

SEED SIZE AND LIGHT REQUIREMENTS

IN

SOUTHERN CAPE FOREST SPECIES

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BOTANY HONOURS PROJECT

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**ABSTRACT**

There is very little published information on seed size and light requirements of Southern Cape forest-associated species. In this study 18 different species were subjected to three different light treatments in a phytotron unit for 6 months: total darkness, 100% and 15% of full light, as measured in forest conditions. Initial seedling performance was monitored and related to seed size and light treatment.

There was much variation in response of individual species to the different light treatments. In general, it was found that most species, over the whole range of seed sizes, were more shade-tolerant than expected. Small-seeded species, however, benefitted more from increased light intensities than large-seeded ones. Relative growth rates were negatively correlated with seed size.

INTRODUCTION

The concept of pioneer species that are light-demanding and climax species that are shade-tolerant is widely accepted in forest ecology.

Pioneer species would inhabit the forest edge, form large seed banks and would only establish^v in gaps with a sufficiently high light intensity for their survival. Climax species are shade-tolerant and can establish under the forest canopy, where they form seedling banks that can persist in shade for extended periods, waiting for a gap before they eventually reach the canopy.

Salisbury (1942) was the first to investigate the relationship between seed size and habitat preference. He demonstrated that, in moist environments in Great Britain, seeds of species that establish in closed, shaded habitats tend to be larger than those of species that typically inhabit sunlit, early successional areas.

Baker (1972) documented a similar relationship for Californian shrubs, but not for herbs and trees. He worked in a more arid environment, where desiccation^c stress led to increased size of seeds. Desiccation^c would of course be greater in sunlit areas and therefore the contrasting effect of shade on seed size in this environment would ^{way} not correspond to that found in a moist environment.

Foster and Janson (1985) demonstrated that, in moist tropical forests, species with larger seeds tend to become established in more stable, shaded plant associations, than do those with smaller seeds. Moist tropical forest trees that require large light gaps for seedling establishment tend to have smaller seeds than do those that become established beneath closed forest canopies.

Grime and Jeffrey (1965) found large differences in adaptation to shade between grassland and woodland species. In a grassland, seedlings would grow out of the shaded stratum within a few days, whereas in a woodland shading continues past the seedling stage and may last several years. Among seedlings of large-seeded tree species, they found greater initial growth, but a lower relative growth rate than in small-seeded species.

Fenner (1983) confirmed this slower relative growth rate in seedlings from larger seeds for 24 species of Compositae. Small seeds in this group also had a higher ash content than the large seeds. *per seed & per unit dry mass*

Seiwa and Kikuzawa (1991) studied vertical growth patterns and leaf dynamics of seedlings of deciduous broad-leaved tree species with different seed sizes under open and shaded conditions. In the open there was little difference in final seedling height of small- and large-seeded species. However, final seedling height was reduced by shading in the small-seeded species, but not for the large-seeded ones. The total number of leaves produced was more negatively affected by shading in small-seeded species than in large-seeded ones.

Most studies on the effects of seed biomass on germination and early seedling growth demonstrate that large seeds have many advantages over small seeds. Large seeds usually have a greater *intra-species?* percentage germination, e.g. than small seeds (Cidecyan and Malloch 1982). Large seeds usually have less stringent requirements for emergence with respect to litter and herbaceous cover (Winn 1985). They also form large seedlings that open their leaves quickly (Seiwa and Kikuzawa 1991). As a consequence of these effects, large seeds may give rise to better competitors (Wulff 1986).

However, small seeds may germinate earlier (Black and Wilkenson 1963), and because of their faster relative growth rate, eventually reach the same height as a large-seeded species in the presence of enough light (Seiwa and Kikuzawa 1991). Hendricks et al. (1991) have found that seedlings from small seeds are more drought resistant during short-term droughts. This could be explained by the negative relationship between seed biomass and the ratio of maximum root length/total leaf area. In other words, these seedlings will lose less water through transpiration due to their relatively smaller leaf area. *or greater supply through deeper rooting*

Despite these and numerous other publications (eg. Harper et al 1970, Salisbury 1973, Winn 1985, 1988, Hodgson and Mackey 1986, Wulff 1986, Mazer 1987, Silvertown 1989, Shipley and Parent 1991) on the effects of seed size and gap dynamics in various habitats, the regeneration dynamics of the southern Cape forests ^{are} still poorly understood. The fact that these forests are considered to be temperate, but also subjected to periodic droughts, make them different from most of the ecosystems studied so far.

Locally, Holmes and Cowling (1992) studied the effect of shade on growth and morphology in seedlings of subtropical shrubs in the eastern Cape. They grew seedlings in full sun and under 15% and 50% of light. Although there were species differences in growth rate and morphology, there were general broad overlap in response to shade treatment amongst species. *Expand*

Midgley et al. (1990) have also found that most Southern Cape forest species seem to be shade tolerant. This tolerance could reduce the effect of gaps in determining spatial variation in species distribution. *But gaps will affect distribution of canopy plants reaching the canopy*

Although much has been published on the relationship between seed size and growth patterns, it is not clear whether all of the demonstrated patterns are generalizable. For example, Stock et al (1990), have shown that, in the Proteaceae, there is no relationship between seed size and relative growth rate. That might be an exceptional case, since the Proteaceae selectively store important nutrients in their seeds, but then there might be many other deviations from the predicted trends published so far. Except for Midgley et al (1990) and Holmes and Cowling (1992) there is virtually no published information available on light requirements for germination and establishment of Southern Cape forest species. These are very important issues in understanding and managing forests. If seed size is an indicator of light requirement or shade tolerance, it could be used for assessments of the ability of species to invade and/or persist in a particular habitat.

Therefore this study is aimed at determining the light requirements of Southern Cape forest associated species, and to see if seed size could be used as a predictor of growth patterns or habitat preferences.

Key questions have been set to elucidate various aspects of these issues. These will be dealt with separately in the methods, results and discussion.

MATERIALS AND METHODS

Seed from as many as possible species of mainly forest trees, but also of species growing on forest margins, were obtained to get as wide as possible a sample of different seed sizes and possible light requirements.

Seed were obtained from the Seed Store in Pretoria, Grootvadersbos and Orangekloof Forests, Newlands Nursery, Kirstenbosch-, and Harold Porter Botanical Gardens.

Some of the information on germination procedures has been obtained from Geldenhuys (Forestry Pamphlet 150).

Seed mass and embryo mass were determined for most species. It was impossible to obtain the embryo mass for six species, since their testa were very thin and inseparable from the embryo. In their case, the thickness of the testa was matched with those of the other seeds, where the testa could be removed. Embryo mass was then estimated as a percentage of seed mass as measured in the closest match. It was then compared to an extrapolation of embryo mass from a graph (figure 1). Number of seeds weighed per species varied between 5 and 100. This depended on how many seeds were available to "sacrifice" for removal of the testa, as well as the size and variability in individual mass.

Seed was sown at a depth of more or less the diameter of the seed, directly into black bags (8cm x 15cm) to avoid mortality with transplanting. The soil mixture used was 2/3 coarse acid washed sand (sand blast no.1 from Consol Glass) and 1/3 sterilized peat. Some species needed special pre-germination treatment, for example stratification, boiling water, or scarification. All seeds were transferred to the phytotron chambers immediately after treatment, so that all germination occurred in the three specified light environments.

The number of seeds sown depended on availability and expected germination rate for each species, aimed at 30 seedlings per species after mortality.

A minimum of 10 seeds (in a few cases only three seedlings germinated from these) of each species were subjected to three different light treatments: Total darkness, to simulate conditions under deep litter in the forest, 15% of full sunlight, to simulate conditions in the forest margin and 100% full sunlight to simulate gap conditions. These treatments are based on averages of measurements of photosynthetically active radiation taken in Orankekloof Forest (open or gap light intensity: $1300 \mu\text{mol m}^{-2} \text{s}^{-1}$, light intensity in forest margin: $195 \mu\text{mol m}^{-2} \text{s}^{-1}$ taken in autumn). In the phytotron a combination of mercury- and sodium fluorescent, as well as incandescent light bulbs were used to get as near as possible to natural sunlight's spectral composition. Shade netting had to be added in the 15% room, since the light intensity could not be adjusted to low enough using the phytotron settings. Different sets of lights were set to switch on and off at 30 minute intervals during the morning and afternoon to simulate light conditions from sunrise to sunset for a 12 hour day.

Temperature was varied between 10°C at "night" and 25°C during the "day" in all three growth chambers, according to averages obtained from Diepwalle Forestry Station.

Humidity was kept at 60% in the 100% sunlight treatment chamber and at 80% in the 15% light- and dark chambers, respectively to simulate conditions in a gap, the forest margin and under litter as measured at Orankekloof Forest.

Seedlings were watered every third day to field capacity with de-ionised water. Observations were made at 3-day intervals for the

duration of the experiment (7 months). Date of first germination for each species were recorded (when cotyledons or first leaves became visible above ground), as well as total number germinated. Survival time in the dark was taken as the time at which 50% of the seedlings have died in species where many seedlings germinated, or when the first seedling started dying in those species where only a few seedlings germinated. At the end of the growth period, seedlings were counted to determine mortality and then harvested. *I don't like this - biased estimate*

Root length, shoot length and hypocotyl length was measured. The number of leaves grown and lost were counted and cotyledon area and leaf area was determined on a leaf area meter. The roots and shoots were then separately oven-dried to constant mass and measured on a Mettler balance.

Since seedlings were harvested at different ages, their biomass at 30 days had to be calculated, assuming logarithmic growth, to be able to compare initial seedling mass with embryo mass.

Quattro Pro was used to generate graphs and to do regression analyses.

but early growth often not logarithmic.

RESULTS

1. Is seed mass an indicator of embryo mass?

Figure 1 shows a positive linear relationship between the logarithms of seed mass and embryo mass. Large seeds have larger embryos than small seeds. (Slope = 0.91, Std err.= 0.02, $p < 0.0001$, $R^2 = 0.96$).

2. Is the embryo fraction of a seed a function of seed size?

Figure 2 shows that there is no relationship between seed size and the ratio of embryo mass / seed mass. Thus there are some small seeds where the embryo makes up a relatively large portion of the seed, as well as some large seeds with relatively small embryo fractions and visa versa.

3. What is the effect of seed size and light intensity on germination time and germination percentage?

Figure 3 shows a very weak relationship between the logarithms of embryo mass and germination time. Only 6% of the variation in germination time is explained by variation in seed mass. The slope is slightly positive (x coefficient=0.101475, std error=0.05 $p < 0.05$), indicating that small seeds germinate slightly earlier than large seeds.

There is no relationship between seed size and germination percentage (see table 2).

4. Is seedling size dependent on embryo size?

Figure 4 shows that there is a positive correlation between the logarithms of embryo mass and the biomass of seedlings at an age of 30 days ($R^2=0.80$, $df=50$, x coefficient=0.85, std error=0.059, $p < 0.0001$). Therefore large seeds produce large seedlings, while small seeds produce small seedlings.

But look at x coeff. Very close to 1, implying little actual growth.

5. Does embryo mass determine the length of time that a seedling can survive in the dark?

Embryo mass has no effect on the survival time of a seedling in the dark (see figure 5). *Podocarpus latifolius* survived the longest, while *Rhus lucida* died the earliest.

6. Is hypocotyl length dependent on embryo mass?

Figure 6 shows that there is no relationship between hypocotyl length and embryo mass. The two species of *Virgilia* had the longest and *Cunonia capensis* had the shortest hypocotyl. ^{growth} conditions ?

7. What is the effect of embryo mass and light intensity on relative growth rate?

Figure 7 shows the negative correlation between the logarithm of embryo mass and relative growth rate. Small seeds have a higher relative growth rate than large seeds.

I have reservations about the way RGR is calculated. No details are given.

This relationship is stronger in full light than in the shade or in the dark (see table 3.) The slope is also more negative in full light than in shade. In other words the relative growth rate of small seeds is increased more in high light intensities, relative to that of large seeds.

This is confirmed by the weak negative correlation (r coefficient = -0.35, std error = 0.30) between embryo mass and the ratio of light / shade relative growth rate (figure 8). Only 21% of the variation in this ratio is explained by embryo mass.

The only species showing a major difference in response to dark versus light treatment is *Podocarpus falcatus* (figure 9).

8. How does light intensity influence above ground growth?

All species, except *Erythrina caffra*, exhibited greater shoot growth with increased light intensity (see figure 10).

9. Does seed size influence response to different light treatments?

Figure 11 shows a slightly negative relationship between the logarithms of seed size and the ratio between shoot mass in light and in shade (x coefficient = -0.804 , std error = 0.32 , $df = 13$, $p < 0.05$). 32% of the variation in log light / shade shoot mass is explained by variation in log seed mass. That indicates that small-seeded species show a greater response to increased light intensity than large-seeded species. *Re-issue of RGR*

10. Does light intensity have an effect on root growth?

Figure 12 shows that all species increased root growth in higher light intensity.

11. Is there a difference in allocation to roots and to shoots by different seed sizes?

Figure 13 shows the difference in root- and shoot allocation (than in roots.) All species invested more in above ground growth. Small seeds produced small roots and shoots and big seeds grew bigger shoots and roots. There is no significant difference in allocation patterns to roots and shoots between large and small seeds.

12. Do different light intensities cause differences in allocation to roots or shoots?

There is no relationship between light intensity and allocation to roots versus shoots. Figure 14 shows enormous species-specific variation in allocation patterns under different light regimes.

13. Is the ratio root length / leaf area dependent on embryo mass?

There is a negative relationship between the logarithms of embryo mass and the length of roots compared to leaf area (slope = -0.39 , std. err. = 0.07 , $R^2 = 0.37$, $p < 0.0001$). In other words, small-seeded species produce long roots and smaller leaf

areas, while large-seeded species produce shorter roots and larger leaf surfaces (see figure 15).

DISCUSSION

1. and 2. Although embryo mass increases with seed mass, as expected (figure 1), there is no correlation between the embryo fraction of the seed with seed size (figure 2). This is contrary to Fenner's (1983) results with Asteraceae, where a negative relationship between seed size and embryo fraction was reported. That reflected the common view that large seeds have smaller embryo fractions, compared to small seeds, implying that large seeds have relatively thick seed coats. Therefore large seeds were thought to be at a double disadvantage: they would have relatively less embryo reserves for seedling establishment, and their dispersibility would be adversely affected by the relatively large testa. Here it is shown that this does not necessarily hold for all taxonomic or ecological groups. Even within the leguminosae, *Erythrina caffra* has a higher embryo fraction than the smaller-seeded *Virgilia*s and *Acacia melanoxylon*. *Olea europaea ssp africana* is a middle-sized seed, but has a very thick testa with a small embryo, while *Diospyros lycioides* is a relatively large seed with a very large embryo fraction. It is also interesting to note that *E. caffra* and *D. lycioides* have very similar seed masses, but *D. lycioides* has a greater embryo fraction. Despite that, however, *E. caffra* has both a greater initial seedling mass (Figure 3) and relative growth rate (Figure 7), than *D. lycioides*.

3. Thompson and Grime (1979) have found that large-seeded herbaceous species germinate more rapidly, and under a wider range

of environmental conditions, than small-seeded ones. Figure 3 shows exactly the reverse, but the slope of the graph is very slight and the correlation between seed size and germination time is weak. Thus there is not much difference in germination time of large- and small-seeded species in our forests. If large seeds do germinate faster, it explains the formation of seedling banks, rather than seed banks. Germinating earlier could be an anti-predation mechanism, since large seeds are more sought after for their nutritional rewards to predators. Small seeds are mostly long-lived (Thompson, 1987) and can therefore survive in seed banks. There they can wait until conditions for germination become favourable, for example increased light intensity in a newly formed gap, or decomposition of a deep litter layer, that could also provide sufficient nutrients for establishment. Small seeded species are initially more dependent on soil nutrients than large-seeded species with large reserves, except, of course, where nutrients are selectively stored in the seed.

There remains much unknown about germination requirements. Although Thompson and Grime (1979) have found that small seeds have more stringent germination requirements, while large seeds usually have a greater percent germination (Cideciyan and Malloch 1982) this study finds no support for that. Table 2 shows that there is no trend in the germination percentages of large seeds to be higher than in small-seeded species, while they were all subjected to the same germination conditions. On the other hand, these conditions were what is generally thought to be ideal for germination. Therefore germination percentage might have been lower in the small-seeded species if germination conditions were generally less favourable, eg. low temperature and humidity.

Not really depends on mineral cues and desiccation sensitivity

But even your light treatment is in the dark for germination 14
- seed is buried.

It is interesting to note that *Rhus lucida*, which is supposed to be a light-demanding small-seeded species, germinated better in the dark than in shade, and did not germinate at all in full light. That might be an adaptation to ensure that it would only germinate under some litter, that can provide an initial moist enough microclimate for seedling establishment, considering the minute water reserve in the seed.

The two species of *Virgilia*, as well as *Scolopia mundii* and *Kiggelaria africana*, exhibited increased germination percentages with increased light intensities, confirming their "pioneer status". Most other species germinated better in shaded conditions.

The very low germination percentage of *K. africana* is probably due to it being adapted to bird-dispersal, with a thick testa that need to be scarified by the bird's digestion.

The high percentage germination in the dark by *Acacia melanoxylon* shows one of the reasons why it is such a successful invader in the southern Cape forests. It should be able to germinate under a thick litter cover of up to 10 cm (figure 6) as is often formed through pods and leaves dropped by this species.

4. Anderson (1971), Wulff (1986), and Hendrix et al (1991) have shown that large seeds give rise to better competitors within a species. Fenner (1983) showed that, within a family, larger seeds give rise to larger seedlings. Figure 4 shows that it also holds for southern Cape forest species. The larger size of seedlings from large seeds would enable them to be superior competitors in the initial stage of seedling establishment. The large embryo reserves would sustain the seedling during the initial, vital period of emerging from litter and opening of leaves for photosynthesis. If a small - and a large seed were to germinate

Find this discussion unconvincing, as we know very little about germination requirements + storage behaviour of most of these species. Some germinate to one way low - why?

in close proximity at the same time, the seedling from the small seed would probably be shaded out by the larger seedling from the large seed. It seems, however, that the benefit from increased embryo size takes a turn for the worse at embryo sizes greater than that of *Erythrina caffra*. This trend is also reflected in figures 10 and 12.

5 and 6. Grime and Jeffrey (1965) demonstrated an inverse relationship between seed size and the rate of seedling mortality under adverse light conditions, suggesting that the seedlings from smaller seeds exhausted seed-bourne resources faster. Figure 5. shows that there is no relationship between seed size and survival time in the dark for the southern Cape forest species considered here.

Podocarpus latifolius, however, stands out as the species most tolerant to dark conditions (see also figure 9). Although it also has the largest seed size, its dark tolerance might be attributed to the fact that it is a gymnosperm, with a slow growth rate and therefore slow depletion of embryo resources. Midgley and Bond (1989) argued that conifers like podocarps should only be able to survive in forests where access to the canopy is not based on fast growth in gaps. In the Southern Cape the podocarps are extremely shade tolerant, with a large, persistent seed bank. When a gap is then formed, its large seedlings are already established and can favourably compete with smaller-seeded faster growing angiosperms that might only germinate then in the increased light intensity caused by the gap.

The species most adversely affected by lack of light is *Rhus lucida*. This, together with its very short hypocotyl length (figure 6), singles out *R. lucida* as the only real shade intolerant species. *Erythrina caffra* and *Acacia melanoxylon* were

the only two other species that did not survive for longer than 50 days in the dark, indicating that most of the southern Cape small-seeded, "pioneer" species are less light-demanding than would be expected. This agrees with Midgley's (1990) theory that the effect of gap size in determining variation in the species composition is not as important as is commonly accepted.

The two species of *Virgilia* stands out amongst the others for their much longer hypocotyls. This seems strange, if considered that these are "pioneer" species that often germinate after fire, when litter should be absent. Their hypocotyl lengths in full light is, however, only about half the length it reaches in the dark (own unpublished data). Therefore it seems that these trees are extremely plastic in their response to light, enabling them to establish in a wide range of environmental conditions, as is observed in the field, where they often form the forest margin, but individuals can also persist in the forest (pers obs).

7. The initial handicap experienced by small-seeded species in producing smaller seedlings than large-seeded species is eventually eliminated through their higher relative growth rates in the presence of enough light and nutrients. The negative slope of the correlation between embryo mass and relative growth rate in figure 7 is steeper in light than in shade and dark, showing an increased relative growth rate response by small-seeded species, compared to large-seeded ones. Thus, although these small-seeded species are able to grow in shade, they benefit more from increased light intensities than do the large-seeded species (see table 3). It is interesting to note that, however small, even *Podocarpus latifolius* experienced an increased relative growth

rate in higher light intensity, indicating that none of these species are shade loving, they are just shade tolerant.

There is contrasting evidence for this negative correlation between seed size and relative growth rate shown in figure 7. Grime and Hunt (1975) show no similar correlation to that found by Fenner (1983) for a similar group of species. However, Fenner's seedlings were grown in distilled water, while Grime and Hunt used a complete nutrient solution. Fenner (1983) has shown that large seeds contain relatively little minerals. Therefore their seedlings' growth could be retarded very soon after germination in the absence of enough nutrients. This study should suffer the same consequence, because seedlings were grown in a very nutrient-poor medium of sand and peat and were given de-ionised water. On the other hand, a slow relative growth rate could be an adaptation to low light intensities, so that seed reserves will be depleted slower, leading to longer persistence in deep forest conditions close to the light compensation point for even shade-tolerant species. The negative growth rate exhibited by many species (figure 9) could be due to high respiratory losses in the production of roots, without a balanced growth in photosynthetic tissue to compensate by supplying energy and carbon. This negative relative growth rate should later be cancelled out by increased above ground growth once the seedling's roots become established and can supply enough minerals for increased shoot growth. It should be interesting to look at actual relative growth rates over the whole duration of seedling development, to look at allocation patterns during the critical establishment period. That should give an indication of the potential of different species to establish in different conditions. Xes

8. All species, except *Erythrina caffra*, capitalised on full light intensity by increased shoot production (see figure 10). That might be an indication of lower light requirement of broad-leaved species, since *E. caffra* is the only representative of this group amongst the species studied.

9. The greater ratio of light / shade shoot production in the small-seeded species is evidence for their adaptation to higher light intensities (figure 11). Although the ratio is greater than one for all species ($p < 0.05$), the large-seeded species exhibit the smallest benefit from full light instead of shaded conditions .

10. All species exhibited increased root production in higher light intensities (figure 12). This would be necessary to absorb enough minerals for the building of new tissue, during increased productivity due to increased rates of photosynthesis.

11. Foster (1986) suggested that species forming persistent seedlings in light levels close to their plant light compensation points, would need to be large-seeded, to have enough reserves to produce higher ratios of photosynthetic to non-photosynthetic tissue necessary for positive net productivity. Although all species in this study allocated more reserves to shoot production at 30 days, there remained a more or less similar balance in above- and below ground growth for all seed sizes. In other words, large seeds did not grow more above ground compared to below ground, than the small-seeded species in this study (figure 13), as suggested by Foster (1986). This could be an indication of low light compensation points among all seed sizes within the Southern Cape forest species. On the other hand, it might be that the age of the seedlings would make a difference in these results. Hendrix et al (1991) have shown that the ratio root/shoot biomass

initially is constant for all seed sizes, but then it increases with age and seed size.

12. The plasticity in light response of these species is demonstrated clearly in figure 14. All species, except *Halleria lucida* and *Rhus lucida* (which did not germinate in full light), responded to shade treatment by increased shoot/root ratios. In the dark, most species allocated the maximum possible amount to formation of shoots, to try and make use of any small amount of light that might become available.

13. The negative relationship between embryo mass and the ratio of root length / total leaf area could indicate that the smaller-seeded species are more drought-resistant than the large-seeded species. When the soil dries out, it does so from the surface downwards. In other words, seedlings with shorter roots would suffer from dessication first. Seedlings from small-seeded species would be able to survive, since their roots are in a deeper, moist level and they have a relatively smaller surface area of leaves losing water through transpiration.

CONCLUSION

Salisbury (1942) was probably correct to link the increase in seed size from open to closed herbaceous vegetation to competition for light. However, that argument cannot unconditionally be applied to forest, and especially temperate forest, conditions. Here the ability to emerge from litter might be equally important in determining seed size.

If low light levels were the only factor that favours large seeds, the sizes of pioneer and climax seeds should be strictly dependent on light intensity in gaps and under the canopy. However, in

large gaps the light intensity will be high enough for even the most light demanding species to reach maximum productivity shortly after germination. Thus large seeds would not need their reserves as much as in shade, but in subcanopy conditions the advantage of large embryo reserves to enable the seedling to grow to a better light regime, may be relatively much greater. There are, however, many other influences on seed size, apart from light intensity, eg. moisture conditions, soil nutrient conditions, resistance to pathogens, and need for dispersal or escape from predators. The combination of all these factors make seed size and its implications a very wide topic to study, since there are so many species-specific variations in adaptation. Thus the few predictions made in this field so far are valuable, but must always be seen against the background of enormous variation in different habitats, as well as in ecological and taxonomic groups. That should, however, not call for despair about making any useful predictions, but should rather stimulate further investigation, to test if the published theories hold true for a more representative portion of our local flora.

To test for real shade tolerance, as in deep forest conditions, future studies should subject plants to very low light intensities, eg. 1% or 2%. If there are true "pioneer" and "climax" species in our forests, that should clearly show in such a study.

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LIST OF TABLES REFERRED TO IN THE TEXT:

Table 1. list of species and abbreviations used in the text and graphs.

am	<i>Acacia melanoxylon</i>
ca	<i>Celtis africana</i>
cm	<i>Carissa macrocarpa</i>
cu	<i>Cunonia capensis</i>
dl	<i>Diospyros lycioides</i>
ec	<i>Ekebergia capensis</i>
er	<i>Erythrina caffra</i>
gt	<i>Gardenia thunbergii</i>
hl	<i>Halleria lucida</i>
ka	<i>Kiggelaria africana</i>
ma	<i>Myrsine africana</i>
oe	<i>Olea europaea ssp africana</i>
pl	<i>Podocarpus latifolius</i>
rl	<i>Rhus lucida</i>
sm	<i>Scolopia mundii</i>
vd	<i>Virgilia divaricata</i>
vl	<i>Vepris lanceolata</i>
vo	<i>Virgilia oroboides</i>

(drk=dark, sde=shade, lgt=light)

Table 3. Summary of regression statistics for the relationship between embryo mass and relative growth rate for different light treatments

light treatment	0%	15%	100%
constant	-0.00666	-0.00311	-0.00077
std err (y-est.)	0.003134	0.00335	0.003766
R ²	0.356395	0.450861	0.546561
df	14	16	15
x coefficient	-0.00279	-0.00387	-0.00511
std err (coeff)	0.001002	0.001067	0.001202
prob. level (coeff)	<0.05	<0.005	<0.005

Table 2. Summary of statistics for germination times and percentages.

spp	% light	no. sown	germ %	germ time (days)	embryo mass (g)
<i>Canonia capensis</i>	0	20	45	17	0.0002
	15		35	15	0.0002
	100		60	14	0.0002
<i>Halleria lucida</i>	0	100	39	19	0.00136
	15		70	14	0.00136
	100		44	17	0.00136
<i>Scolopia mundii</i>	0	100	70	10	0.0017
	15		75	11	0.0017
	100		80	12	0.0017
<i>Vepris lanceolata</i>	0	100	40	73	0.00779
	15		16	42	0.00779
	100		22	61	0.00779
<i>Acacia melanoxylon</i>	0	50	30	23	0.0085
	15		16	34	0.0085
	100		12	24	0.0085
<i>Myrsine africana</i>	0	100	32	71	0.00902
	15		15	93	0.00902
	100		22	95	0.00902
<i>Rhus lucida</i>	0	50	6	41	0.00978
	15		4	31	0.00978
	100		0		0.00978
<i>Carissa macrocarpa</i>	0	50	82	28	0.00995
	15		78	22	0.00995
	100		72	36	0.00995
<i>Olea europaea</i> <i>ssp africana</i>	0	50	10	67	0.01357
	15		8	37	0.01357
	100		6	105	0.01357
<i>Celtis africana</i>	0	50	72	17	0.0179
	15		86	12	0.0179
	100		56	16	0.0179
<i>Gardenia thunbergii</i>	0	100	10	69	0.01912
	15		39	40	0.01912
	100		17	58	0.01912
<i>Virgilia oroboides</i>	0	50	42	12	0.02096
	15		46	9	0.02096
	100		56	10	0.02096
<i>Kiggelaria africana</i>	0	100	0		0.0222
	15		2	70	0.0222
	100		7	56	0.0222
<i>Virgilia divaricata</i>	0	50	12	13	0.03063
	15		24	10	0.03063
	100		34	11	0.03063
<i>Erythrina caffra</i>	0	20	15	26	0.1243
	15		15	20	0.1243
	100		15	21	0.1243
<i>Ekebergia capensis</i>	0	40	38	24	0.1257
	15		76	23	0.1257
	100		58	22	0.1257
<i>Diospyros lycioides</i>	0	30	17	94	0.15
	15		20	38	0.15
	100		13	70	0.15
<i>Podocarpus latifolius</i>	0	50	56	57	0.1947
	15		62	43	0.1947
	100		52	60	0.1947

Seed age + desiccation sensitivity

LIST OF CAPTIONS FOR FIGURES REFERRED TO IN THE TEXT:

Fig. 1. Relationship between log seed mass and log embryo mass.

Figure 2. Relationship between seed size and the ratio of embryo mass/seed mass

Fig. 3. Relationship between log embryo mass and log germination time.

Table 2. Summary of germination results.

Fig.4. The relationship between log biomass at 30 days and log embryo mass.

Fig.5. Survival time in the dark of species with different seed sizes

Fig.6. Hypocotyl length for species with different embryo masses.

fig.7. Relationship between relative growth rate and log embryo mass.

Fig.8. Relationship between the ratio light/shade relative growth rate and embryo mass.

Fig.9. Relationship between dark/light relative growth rate and embryo mass.

Fig.10. Shoot biomass of different species after different light treatments for 30 days.

Fig.11. Relationship between log light/shade shoot biomass at 30 days and log embryo mass.

Fig.12. Root biomass after 30 days under different light regimes for different species.

Fig.13. Root and shoot biomass at 30 days for different seed sizes.

Fig.14. Shoot biomass/root biomass after 30 days in the dark, shade and full light.

Fig.15. The relationship between log root length/total leaf area and log embryo mass.

Fig. 1. Relationship between log seed mass and log embryo mass.

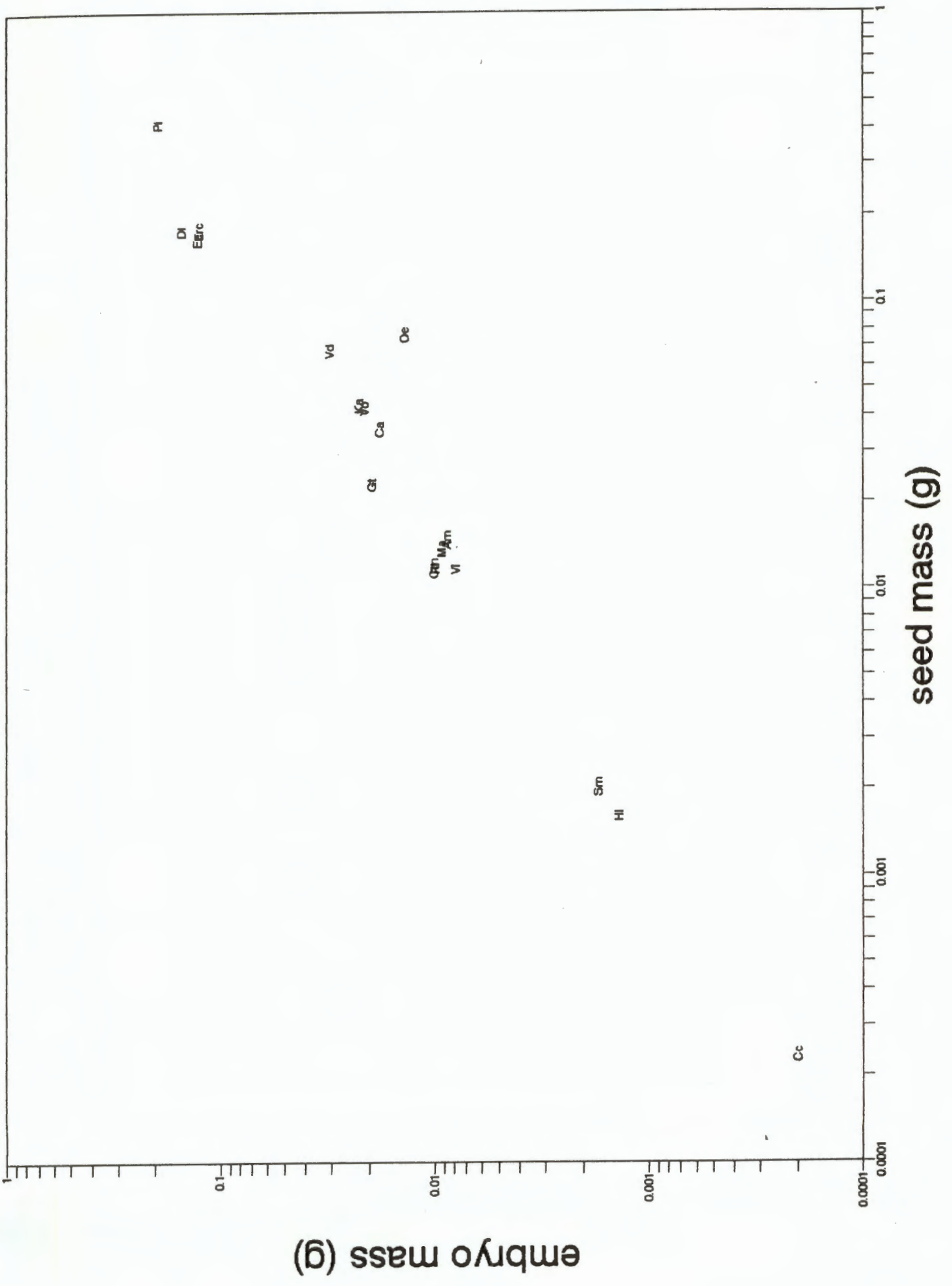


Figure 2. Relationship between seed size and the ratio of embryo mass/seed mass

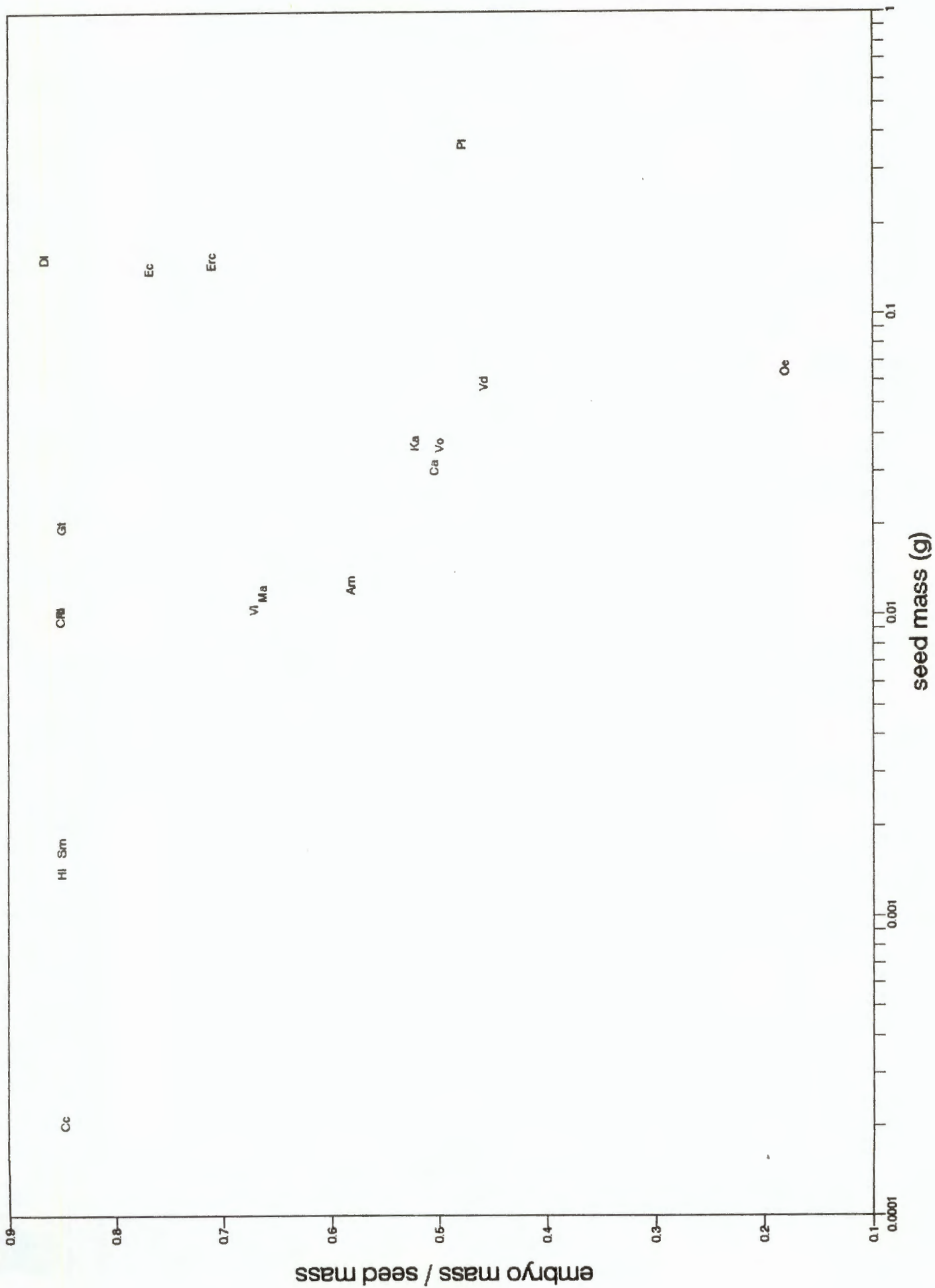


Fig. 3. Relationship between log embryo mass and log germination time.

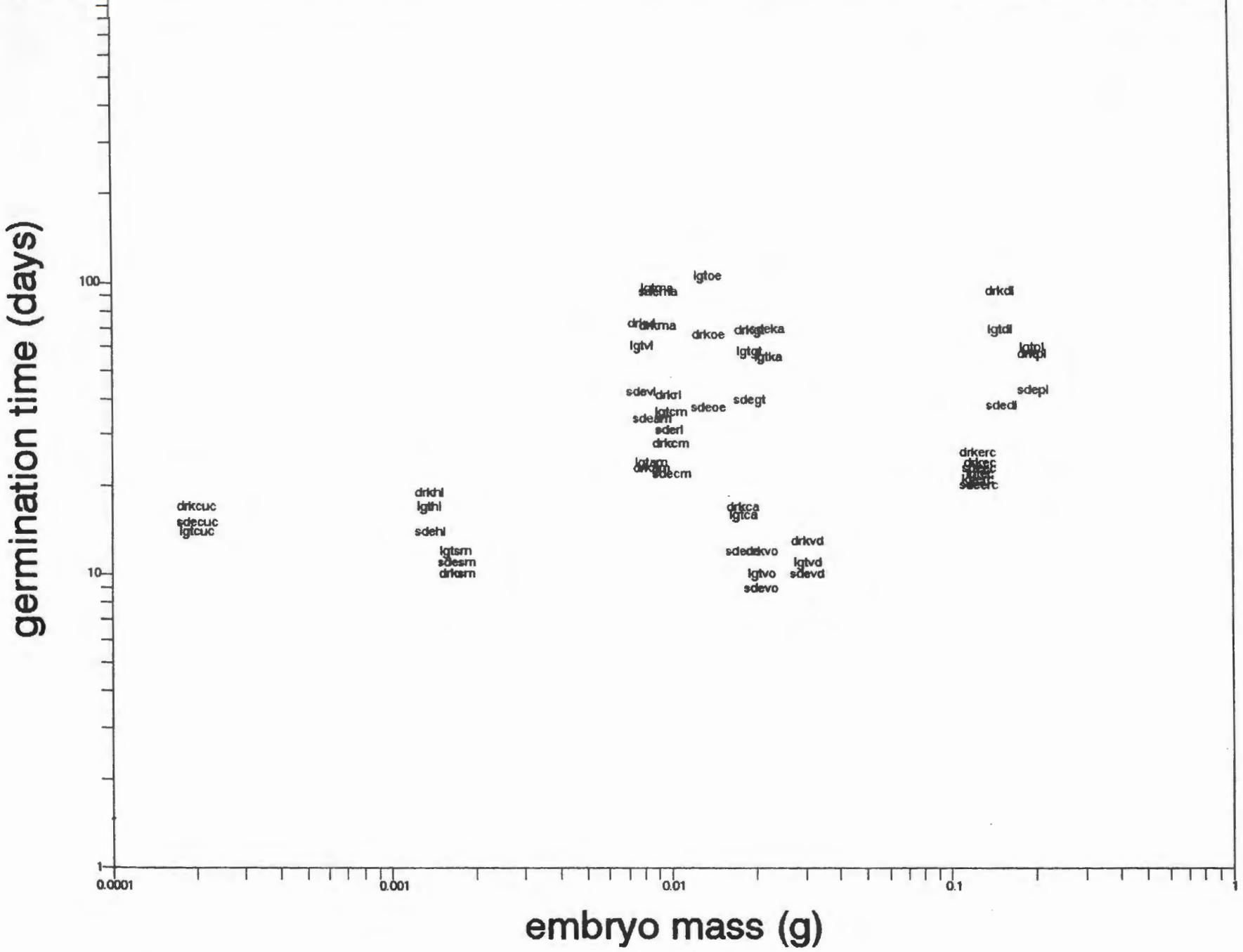


Fig.4. The relationship between log biomass at 30 days and log embryo mass.

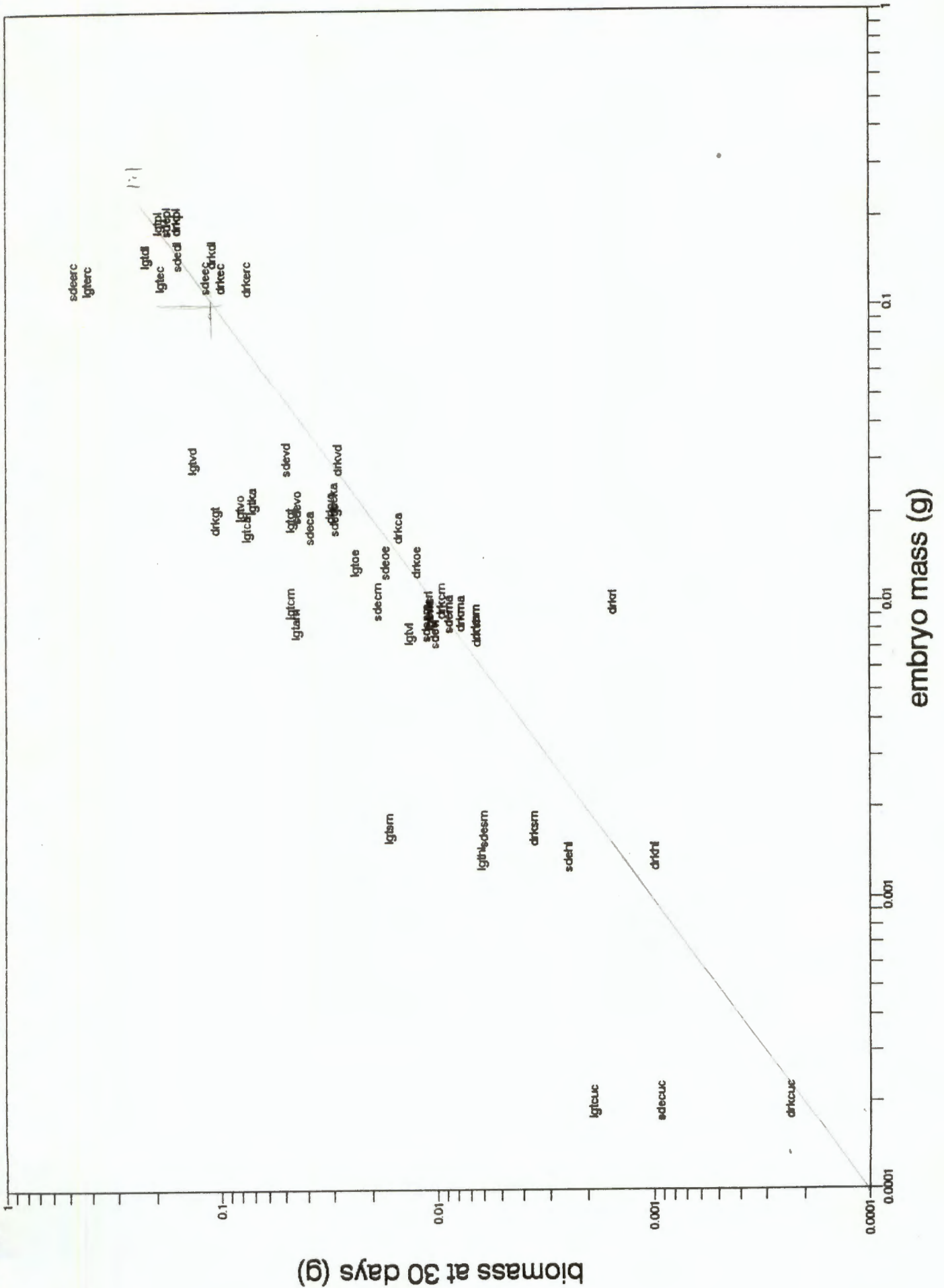


Fig.5. Survival time in the dark of species with different seed sizes

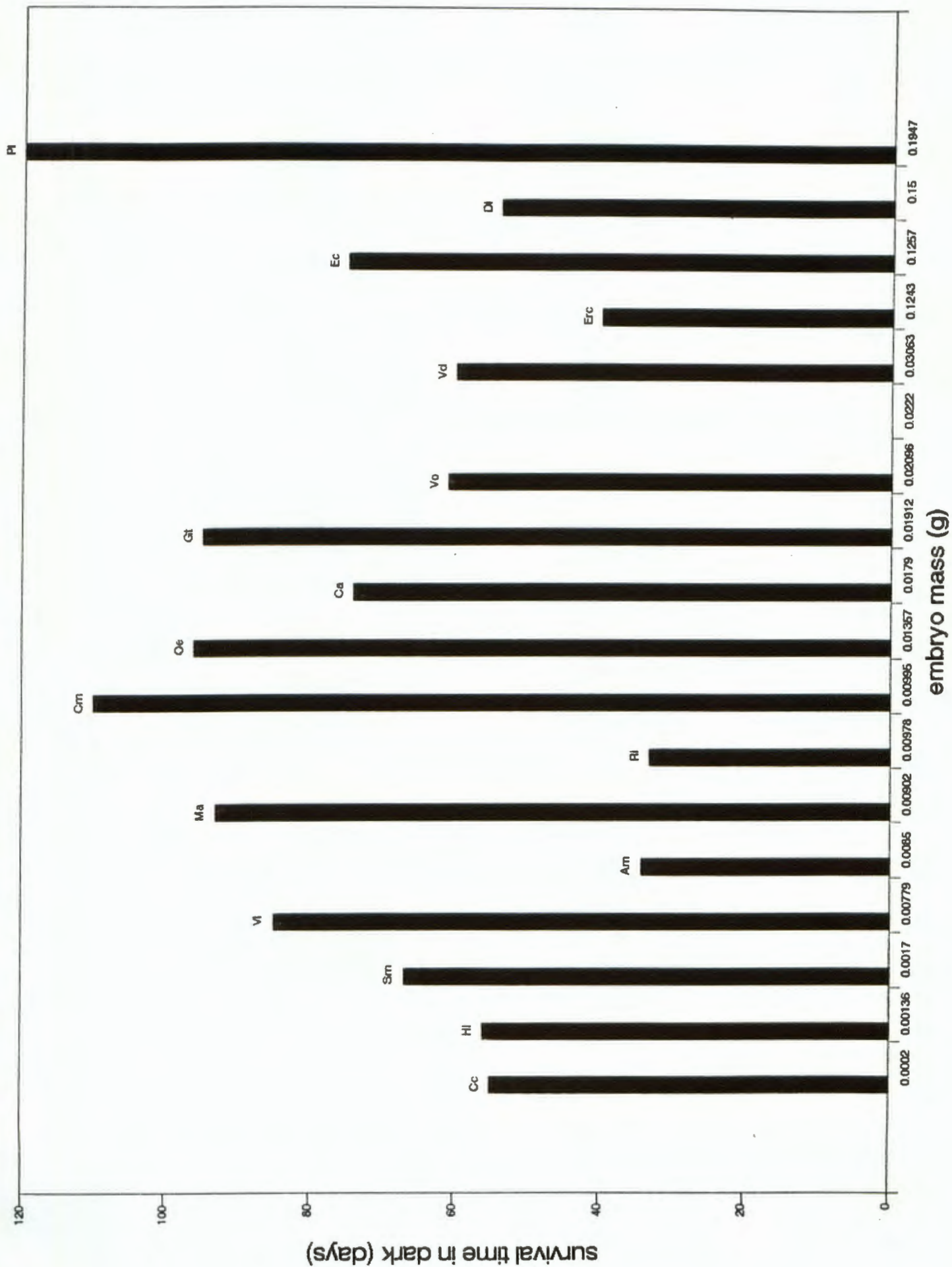


Fig.6. Hypocotyl length for species with different embryo masses.

Different light treatments?

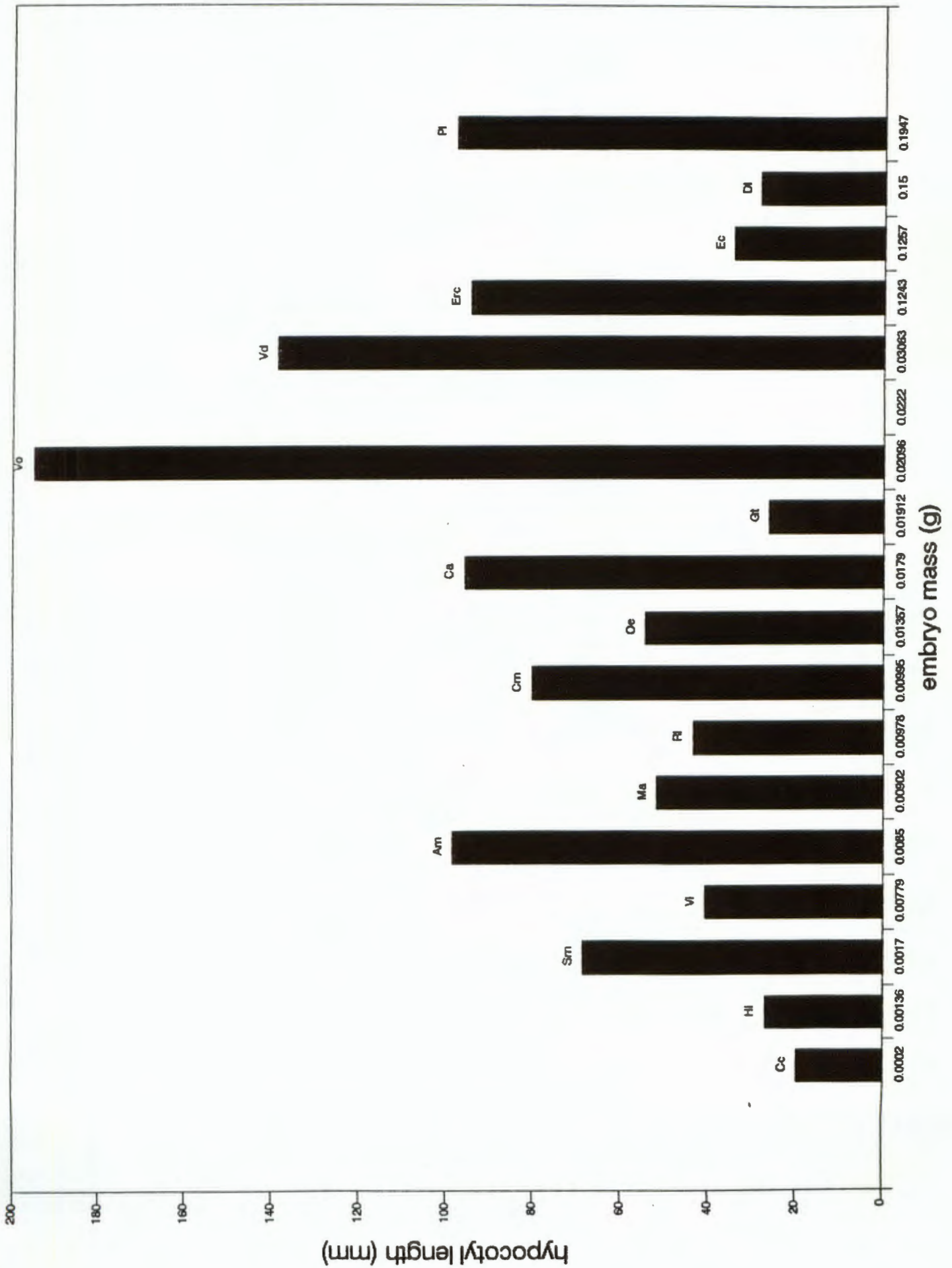


Fig.8. Relationship between the ratio light/shade relative growth rate and embryo mass.

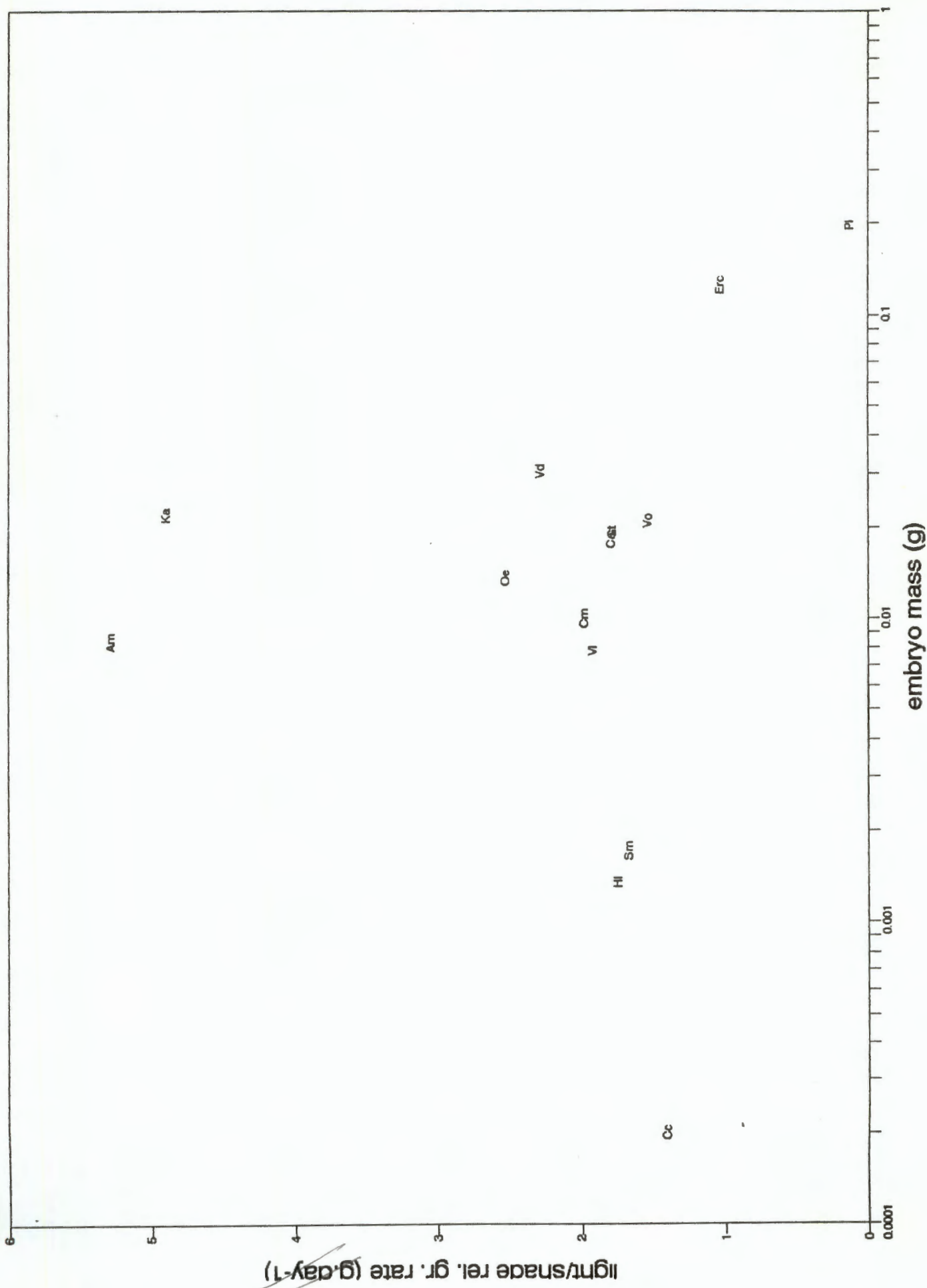
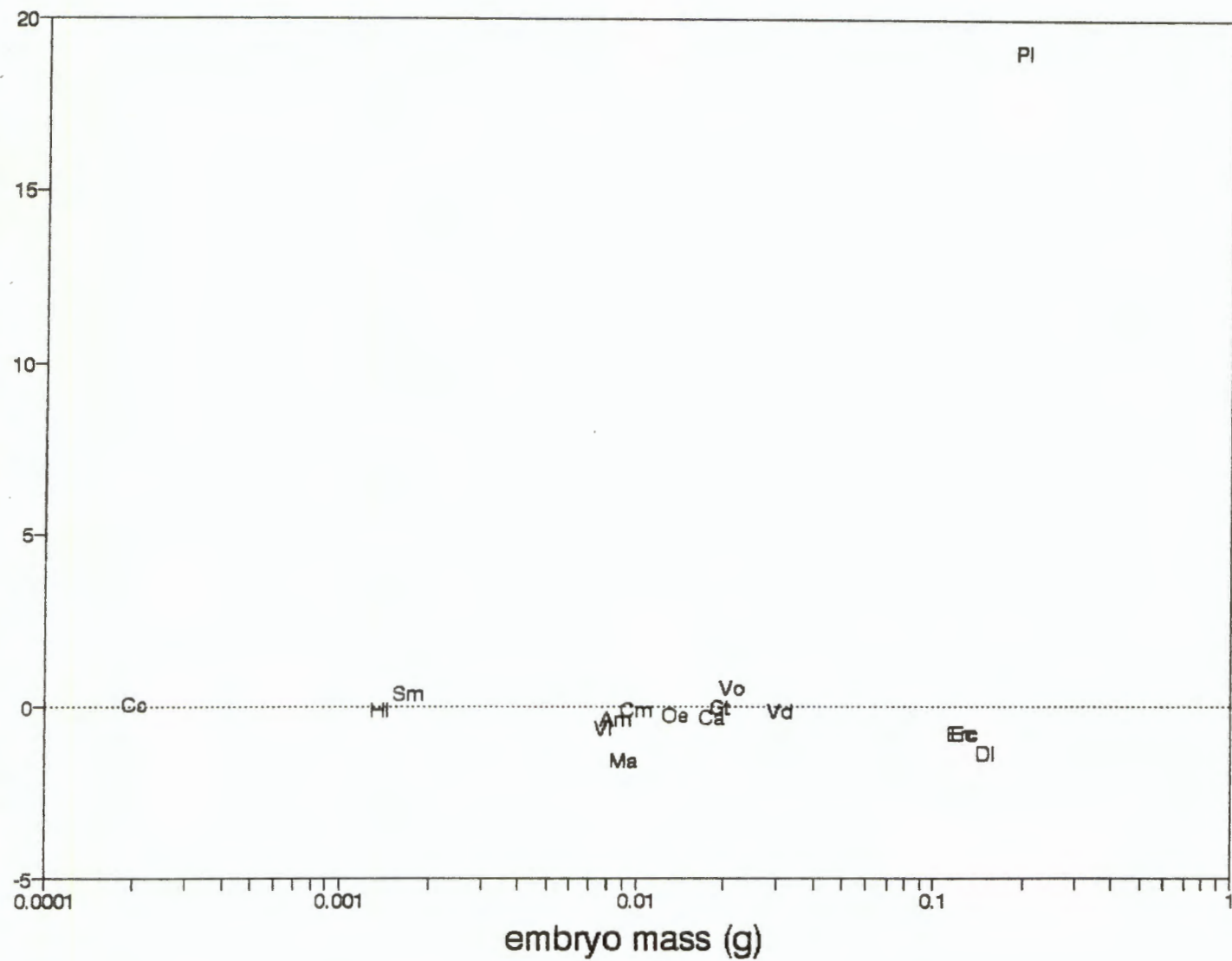


Fig.9. Relationship between dark/light relative growth rate and embryo mass.

light/dark ?



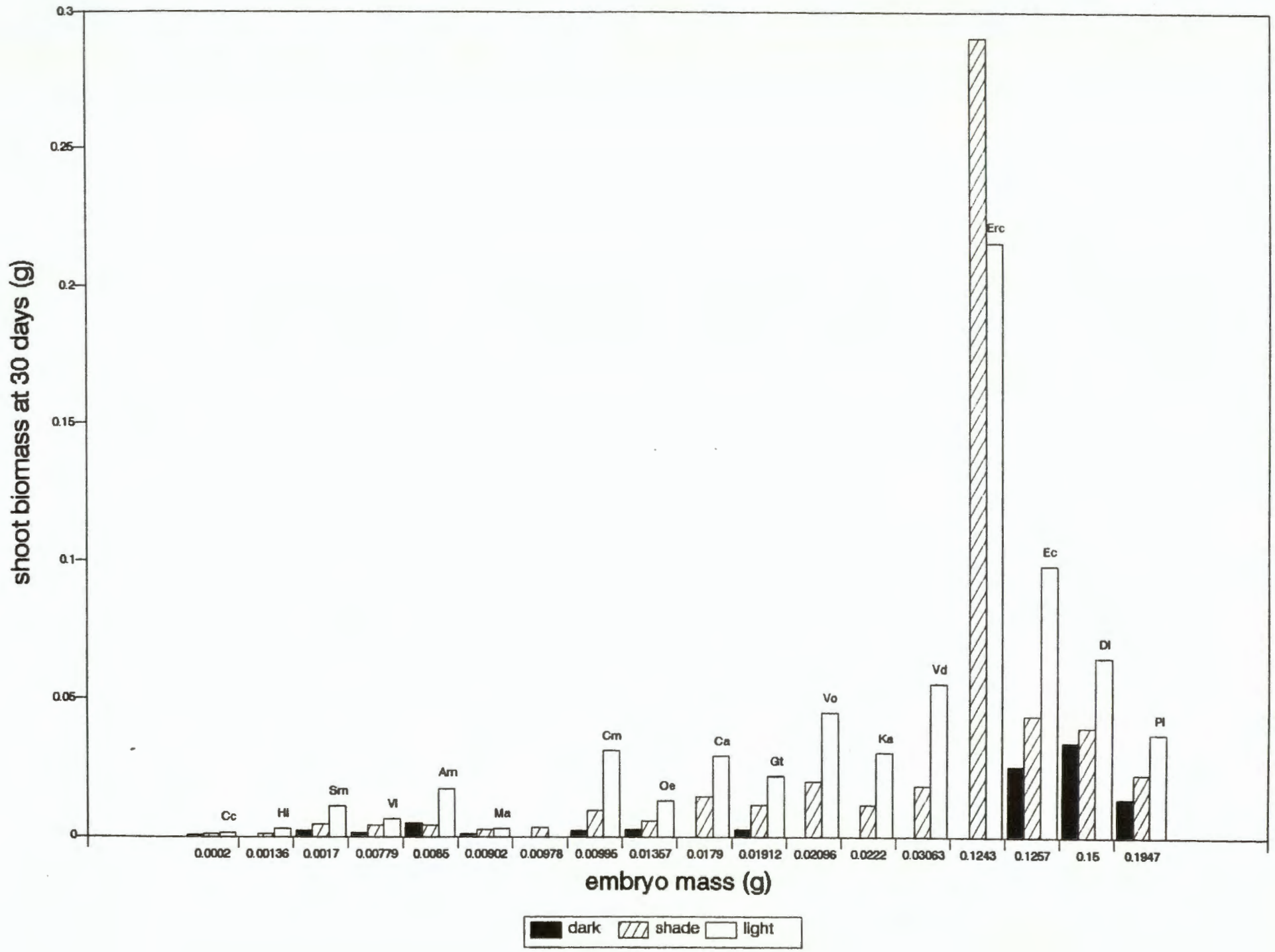
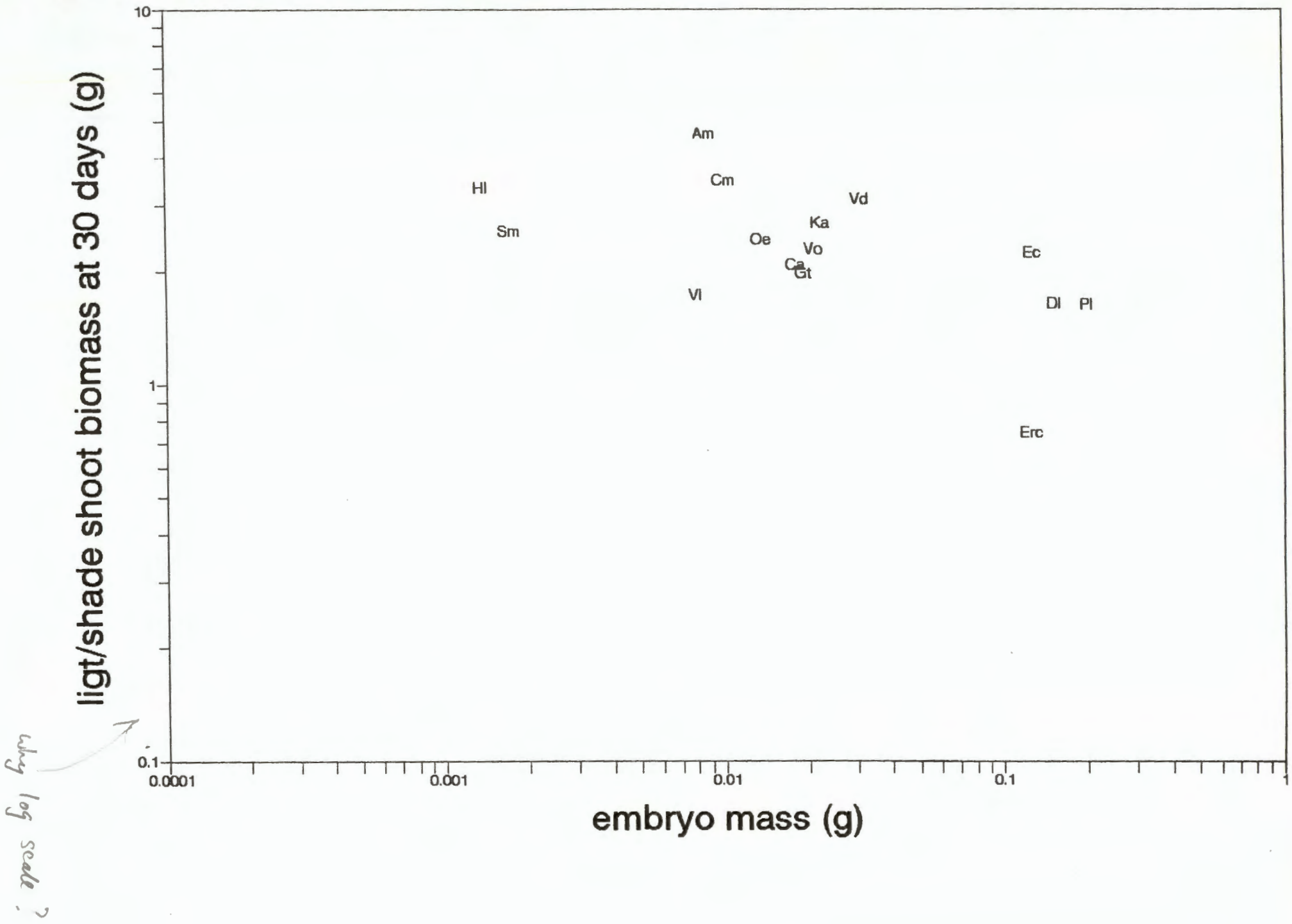


FIG. 10. Shoot biomass of different species after different light treatments for 30 days.

Fig. 11. Relationship between log light/shade shoot biomass at 30 days and log embryo mass.



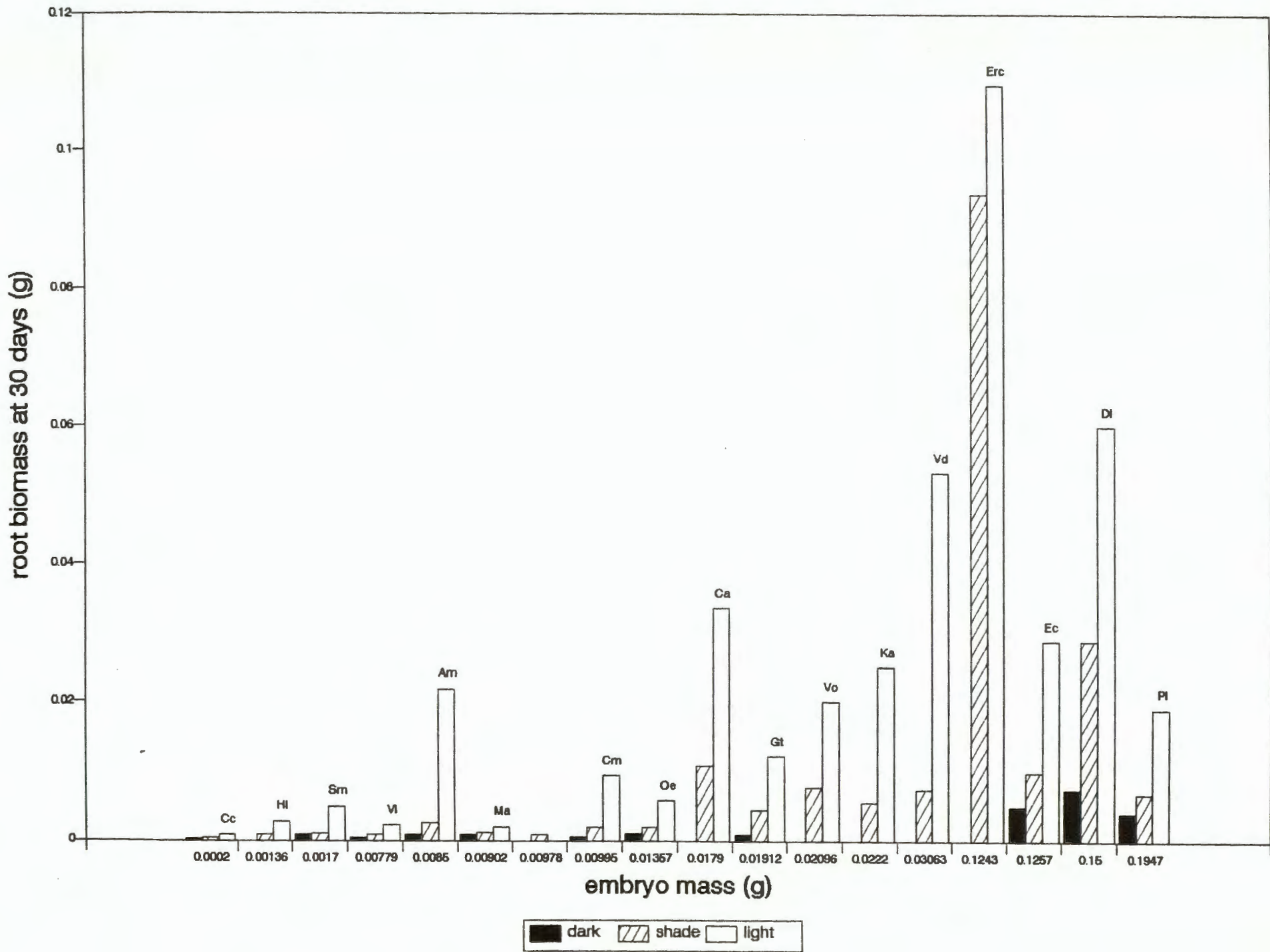
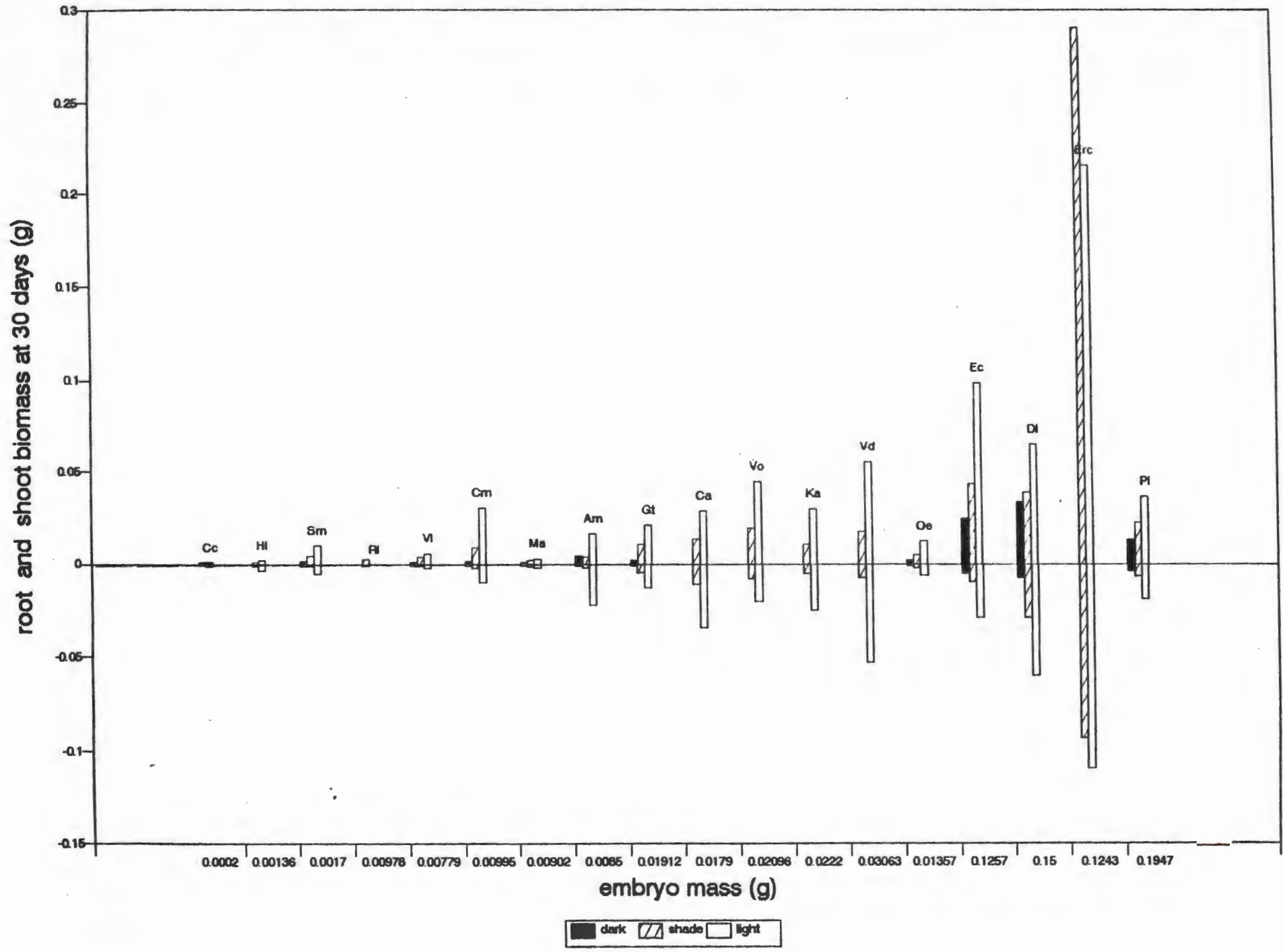


Fig. 12. Root biomass after 30 days under different light regimes for different species.

Fig. 13. Root and shoot biomass at 30 days for different seed sizes.



shoot/root biomass at 30 days (g)

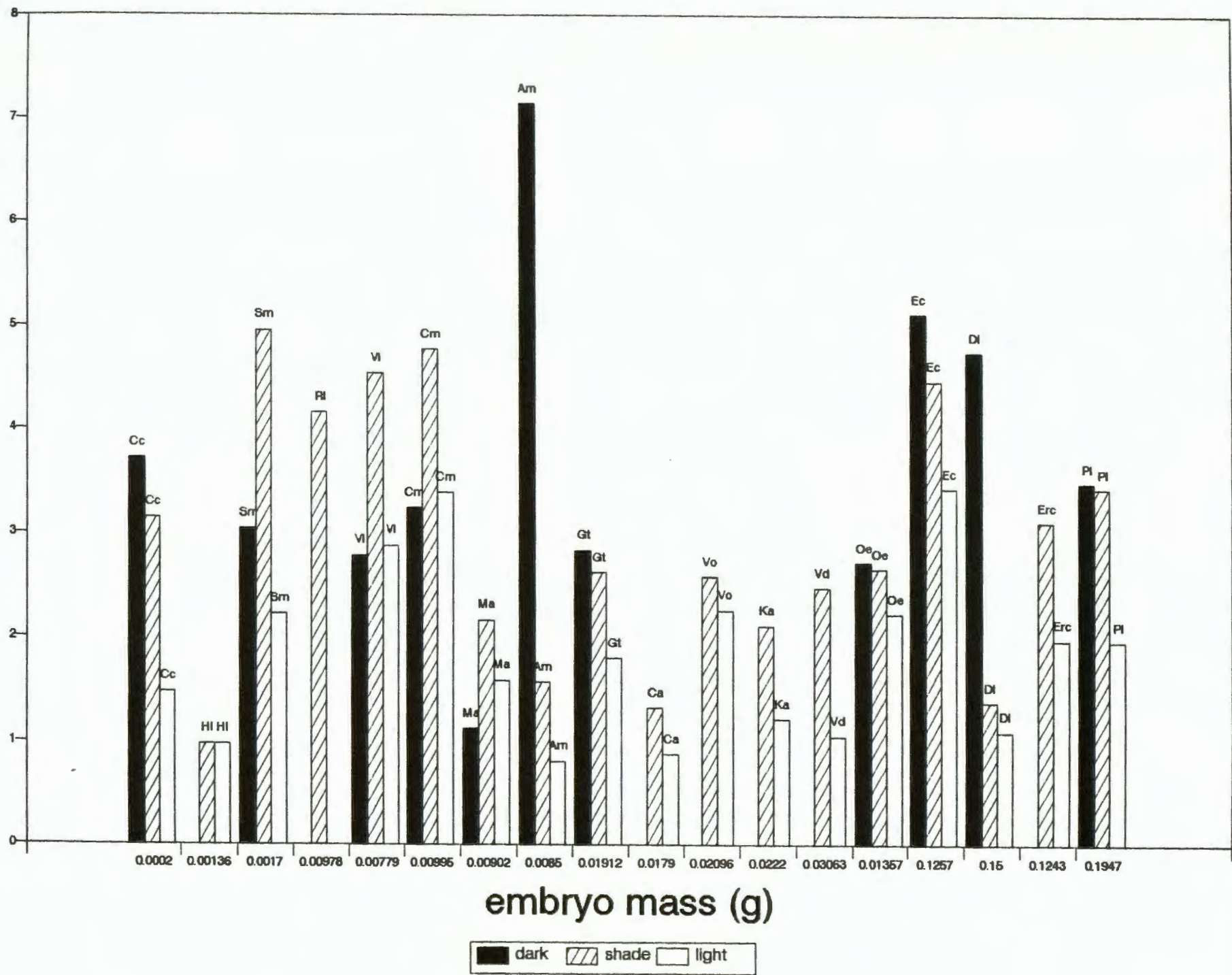
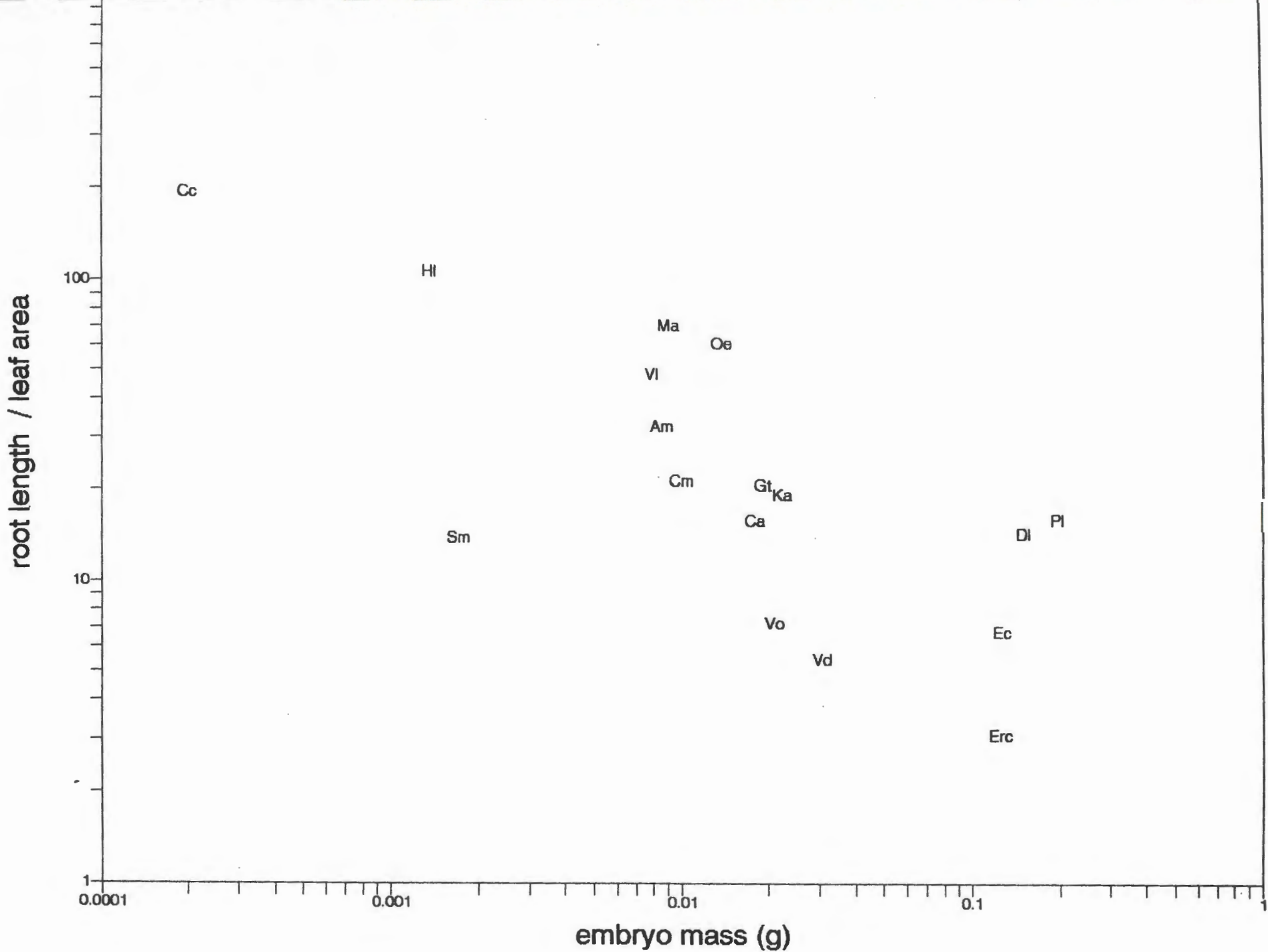
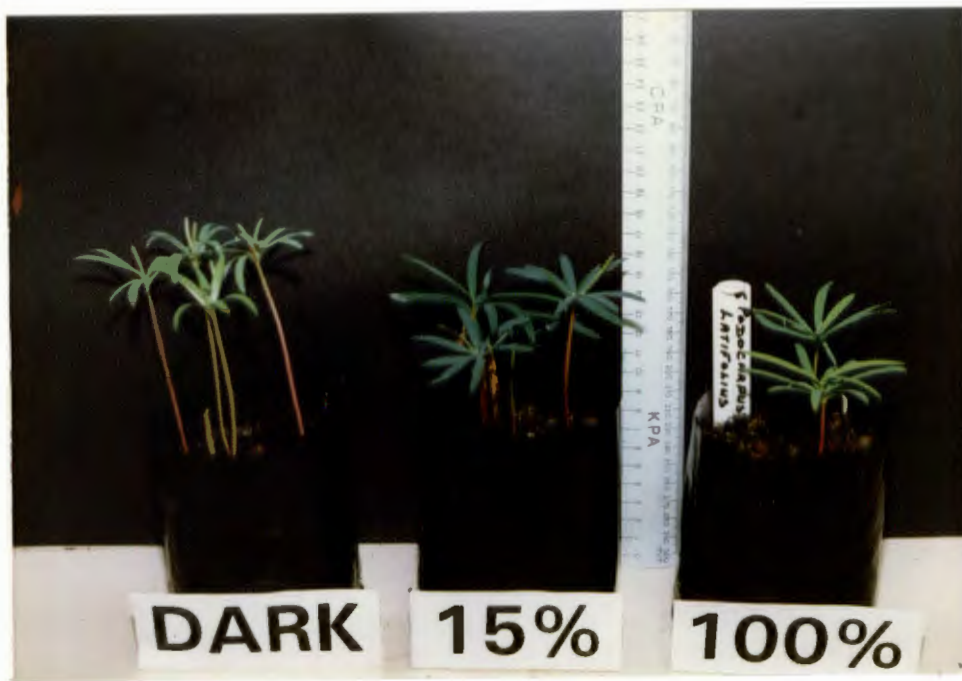


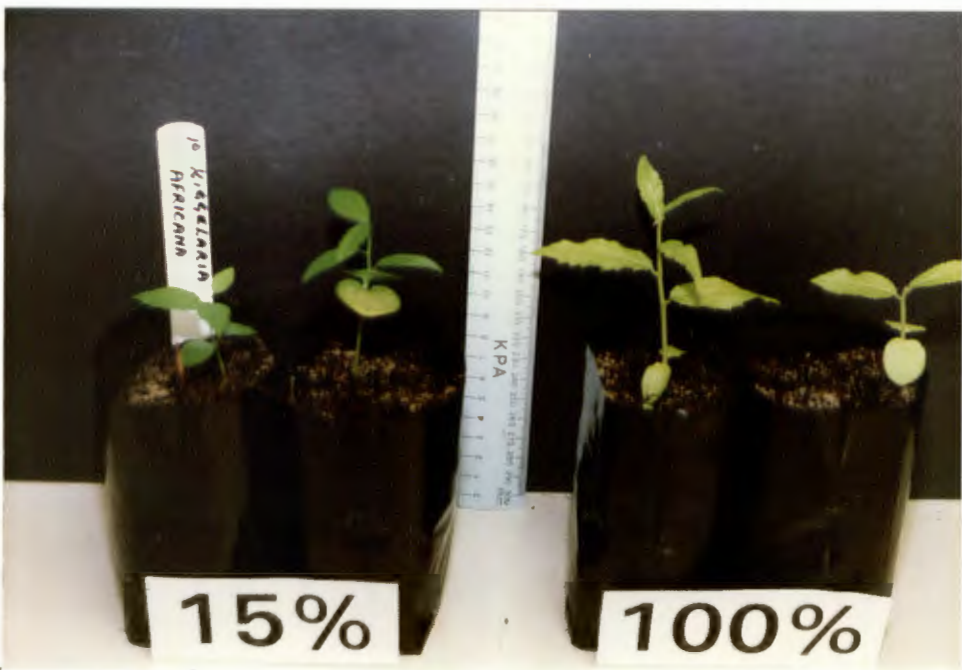
Fig. 14. Shoot biomass/root biomass after 30 days in the dark, shade and full light.

FIG. 15. The relationship between log root length/total leaf area and log embryo mass.



SOME PHOTOGRAPHS ILLUSTRATING RESPONSES TO DIFFERENT LIGHT TREATMENTS FOR A FEW SPECIES.







(HALBERIA LUCIDA)