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Gas Exchange and Crop Yield of the Reproductive Organs in Hybrid Larch (*Larix decidua* x *L. kaempferi*) in Relation to the Vegetative Carbon Demand

By

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Key words: *Larix*, reproduction, gas exchange, refixation, cones, flowers, biomass, carbon balance.

Summary

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Little is known about the gas exchange of naturally growing, reproductive organs in larch trees, in particular, in comparison with the vegetative carbon (C) demand. The study focuses on the hybrid between European and Japanese larch, known for high capacities in stem growth and flowering. Male flowering mass can be as high as 1.6 mg cm^{-1} , i.e. per unit length of twig section, while respiring $1.2 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ at 15°C . The respiratory C release during the short flowering period in early April was about 11 % of the C content of male flowers. The dark respiration rate of cones was, in July, only half as high as in male flowers, however, up to 60 % of the respired CO_2 was photo-synthetically refixed in cones under high-light and moderate temperature conditions. Cone photosynthesis, being saturated at $900 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and declining with increasing temperature, lowered the daily respiration by about 22 % under variable light conditions. While overheating three times as much above the ambient air temperature as did larch needles, cones displayed a lower transpiration rate and water vapour conductance, the latter being insensitive to the climatic factors.

The annual cone yield related to reduction in the radial stem increment, whereas radial branch growth was hardly affected. Reserves for male flowering appeared to be accumulated during preceding years favourable to stem growth. The carbon respired by the short-lived male flowers only demanded a minor portion of the annual, whole-tree C balance. However, at high cone yield of about 25 % of the biomass of radial stem increment, C costs of cones including respiration become significant in the tree's C balance. The abundant flowering of hybrid larch may be regarded as an-

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other expression of heterosis, as the high annual C gain apparently ensures ample reproduction. Given the high reproductive biomass, CO₂ refixation of cones alleviates the C balance at the whole-tree level.

Introduction

Although the biomass of the reproductive organs of adult forest trees is rather small in relation to the vegetative biomass (WHITTAKER & WOODWELL 1968), the share of reproduction costs may be significant within the trees' annual carbon (C) balance (LINDER & TROENG 1981). The cone production of coniferous trees is known to be highly C demanding so that tree-internal competition may arise with the C allocation into stem and needle growth (EIS & al. 1965, TAPPEINER 1969, SELAS & al. 2002), although recent reports on C saturation of trees under the rising atmospheric CO₂ supply may suggest vanishing tradeoffs between reproductive and vegetative C fluxes (KÖRNER 2003a). A particular role may be ascribed to some varying degree to cone photosynthesis in coping with the reproductive C demand, which is in line with discussions about the effect of the photosynthetic activity in shoot axes on the whole-tree C balance (BENECKE 1985, ASCHAN & PFANZ 2003). Although some physiological aspects of C uptake and allocation have been unravelled in cones (e.g. DICKMANN & KOZLOWSKI 1970, ROOK & SWEET 1970), little is known about the gas exchange performance of intact cones under field conditions, as studies were performed on excised material (e.g. LINDER & TROENG 1981, KOPPEL & al. 1987).

The present study investigates the gas exchange of naturally growing reproductive organs (cones and male flowers) in hybrid larch (*Larix decidua* x *L. kaempferi*), including aspects of the energy balance of cones. Moreover, as male flowers and cones generally differ in terms of their number and longevity, attention was directed to their biomass production each in relation to the increment of other tree organs and the annual whole-tree C balance. The study was part of a larger analysis that exemplified the C balance and significance of crown architecture on the growth of adult forest trees of the genus *Larix* (BENECKE & al. 1981, MATYSSEK & SCHULZE 1987a,b, 1988) which is characterized by light-demanding and both frequently and heavily seeding pioneer species. Hybrid larch, an offspring of the parent species *Larix decidua* (European larch) and *L. kaempferi* (Japanese larch), was studied because of its capacity for stem heterosis and abundant flowering during mast years (SCHOBER 1953, MATYSSEK & SCHULZE 1987b). The analysis of hybrid larch was expected, therefore, to readily uncover reproductive versus vegetative C demands.

Material and Methods

The study introduced here was part of a larger investigation which has been reported in detail by MATYSSEK & SCHULZE 1987a,b, 1988.

Study site and species

The study site was located in a hill range near Bayreuth/Germany ('Hohe Warte', 450 m a.s.l.) within a planted multi-species forest which was mainly composed of *Larix decidua*, *L. kaempferi* (syn. *L. leptolepis*) and their hybrid (referred to as *L. decidua* x *leptolepis* in MATYSSEK & SCHULZE 1987a,b; 1988) as well as *Picea abies* and *Pinus sylvestris*. Trees of all species had an age of 33 years at the time of investigation and formed a closed canopy. The study reported here focused on hybrid larch which displayed heterosis in the formation of tall and thick stems (MATYSSEK & SCHULZE 1987a,b). The stem of the investigated hybrid larch tree was 20 m high, carrying a foliage dry mass of 9.8 kg between 9 and 20 m aboveground and overtopping individuals of the other species by about 4 m. The stem diameter at breast height was 26 cm and 40 % larger than in neighbouring trees of the parent species, and the latter had a foliage mass of only half the amount in the hybrid. The mean annual air temperature inside the canopy was 8.2°C, and the frost-free season extended from June through September. Soil temperature never dropped below 5°C within the uppermost 30 cm from May through October. The mean annual soil temperature was 6.6°C at 15 cm belowground. Precipitation was rather evenly distributed throughout the annual course (750 mm), with a slight maximum in summer.

In 1980, the opening of the male flowers, i.e. pollination, began in mid-April, shortly after vegetative bud break. At this time, cone flowers were open after conelet growth had begun on April 9. By April 29, the conelets were 2 cm long, displaying bract colouring from pale green to red in the hybrid larch. The cones investigated possessed green scales phasing into red towards the outer distal edge. Cones grew rapidly and were close to final size (4 cm long, 2.9 g dry mass) at the time of the gas exchange investigations in early July. On Sept. 25, 50 % of all cones in the tree crown were brown (4 cm long, 3.5 g dry mass), indicating photosynthesis to be possible during a period of at least 5 months. Cones were absent in the shade crown. In 1981, no reproductive organs were formed. After an initial amount of developing, reproductive buds similar to that in 1980, a late-frost episode in April 1982 destroyed 90 % of all conelets in the crown.

Gas exchange

Gas exchange was measured with thermo-electrically controlled cuvettes (Walz, Efeltrich, Germany), the operation of which has been described by KOCH & al. 1971, SCHULZE & al. 1972 and SCHULZE & KÜPPERS 1979. At 13 m stem height, sun twigs carrying cones (July 1980 and 1982) or male flowers (April 1982) were enclosed while still being attached to the tree. A few days before enclosure, twig sections distal to those carrying cones or male flowers had been removed, while the enclosed parts were free of needles. Gas exchange was monitored in response to diurnal courses of the ambient climatic factors (Fig. 1A) as well as to step changes of either cone temperature or photosynthetic photon flux density (PPFD). Steady-state responses upon step changes were assessed under an artificial light source (Osram HQI-TS 'Powerstar', 400 W, 5200 K). Cone temperature was measured by inserting a copper/constantan thermocouple (diameter 0.1 mm) between the scales close to the cone surface. Gas exchange rates were expressed per unit of cone dry mass or surface area, as the latter was determined by means of a modified glass bead technique (DAVIES & BENECKE 1981).

Biomass

Biomass and annual growth increments of the entire branch system were determined by harvesting about 15% of all live branches of the crown, and by relating branch biomass to branch length. The obtained correlation along with the length assessment of all live branches were used to calculate wood biomass and increments, foliage mass and the amount of male flowers in the crown (MATYSSEK & SCHULZE 1987b). The annual biomass increment of stems was derived from core sampling (by one-meter intervals) after the determination of wood density and calculation of the total annual increment in stem volume. The number of cones was obtained by counting, and their total biomass was assessed on the basis of harvested samples.

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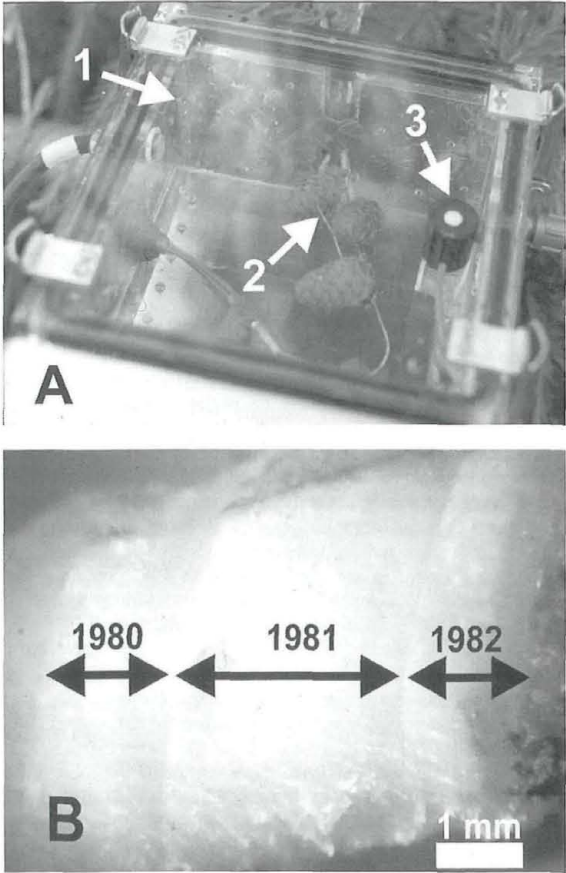


Fig. 1. A: Cones of hybrid larch as sealed into the thermo-electrically controlled cuvette during assessment of diurnal course in gas exchange: 1 = transparent part of the cuvette; 2 = thermocouple; 3 = PPF sensor. B: Annual rings in the stem of hybrid larch at breast height.

Annual carbon gain

The annual net carbon gain was calculated from an empirical CO₂ assimilation model which was based on the gas exchange data of needle-bearing twigs under ambient climate conditions, taking into account the crown-internal distributions of PPF and the biomass of sun and shade foliage (MATYSSEK & SCHULZE 1988).

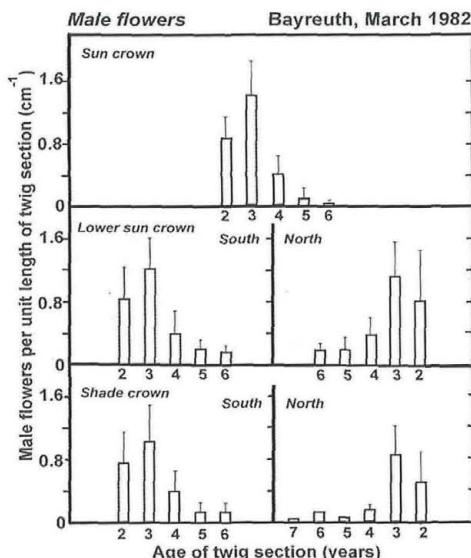


Fig. 2. Number of male flowers in hybrid larch per unit length of twig section as related to the age of section (means $\pm$ SD).

Results

Amount and respiration of male flowers

Since male flowers in larch develop from vegetative buds of the previous year, their abundance may limit the annual carbon gain during the current year. Current-year and 1-year-old twig sections did not carry male flowers in hybrid larch, whereas a high number of flowers was reached per unit length of 2 and 3-year-old sections ($1.2 - 1.6 \text{ cm}^{-1}$; Fig. 2). The flowering density sharply declined to about 0.4 cm^{-1} on 4-year-old sections, and only few flowers were found on 6-year-old sections. Flowering density on sections of same age was similar across the different crown zones and exposures. The crown carried a total of about 170,000 male flowers in 1982, which represented a dry mass of about 5.2 kg. As the entire branch system (including lateral twigs) totalled to about 4200 m, mean flowering density resulted in 0.4 cm^{-1} (corresponding to 12.4 mg cm^{-1}) at the crown level.

Since male flowers are greenish only during early stages of their development, their maintenance must be covered by carbon reserves. At a Q_{10} of 2.6 between 10 and 20°C , the dark respiration rate of male flowers was $1.2 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ at 15°C in early April (Fig. 3). Hence, the respiration rate of flowers was similar to that of larch needles during mid-summer (MATYSSEK & SCHULZE 1987a, 1988). During the first 10 days in April, which was the climax period of male flowering, the respiratory CO_2 release was 197 mg g^{-1} or, at a mean flower dry mass of 30 mg,

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1 kg per whole crown. Thus, the respiratory C demand was about 11 % of the C content of male flowers.

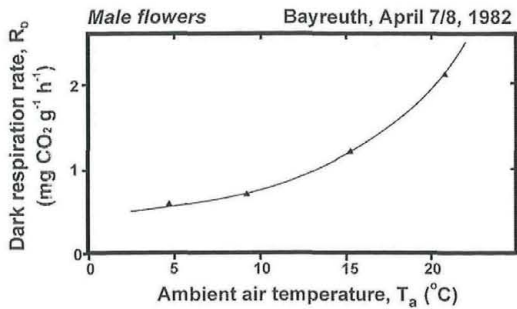


Fig. 3. Dark respiration rate of twigs carrying male flowers in hybrid larch in relation to air temperature (expressed on a flower mass basis).

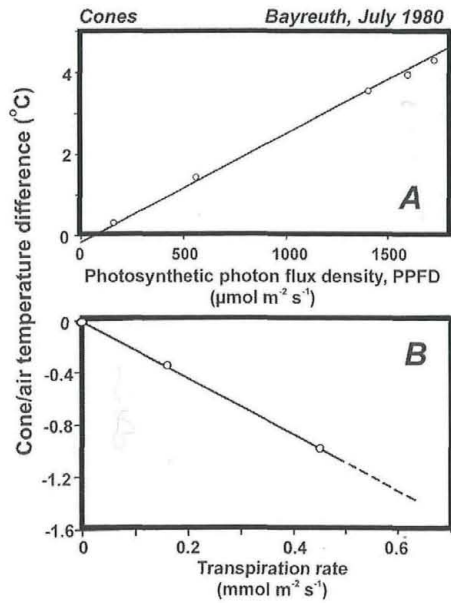


Fig. 4. A, Overheating of cones in hybrid larch above air temperature as related to photon flux density (PPFD). B, Cooling of cones in relation to transpiration rate.

Gas exchange of cones

At an air temperature of 18°C, low evaporative demand ($\Delta w < 5$ mbar bar⁻¹) and PPFD of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, cones overheated three times as much above the ambient air temperature (i.e. by about 2.6°C; Fig. 4A) as did the needles. Besides the probably reduced heat dissipation through convection, this thermal behaviour of cones was due to their stomataless scales, the diffusive conductance of which for water vapour was four times lower (13 mmol m⁻² s⁻¹) than that of needles (Fig. 5, MATYSSEK & SCHULZE 1987a, 1988). In the absence of stomata, the cone conductance did not respond to changes in any of the climatic factors, and a transpiration rate of about 0.13 mmol m⁻² s⁻¹ as occurring in cones at $\Delta w = 10$ mbar bar⁻¹ was reached in needles already at much lower Δw . Nevertheless, the transpiration rate had a cooling effect on the cone temperature (Fig. 4B).

The dark respiration rate at a cone temperature of 15°C was, on a dry mass basis, only half as high (0.7 mg CO₂ g⁻¹ h⁻¹, Fig. 6) as in male flowers (cf. Fig. 2) or in needles (MATYSSEK & SCHULZE 1987a, 1988). However, when expressed per unit of cone surface area, the dark respiration rate was 10 times higher than the corresponding, area-related rate of needles. At high PPFD, the rate of cone respiration was lowered across the assessed temperature range, reflecting photosynthetic activity of the cones (Fig. 6). Although depending on the stage of cone maturation, in July photosynthetic CO₂ refixation (cf. LINDER & TROENG 1981) of about 60 % of the dark respiration rate became manifest at 18°C. Refixation was saturated at PPFD of 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$, however, the efficiency in regaining respired CO₂ decreased with increasing temperature (Fig. 7).

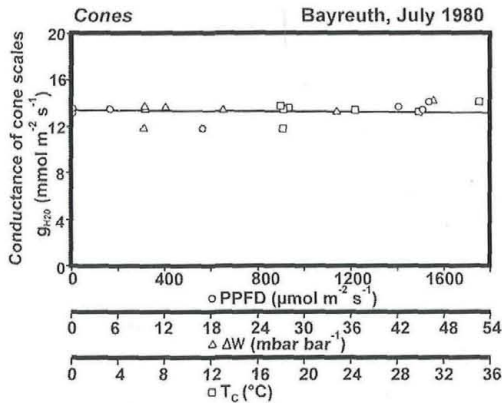


Fig. 5. Cone conductance for water vapor in hybrid larch as related to photon flux density (PPFD), cone temperature (T_c) and evaporative demand (Δw , i.e. the difference in the mole fraction of water vapour between cone surface and ambient air).

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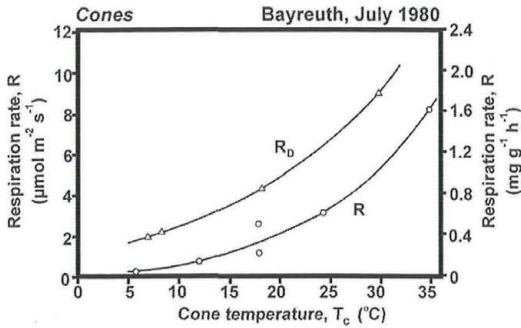


Fig. 6. Temperature dependence of the cone respiration rate of hybrid larch in the dark (triangles, R_D) and under light saturation of photosynthetic CO_2 refixation (circles, R).

Cone photosynthesis was also reflected during diurnal courses under the ambient climatic conditions at the forest site, as at high PPFD in the afternoon, CO_2 refixation lowered the respiration rate by almost 60 % (Fig. 8). For the day depicted, the daily cone respiration amounted to 120 mmol m^{-2} , which is an amount 22 % lower than that expected without the capability of photosynthetic CO_2 refixation.

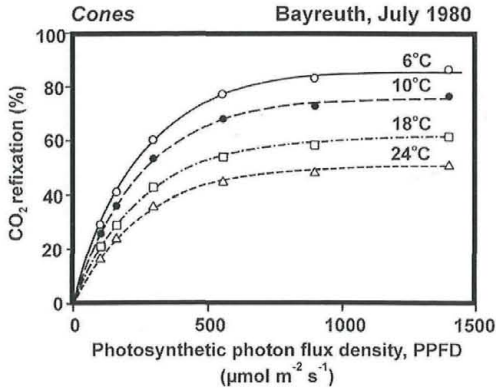


Fig. 7. Light and temperature dependence of cone CO_2 refixation (= decrease in respiration rate; function of 18°C directly measured, other functions derived from Fig. 6 and from the relationship at 18°C ; confirmed in July 1982).

Male flowers and cones in relation to the annual whole-tree production

After about 650 cones (= 2 kg dry mass) had matured in the studied hybrid larch tree by the autumn of 1980, no cones developed in 1981. In 1982, the amount

of cone buds was comparable with that in 1980, however, only about 60 conelets continued to develop after a late-frost episode in early April. The annual ring that developed during the coneless year of 1981 was distinctly wider along the entire stem length than the rings that were formed in 1980 and 1982 (Fig. 1B). This ring pattern was reflected in the total amount of annual stem wood production (Fig. 9), which in 1981 was approximately twice as high (17 kg) as in the preceding or succeeding year. This contrasted with the stem wood production of neighbouring Japanese larch, which was coneless during 1980 through 1982 and displayed rather similar radial growth increment in each of these years, despite different weather conditions (MATYSSEK 1985). Adjacent European larch, which had no cones in 1981 and 1982, displayed similar annual stem production in these two years. However, in 1980, when European larch did produce cones, stem production was distinctly reduced (MATYSSEK 1985). In hybrid larch, changes in cone yield were less reflected in the annual biomass production of the entire branch system (Fig. 9), whereas the annual increments in stem length which are regarded to be fuelled from previous-year reserves (ODIN 1972) remained unchanged (MATYSSEK 1985).

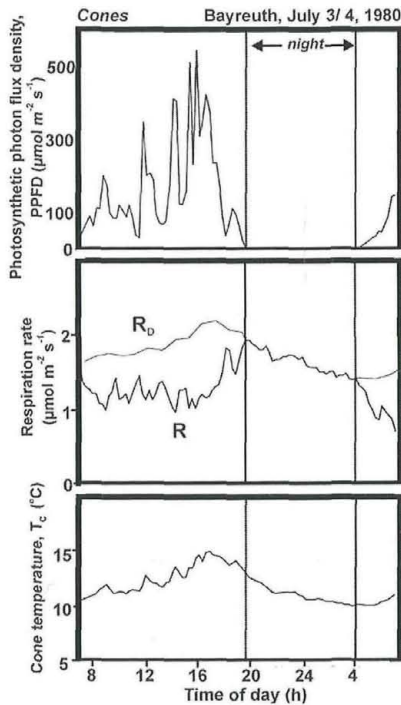


Fig. 8. Diurnal courses of cone respiration rate, photon flux density (PPFD) and cone temperature in hybrid larch; during daylight hours, the dark respiration rate of cones (R_D) was interpolated (thin line) according to the functions of Figs. 6 & 7.

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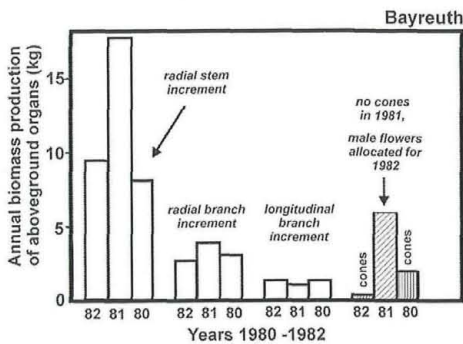


Fig. 9. Biomass increment (dry mass) of tree organs during the years 1980 through 1982.

Table 1. The reproductive organs in relation to the whole-tree C balance of hybrid larch (adapted from MATYSSEK & SCHULZE 1988).

A)	1982		
	Biomass increment kg	Carbon (increment + respiration) (kg)	Proportion of annual C gain (%)
Stem	9.3	12.0	38
Branch system	4.0	5.9	18
Root system	---	8.6 ¹	27
Needles	9.8	4.9 ²	15
Cones ⁵	0.4	0.3	0.9
Male flowers	5.2	0.3 ³	0.8
Annual C gain		32.0	100
B)	1980		
	Biomass increment kg	Carbon (increment + respiration) (kg)	Proportion of annual C gain (%)
	7.9	10.3	32 ⁴
	4.0	5.9	18 ⁴
Cones ⁵	2.0	1.5	5 ⁴

¹ no direct assessment, C costs of the root system calculated as the difference between the annual C gain and the aboveground C costs.
² respiratory costs accounted for in annual C gain (= net C gain).
³ structural C costs assigned to 1981 (see text)
⁴ same C gain and costs of respiration assumed as in 1982.
⁵ annual C costs of cone respiration assumed to be half of the C content of the matured cone biomass (according to LINDER & TROENG 1981 for *Pinus sylvestris*)

Since the C allocation to male flowers must be fuelled from the C gain of the preceding year (see above), in Fig. 9 the biomass of male flowering in 1982 was assigned to 1981. Apparently, ample reserves for male flowering may be formed during years which are favourable to stem production. Although the total flower biomass is rather high, the carbon respired by the male flowers makes up a

minor portion only of the annual carbon balance in hybrid larch (Table 1A, 1982), because of the short time span of flowering. Hence, these carbon costs may be similar to the total (structural + respiratory) annual C demand of a small number of cones, as was the case in 1982, when the annual C balance was mainly determined by the vegetative organs. However in years of ample cone yield (1980, Table 1B), the C costs of cones may rise up to about 5 % within the annual whole-tree C balance, when assuming annual C gain and foliage biomass to be similar to those in 1982. In 1980, the biomass of the cones was 25 % of that in stem increment. Assuming the annual C costs of cone respiration to be half the C content of the matured cone biomass (cf. LINDER & TROENG 1981), the total C costs of cones may have been only 15 % of those of the stem, when including the influence of cone photosynthesis.

Discussion

Although the gas exchange of the reproductive organs was determined by CO₂ release, the latter would have been distinctly larger without CO₂ refixation. Contrasting with the short-lived male flowers which were greenish only during the early stages of development, CO₂ refixation is substantial, in particular, for the C balance of the female cones on a seasonal basis. Already under changing cloudiness, the daily respiration was lowered by about 20 %, and given combinations of low temperature and high PPFD, photosynthetic compensation of the respiratory CO₂ release may be achieved (cf Figs. 6, 7). At similar stage of cone development, also in *Pinus sylvestris* (LINDER & TROENG 1981) and *Pinus resinosa* (DICKMANN & KOZLOWSKI 1970) expected dark respiration rates were lowered by about 50 to 75 % at high PPFD and moderate temperature. Similar to *Pinus sylvestris*, the CO₂ refixation in hybrid larch was saturated at PPFD of about 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$. KOPPEL & al. 1987 found CO₂ refixation to reduce the respiratory loss of spruce cones (*Picea abies*) by about 17 % on an annual basis. Although the proportion of the entire C costs of cone production within the annual whole-tree C balance could only be estimated in hybrid larch (< 10 % in years of ample cone yield, cf. Tab. 1), consistency in cone gas exchange may suggest a proportion similar to that in other conifers (LINDER & TROENG 1981, KOPPEL & al. 1987). Cone photosynthesis appears to fulfil a function similar to the photosynthesis of other so-called “non-green” organs like shoot axes which in fact possess chloroplasts (e.g. 23% annual CO₂ refixation: BENECKE 1985). The latter, depending on axis age and tissue type, counteract CO₂ release and, by this, alleviate the C balance of the tree (MATYSSEK & al. 2002, ASCHAN & PFANZ 2003).

As shown for *Pinus resinosa*, both the photosynthesis of the cones and neighbouring needles had to cover the C demand of cone development (DICKMANN & KOZLOWSKI 1968) so that the assimilate influx from the needles, which can eventually limit stem and needle growth (EIS & al. 1965, TAPPEINER 1969, SELAS & al. 2002), may be determined by the extent of CO₂ refixation. However, increasing fecundity and accelerated sexual maturity of trees, being viewed in the context of

global-change effects (LADEAU & CLARK 2001), along with presumed C saturation under elevated CO₂ (KÖRNER 2003a), suggest the tree-internal competition for carbon between reproduction and radial stem growth may vanish during the upcoming decades (as posed for non-limiting conditions: MENCUCINI & PIUSSI 1995). Apparently, hybrid larch still showed a distinct trade-off between reproductive and vegetative growth during the early eighties of the 20th century. As the extent of C autonomy during the growth of cones depends, besides the developmental stage, on light and temperature conditions (see above), the location of cones in the tree crown appears to be crucial. Consistent with hybrid larch, aggregations of cones were typically found in the sun-lit parts of crowns or forest canopies (DESPLAND & HOULE 1997, GREENE & al. 2002). Since the transpiration rate of larch cones was rather low in the absence of stomata, and the heat dissipation from cones may be reduced relative to that facilitated by small needle dimensions, low PPFD was already able to markedly raise the cone temperature above the temperature level of the ambient air. This appears to be disadvantageous, since the CO₂ refixation was reduced at high temperature (cf. Fig. 7). However, especially in the natural habitats of larch at polar and alpine timberlines (ELLENBERG 1996, HORIKAWA 1972, RICHARDS 1981), overheating may counteract, during cool periods, temperature inhibition of cone growth (cf. TRANQUILLINI 1979, KÖRNER 2003b).

The bud initiation of the reproductive organs is known to occur during the year preceding flowering (WARING & SCHLESINGER 1985), and species-specific climatic conditions are concluded to stimulate the initiation of cones (EIS & al. 1965). Hence, the coneless year of 1981 appears, in hybrid larch, to be a consequence of the cool and humid early summer of 1980 (MATYSSEK 1985), whereas after the warm summer of 1981, a substantial amount of reproductive buds did exist in 1982. Once cones and male flowers have been initiated, their further differentiation during the year of flowering may be driven by factors that are able to induce sinks for assimilates in the reproductive organs. Moderate drought conditions (EIS & al. 1965, WARING & SCHLESINGER 1985, SELAS & al. 2002) may lead, at reduced rates of phloem transport, to assimilate accumulation within the crown and, by this, favour such sinks. The latter once initiated in the reproductive organs then compete with the assimilate flux into, in particular, the tree organs farthest from the crown (ROOK & SWEET 1971, but see KÖRNER 2003a). Such a trade-off appears to be reflected in the reduced stem increment of 1980, when the total cone dry mass amounted to 25 % of the stem production (cf. Fig. 9).

Nevertheless, the reduction in stem growth during 1980 was not quantitatively explained by the reproductive C costs (cone mass plus estimated annual respiration) when compared with the ample stem increment during the coneless year of 1981. This may be due to the short experimental coverage of CO₂ refixation in this study and/or summer conditions, C gains and allocation that varied between the three observed years (cf. MENCUCINI & PIUSSI 1995). Remarkably, stem growth was similar in 1980 to that in 1982, although in the latter year only 10 % of the initiated cone number (which was similar to that in 1980) eventually reached maturation. Perhaps, cone respiration is rather high during early cone development (prior to pollination), as suggested by CHING & CHING 1962. If so, and if fuelled

from reserves, stem growth may stay limited during the later course of the season even after cone loss, if the refilling of such reserves created a strong sink for the current assimilate production relative to the sink strength of stem growth.

Since the male flowers of larch mainly appear prior to the needle flush in spring (MATYSSEK 1985), their sink induction for assimilates probably occurs during the preceding year. As indicated by the large radial stem increment in 1981 (cf. Fig. 1B), extensive male flowering as observed in 1982 appears to be favoured after conditions that are advantageous for biomass production during the preceding year. Ample yield in reproductive organs has also been reported from *Larix laricina* (POWELL & al. 1984). Nevertheless, the yield of cones and male flowers in hybrid larch largely exceeded that observed in the parent species, comparing trees of same age and at the same site. While hybrid larch carried 650 cones in 1980, it was less than 10 % of this number in neighbouring individuals of either parent species. In 1982, branches of 2 m length in hybrid larch did carry about 2000 male flowers, whereas the total number was less than 1500 in trees of the parent species. Characteristic distribution patterns along branch sections were found in male flowers (cf. Fig. 2) and cones which resembles observations in other conifers (CARON & POWELL 1993, CLARKE & MALCOLM 1998). Estimates of seed yield may be based on the number of developing cone buds (PHILIPSON 1997, in the absence of cone loss later in the season).

The extensive flowering in hybrid larch may be regarded as another expression of heterosis which is most evident in the rapidly growing, tall and thick stems relative to the parent species (SCHÖBER 1953, GÖTHE & SCHÖBER 1971). The increased annual C gain necessary as a pre-requisite of the ample stem growth in hybrid larch was found to be mediated through a "complementation principle" (SINHA & KHANNA 1975): high foliage density similar to *Larix decidua* in combination with a spacious crown architecture (based on extending branches) similar to *L. kaempferi* (MATYSSEK & SCHULZE 1987a,b). The annual C gain of hybrid larch appears to be high enough for ensuring ample reproductive yield. In addition, taking into account the potential trade-off between stem and cone production, sufficient C investments into the structure and transport capacity of the trunk can be afforded to meet the resource demands (water, nutrients) of the highly productive foliage. It appears that the facilitated high number of offspring may compensate for the phenomenon that in hybrid larch the capacity of stem heterosis is inherited only to variable extent (REEMTSMA, pers. comm.), perhaps representing another reason of mast years (cf. KELLY & SORK 2002). One has to keep in mind, of course, that individuals of hybrid larch typically are the result of selective plant breeding. The extraordinary cone yield which can be reached in hybrid larch emphasizes the alleviating role of cone photosynthesis (i.e. CO₂ refixation) within the whole-tree C balance.

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