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The Carbon Balance of European Larch (*Larix decidua*) at the Alpine Timberline

By

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Key words: Whole-tree carbon balance, carbon gain, respiration, allocation, storage, roots.

Summary

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The annual course of the carbon (C) balance of a 65-year-old larch tree (*Larix decidua* Mill.) growing at the timberline was determined, as based on continuous measurements of the net photosynthesis and dark respiration rate of sun and shade twigs, the stem and branch respiration rate and on assessments of the light and biomass distribution within the crown. Response curves of photosynthesis to light, temperature, and air humidity provided the basis for modelling net photosynthesis and dark respiration of the various crown parts. The dry matter increment of needles and radial stem growth were followed throughout the year, and newly formed stem, branch and coarse-root material was examined microscopically at the end of the growing season. Daily and seasonal C balances were calculated from the C gain, respiratory C release and dry matter increment of the various tree organs. The annual C gain by net photosynthesis of the whole tree was 12.19 kg (100%), with the needles (including foliated twigs) releasing 1.77 kgC (14.5 %) by dark respiration. 3.28 kgC (26.9 %) were invested into the annual increment of wood and bark in stem, branches, and coarse roots, with the annual respiration of these organs amounting altogether to 2.89 kgC (23.7 %). 0.88 kgC of the 1.95 kgC (16.0 %) invested into needles originated from C reserves. From November through mid-June, the period of a permanently negative C balance, 1.87 kgC (15 %) were supplied from reserves. Assuming new C storage similar to the amount used during the current year, a surplus of 2.30 kgC (19.0%) was calculated to cover the C demand of the fine roots. The C balance of larch at the timberline was compared with findings from other tree species and habitats. Annual C gain of trees from subalpine sites was lower in absolute terms but in relation to the C gain, allocation to aboveground woody organs was higher, while respiration per unit dry matter produced was lower than at low elevation sites. Besides temperature and length of growing season, the above-ground C demand of rapidly growing, light-demanding pioneer species is reflected in the C balance

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of larch relative to the late-successional, evergreen competitors even under harsh timberline conditions.

Introduction

Comparative ecophysiological field studies were conducted on trees of the deciduous conifer *Larix decidua* growing in different habitats, near Bayreuth at 450m a.s.l., at the Austrian timberline near Innsbruck at 1930m a.s.l., and outside its natural range along an altitudinal gradient in New Zealand (BENECKE & al. 1981). This comparison showed *Larix decidua* to respond in similar ways, after completion of foliage growth, to climatic influences regardless of the habitat, whereas the length of the growing season was crucial in determining productivity. Comprehensive studies at the Bayreuth site, including C balance, nutrition and water economy of *Larix decidua*, *L. kaempferi* and their hybrid, and of evergreen conifers, were published in several papers (MATYSSEK 1985a,b, 1986, MATYSSEK & SCHULZE 1987a,b, 1988, SCHULZE & al. 1985, OREN & al. 1986, MATYSSEK & BENECKE 2005). Regarding the Austrian timberline, the interrelations between annual wood increment and respiration of stem and branches have been outlined previously in relation to the site conditions and phenology (HAVRANEK 1985). The present paper completes the analysis of the C balance for the whole *Larix decidua* tree at the timberline.

Trees of the genus *Larix* are light-demanding and eventually outcompeted by shade-tolerant tree species (SCHÜTT & al. 1992, ELLENBERG 1996). In the open timberline forests, air and soil temperature as well as length of growing season rather than light are most decisive for growth (TRANQUILLINI 1979, KÖRNER 2003). Although rough estimations on the annual C balance of *Larix decidua* at the timberline were published by TRANQUILLINI & SCHÜTZ 1970, a detailed account that would quantify, throughout the whole year, C gains versus demands by growth and respiration of the various tree organs has been lacking so far. This deficit constrains interpretations of source-sink relationships (BAZZAZ 1997). As a deciduous tree, larch faces the particular challenge in resource turnover under harsh timberline conditions to completely renew its foliage each year (MATYSSEK 1986); however, interaction with reserve storage prior to and during the period of a positive C balance of the foliage to meet the metabolic demand of the other tree organs is still unknown. How do allometric relationships between green and non-green organs perform at the timberline, in terms of source *versus* sink strengths and in comparison with other site conditions, including altitude, and - in particular - evergreen conifer species (cf. GOWER & RICHARDS 1990)? The hypothesis is tested that even under harsh timberline conditions traits of carbon balance and allocation characteristic of pioneer species are apparent in deciduous larch relative to its late-successional, evergreen competitors.

Material and Methods

The annual C balance was investigated in a dominant 65-yr-old *Larix decidua* tree (8.2m tall, 16.6 cm d.b.h.) in the open subalpine *Pinus cembra*-*Larix decidua* forest at 1930 m a.s.l. on Mt. Patscherkofel (PK) near Innsbruck, Austria. Annual ring growth approached the potential maximum productivity at this site. Exposure was open to the south, whereas neighbouring *Pinus cembra* trees slightly cast shade from NE and NW. Soil was a podsol with a 15-20 cm humus layer on a wet, but well-aerated C horizon of weathered schist mixed with sand and clay. Climatic data for Mt. Patscherkofel are given in BENECKE & al. 1981 and HAVRANEK 1985.

Aluminium scaffolding provided access to the tree crown. Gas exchange was measured continuously for 12-14 days each month from May through September, and less frequently during winter. Radiation above-stand, air temperature and relative humidity were recorded continuously by a pyranometer and a standard thermo-hygrograph at the station Klimahaus 50 m apart. These data were transformed according to the climatic conditions measured in the tree crown and used for interpolating gas exchange between the measuring periods. In the sun crown, gas exchange was measured at 4 to 5 m aboveground with a climate-controlled cuvette system (Walz, Effeltrich, FRG) on south-facing unshaded twigs, which were changed by weekly intervals. The climate in the cuvette tracked ambient conditions. On a monthly basis, step changes of one out of the other climatic factors (which were kept constant) were performed in the cuvette to assess steady-state response curves in gas exchange (BENECKE & al. 1981, MATYSSEK & SCHULZE 1987a, 1988). Such experiments required the use of an artificial light source (Osram HQI-TS Powerstar 400W, 5200 K colour temperature). In the inner shade crown at 1.2 m aboveground, CO₂ gas exchange was measured with a non-climatized cuvette in the absence of needle overheating.

PAR was measured with PPFD sensors (LICOR) during summer days along a 0.4*0.4 m grid system in order to assess crown-internal light gradients. Assessments were averaged per unit of crown height. Light gradients and needle biomass were used for up-scaling daily net photosynthesis (P_n) and nightly respiration per unit of crown length, employing an empirical model of CO₂ assimilation. Model calculations were within ± 5% of measured P_n (MATYSSEK 1985a). Since twigs were used in gas exchange assessment, the respiration of the needle-bearing twigs and branches is included in "P_n" during daylight hours, and in "needle dark respiration" during the night.

Stem respiration rate was assessed by means of non-climatized clear perspex chambers that were sealed to the north-facing part of the stem at 1.2 and 4.6 m aboveground (covering a stem surface of 0.03 m² each). Branch respiration rate was measured at 3 m aboveground on two branch sections (23 mm diameter each; enclosure in clear perspex cuvettes) that were representative for the mean diameter of all living branches in the crown. Stem and branch respiration data were up-scaled to the crown level via the respective measured annual dry matter increments (DMI; further details see HAVRANEK 1985). Respiration of the root collar (16.0 kg DM) and the coarse roots (diameter >3 mm, total length 173 m, 19.9 kgDM) was calculated assuming the DMI-respiration relationship of the stem.

The daily C balance throughout the entire growing season of 1982 was calculated from the daily sums of P_n and the dark respiration of needles which included the respiration of needle-bearing parts of the branches, and from branch, stem and coarse root respiration. The daily increases in needle DM were interpolated from weekly measurements, but the daily DMI of the stem, coarse roots and the branches had to be estimated. Since respiration during the growing season (May - September) is strongly linked to the metabolic activity and is a reliable indicator of changes in radial growth and lignification processes (HAVRANEK 1981, 1985, MORI & HAGIHARA 1988), a linear relationship was assumed between respiration and DMI for calculations on a daily basis according to (1).

$$(1) \text{ Total respiration}_{\text{growing period}} / \text{Total DMI} = \text{daily respiration} / \text{daily DMI}.$$

To track the seasonal course of cambial activity and xylem cell growth, small cores from the vicinity of the respiration chambers were taken with a bone borer. The growth activity of the roots was not investigated.

The aboveground biomass of the tree was completely harvested during late September before needle-yellowing, and roots were excavated in October 1982. All branches were numbered and cut to 0.4m sections. To map the exact distribution of the biomass in the crown, all sections were divided into long-shoots, needles as well as living and dead branches. Branches were selected for exemplifying "specific leaf mass per area" (LMA, as needle dry mass per unit of total needle surface area) on each branch section, using the glass bead technique (THOMPSON & LEYTON 1971). Annual wood increment was measured microscopically from stem disks taken every 0.5m along stem height, from 360 random branch samples of all crown positions, as well as from 80 coarse-root samples of all diameter classes (bark increment being estimated from subsamples).

Results

Biomass data

Biomass data of the investigated *Larix decidua* tree at Mt. Patscherkofel (PK) were compared with *L. decidua*, *L. kaempferi* and *L. hybrid (decidua x kaempferi)* in Bayreuth (BT, Table 1). The data of the subalpine *L. decidua* were expressed as percent of the same species and of the hybrid larch at BT. The most striking differences between the two *L. decidua* trees were age and tree height, while lengths of the living crown were similar. During a longer growth period, *L. decidua* at BT was more productive (greater total length of branches, long-shoots, greater needle mass and area, net assimilation and annual DMI). However, DMI per unit of needle mass and net assimilation were higher in the timberline larch. Similarity between *L. decidua* trees growing at contrasting sites was greater than between *L. decidua* and the hybrid larch at the same site.

Phenology and growth

In 1982, the sum of daily mean air temperatures, after staying continuously above freezing point, reached 105°C by May, 24. This heat sum, similar to 1981, was necessary to initiate needle growth. Short-shoot needles reached 13% of their final area and dry mass by June 1. Until June 16, when long-shoots began to grow, the area of short-shoot needles had reached 90% of its final extension at the end of June. Extension growth of long-shoot needles was completed by mid-July, although lignification of long-shoots and bud growth continued. Long-shoot needles which had slightly enhanced LMA and net photosynthetic rates amounted only to 11 percent of the foliage mass so that their dry mass was pooled with that of the short-shoot needles (Table 2). Favourable weather conditions in spring and summer 1982 allowed a rather luxurious growth of needles and long-shoots, as compared to previous years (HAVRANEK 1985). Needles gradually turned yellow after October 5 and were shed during the second half of October. In 1982, only few male flowers and cones developed (cf. MATYSSEK & BENECKE 2005).

Table 1a. Biomass data of the experimental trees of *Larix decidua* at Mt. Patscherkofel, 1930m (PK), and near Bayreuth at 450m a.s.l. (BT), and of *L. kaempferi* (BT) and *L. hybrid* (*decidua* x *kaempferi*, BT) in the year of harvest, 1982. "Sapwood" marks the sapwood cross-section area at b.h.d, sapwood volume is related to the whole stem. Net assimilation (NA) is defined as net photosynthesis minus dark respiration. Dry matter increase of aboveground organs (DMIab) comprises long shoots, branches and stem but no needles (N). Growth period (days): from 5mm needle length until yellowing. Coarse roots: diameter >3mm.

1b. Carbon content of the biomass of the *L. decidua* tree at PK.

(a)	L.dec.PK	L.dec.BT	L.kae.BT	L.hyb.BT	PK:BTdec	PK:BT _{hyb}
Tree age, yrs	65	33	33	33	200%	200%
Tree height, m	8.2	15.3	16.2	19.8	54%	41%
Crown length, m	7.0	7.0	7.0	11.0	100%	64%
B.h.d., cm	16.6	15.8	17.4	26.1	105%	64%
Branches, m	1360	1750	2390	4210	78%	32%
Long-shoots, m	252	352	443	994	72%	25%
Sapwood, cm ²	97	88	79	185	110%	52%
Needles, kgC	1.95	2.55	2.40	4.90	76%	40%
N. area, m ²	104	124	124	243	84%	43%
LMA, g _{DM} , m ⁻²	37.5	41.1	38.7	40.3	91%	93%
NA., kgC	10.42	16.09	16.44	32.0	65%	33%
DMI stem, kgC	1.65	2.15	2.35	4.75	77%	35%
DMI ab, kgC	2.79	3.15	3.15	6.8	89%	41%
Growth period	136	170	170	170	80%	80%
DMIab/NA, gg ⁻¹	0.267	0.196	0.192	0.213	136%	125%
DMIab/N, gg ⁻¹	1.43	1.23	1.31	1.39	116%	103%
DMIstem/N, gg ⁻¹	0.84	0.84	0.98	0.97	100%	87%
Sapwood vol., m ³	0.04	0.10	--	--	--	--
(b)						
<i>L. decidua</i> -PK	Stem	Branches	Stump	Co-roots	Cones	Tot.biomass
(kgC)	25.42	12.31	8.00	9.95	0.42	58.1

Table 2. Seasonal course of total surface area and dry matter of pooled short- and long-shoot needles, given as percentages of the levels at tree harvest in mid-September.

Date	Needle area (%)	Needle DM (%)
May 25	1	5
June 01	13	13
04	33	24
13	75	53
19	86	68
25	92	78
July 01	95	85
10	98	91
20	100	97
31	100	100

The radial increment of the stem, which started with the formation of new phloem cells prior to the onset of xylem cell production at the beginning of June, peaked before mid-July and ended during the first days of September (cf. Fig. 8).

Stem respiration in general showed the same pattern but peaked later and lasted for a longer period, indicating high metabolic activity of the newly formed, still living cells (cf. HAVRANEK 1985). Cell-wall lignification of late-wood cells was still active when the tree was harvested in mid-September but was completed by the second week in October, as checked in neighbouring larches.

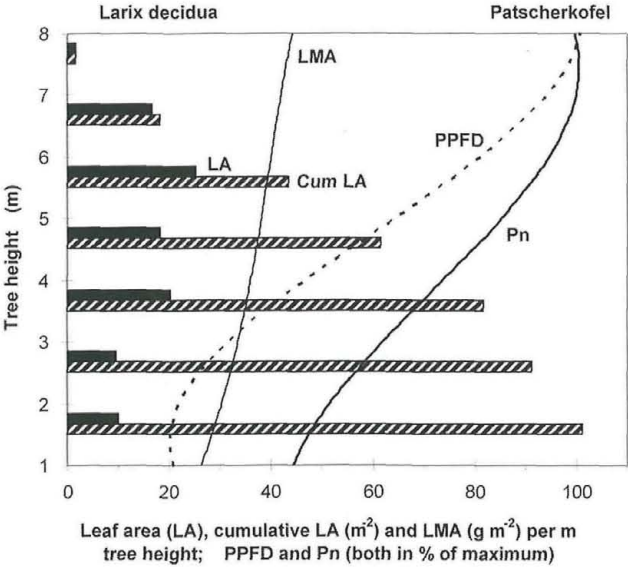


Fig. 1. The crown structure of the experimental larch tree. Distribution of the leaf area (LA) and the leaf mass per area (LMA, g m^{-2}) is shown for crown layers by one-meter intervals. From top to base of the tree (x), PPFD(y), LMA(y) and Pn (y) decreased according to the polynomial regressions: $y = -0.51x^3 + 7.31x^2 - 7.2x + 31.21$; $y = 0.039x^3 - 0.676x^2 + 5.81x + 21.06$; $y = -0.3x^3 + 3.42x^2 - 0.99x + 42.2$, respectively (for all $r^2=0.99$). LAI (total LA) = 8; LAI (projected LA) = 3.7.

Net photosynthesis and crown architecture

Along the vertical crown extension, PPFD positively correlated with LMA and with Pn/ m^2 (Fig. 1). As even the lowest branches in the open stand were sun-exposed, to some extent at least, mean PPFD within the first meter aboveground still approached 20% and Pn nearly 50% in relation to the respective levels under full sunlight. In the shaded inner part of the lower crown, where PPFD was only 10%, LMA was lowest (20g m^{-2}). On the contrary, LMA was twice as high under full sunlight at the top of the tree. During sunny summer days, maximum rates of Pn were between 3.4 and $3.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in sun needles and 2.0 - $2.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in shade needles. Maximal daily CO_2 uptake of sun needles reached 120 - 135

mmol CO₂ m⁻² d⁻¹ (5.3-5.9 g CO₂ m⁻² d⁻¹) and of shade needles 60 -70 mmol CO₂ m⁻² d⁻¹ (2.6-3.1 g CO₂ m⁻² d⁻¹).

The annual Pn of needles in the upper sun crown (528g CO₂ m⁻², 144g C m⁻²) was more than twice that of shade needles (235g CO₂ or 64g C m⁻²). This difference was smaller when Pn was based on needle DM: Sun needles produced about 12.3g CO₂ g⁻¹DM yr⁻¹ and shade needles 8.9g CO₂ g⁻¹DM. The high C gain between 3 and 7m aboveground, which approached 83% of the whole tree's gain, originated mainly from the large needle mass of this region (80% of foliage DM, and 77% of foliage area, being 104m²).

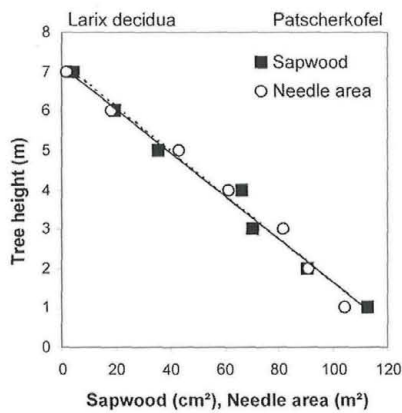


Fig. 2. The amount of needle area above any tree height correlates with the stem sapwood area at that cross section. On average 1 cm² sapwood supplies 1m² of total needle area.

Water relations during the growing season hardly limit production at the alpine timberline and are not presented here. The share of the sapwood cross-sectional area and, hence, the water conducting capacity in the stem indicate in comparison with the cumulative needle area, that about 1cm² of conducting sapwood area is available for the water transport per m² needle area (Fig. 2). Related to projected needle area, 1cm² sapwood area would supply about 0.47 m² LA.

C balance of the various crown layers

The annual net C gain is compared to the annual C demand for the crown layers by one-meter intervals in Fig. 3A. Demand comprises C for DM production of needles and new shoots, annual wood and bark increments of branches and the stem as well as respiration of these organs.

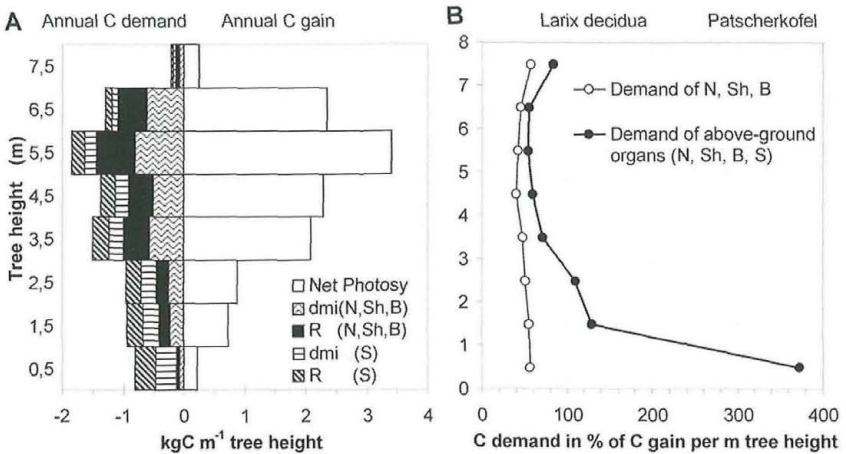


Fig. 3A. Annual net photosynthetic C gain is compared to the C demand for the crown layers by one-meter intervals. Demand comprises C for DM production (dmi) of needles (N) and long-shoots (Sh), annual wood and bark increments of branches (B) and the stem (S) as well as respiration (R) of these organs. 3B. The C demand of aboveground organs as a percentage of the C gain for the crown layers, without (○) and with the stem (●).

The C demand for DMI and respiration of needles, new shoots and branches, expressed as a percentage of the photosynthetic C gain was 40% in the middle of the crown and increased to 57% towards the upper and lower crown parts (Fig. 3B). Branches of the most productive crown layers between 3 and 7m above ground exported 56% of their C gain into the stem. 46% were exported from the top layer and the shade crown. Because the absolute contribution of shade branches was small, the mean C export of all branches into the stem amounted to 55% of their C gain. Balancing C gain versus C demand yields a surplus of carbon above 3m tree height but deficits below. 4.2kg, i.e. 40% of the total C produced above 3m height were translocated towards the stem base, with some proportion of this C flux being consumed by the stem below 3m height so that 27% of the C gain was left to cope with the C demand (growth and respiration) of the belowground organs (coarse and fine-roots, mycorrhizae).

Seasonal course of the daily C balance

During May, DMI and respiration fully depended on stored reserve material (Fig. 4). Beginning on June 5 (day 156), daily Pn began to exceed dark respiration and, hence, to contribute to the DMI of the needles. Nevertheless, the C balance of the whole tree remained permanently negative through mid-June, mainly because of the high C demand of the developing needles and the onset of cambial

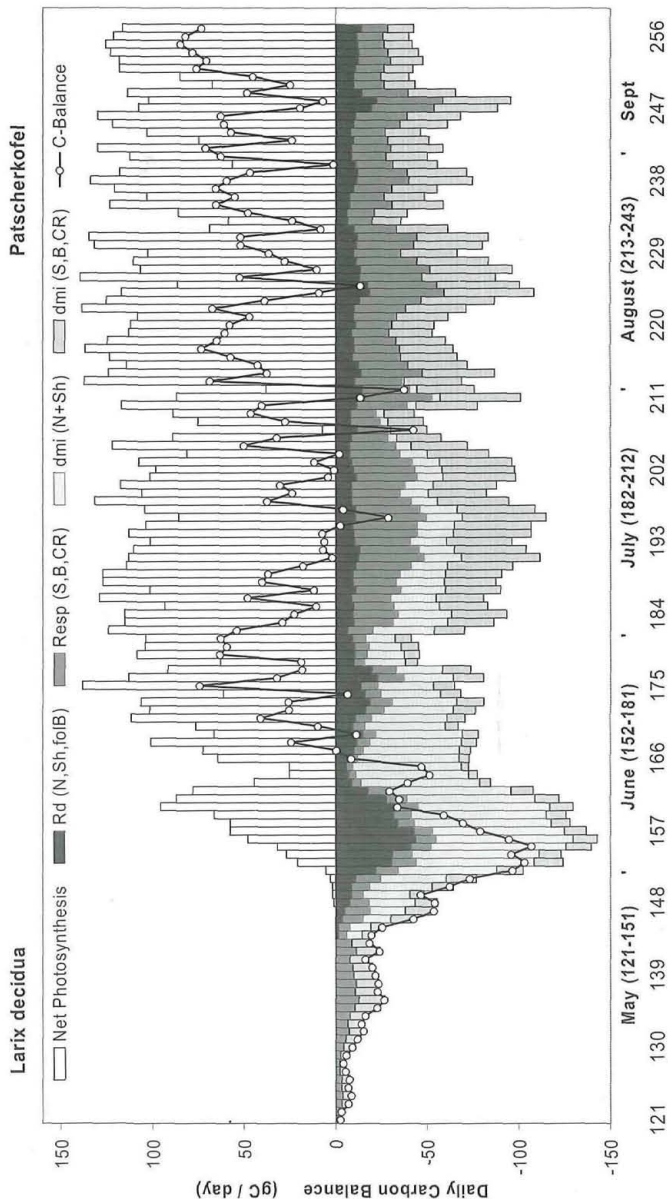


Fig. 4. Seasonal course of the daily C balance of the *L. decidua* tree. Daily C gain by net photosynthesis (Pn) is compared with daily C demand by dark respiration of needles, long-shoots, and foliated branches (N, Sh, folB), by the respiration of stem, the leafless parts of branches and the coarse roots ((S,B,CR), as well as by the daily dry matter increase (dmi) of needles, long shoots, stem, branches and coarse roots. During periods of a negative C- balance, C must be supplied from stored reserves, which should be refilled when balances were positive. Not included in this balance is the C demand for fine roots and mycorrhizae.

and phloem activity. From mid-June onwards, more C was produced than used so that contrasting with short-shoot needles the C demand of the newly growing long-shoots (flushing on June 16; day166) was entirely covered by the current Pn. In July, when the demand of needles and twigs decreased, the C consumption of branches, stem and coarse roots gained in importance. The intense DMI and respiration of these latter organs consumed the C-gain during this time of the year almost entirely (in particular, between July 10 and 23; days 191-204). In August, needle DW had ceased to increase. Although the C consumption of branches, stem and coarse roots continued at a rather high level, a considerable surplus of carbon was available for the belowground organs and storage. The surplus even increased in September, when sunny weather conditions still allowed high C gains in parallel to ceasing radial stem growth and lignification of the latewood cells. In early October, the C balance (Fig. 5) stayed positive, as needles gradually turned yellow upon early-frost episodes before being shed during the second half of October. Sporadic depressions occurred in the C balance during the seasonal course, being caused by frost, snow or rainfall events (days 165, 232) or low radiation (days 207, 212), or by high respiration during warm and cloudy days (196, 225, 248).

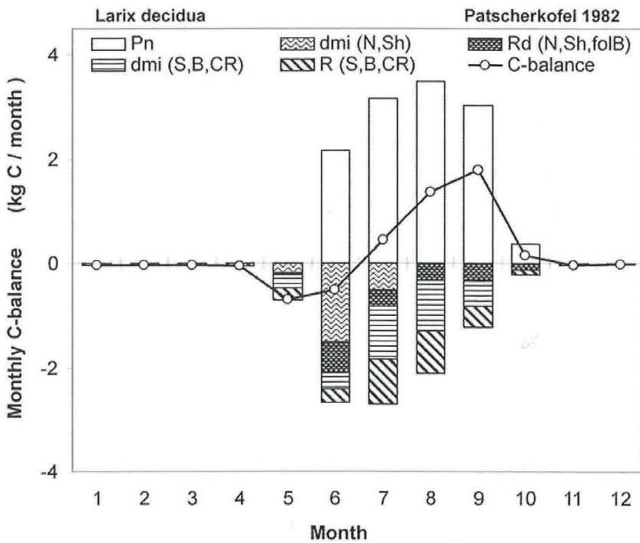


Fig. 5. Monthly C balance of *Larix decidua* at the timberline. Abbreviations as in Fig. 4.

During the leafless period from November 1981 through April 1982, the C release through maintenance respiration of twigs, branches, stem and coarse roots amounted to 0.22 kgC, which is only 1.8% of the annual C gain in 1982 (Fig. 5). A total of 1.87 kgC (15% of the annual C gain) was supplied from stored C reserves

to compensate for the respiration in winter as well as the new needle growth and cambial activity from May through mid-June (1.65 kgC), when the C balance was permanently negative. Not included in the balance are the negligible C amounts of the sparse male flowering in spring 1982. Also omitted were the cones (0.06 kgC) and their respiration which drew less than 1.0 % of the C gain in 1982 (adopting estimates by LINDER & TROENG 1981). Between mid-June and needle yellowing in October, the C balance yielded a total surplus of 4.17 kgC. Assuming new C storage similar to the amount used during the current year (i.e. 1.87 kgC), a surplus of 2.30 kgC (19.0%) was calculated to cover the C demand of the fine roots and mycorrhizae.

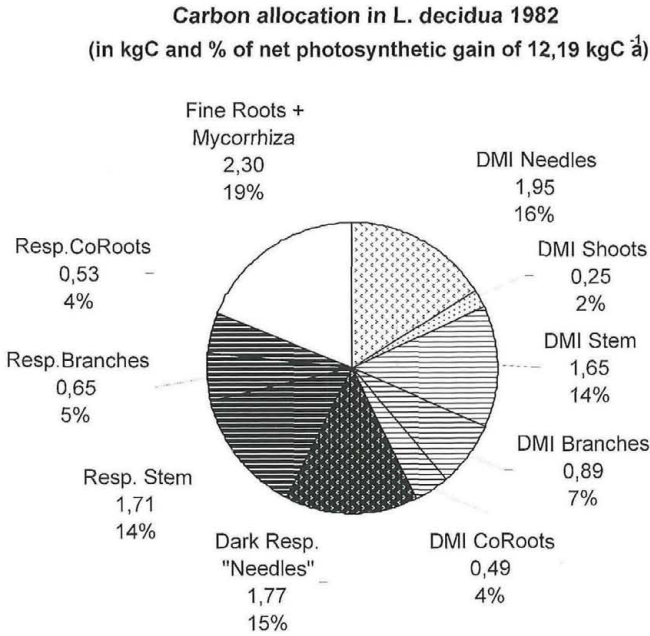


Fig. 6. The annual C allocation into dry matter (DMI) and respiration (Resp.) of the various parts of the larch tree in the year 1982.

Annual carbon allocation

In 1982, a total C gain of 12.19 kg was produced and allocated to the various tree organs (Fig. 6): A total of 1.95 kgC (16%) was invested into needle DM and 3.28 kgC (27%) into the annual wood and bark increments of the stem, branches (new shoots included) and coarse roots. For the respiration of all above-

ground parts and the coarse roots, a total of 4.66 kgC (38%) was used, leaving 2.30 kgC (19%) for fine roots and mycorrhizae.

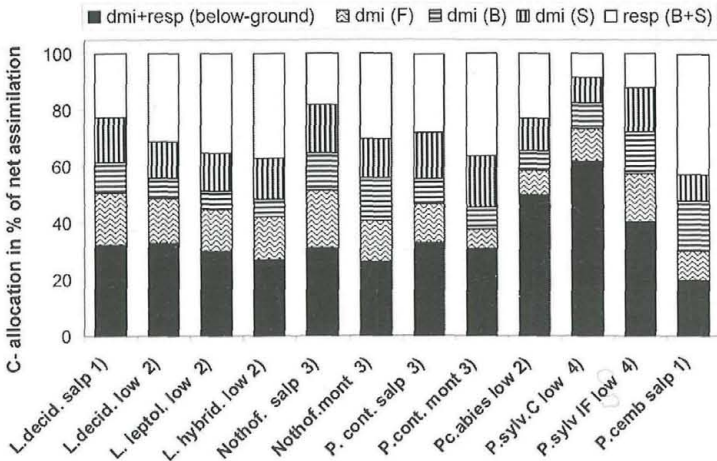


Fig. 7. Annual C allocation to belowground organs, to dry matter (dmi) and respiration (resp) of foliage (F), branches (B) and stems (S) as percentage of the net assimilation, for trees from subalpine (salp, 1320-1930m), montane (1000m) and low elevation (low, 185-450m) sites. (1) *Larix decidua*, Innsbruck (1930m); (2) *L. decidua*, *L. leptolepis*=*L. kaempferi* and *L. hybrid* (*decidua* x *kaempferi*), Bayreuth (ex MATYSSEK 1985, 1986); (3) *Pinus contorta*, ssp. *contorta* and *Nothofagus solandri*, var. *cliffortioides* (ex BENECKE & NORDMEYER 1982); *Pinus sylvestris*, C=control plot, IF = irrigated and fertilised plot, Central Sweden (ex LINDER & AXELSSON 1982).

Comparison between C balance of subalpine larch and other tree species

For reasons of comparability with C balances of other studies, C partitioning had to be related to "net assimilation", defined as the net photosynthetic C gain after subtraction of the needle dark respiration (Fig. 7). Annual C investment into foliage was greater in deciduous (15-20%) than in evergreen species (7-14%). C allocated to foliage and branches was 11-31% higher in trees of the same species at subalpine sites than at low elevation. By contrast, respiration of aboveground woody parts used 23-40% less carbon at subalpine than at low sites. The amount of C calculated for belowground organs was rather similar in all species (26-33%) except for spruce (50%) and pine in Sweden (62 % in control, 40% in the IF-stand). Variation in site characteristics relating to water and nutrient supply can change C allocation distinctly, as exemplified by *Pinus sylvestris* in Sweden. The respiration of aboveground woody parts relative to their DMI was low (40-47%) in these latter pine stands compared to other low elevation sites (mean 146% of DMI), and it was intermediate (mean 85% of DMI) in subalpine stands.

Discussion

Explaining the existence of given tree individuals, in particular, under harsh environments, in terms of a case study, and exploring complex, functional relationships within such trees with satisfactory precision, necessitates analytical focus on the scale of single trees with their intrinsic, ecologically relevant response patterns. Our larch tree was, at its given age, representative for the open timberline ecotone in the Austrian Central Alps with respect to biomass development, as reported by TRANQUILLINI & SCHÜTZ 1970 at the same site. However, weather conditions may modify tree responses between years even more distinctly than does individual variation between trees: In 1980 a very late bud burst occurred that shifted the growth period towards autumn when the fully active green needles were killed rapidly by a heavy frost event that prevented retranslocation of needle N. In 1981, a rather warm spring induced bud burst one month too early so that late-frost destroyed many needles and a large number of male flowers, cutting the needle mass of the tree in half as compared with the "average" year of 1982. Measurements of gas exchange on needles in 1981 revealed the same dependence of Pn and conductance on climatic variables as in 1982 (BENECKE & al. 1981), but the DMI of stem, branches and coarse roots was only about 50% of that in 1982, mainly according to the reduced needle mass, as weather conditions were similar in both growing seasons. Such a pronounced, inter-annual variability would not be compensated for statistically even if working with a large sample size of trees.

Overviews on the growth and the carbon balance of trees at the timberline are given by TRANQUILLINI 1979 and KÖRNER 2003. The ratio of leaf mass versus total plant mass is difficult to interpret. Tree age doubtlessly plays an important role but there are also typical changes that relate to the altitude. The needle mass of our 65-year-old *Larix decidua* was 3% (1.5% in 1981) of the total plant mass and 7% in 23-year-old larch (BERNOULLI & KÖRNER 1999), both growing at the alpine timberline. 33-year-old European larch near Bayreuth (450m a.s.l.) with a similar length of the living crown as our larch, bore 5% needles, but the stem length was twice that of the PK tree, yet without foliage up to 8 m height (Table 2). The DW ratio of branches to stem also increases with altitude, leading to increasingly shorter stems. The BT larches grew in a closed forest, and branches of the lowest shade crown below 8 m height died due to light deficiency (<15% of full sunlight, MATYSSEK 1985a, MATYSSEK & SCHULZE 1988), whereas branches of the PK-larch reached almost the ground where the mean radiation was still about 20%. Under a dense stand in NZ only 5 % of full sun light was reported (TURTON 1982). The lowest mean PPFD measured in the lower inner crown of the timberline larch was 10%, presenting obviously the limit, where small branches already died, and the inner sections of large branches were leafless. However, it should be mentioned here, that in the dense part of the subalpine forest, larches existed that were shaped similarly to those growing in BT. In competition for light with Norway spruce and cembra pine, these larches possess only a small living crown of 2-3m on top of thin stems with minor annual ring growth, having lost all branches of the shaded lower crown up to a stem height of 8-10m. The C balance of such light-limited

subalpine larch trees has not been investigated yet. Our biomass analysis (cf. Table 2) confirms the annual increase in the length of the leader and the long-shoots to be a key quantity for growth (and for success in the competition for light).

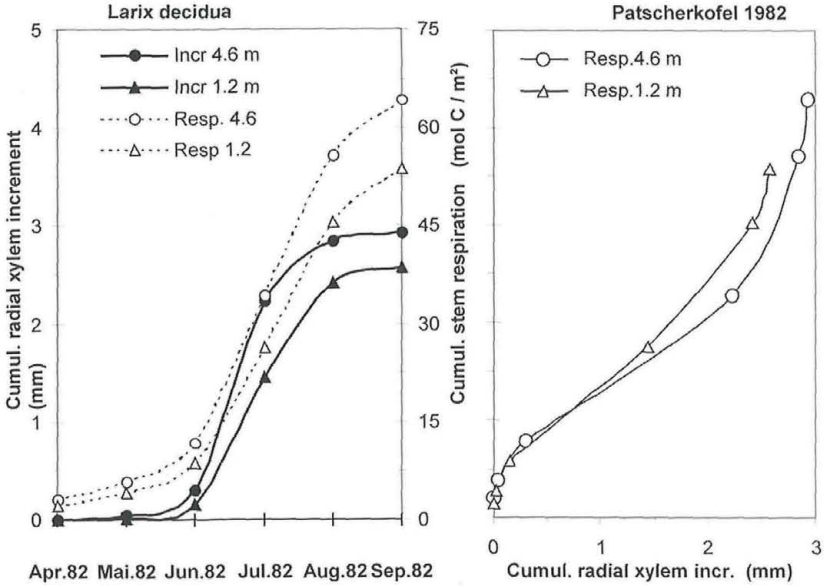


Fig. 8. Left: Course of the cumulative radial xylem increment and the cumulative stem respiration at the positions of the respiration cuvettes, at 1.2m and 4.6m stem height. Right: Total stem respiration vs. radial xylem increment. The higher stem respiration per xylem increment is caused by the greater sapwood depth at 1.2 m height.

Although the sums of the annual net assimilation of the *L. decidua* trees at 450 m and 1930 m were expectedly quite different due to the length of the growth periods, the C allocation to the various tree organs in proportion of the annual C-gain was similar in all studied larches (cf. Fig. 7) However, the same tendency as in the long-term biomass distribution mentioned above, was also visible in the annual C allocation, namely that at the timberline a higher percentage of C was allocated to foliage, branches and the stem. On the contrary, the share of C used for respiration was considerably smaller than at low altitude. In other words, DM production of aboveground woody organs seems to be more economic at the timberline, because less C is respired per g DMI. Why do trees that grow larger and faster at low altitude, respire relatively more C than trees at the timberline? Is this a tribute to higher "maintenance costs" along longer stems or/and due to the higher temperatures? If the temperature-independent respiratory costs for the conversion of as-

similates into new structures are similar, it appears that the maintenance respiration must be higher. The maintenance costs are thought to stem from the temperature dependent cell metabolism of the living stem tissue, mainly ray parenchyma in the sapwood and in the phloem (cf. STOCKFORS & LINDER 1998).

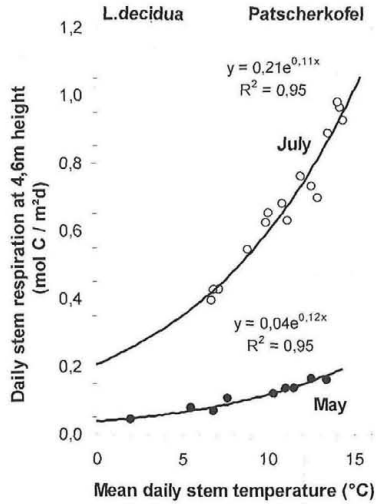


Fig. 9. Relation between the daily sums of stem respiration and the daily mean stem temperatures in May and July 1982. Q10 between 5 and 15°C was 3.2 in May and 2.9 in July.

As demonstrated in this study, distinct differences existed in the seasonal courses of radial xylem increment and stem respiration (Fig. 8). It should be emphasized that radial xylem increment peaks earlier than stem respiration, the latter exhibiting high metabolic activity until September both at the timberline and the low elevation site (cf. HAVRANEK 1985, MATYSSEK & SCHULZE 1988). At the timberline the cambium was dormant until mid-May and only few phloem cells were produced towards the end of May. Xylem growth started in June and peaked in July. During May, most of the stem respiration should therefore be R_m , whereas in July, at a given temperature, stem respiration was much higher due to the high metabolic demand of the intensive growth (Fig. 9).

At any stem temperature, the May values were about 20 % of the July values indicating roughly the temperature-dependent R_m rate. For the whole year, R_m of the 8m-stem was 0.512 gC (or 12.8 kgC m⁻³ sap wood), which makes about 30 % of the total annual stem respiration. For comparison, R_m should have amounted to at least 1.28 kgC in *L. decidua* at low elevation (BT), as based on the sapwood volume of ca. 0.1m³ along the 15m long stem. Taking into account higher summer

temperatures and a milder winter at BT, R_m may amount to more than 40 % of the total stem respiration (of 3.4 kgC a^{-1}).

The calculated seasonal course of the daily C-balance of the PK larch allows a rather exact balance for the whole tree, being aware, however, of uncertainty in time and space regarding the proportion of DWI of the stem in relation to its respiration rate. A great fraction of respiration may be located in the phloem (cf. STOCKFORS & LINDER 1998) where functional sieve cells occupy a wide band in *Larix* during summer (SCHMITZ & SCHNEIDER 1989), but where only mature phloem elements that were formed early in the season translocated ^{14}C assimilate in June. Transport and metabolism of sucrose, the main transport form in larch (SCHNEIDER & SCHMITZ 1989), and of proteins, from and into sieve cells are associated with intense respiration (SAUTER & BRAUN 1972). Across the contact of sieve elements with phloem rays not only the substrate for the cambial growth but also uptake during mobilisation from rays, and deposition of reserve material (WETZEL & GREENWOOD 1989) into the rays, needs to be managed. Strasburger cells represent those specialised phloem ray cells that are in direct contact with sieve cells, and show high metabolic activity in longitudinal and radial transport of assimilates in *Larix* (SAUTER 1982).

Concerning the C-balance of the PK larch, locations and size of the tree's storage capacity remains a black box. Root growth was reported to start slightly earlier than shoot growth in young larch at the timberline (HÄSLER & al. 1999), powered at least initially by reserve material, and maximum root growth occurred in summer when soil temperatures were highest. If this also applies to the adult PK larch, fine roots would compete for carbon at the time of the highest overall C demand. In 5-yr-old larch at low elevation, ^{14}C -experiments revealed that radiocarbon moved basipetally into the roots at all times between April and September, particularly in spring and late summer with a velocity of $10\text{--}20 \text{ cm h}^{-1}$ (SCHNEIDER & SCHMITZ 1989), a speed similar to that calculated for basipetal phloem sap movement in 45-yr-old *Pinus sylvestris* by MÜNCH 1930. Assuming a similar transport velocity for the PK larch would translocate C from the top to the roots within 50 to 100 hrs. Sucrose from the base of the crown could arrive in roots within a day.

Highest priorities within C allocation typically have buds, new foliage and new roots, followed by storage tissue and diameter growth (cf. WARING & SCHLESINGER 1985). This seems to be true also in larch. Besides light limitation mentioned above, also stress caused by low soil temperature seems to allocate C primarily into needles and roots leaving little for the stem diameter to increase. According to KAJIMOTO & al. 1999, old *Larix gmelinii* growing on permafrost soils in Central Siberia allocates annual C gain largely into needle production (56% of total NPP) and roots (27%) at the expense of aboveground woody parts (17%). In our PK-larch 30% of the annual DMI was allocated to the needles, estimated 26% to fine and coarse roots and 44% to the aboveground woody organs. So far no data of larch were available to be compared with *Pinus cembra* and *P. montana* afforested at extreme subalpine sites in Switzerland (TURNER & al. 1982). On the colder N-exposed slope with less radiation, total dry matter of *P. cembra* and *P. montana* was 60% and 31%, respectively, of the plants growing on the warmer E-slope.

However, C-allocation to the various organs seems to be very conservative in these species with little difference between both sites, indicating a balance between C source and sinks. SAIKKONEN & al. 1999 report a similar relationship when defoliation of *P. sylvestris* (except current foliage) did not alter the ratios of produced needle biomass to the biomass of fine roots or living fungi in fine roots. These outcomes were considered as a functional balance between C sources in plant foliage and belowground sinks (growing roots and mycorrhizae).

In the case of our well-growing timberline larch, surplus C production may have been poor in the growth period 1980, as mentioned above. Nevertheless, in the following warm spring of 1981 a great number of male flowers were produced and, along with needle destruction by late-frost, needle mass was cut in half of that in 1982. Diameter growth of stem, branches and coarse roots was proportionally reduced with the needle mass in 1981, but again no signs of low storage reserves could be detected, concerning the supply of the new foliage in 1982. However, for extreme subalpine sites a distinct reduction of the tree ring-width in young *L. decidua* was reported for years following harsh autumn conditions in the previous year (TURNER & SCHÖNENBERGER 1981). From the seasonal course of the C balance one would expect that autumn is indeed a very important period for surplus production and probably bud initiation in larch.

In conclusion, besides temperature and length of growing season, the aboveground C demand which appears to be characteristic of a rapidly growing, light-demanding pioneer species determines the C balance and allocation of larch relative to the late-successional, evergreen competitors even under timberline conditions- indicating confirmation of the hypothesis posed at the beginning.

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