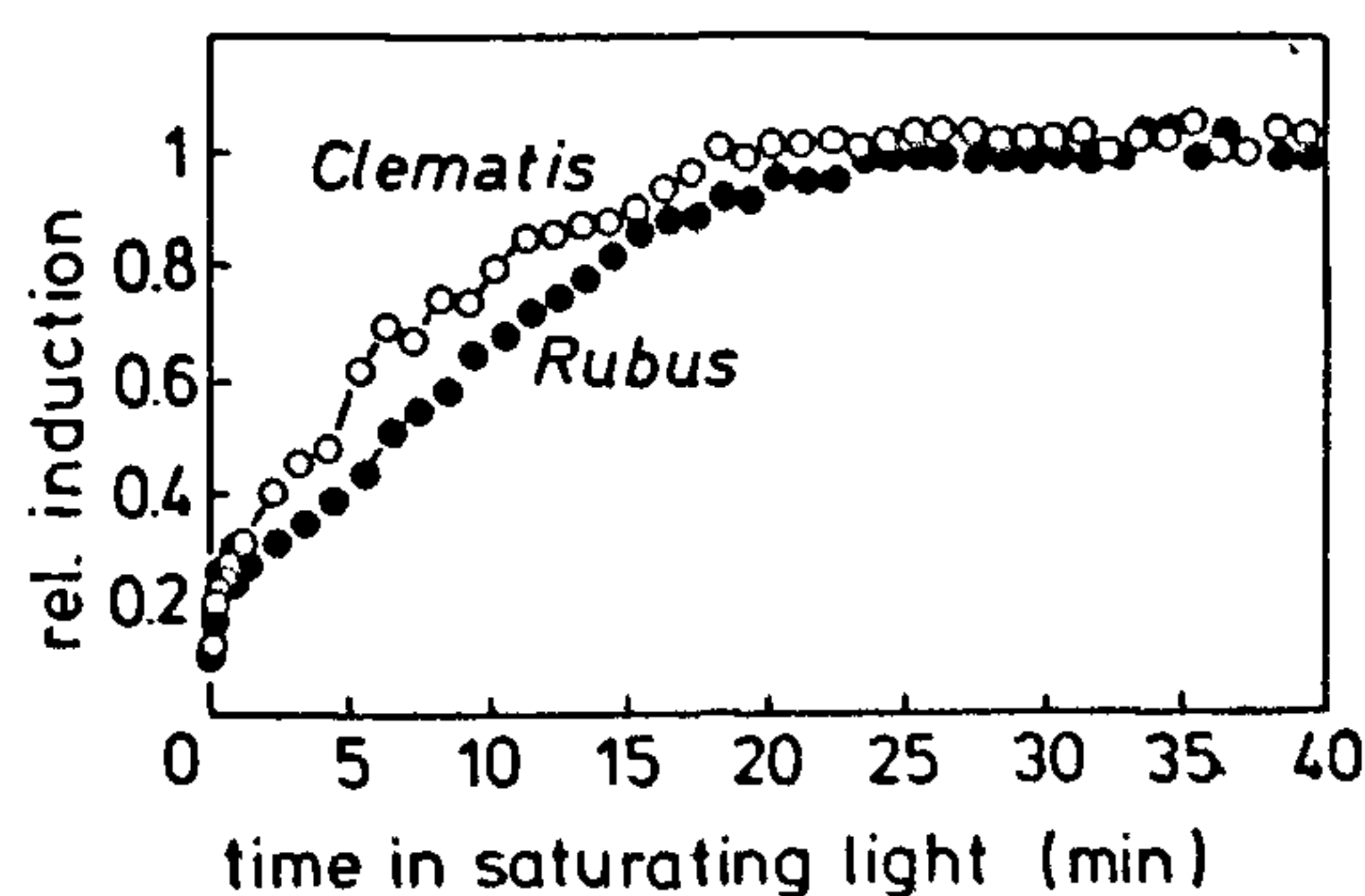

Figure 1. Increases in relative photosynthetic induction after a step change from dim light to continuous saturating light, in the two vines, *Rubus fruticosus* agg and *Clematis vitalba*, of differential successional range.
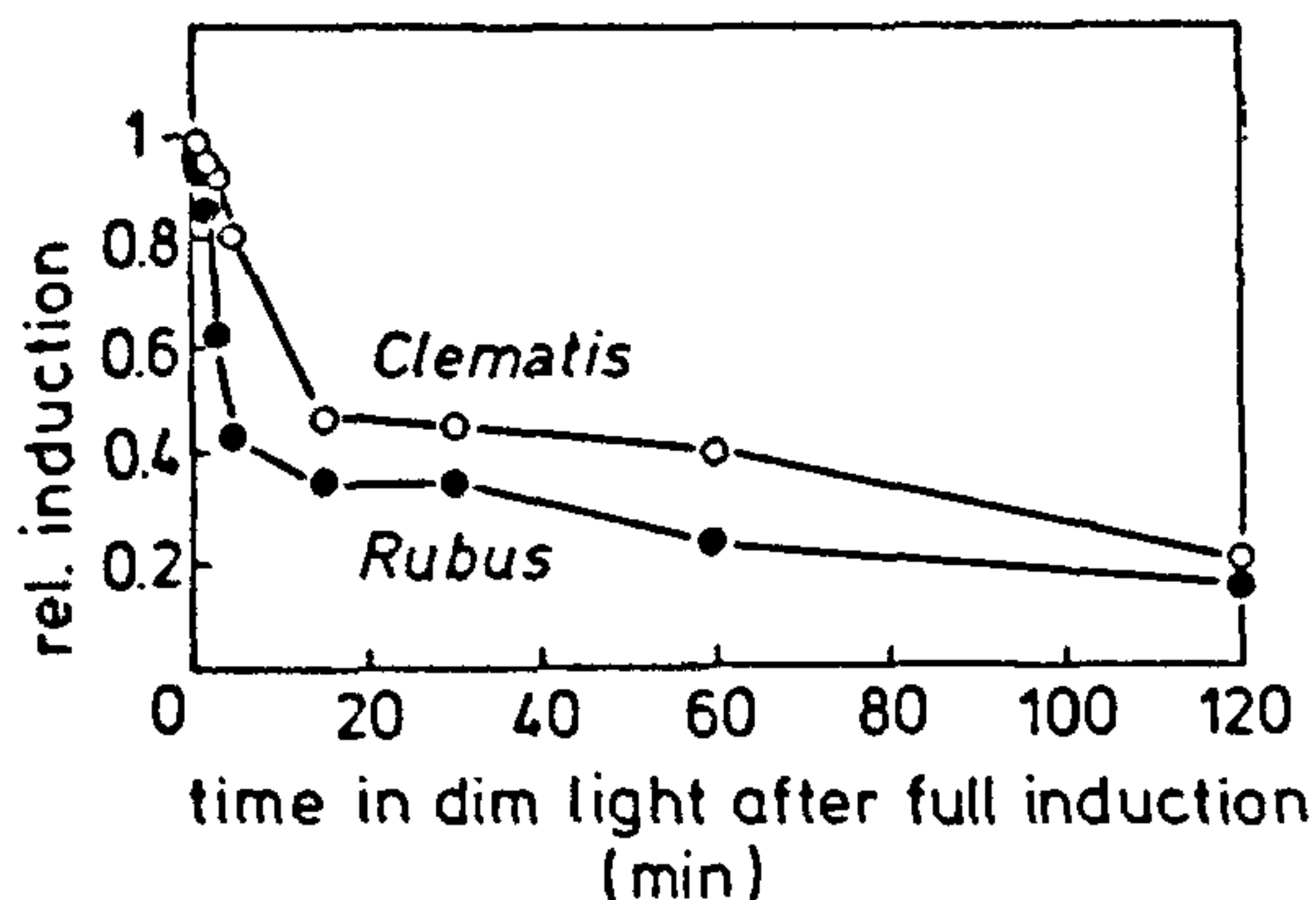
Figure 2. Decreases in relative induction in *Rubus* and *Clematis* after a step change from saturating to continuous dim light, starting with full induction
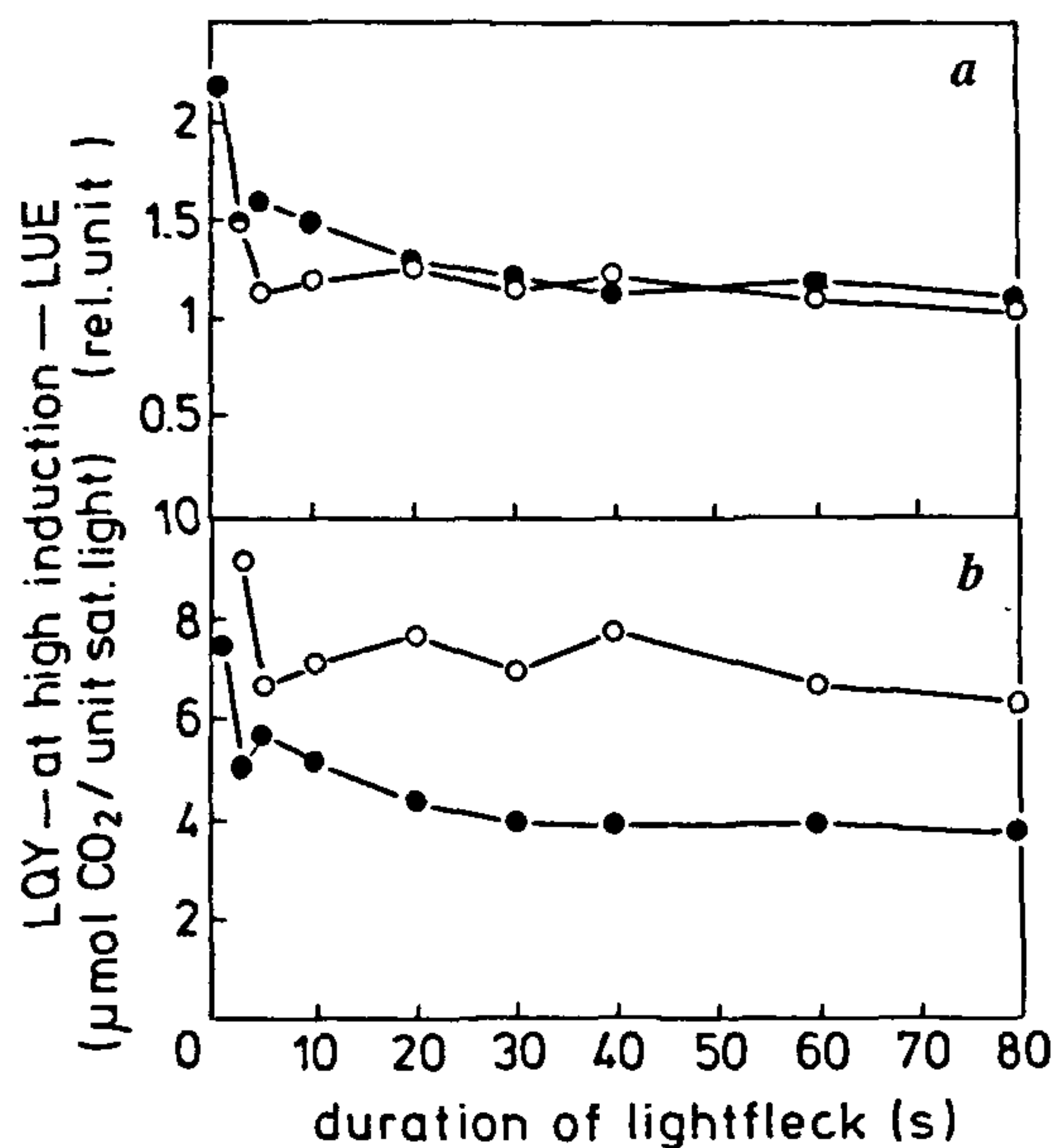

Figure 3. *a*, Amount of total carbon gained attributable to a fleck (LF) of 30 s saturating light, as dependent on relative induction, in *Rubus* and *Clematis*. *b*, Fraction of postillumination versus total carbon gain attributable to a 30 s lightfleck, as dependent on relative induction, in *Rubus* and *Clematis*.

this is a general characteristic.

Except at low photosynthetic induction when both plants are similar, *Clematis* gains more carbon attributable to a 30 s lasting lightfleck (Figure 3 *a*). This difference is not a consequence of its 'better' induction dynamics but a result of its higher photosynthetic capacity maintained in these shade leaves (not shown). From this and the previous result we conclude that in the same light environment, *Clematis*, gains more carbon.

Following a lightfleck there is a clearly noticeable postillumination carbon fixation[11, 22] which may last as

long as 84 s[8]. We observed that the fraction of carbon gained postillumination is higher the shorter a lightfleck (Figure 3 *b*) which fully agrees with the other observations[8, 11]. Despite differences in total carbon gain (Figure 3 *a*) the two species do not differ in this fraction at variable induction (Figure 3 *b*). Very likely, the underlying biochemical mechanisms are identical.

Efficiency of utilizing lightflecks

The question remains of how lightflecks of different lengths are utilized to fix carbon at constant full induction. In general agreement with Pearcy[23] and Küppers and Schneider[8] we observed that LUE is highest in short lightflecks (1 to 5 s) and declines with longer lightfleck (Figure 4 *a*). At full photosynthetic induction, LUE may be up to 220% if the response is instantaneous or compared to steady-state conditions. Thus, postillumination carbon fixation, being more important, the shorter the fleck leads to considerable rise in LUE. Similarly, LQY is highest in short lightflecks (Figure 4 *b*). While we did not find any differences in LUE among species, LQY is generally higher in *Clematis* due to its higher photosynthetic capacity.

Induction dynamics and successional range of species

We have already seen that short lightflecks are more efficiently used for carbon gain than for long ones. This
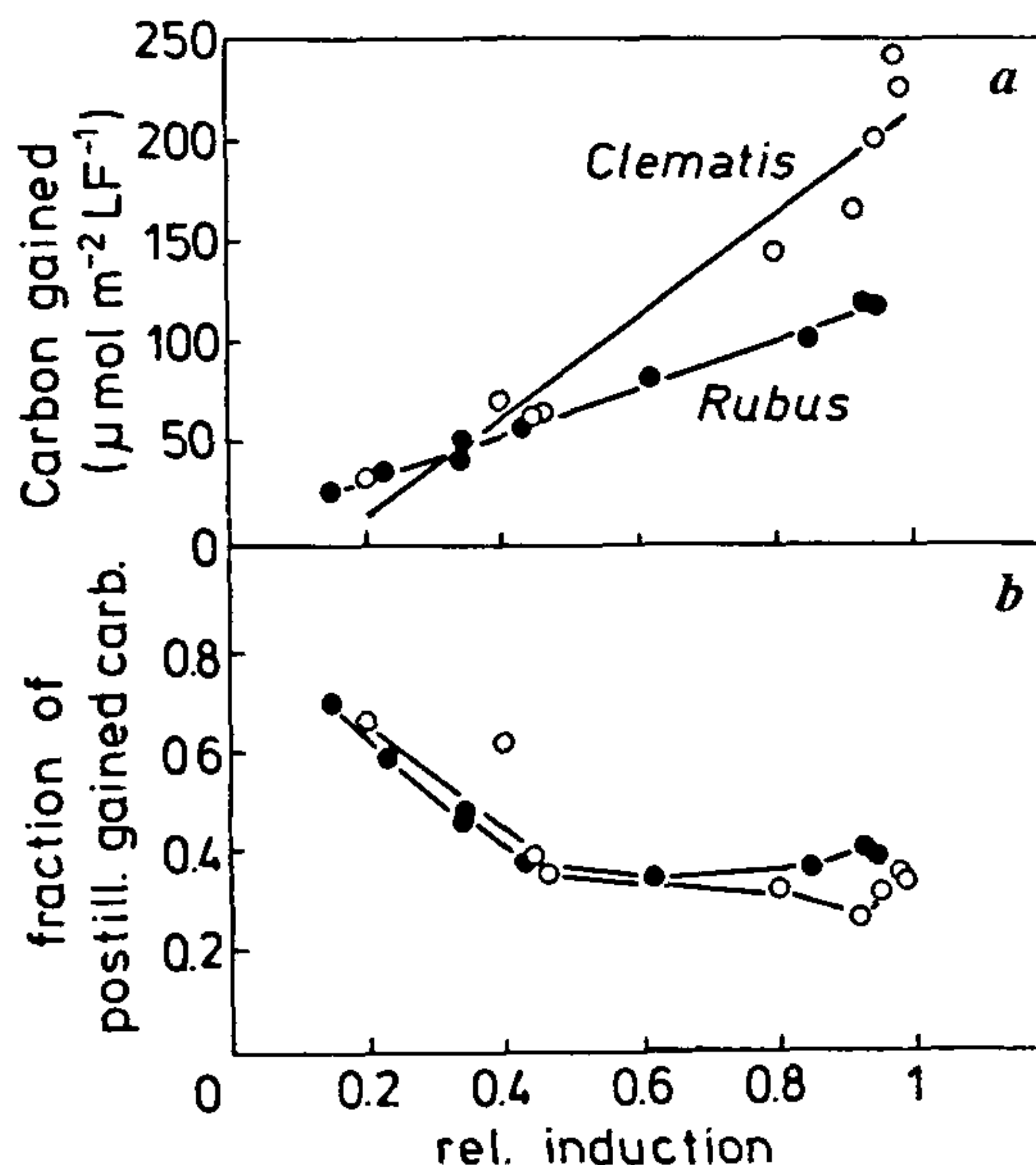

Figure 4. *a*, Lightfleck utilization efficiency (LUE) and *b*, lightfleck quantum yield (LQY in saturating light) as dependent on lightfleck length in *Rubus* and *Clematis* (symbols as in Figure 3).

Table 1 *b*. Successional categories (as in Table 1 *a*) and half-times (in min) (means ± S.D) of induction increases and losses

State of succession	Early pioneer	Pioneer	Mid-successional	Mid- to late successional	Late successional
Induction increases	2 5 ± 3.5	2.3 ± 2.5	1.4 ± 1.2	1.1 ± 0.4	0.8 ± 0.5
Induction losses	5.1 ± 5.5	9 0 ± 5 6	11.7 ± 5 8	17.0 ± 9.2	19.5 ± 12.7

characteristic fits well with predominantly short sunflecks found in understorey and lower canopy sections[4]. Additionally, higher induction supports LUE, LQY and carbon gain[8,23]. So the question arises, if species of different successional ranges (compare Table 1) differ when they co-occur in the same understorey at identical conditions and, why are early successional plants gradually removed from the understorey.

Most of the species do not differ with respect to LUE at the same induction (not shown, but compare Figure 4 *a*), so we study their induction dynamics, in particular, since induction state controls LUE, LQY and carbon gain (see above). Table 1 *b* shows means of the half-times (i) to reach induction after a step to saturating light starting from dim light and (ii) to lose half of induction in dim light beginning with full induction. The results clearly show that pioneers need much longer (2.5 min) to be half induced as compared to late species (only 0.8 min), whereas they lose half of their induction already within 5.1 min as compared to 19.5 min in the later species. Obviously, late species are much better adapted on the leaf level to a dynamic sunfleck environment than early ones (see also ref. 24).

Discussion

Most plants in a temperate forest of the northern hemisphere have to establish and adapt in the understorey where light is generally limited and only available in short sunflecks. Pioneer species that are overgrown during secondary forest succession may survive in such an environment in a few subsequent generations. Consequently, in intermediate states of succession they may be found beside mid- and late successional species, as was the case in this study (Table 1). Therefore, we were able to directly compare potential behaviour to a highly dynamic light environment for species originating from exactly the same locality and environment. Since limited adaptability to dynamic light could be one factor determining why early successional species are gradually outshaded from the understorey, we addressed this question in the present comparative study (see also Schneider et al.[24]).

Our results show that, in general, photosynthetic efficiency is highest in short lightflecks and that species do not differ with respect to LUE (Figure 4 *a*). But we observed distinct differences in the velocity of photosynthetic induction increases and losses. Pioneer species needed 3 times longer to reach half induction in continuous saturating light as compared to late successional representatives, while they, additionally, lose their induction 4 times faster than the other species. Since most sunflecks last for seconds, only shade-adapted leaves of pioneers will not reach their full photosynthetic induction. With respect to this shade leaves of pioneers behave like half-shade or sun leaves of late successional species such as *Fagus sylvatica*[8]. Although early successional plants have, in general, higher photosynthetic capacities than late species (for comparable light adaptation at full induction of leaves[17,25-29]) they cannot utilize this potential for lack of sufficient induction in a sunfleck climate. However, there are exceptions from the rule of declining photosynthetic capacity with proceeding succession (as observed in *Clematis* and *Rubus* and indicated by Figure 3 *a*), so that higher carbon gain at the same induction state together with better induction dynamics gives *Clematis* a clear advantage over *Rubus* with respect to carbon gain in the understorey (Figures 1, 2 and 3 *a*).

Since leaves generally lose photosynthetic induction in dim light or darkness it is highly likely that maintaining a high induction is costly to the leaf[23]. One may speculate that shade plants invest relatively more into these costs than sun plants, since they are highly dependent on utilizing any sunfleck. However, nothing is known about this aspect, although it may have a species-specific, genetic component, as is implied by our experiment. Several enzymes of the Calvin cycle become gradually induced by light, and their individual induction dynamics may improve sunfleck utilization e.g. by post-illumination carbon fixation. For example, it is known that in shade leaves a higher restriction for triose-P-pools to be metabolized to RubP-pools exists than in sun leaves[30] which helps to prevent inhibition of electron-transport capacity by $NADP^+$ limitations. Similar processes may be important in the induction differences of early and late successional species.

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