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Potential negative effects of atmospheric CO₂-enrichment on insect communities in the canopy of a mature deciduous forest in Switzerland.

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Since atmospheric CO₂-enrichment has been shown to affect leaf tissue quality, changes in the consumer community can be expected. In this paper I report data of the impact of whole forest canopy CO₂-enrichment in a mature deciduous forest near Basel on the canopy arthropod fauna. I compared the abundance, species richness and guild composition of arthropods in the canopy of beech (*Fagus sylvatica*) and oak (*Quercus petraea*) under different CO₂-treatments. Crown-inhabiting insects were collected with the beating tray method from the gondola of a 45 m tall forest canopy crane. A total of 1253 arthropods (1155 of them insects) in at least 59 morphospecies were found which belong to five different feeding guilds. Heteroptera (bugs, 31%), Coleoptera (beetles, 24%) and Auchenorrhyncha (cicadas, 18%) were the largest taxonomic groups. On both tree species there was a significant decrease of the insect diversity under elevated CO₂. This reduction might result from shifts in the composition of the feeding guilds: chewing phytophagous (on beech) and sap-sucking insects (on oak) profited over-proportionally from CO₂-enrichment. Guild composition (percentage of chewing phytophagous insects) correlated with plant quality data (specific leaf area SLA, content of non structural carbohydrates NSC). I conclude that the atmospheric CO₂ increase will affect forest canopy insect diversity, and is likely to change the insect impact on forests too.

Keywords: Diversity, morphospecies, feeding guilds, carbon dioxide, global change, *Fagus*, *Quercus*.

INTRODUCTION

The ongoing enrichment of the atmosphere with CO₂ will not only affect the climate system but will also influence the biosphere directly via its consequences for plant photosynthesis. There is a rich literature which documents that plant photosynthetic stimulation will translate into enhanced plant growth when resources other than carbon are non-limiting (Körner 2000). In all other cases plants get carbon enriched and nutrient depleted (Ceulemans et al. 1999), causing plant products to lose attractiveness for many plant consumers (Körner 2000). Higher concentration of carbon-based allochemicals and increases in leaf toughness have also been observed (Lindroth et al. 1993).

Most of these tests were made with juvenile plants mainly in controlled environments. Therefore little is known about such changes in natural plant communities and mature forests in particular. Given that forests represent more than 80% of the terrestrial global biomass carbon pool, this is a severe gap in our understanding.

Insects are one of most dominant and important players in all terrestrial ecosystems (Zwölfer 1999). They are not only the most important herbivores, but have

key roles as pollinators and parasites or parasitoids of potential pest species. Via its effect on plants, the increase of the atmospheric CO₂ concentration within the last 200 years (from 280 to 365 µmol mol⁻¹) is very likely to exert influences on animals in a direct way. Associated with differential CO₂ responses of plants, some animal species could even lose their host species in the long run.

Different animal species and developmental stages will have different abilities to cope with the new conditions. Host specific species may be more affected than generalists and winged and mobile adults can more easily escape than juveniles (Coviella & Trumble 1999). Whole feeding guilds (e.g. sap suckers versus leaf-chewers) could be influenced in different ways, some may win and some may lose. Clearly this is of great importance for local and global biodiversity and conservation (Coviella & Trumble 1999). Insects are representing up to 80% of all animal species on earth and therefore even small changes could decrease the biodiversity significantly. On the other hand, insects have a very short generation time, which may allow rapid evolutionary adaptation.

In my study, I investigated the abundance of crown inhabiting insects in the crowns of mature deciduous forest trees in a natural forest, part of which received artificial CO₂-enrichment. I compared insect diversity and the feeding guild responses in two tree species (beech and oak) under ambient and elevated CO₂. I expected different species as well as different feeding guilds to respond differentially to the new conditions leading to a reduction in diversity. I also explored whether some of the community changes correlated with leaf quality parameters.

MATERIAL AND METHODS

The experimental forest is located in Hofstetten, 15 km south of Basel, Switzerland (47° 28' N, 7° 30' E; 550 m asl). The forest belongs to the study area of the Swiss Canopy Crane Project. The investigated trees are 80–120 years old beeches (*Fagus sylvatica* [L.]) and oaks (*Quercus petraea* [L.]), with heights between 30 and 36 m. Companion species are *Carpinus betulus* (L.), *Tilia platyphyllos* (L.), *Acer campestre* (L.), *Prunus avium* (L.) and some conifers (*Larix decidua* [Mill.], *Picea abies* [L.], *Pinus sylvestris* [L.] and *Abies alba* [Mill.]).

14 trees from different species are exposed to elevated CO₂ with the web-FACE method, simulating future atmospheric conditions (Pepin & Körner 2002). This new method is based on a web of thin plastic tubes woven into the crown of the trees (300 to 1000 m tubing per tree), which emit pure CO₂ through tiny pores during daylight hours. The CO₂-release is controlled by a computer in connection with a 25-channel infrared gas analyzer (IRGA). Within the upper crown of CO₂-treated trees, the daily mean concentration of CO₂ in the air is between 526 and 566 µmol mol⁻¹. The treatment started in September 2000 and was interrupted between end of October and mid April, when deciduous trees have no green leaves.

I collected insects on beech and oak trees under ambient CO₂ (365 µmol mol⁻¹) and elevated CO₂ (ca. 540 µmol mol⁻¹). With the help of a crane of 45 m height, I had gondola access to every position of the trees. On six different days (21. 05. 01, 13. 06. 01, 03. 07. 01, 06. 05. 02, 08. 05. 02, 15. 05. 02) I sampled the crowns of all test trees as follows: I chose four different branches per tree (exposed to direct sunlight) in the upper part of the crown and collected insects with a modified beating tray method (Piechocki & Händel 1996). While I held a square fabric-frame (60x60 cm) underneath the branch, I shook the branch three times in a standardized way. Because of risk of damaging the branches, I could not beat with a stick. In

2001, three beeches and three oaks under ambient CO₂ and three beeches and three oaks under elevated CO₂ were sampled, in 2002 there were four trees in each treatment (because of a lack of CO₂-treated trees, on the largest CO₂-treated beech and oak two different sites were sampled and taken as two independent samplings). Every time the collection was balanced, so that an equal number of samples per tree species and CO₂-treatment are collected.

All arthropods (insects and spiders) that fell in the collecting frame were preserved in alcohol for later determination. I always pooled the four branch samples of a tree in one tube. Samples were taken on warm, more or less sunny days without precipitation or strong wind.

In the lab I determined the arthropods with the help of a stereomicroscope as precise as possible (if possible, species, genus or family level, at least order level, after Hannemann et al. 2000) and classified them as different morphospecies. I also classified all animals into five different feeding guilds that were chewing phytophagous insects (leaf chewers), sap-sucking phytophagous insects (phloem- and xylem-feeders), carnivorous insects (predators), parasites/parasitoids and omnivorous insects after Moran & Southwood (1982), modified.

Leaf data such as % nitrogen, non structural carbohydrates (NSC in % per dry mass and in g m⁻²) and specific leaf area (SLA in dm²g⁻¹ d.m.) were collected during the summer 2002 and analysed using standard methods as described in Körner & Miglietta (1994). These data will be published in detail elsewhere, but are used here to test possible correlations with insect responses.

For statistical analysis, the diversity of insect species (Shannon-Weaver-index, H_s) was determined for each tree species and CO₂-treatment. Diversities between the different treatments were compared with a modified t-test for this purpose (the variance and the degrees of freedom of each H_s are approximated; Hutcheson 1970). The abundance of individuals and species belonging to the different feeding guilds per tree and day and differences between the CO₂-treatment were compared with the Mann-Whitney-U test. Leaf traits were correlated with guild composition and species diversity with a linear regression.

RESULTS

Overall diversity

In total, I collected 1253 arthropods (1155 insects and 98 spiders) of 59 different morphospecies in the two seasons (Tab. 1). All spiders were grouped into one single "morphospecies" and were treated in the evaluation as if they were one carnivorous insect morphospecies. This was done because many juvenile stages are difficult to determine. In comparing individuals, Heteroptera (bugs; 31%) were the most prominent group, followed by the Coleoptera (beetles; 24%) and the Auchenorrhyncha (cicadas; 18%). The different morphospecies included very different numbers of individuals. Exactly 50% of all collected individuals belonged to the five most frequent morphospecies. In the following these were named morphospecies: Curculionidae A, Heteroptera C, Araneae, Miridae A and Cicadellidae C (Tab. 1). The twelve most frequent morphospecies still amounted to 74% of all individuals. 39 morphospecies contributed less individuals than 1% of the total.

The diversity (Shannon-Weaver-Index H_s) of the insects decreased under elevated CO₂ on both tree species (Fig. 1). On beech this decrease was highly signifi-

Tab. 1. Number of collected insects (morphospecies). F.s. *Fagus* (beech), Q.p. *Quercus* (oak); A, ambient CO₂-concentration, E, elevated CO₂-concentration.

Order	Morphospecies	year 2001				year 2002			
		F.s.A	F.s.E	Q.p.A	Q.p.E	F.s.A	F.s.E	Q.p.A	Q.p.E
Neuroptera	<i>Chrysopa</i> sp.			1		1	1		1
	Neuroptera A	1							
Ensifera	Ensifera	1		2	1			1	
Raphidioptera	Raphidioptera			1	1				
Sternorrhyncha	Aphidina	28	28		1	6		3	1
Auchenorrhyncha	Auchenorrhyncha A					3	4	30	7
	Auchenorrhyncha B					4		3	8
	Cicadellidae A	19	12	28	17				
	Cicadellidae B		1	10	4				
	Cicadellidae C	11		21	49				
Heteroptera	Heteroptera A					1	2	1	7
	Heteroptera B					1		8	10
	Heteroptera C					9	3	44	43
	Heteroptera D					7	9	2	10
	Heteroptera E						1		3
	Heteroptera F					1	1	7	18
	Heteroptera G						3	10	33
	Anthocoridae						1	1	
	Miridae A	8	4	42	38				
	Miridae B		12	16	6				
	Miridae C			8	2				
	Coreidae	1		1					
	Pentatomidae					3	1	3	2
	Acanthosomidae	1							
Coleoptera	Curculionidae A	31	15	5	7	14	188	2	
	Curculionidae B			1				1	
	Curculionidae C								3
	Curculionidae D						1		
	<i>Curculio</i> sp.			3	1				
	Agrilinae					3	1	4	2
	<i>Agrilus</i> sp.			1	1				
	Coccinellidae	1		1					
	<i>Adalia decempunctata</i>				1				
	<i>T. sedecimpunctata</i>					2		4	6
	Staphylinidae				2				
	Anthribidae				1				
Hymenoptera	Tenthredinidae A	1	1	9	5	2	1	2	3
	Tenthredinidae B							1	
	Tenthredinidae C							1	2
	Formicidae			16	5				
	Parasitica			1	1				
	Chalcidoidea A	1	1	1	1		9	3	
	Chalcidoidea B	1		1	1				
	Chalcidoidea C			1					
	Braconidae A	2				1		4	
	Braconidae B							2	
	Chrysididae							1	
Lepidoptera	Geometridae	2		1		1			
	Lepidoptera A		1					1	1
	Lepidoptera B							2	1
	Noctuidae								1
	Gracillariidae					1		2	
Diptera	Diptera A	3			3	5	1	3	15
	Diptera B				2	3		1	3
	Diptera C				1			5	2
	Diptera D					3	2	4	2
	Diptera E							2	2
	Diptera F							1	1
Araneae	Araneae	12	10	4	2	19	14	20	17
Total per tree species and CO₂-treatm.		124	85	175	153	90	243	179	204
Total per tree species (A + E)		F.s. =	209	Q.p. =	328	F.s. =	333	Q.p. =	383

cant in both years (2001 and 2002). On oak the decrease was only marginally significant in 2001 and not significant in 2002.

Feeding guild responses

In 2002, the numerical size of the five different feeding guilds depended on the tree species and the CO₂-treatment (because of a slightly different sampling design, the data from 2001 could not be analyzed in this way). Chewing phytophagous insects were the most abundant group on beech (totally 67% of all individuals) in 2002, and this difference increased significantly under elevated CO₂ (Mann-Whitney-U tests, $p = 0.0023$). On oak, sap-sucking insects were most abundant (66% of all individuals) and they also profited from CO₂-enrichment (marginally significant, $p = 0.081$). In contrast, the number of chewing phytophagous insect individuals significantly decreased on oak under elevated CO₂ ($p = 0.043$).

When the proportions of the different guilds per tree were compared with leaf quality data, two significant correlations could be found: On oak the proportion of chewing phytophagous insect individuals per tree is positively correlated with the SLA (Fig. 2) and negatively correlated with the concentration of NSC (Fig. 3). Both correlations are no longer significant after a Bonferroni-correction.

DISCUSSION

Overall diversity

It is not surprising that almost all of the collected arthropods were insects. Their dominance both in number of species and individuals in the canopy fauna had been demonstrated several times (e.g. Moran & Southwood 1982). Because the aim here was not to classify all the individuals to species level, the number of 59 morphospecies underestimates the actual species number by far. Particularly in Hymenoptera, Heteroptera, Auchenorrhyncha and Diptera several taxonomically different species were grouped in one morphospecies. One reason for this was the large number of individuals found in larval stages, where a determination is often more difficult than in adults. The composition of the morphospecies and their relative frequencies shows very clearly that only few species are highly abundant, while most of the species are rare. Hence, these “rare” species contribute much to the species diversity. This is important, when changes due to elevated CO₂ are considered. Most of the collected insects were herbivorous insects (leaf chewers or plant-sap suckers). The sampling method excludes leaf miners. This sampling effect is also reflected in the representation of orders: typically plant associated orders as Auchenorrhyncha, Heteroptera or Coleoptera have a strong weight. Under elevated CO₂ mutual relationships between plants and plant feeding insects may become more pronounced. CO₂-dependent abundance changes in one group can provoke changes in other groups. So plants will effect insects and insects effect plants.

The most interesting result of this study was the finding that the insect species diversity on trees decreases under elevated CO₂ (Fig. 1). The reduction was found in both years and on both tree species and might be the direct consequence of shifts in the prominence of certain feeding guilds. The reduction was more pronounced in the second year of treatment in 2002 than in 2001. A cause of these shifts may be the disproportional increase of chewing phytophagous insects on beech and the in-

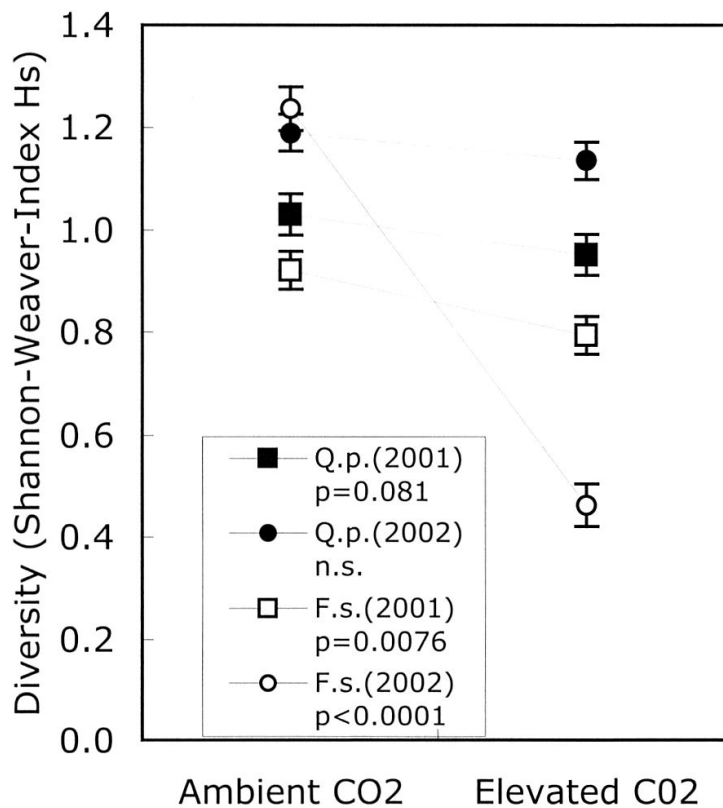


Fig. 1. Insect-diversity (H of morphospecies \pm s.d.) on oak (*Quercus*, Q.p.) and beech (*Fagus*, F.s.) under different CO_2 -levels (ambient and elevated) for two sampling years.

crease of sap-sucking insects on oak under elevated CO_2 in the year 2002. In both cases, numerically already leading morphospecies profit, suggesting that the most abundant herbivores become more abundant under this atmospheric change. It is possible that more mobile insects moved to other host plants. If true, real differences would be flattened, but this could be attributed to the isolated nature of CO_2 -enrichment and would not be an option in a CO_2 -rich world. Since my collections in 2002 started very early in the season, they covered a lot of still non-winged and non-mobile larval stages. This might explain the stronger signal in 2002 than in 2001. Another reason for this phenomenon might be that in 2002 community effects had already passed through initial adjustments. Most insects collected in 2001 had been “placed” by their parents as eggs on substrate that had not experienced season-long CO_2 -enrichment. So direct influences of elevated CO_2 or CO_2 -mediated effects via plants in this season were important. In 2002, however, parental substrate preferences during 2001 for egg deposition became important. Brooks & Whittaker (1998) showed such generation effects in changes within life histories of insects, where egg number and weight as well as larval weight of a beetle species on *Rumex obtusifolius* decreased after two or three subsequent generations under elevated CO_2 .

Feeding guild responses

The more pronounced reduction of insect diversity on beech than on oak is not easy to explain. On oak, insects may face different constraints than on beech. For example, oaks have a higher content of tannic compounds, tougher leaves and the leaves contain more lignin and cellulose, clearly not an ideal diet (e.g. Schütt et al. 1994–2003). If the plants reacted to CO_2 -enrichment in a way, that their tissue

quality becomes more “oak-like”, sap-sucking insects may be better adapted to this, since they are used to high C:N ratios. They might be pre-adapted to such a change in food quality which thus, leads to less marked effects. Unfortunately we have no phloem sap data to substantiate this. Negative consequences for the trees could include an increase of microbial diseases often transmitted by sap-sucking insects. On beech, leaf chewers are more prominent. They consume complete leaf tissue and do not select or avoid certain tissue fractions. This means that they should be more sensitive to changes of total leaf composition. Nevertheless, chewing phytophagous insects also profited under enhanced CO₂, but this was due to a huge increase of one single curculionid species.

Guild composition changes due to elevated CO₂ may also have been more pronounced in 2002, because of the shorter observation period of two weeks. In 2001, collections were made over a period of six weeks. Over a 6-week period insect fauna changes by natural phenology may override CO₂-effects.

Possible plant tissue influence and predictions

Only on oak correlations between feeding guilds and leaf tissue data could be found: the percentage of chewing phytophagous insects per tree is positively correlated with the specific leaf area (SLA; Fig. 2) and negatively correlated with the concentration of non structural carbohydrates (NSC; Fig. 3). Obviously, a lower SLA

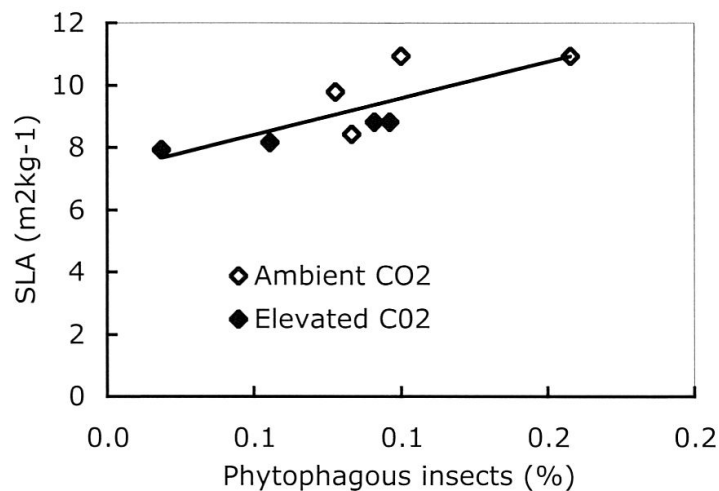


Fig. 2. The relationship between the average percentage of phytophagous insects per tree and specific leaf area (SLA) of oak (*Quercus*; $p = 0.023$). A, ambient and E, elevated CO₂; data for 2002.

(commonly this means “tougher” leaves) is unattractive for chewing insects and they decrease (or change hosts). For sap-sucking species the change in SLA does not affect their food quality. Lower SLA was expected and found under high CO₂-concentrations, which should have exerted a direct influence on guild composition. For the negative correlation between the percentage of chewing phytophagous insects and NSC concentration, I did not find a satisfying explanation. It should be noted that all correlations are no longer significant under a Bonferroni-correction. So their significance could be also an artefact and they should be viewed rather as a trend. Future investigations should focus on such possible relationships.

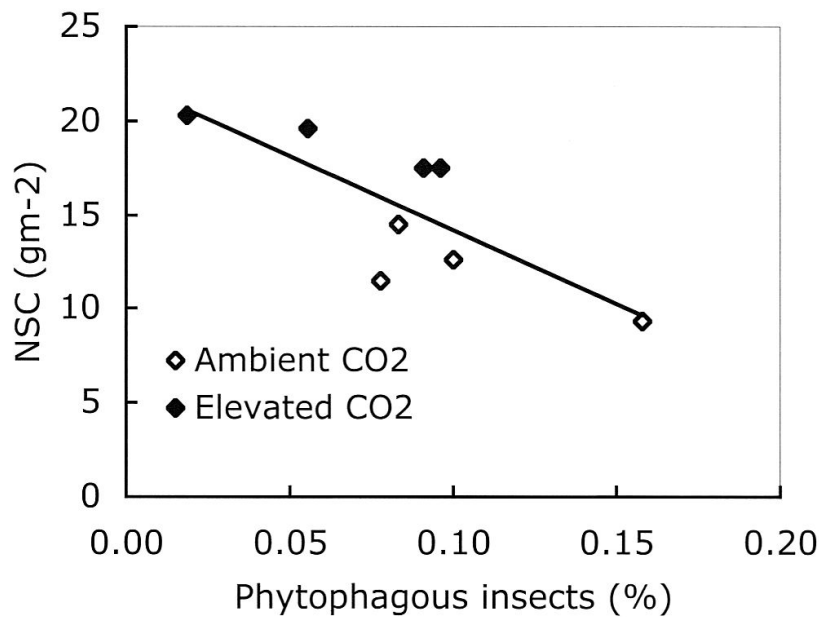


Fig. 3. The relationship between the average percentage of phytophagous insects per tree and the concentration of non-structural carbohydrates (NSC) in oak (*Quercus*; $p = 0.021$). A, ambient and E, elevated CO₂; data for 2002.

It is concluded, that the increase of atmospheric CO₂ will have various effects not only on plants but also on plant inhabiting animals such as insects. The data presented here suggest a reduction of insect diversity. At the same time some insect species may profit: They are better able to cope with the new conditions. If such changes in insect communities would materialize on larger scales, they would definitely provoke counter-reactions in the ecosystem. One possible effect could be changes in competition between trees due to changed feeding habits of insects. Because of the short generation time of insects such effects can occur more rapidly than direct CO₂-effects on long-living trees.

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ZUSAMMENFASSUNG

In einem Laubmischwald wurde die CO₂-Konzentration der Atmosphäre simuliert, wie sie in Zukunft auftreten wird. Dabei wurden ganze Bäume an ihrem natürlichen Standort mit zusätzlichem CO₂ begast. In dieser Arbeit untersuchte ich, was das für Auswirkungen auf die kronenbewohnende Arthropodenfauna hat. Ich sammelte Insekten und Spinnen von einer Krangondel aus und verglich Häufigkeiten der Arten, die Diversität auf Morphospeziesniveau und Frassgildenzusammensetzung der Insekten auf Buche (*Fagus sylvatica*) und Eiche (*Quercus petraea*) unter normalem und erhöhtem CO₂. Unter erhöhtem CO₂ nimmt nicht nur die Diversität signifikant ab, sondern die einzelnen Frassgilden profitieren unterschiedlich. So nehmen unter der veränderten Umgebung auf Buche die kauend-beisenden Insekten zu, während es auf Eiche die saftsaugenden sind. Ich ziehe die Schlussfolgerung, dass der anthropogen verursachte Anstieg von CO₂ in der Atmosphäre die Insektenfauna negativ beeinflusst und dies indirekt Einfluss auf die Pflanzengemeinschaften hat.

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