TECHNISCHE UNIVERSITÄT MÜNCHEN

Lehrstuhl für Renaturierungsökologie

Population biology of *Typha latifolia* L. and *Typha angustifolia* L.: establishment, growth and reproduction in a constructed wetland

Sabine I. Heinz

Vollständiger Abdruck der von der Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt der Technischen Universität München zur Erlangung des akademischen Grades eines

Doktors der Naturwissenschaften

genehmigten Dissertation.

Vorsitzender:		Univ. - Prof. Dr. L. Trepl
Prüfer der Dissertation:	1.	Univ. - Prof. Dr. J. Pfadenhauer (i.R.)
	2.	Univ. - Prof. Dr. A. Fischer

Die Dissertation wurde am 15.11.2010 bei der Technischen Universität München eingereicht und durch die Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt am 23.02.211 angenommen.

Berichte aus der Biologie

Sabine Heinz

Population Biology of *Typha latifolia* L. and *Typha angustifolia* L.

Establishment, Growth and Reproduction in a Constructed Wetland

Shaker Verlag
Aachen 2012

Bibliographic information published by the Deutsche Nationalbibliothek
The Deutsche Nationalbibliothek lists this publication in the Deutsche Nationalbibliografie; detailed bibliographic data are available in the Internet at http://dnb.d-nb.de.

Zugl.: München, Techn. Univ., Diss., 2011

Printed in Germany.

ISBN 978-3-8440-0715-2
ISSN 0945-0688

Shaker Verlag GmbH • P.O. BOX 101818 • D-52018 Aachen
Phone: 0049/2407/9596-0 • Telefax: 0049/2407/9596-9
Internet: www.shaker.de • e-mail: info@shaker.de

Vorwort

Mit dem Projekt „Rohrkolbenanbau in Niedermooren – Integration von Rohstoffgewinnung, Wasserreinigung und Moorschutz zu einem nachhaltigen Nutzungskonzept“ (DBU Projekt Nr. 10628) wurde im Donaumoos der Anbau einer Röhrichtpflanze als nachhaltige Kulturpflanze getestet. Die vorliegenden Untersuchungen zu Etablierung, Wachstum und Reproduktion von Rohrkolben wurden am Lehrstuhl für Vegetationsökologie (seit 2010 Lehrstuhl für Renaturierungsökologie) im Rahmen dieses Projektes durchgeführt sowie durch ein Stipendium der Deutschen Bundesstiftung Umwelt (DBU) und ein Stipendium für Doktorandinnen im Rahmen des Programms „Chancengleichheit für Frauen in Forschung und Lehre“ der Technischen Universität München unterstützt.

Mein besonderer Dank gilt Herrn Professor Dr. Jörg Pfadenhauer und Herrn Dr. Ulrich Wild für die Bereitstellung des Themas und die Begleitung der Arbeit. Bei Herrn Professor Dr. A. Fischer bedanke ich mich für die Übernahme des Koreferates.

Allen Beteiligten des Projektes „Rohrkolbenanbau in Niedermooren“ danke ich für die gute Zusammenarbeit auf den Projektflächen. Bei der Landesanstalt für Bodenkultur und Pflanzenbau (heutige Landesanstalt für Landwirtschaft, LfL) möchte ich mich für die Trocknung und Inhaltsstoff-Analyse der Biomasseproben bedanken. Vom Fachgebiet Geobotanik (TUM) wurden mir freundlicherweise Gewächshausflächen zur Verfügung gestellt.

Allen Kolleginnen und Kollegen am Lehrstuhl für Vegetationsökologie danke ich für die freundschaftliche Aufnahme und die Unterstützung. Für Ratschläge rund um Makros und Datenbanken möchte ich Maren Belde danken. Ebenso danke ich all den studentischen Hilfskräften, Zivildienstleistenden und Praktikanten, ohne deren Unterstützung die Gelände- und Gewächshausarbeiten nicht zu bewältigen gewesen wären.

Für Ihre Geduld und Unterstützung beim Erstellen des Manuskriptes durch zahlreiches Korrekturlesen und wertvolle Anregungen möchte ich mich bei Dr. Franziska Mayer und Dr. Gisbert Kuhn, sowie bei Dr. Ulrich Wild bedanken. Dr. Kathrin Kiehl danke ich für Anregungen und Diskussionen besonders zum Kapitel 3.

Contents

1 Introduction

Typha latifolia L. and *T. angustifolia* L. are closely related emergent wetland plants native to Europe with a distribution in the temperate northern hemisphere. They are tall erect perennials with long linear leaves and flower spikes. Their habitat ranges from temporary flood plains, ditches, ponds and lakes to slow flowing rivers (STACE 1997). Both *Typha* species are common and widespread in Europe and often build mono-dominant stands characterised by a low plant species diversity. Because of their extensive distribution and commonness *Typha* communities form an important and widespread wetland type under more eutrophic conditions.

Wetlands provide natural protection against extreme floods, store freshwater and enhance the water quality. They function as habitat for many invertebrate and vertebrate species, providing a spawning habitat for fish and amphibians and offering hide and nesting for birds (MITSCH & GOSSELINK 2000). Wetlands and especially peatlands provide a net sink of carbon dioxide (BOBBING et al. 2006). In the last centuries an estimated 50 % of the wetland area has been lost and wetland protection has become a high priority worldwide (MITSCH & GOSSELINK 2000). It is supported by international agreements such as the Ramsar convention (RAMSAR 1971) and the International Convention on Biological Diversity (RIO 1992).

Typha populations can provide all these services to human welfare and sustainable natural resource management. But eutrophication and changes in water regime can turn *Typha* with its extensive dispersal and fast growth into an invasive species, displacing more diverse plant communities and blocking drainage systems (ZEDLER & KERCHER 2004; BOERS et al. 2007). In constructed wetlands *Typha* species are among the desired vegetation because of their high capacity to absorb nutrients and clean water even when heavy metal contamination is involved (SAYDEGER et al. 2004; CIRIA et al. 2005).

This study investigates the establishment, growth and reproduction of *T. latifolia* and *T. angustifolia* using the approach of population biology. Population biology studies the numbers of organisms and attempts to explain the structure of populations. It describes the processes underlying population growth and individual survival (HARPER 1977, SILVERTOWN & CHARLESWORTH 2001). The population biology approach enables not only to study the effect of environmental factors but also to quantify the effect and to compare the dimension different factors have on growth and reproduction. *Typha* is studied following the plant´s life cycle from germination, over seedling establishment and growth to reproduction and death (Fig. 1-1). The focus is set on the colonisation of new habitats, the population establishment and the first years of population development.

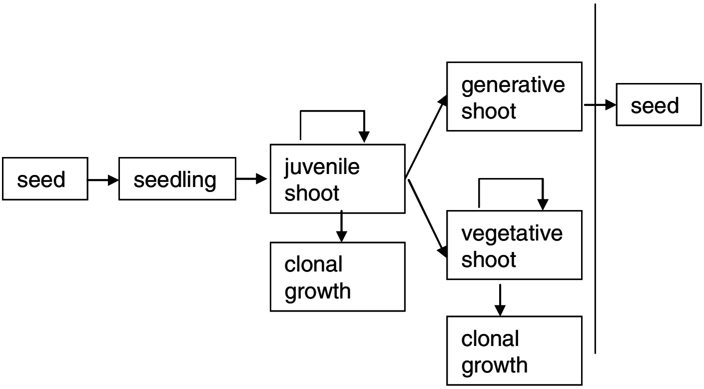

Figure 1-1: Schematic life cycle of *Typha*.

Typha latifolia and *T. angustifolia* largely share the same morphology. Both are erect, rhizomatous perennials (STACE 1997). Shoots are formed by long linear leaves sheathing at the base. In June and July erect culms with terminal inflorescences are developed. Flowering shoots achieve heights of 2.5 m to over 3 m. The flowers are unisexual, the pistillate spike is borne below the staminate spike (GRACE & HARRISON 1986). The flowers are wind-pollinated, protogynous but usually self-pollinated (KRATTINGER 1975). Diaspores are light-weight one seeded dry fruits with basal hairs of up to 1.4 mm size (GRIME et. al 1988). In each flower-spike more than 100 000 diaspores mature, which are dispersed by wind from October to January (COOPS & VAN DER VELDE 1995). In autumn nutrients are stored in the underground rhizome (GARVER et al. 1988). While generative shoots complete their growth with flowering and die after reproduction, some vegetative shoots survive winter and show re-growth in spring (DICKERMAN & WETZEL 1985). Established plants spread rapidly by lateral rhizomes produced at the base of the leaves. One individual plant (genet) is able to produce more than 40 new daughter shoots (ramets) in the first growing season (FIALA 1978). Polycormones are able to cover up to 16 m² at the end of the first growing season (FIALA 1978). Shoots and rhizomes have a well-developed aerenchyma, providing underground organs with oxygen (GRIME et al. 1988).

Typha latifolia and *T. angustifolia* are morphologically distinguished by the width of their leaves (*T. latifolia* 8-24 mm, *T. angustifolia* 3-10 mm), but the best characteristic is the composition of male and female parts of inflorescence in summer. In *T. latifolia* male and female parts of the spike are usually contiguous, while the inflorescence of *T. angustifolia* is intermitted by a 3 to 8 cm gap (STACE 1997). Shoot anatomy differs gradually as well: *T. latifolia* produces longer rhizomes between daughter shoots (ramets) (GRACE & WETZEL 1982). Ecologically *T. angustifolia* is characterized by a higher salt-tolerance than *T. latifolia* (GRACE & HARRISON 1986). While *T. latifolia* is a very frequent species, *T. angustifolia* occurs more scattered (STACE 1997).

Previous studies investigated *Typha* spp. under different aspects. BASKIN & BASKIN (1998) present a review of different factors affecting *Typha* spp. germination.

Comparative descriptive studies on the morphology and phenology (KRATTINGER 1978) and the growth of the underground organs (FIALA 1978) of both species were conducted in Europe. In North America GRACE & Wetzel (eg. 1981 a, 1982; 1998, i.e. parts reviewed by GRACE & HARRISON 1986) investigated the growth of *Typha* spp. in different experiments focussing on development and competition between species along a water level gradient. DICKERMAN & WETZEL (1985) studied the demography of *T. latifolia* ramets in a natural wetland in Michigan (US) in two successive seasons. Also studies in community ecology concerned with the early development of vegetation zonation and the ecological niche along water-level gradients incorporated *T. latifolia* and *T. angustifolia* and investigated the establishment of the species (e.g. MOORE & KEDDY 1988; SHIPLEY et al. 1989; COOPS & VAN DER VELDE 1995). In the last decades the attention shifted towards the invasion and control of *Typha* spp. Invasive developments of *Typha* are mainly caused by nutrient enrichment and changes in hydro-periods, studies focus on *Typha domingensis* and the hybrid species *Typha* x *glauca* in North America (ZEDLER & KERCHER 2004; MIAO 2004; BOERS et al. 2007; TIAN et al. 2010). Employing data from preceding studies TANAKA et al. (2004) and DAS & TANAKA (2007) modelled long-term competition between *T. latifolia* and *T. angustifolia* and nitrogen budgets of *T. angustifolia.*

Intra-specific differentiation between *Typha* populations was studied by MCNAUGHTON (1966) on different plant traits. More recent studies detected genetic differences between European *Typha spp.* populations in Flanders (LAMOTE et al. 2005) and between populations in the Ukraine using DNA (TSYUSKO et al. 2005).

Currently the uptake potential of *Typha* in treatment plants is in the focus of research (MANDER & MITSCH 2009). In constructed wetlands *Typha* spp. is applied because of its uptake capacity, tolerance of high nutrient concentrations and tolerance even to heavy metal contamination (SAYDEGER et al. 2004; CIRIA et al. 2005; CHANDRA & YADAV 2010). In addition *Typha* stands emit comparatively low amounts of the greenhouse gas methane (KAO-KNIFFIN et al. 2010).

The presented studies investigate the population biology of *Typha latifolia* and *T. angustifolia* following the life cycle from germination, to establishment, growth and vegetative and generative reproduction by performing different experiments and by observing the development of a planted stand in a constructed wetland. The results are combined on the one hand to explore growth and colonising strategies of *Typha* sp. and on the other hand to develop recommendations for cultivation and harvest of *Typha* sp. in constructed wetlands.

Chapter 3 focusses on the effect of temperature and water level on seed germination. Both *Typha* species differ slightly in their water-depth requirements in the adult phase (GRACE & WETZEL 1981 a). Germination tests at different water level and temperature combinations investigate, whether differences already exist in the germination requirements. Further the interaction of both factors and the germination speed is studied to estimate effects on the colonisation of new habitats by *Typha* seedlings.

In **Chapter 4** variations in the germination response of different *Typha latifolia* populations are investigated. Species occurring over wide geographic areas frequently develop populations adapted to the local environments (TURESSON 1922). Also germination requirements differ between populations of different origins (MCNAUGHTON 1966; QIU et al. 2010). In the light of climate change differences in germination requirements among populations may have effects on the competition and the colonisation of new habitats. To quantify population differentiation in germination traits 15 European *T. latifolia* populations from different climatic regions were subjected to five different temperature regimes. Germination success and time lapse were correlated to site characteristics to explore geographical patterns.

Chapter 5 investigates the effect of different water-levels on the seedling growth of *T. latifolia* and *T. angustifolia*. In aquatic plant communities water-level is a key factor structuring vegetation zonation (COOPS & VAN DER VELDE 1995; SEABLOOM & VAN DER VALK 2003). But microhabitats exploited by juveniles may differ from those experienced by the parents (GRIME & HILLIER 1992). In a greenhouse experiment the effect of three different water-levels on seedling growth and biomass development and the establishment capacity of both species was tested.

Chapter 6 describes the development and demography of planted stands of *T. latifolia* and *T. angustifolia* in a constructed wetland. While in non-clonal plants high population densities result in asymmetric competition, with size dependent mortality (self-thinning), growth in clonal plants is regulated by clonal integration (HARPER 1977; COOK 1985). The physiological integration effects a reduction of the production of new shoots as density increases (density dependent natality), prevents over-production (DEKROON 1993), and would ideally regulate the development of new shoots to shoot densities close to the carrying capacity of the environment (HUTCHINGS 1979). Besides mortality and natality (DEKROON 1993), the biomass allocation to the production of daughter ramets and sexual reproduction could be density dependent (OGDEN 1974; VAN KLEUNEN et al. 2001). The study is concerned with the colonisation of new habitats by *Typha latifolia* and *T. angustifolia* and investigates differences in stand-structure and shoot fate depending on stand density and heights.

Chapter 7 develops recommendations for establishment and biomass yield of *Typha* sp. in constructed wetlands. Constructed wetlands are mainly used for water purification (CIRIA et al. 2005; MANDER & MITSCH 2009) and flood control (CAMPBELL & OGDEN 1999). Cultivating wetland plants as raw-material instead of traditional cultures provides a sustainable land use concept for degraded fen soils (PFADENHAUER & GROOTJANS 1999; WILD et al. 2002). The influence of the establishment method - by sawing or planting – on growth and biomass production is investigated in pilot plant scale. Also the effect of different cutting levels for the harvest is tested.

While chapters three to seven cover the different aspects of germination and growth largely independently and offer the opportunity to be read on their own, **chapter 8** concludes the different aspects of the life cycle studied. The different generative and vegetative strategies of *T. latifolia* and *T. angustifolia* and their effects on natural and constructed wetlands and for the cultivation of *Typha* are discussed.

The present study was integrated in the project „Cultivation of *Typha* in a degraded fen area – integration of raw-material production, water purification and soil protection into a sustainable landuse concept“ (Rohrkolbenanbau in Niedermooren – Integration von Rohstoffgewinnung, Wasserreinigung und Moorschutz zu einem nachhaltigen Nutzungskonzept) (e.g. WILD et al. 2002). The objective, the experimental site and results of the project will be reviewed in the following section (**chapter 2**).

2 Cultivation of Typha – Integration of water purification, fen protection and the cultivation of a renewable resource

The aim of the project “Cultivation of *Typha* in a degraded fen area – integration of raw-material production, water purification and soil protection into a sustainable landuse concept“ was to investigate possibilities and effects of cultivating *Typha* spp., a native reed plant, in a degraded fen as raw-material for the production of insulation products for the building trade (WILD et al. 2002). Raw material production, water purification and fen protection were combined to a sustainable land use concept.

Dropping the groundwater table in fens starts the process of peat loss (SUCCOW & JOOSTEN 2001). The peat becomes dry, the structure changes and the peat volume decreases. Aerobe soil conditions start the mineralisation of stored organic matter and carbon-hydrate, nitrate and phosphate, stored in the peat, are set free (SCHMIDT 1994). The oxidation of the fen soil rich in nitrate leads to the eutrophycation of effluents and groundwater (MEISNER et al. 1995; PFADENHAUER 1994). Trace gases enhancing global warming are emitted (carbon dioxide, nitrous oxide, methane; MARTIKAINEN et al. 1993). Mineralisation and erosion of the peat soil reduce the soil level. Drainage ditches have to be deepened to ensure drainage. A vicious circle of drainage and soil loss is started (PFADENHAUER 1994). In the long term the whole fen ecosystem is destroyed.

While traditional agriculture on fen soils requires drainage, reed plants can be cultivated under wet or flooded conditions. *Typha* sp. combines adequate habitat requirements and high productivity. Dry leaves can be used as raw material for the production of insulation products (WILD et al. 2002).

The constructed wetland built as a pilot demonstration site is situated in southern Germany in a fen area called Donaumoos. Since drainage started some 200 years ago the fen area has decreased from 18.000 ha to 12.000 ha (SUCCOW & JESCHKE 1990). In most places only peat-layers of 1 to 2 m remained from a former 8 m peat layer. Beside the soil loss, flooding is another problem in the Donaumoos area: The deepening of the drainage ditches over the last 200 years decreases the slope; in cases of long or heavy rain periods drainage is ineffective and agricultural and settlement areas are flooded (PFADENHAUER et al. 1991). Most parts of the Donaumoos are used for intensive agriculture and the project site was intensively managed grassland before the basins were built.

The experimental basins were built by removing the top-soil and creating a dyke with the material. Three basins with a total area of 62.000 m² were planted with *T. latifolia* (approx. 50.000 m²) and *T. angustifolia* (approx. 4.000 m²) at a density of two shoots/m² in June 1998. A quarter of one basin was left un-planted to test the establishment by sowing the following spring. The basins were supplied with nutrient rich water from a drainage ditch with a permanent flow rate of 10 l/s (cp. table 6-1), the water level was fixed at 0.2 m (basin 1 and 3) and 0.4 m. (basin 2) (cp. figure 6-1).

Apart from a small-scale harvesting experiment in the winter 1998/99 the aerial biomass was harvested in late winter 1999/2000 (second season) for the first time. Due to not permanently frozen soil and heavy harvest machinery with caterpillar drive, soil and plant rhizomes were damaged especially at gateways and turning radii. *T. latifolia* stands were affected more seriously because of the spatial distribution of the experimental sites. The second harvest in winter 2000/2001 was conducted with light-weight machinery with balloon tyres on completely frozen soil and caused minor to no damage to soil and plants.

Establishment and growth of the planted *Typha* stands were investigated in fifteen 5 x 5 m² plots. The development on the sown area was monitored at 36 plots of 1 x 1 m². An interdisciplinary team of scientists investigated the water quality, trace gas fluxes and the colonisation of the basins by invertebrates and birds (cp. LENZ & WILD 2000; WILD et al. 2001; RANFTL 2001). During periods of flooding the constructed wetlands served as retention basins by increasing water levels up to 1 m for a short time.

Nutrient uptake and de-nitrification decreased phosphate loads by up to 70 % and nitrate- loads even at a rate of up to 85 % (LENZ & WILD 2000; WILD et al. 2002). The trace-gas fluxes fluctuated between basins and seasons. In comparison to an intensively managed grassland the global warming potential could not be reduced by the cultivation of *Typha* (KAMP 1998). The *Typha* basins offered an alternate habitat to invertebrates, amphibians and birds in an agriculturally region. A total of 58 different bird species have been detected from 1998 to 2000 in and around the constructed basins (RANFTL 2001). After the passage through basin 1 the effluent provided a fen restoration site with nutrient poor water. Especially the fen-species profited from the rewetting and the elevated water levels (HEINZ 2004).

3 The effect of temperature and water depth on seed germination of *Typha latifolia* and *Typha angustifolia*

Introduction

Seed germination and establishment are critical phases in the life cycle of plants (HARPER 1977). The germination success is determined by (a) physical factors like temperature, hydration, aeration and light and (b) the genetic constitution of the seeds (BEWLEY & BLACK 1994). Species specific germination requirements provide that germination takes place under habitat conditions adequate for establishment and growth. That way environmental conditions control not only germination success but can function as a trigger to start germination. Some environmental factors thereby control a whole set of physical factors; for instance water depth affects not only the availability of water, but influences the oxygen supply, the quantity and quality of light and the fluctuation of temperatures (FRANKLAND et al. 1987).

Generative reproduction of emergent macrophyte species is often related to prolonged water level draw-down uncoupling juvenile and adult niches to some extent (SHIPLEY et al. 1989; COOPS & VAN DER VELDE 1995). Species depending on draw-downs for germination use increasing and especially fluctuating temperatures as an indicator for low water levels.

The natural dynamic of wetlands with periodical high and low water levels controls mortality and recruitment. But human impact increasingly provokes changes in hydrology and nutrient supply and destabilises natural processes. These environmental alterations of wetlands can turn single species into invasive species displacing others (ZEDLER & KERCHER 2004, WEI & CHOW-FRASER 2006). Detailed knowledge of the species specific germination requirements offers the opportunity both to control invasions and to further establishment of decreasing populations (BOERS et al. 2007). Furthermore wetland species get into the focus as renewable resource (WILD et al. 2002; CIRIA 2005) and are employed for water purification in constructed wetlands especially when high loads of heavy metal i.e. lead, zinc are involved (MANDER & MITSCH 2009).

The investigated wetland species, *Typha latifolia* L. and *Typha angustifolia* L., both are common and widespread emergent macrophytes in wetlands of the temperate northern hemisphere. Their extensive distribution and habitat requirements make them suitable experimental species to test a range of temperature and water level treatments.

Typha species colonise new sites by seed dispersal. Due to the production of a high number of small, wind dispersed diaspores (COOPS & VAN DER VELDE 1995) new habitats can easily be reached.

Yet the seed germination of Typha spp. has been researched with differing objectives (i.e. review by GRACE & HARRISON 1986). Overall light turned out to be crucial for the germination (e.g. Lombardi et al. 1997), while oxygen is not required (MORINAGA 1926, SIFTON 1959). Elevated moisture supply in most studies facilitates germination (COOPS & VAN DER VELDE 1995, but see KEDDY & ELLIS 1985) as do elevated and fluctuating temperatures (LOMBARDI et al.1997; EKSTAM & FORSEBY 1999).

The purpose of this study is to examine the effects of temperature and water depth not only on the success but on time lapse of seed germination of *T. latifolia* and *T. angustifolia.* The time lapse of germination gains importance as mudflats as appropriate regeneration niches only exist for a short time period and fast germination gives an essential advantage of pre-empting (GRACE 1987). A focus is set on the interactions between temperature regime and water depth.

Separate studies detected no water level effect on the germination of *T. angustifolia* (KEDDY & ELLIS 1985), but a pronounced increase in germination with increasing water level in *T. latifolia* (MOORE & KEDDY 1988). In the adult phase *T. angustifolia* grows into greater water depth than *T. latifolia* (GRACE & WETZEL 1981 a). Thus the germination response of *T. latifolia* and *T. angustifolia* is tested in direct comparison to investigate whether differences with reference to temperature and water depth requirements exist already in the juvenile phase.

Some studies indicate that *Typha*-populations from different geographical regions differ in their ecological amplitude (HAI et al. 2006) and even in their germination requirements (MCNAUGHTON 1966). To consider regional variation, different populations from Germany and one Hungarian population were integrated in the experiment. This approach offers the opportunity to investigate, if different populations show a shared or distinct germination response to the factor combinations.

Methods

Study material

Ripe spikes of two populations of *Typha angustifolia* and four populations of *Typha latifolia* have been collected in Germany and Hungary from December to January

(Table 3-1). All seeds were stored at room temperature until the start of the experiment in March.

The seeds were separated from adhering structures (pericarp, gynophore and hairs) by blending them in water and a small amount of a detergent (cp. BONNEWELL et al. 1983). The seeds settling to the bottom were placed on filter paper, washed in deionizied water and dried in an oven at 22°C. Seeds from 8-10 spikes per population were combined and thoroughly mixed.

Table 3-1: Origin and seed weight of *Typha* seeds from different populations used in the experiment. Significant differences in seed weight are marked by different letters behind the value.

species	population / origin	abbreviation	seed weight per seed [mg]
Typha angustifolia	Karlskron (Germany) 48°40´N; 11°25´E	Ta 1	0.036 ± 0.004 b
	Lakitelek (Hungary) 46°52´N; 20°0´E	Ta 2	0.034 ± 0.011 b
Typha latifolia	Donaumoos 1 (Germany) 48°42´N; 11°11´E	Tl 1	0.044 ± 0.010 ac
	Donaumoos 2 (Germany) 48°42´N; 11°11´E	Tl 2	0.038 ± 0.004 bc
	Ampertshausen (Germany) 48°28´N; 11°37´E	Tl 3	0.047 ± 0.004 a
	Lakitelek (Hungary) 46°52´N; 20°0´E	Tl 4	0.034 ± 0.006 a

To test the effect of this “cleaning” method on germination four extra replicates with complete propagules from the population Donaumoos 1 (Tl 1) were included in all treatments. “Cleaned” seeds showed a slight acceleration in the onset of germination, but no significant effects could be detected between the whole propagules and cleaned seeds. Both reached a nearly identical mean final germination percentage of 40.4 +/- 5.0 (whole propagules) and 40.5 +/- 4.8 (cleaned) respectively after 24 days. Therefore in the following only the data of the cleaned seeds are taken into account.

Seed weight was determined by weighing twenty samples of 50 seeds of each population.

Experimental design

Germination tests were conducted in transparent plastic boxes (9.5 cm x 7.5 cm x 9.8 cm) with a lid, filled with 50 ml silica sand. The sand was washed with deionized water and was saturated with water before sowing. Four replicates of 50 seeds each evenly distributed in the container were used for each *Typha* population.

Germination was tested in a fully factorial experiment with three levels of water depth and at four different temperature regimes. The applied water depth treatments were: moist (soil kept saturated), surface (water depth maintained at the soil surface), and flooded (water depth maintained 4 cm above the surface). Growth cabinets were set to diurnally fluctuating 5/15°C, 10/25°C, 20/30°C, and constant 25°C. Temperature fluctuations corresponded to a light regime of 16 h light (higher temperature) and 8 h darkness (lower temperature). The temperature fluctuations chosen were based on the average day- and night-temperatures of the months April / May (5/15°C) and July (10/25°C) for a fen area in southern Germany (Donaumoos, 48°42´N; 11°11´E). The higher temperatures were chosen to allow direct comparison with other studies (i.e. SIFTON 1959; BONNEWELL et al. 1983, LOMBARDI et al 1997; EKSTAM & FORESBY 1999).

Germinated seeds were counted every second day for 24 days. A seed was considered to have germinated when the seed coat was broken and parts of the hypocotyl appeared. All seedlings were removed from the boxes and water levels were adjusted if necessary.

Calculated parameters and data analysis

To differentiate between the time lapse of germination and the proportion of seeds which can germinate in a given time period three different germination parameters were determined.

The final percentage germination indicates the proportion of seeds germinating during the experiment. The onset of germination refers to the number of days elapsed between sowing and the onset of germination (EVANS & ETHERINGTON 1990). As a second measure of the time lapse the number of days taken to reach 50 % of the final percentage germination (T_{50}) was determined.

The effects of water level, temperature regime and species or population on germination percentage, onset of germination and T_{50} were analysed by 3-factorial ANOVA´s. To fit the assumptions proportion data was arcsin-square-root transformed before analysis. Differences in seed weights between species and populations were tested by one-factorial ANOVA´s. Post hoc testing was done by the Tukey (HSD) test. Relations between seed weight and germination success and between the different germination parameters were analyzed by Spearman Rank correlation. All tests of significance were done at a predetermined level of significance of 0.05.

Results

Seed weight

The seed weight of *T. latifolia* averaged 0.041 +/- 0.008 mg per seed, *T. angustifolia* 0.035 +/- 0.008 mg per seed and differed significantly between the species (F 14.0, $p < 0.01$). Only the populations of *T. latifolia* showed significant differences in seed mass while between the *T. angustifolia* populations no significant difference was detected (Table 3-1).

Water depth and temperature

Temperature and water depth both had a significant effect on final percentage germination and the germination speed (Table 3-2). In the parameters onset and T_{50} occurred additionally a significant temperature x water depth interaction. *T. latifolia* showed this interaction also for final percentage germination, when tested alone. Significant inter-specific differences occurred only in final germination percentage.

Table 3-2: Result of the analysis of variance (ANOVA) testing the effects of temperature regime (temp), water depth (water) and species (spec) on the final percentage germination, the onset of germination and the number of days taken to 50 % of final percentage germination (T50). *** - $p < 0.001$, n.s. - not significant.

		F		
	d.f.	Final percentage germination	Onset of germination	T_{50}
temp	3	64.5 ***	46.8 ***	96.2 ***
water	2	103.2 ***	13.7 ***	19.8 ***
spec	1	16.8 ***	n.s.	n.s.
temp x water	6	n.s.	5.1 ***	6.9 ***
temp x spec	3	6.3 ***	n.s.	n.s.
water x spec	2	n.s.	n.s.	n.s.
temp x water x spec	6	n.s.	n.s.	n.s.

Generally *T. latifolia* obtained higher final percentage germination than *T. angustifolia* at all factor combinations except for the constant temperature regime (Fig. 3-1 a). Averaged over all water depths the germination was enhanced most by diurnally fluctuating temperatures of 10/25 °C; a further increase in temperature did not stimulate an increase in germination percentage. Raising the water depth effectuated a significant increase of the germination percentage at every temperature regime.

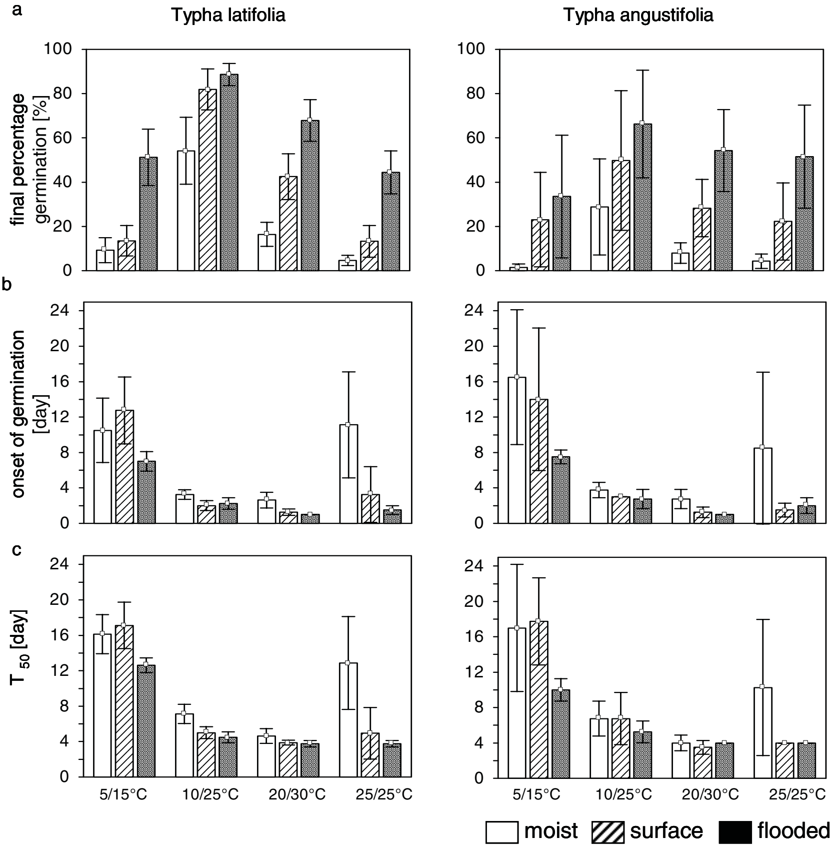

Figure 3-1: Final percentage germination (a), onset of germination (b) and T50 (c) of *Typha latifolia* (left) and *T. angustifolia* (right) at different temperatures and water depths.
Presented are means ± 95% confidence limits.

The time lapse of germination was influenced more severely by the increase of temperature than by the increase of water depth. In both species higher temperatures shortened the lag phase between sowing and the onset of germination and decreased the time till 50 % of the final percentage of seeds had germinated (Fig. 3-1 b, c). Just at the lowest temperature (5/15 °C) and at constant temperatures (25 °C) an increase in water level resulted in a significant reduction of the lag phase. The fastest germination, with the first germinating seeds within 24 h, was obtained by the highest fluctuating temperature (20/30 °C) and flooded conditions.

The direct comparison of diurnally fluctuating 20/30 °C and constant temperatures of 25 °C with an equal average day temperature showed significant effects of the temperature regime on final percentage germination and onset of germination only for *T. latifolia*.

While the T_{50} showed a strong positive correlation to the onset of germination (r = 0.81), the final percentage germination was negatively correlated with T_{50} (r = -0.35) and the onset of germination (r = -0.43).

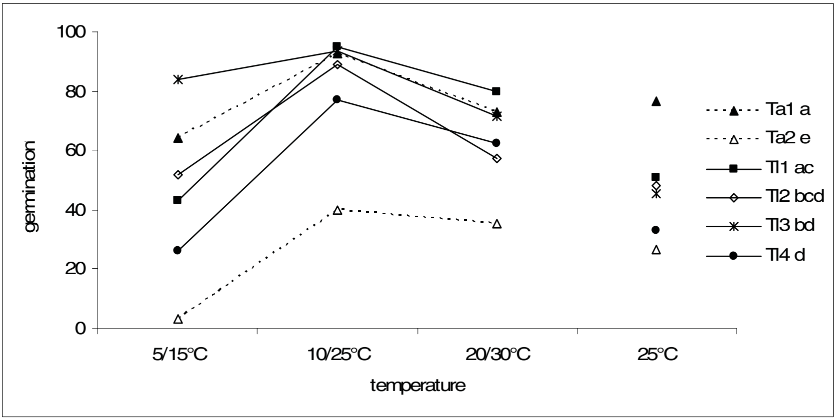

Figure 3-2: Mean final percentage germination of the *T. angustifolia* (Ta) and *T. latifolia* (Tl) populations at different temperature regimes and flooded conditions. Significant differences between populations averaged over all temperature regimes are marked by different characters (Abbreviations shown in Table 3-1).

Population origin

In *T. latifolia* and *T. angustifolia* the populations from different origins differed significantly in the final percentage germination, but showed no significant differences in the onset of germination and T_{50}. The populations show a shared germination reaction to the factor combinations (Fig. 3-2, only flooded conditions presented). The highest germination percentage was obtained at 10/25°C and flooded conditions for all populations. The post hoc test showed that only individual populations differed significantly.

Discussion

Effects of temperature regime and water depth on seed germination

Water depth and temperature both had strong effects on success and time lapse of the seed germination of *Typha* spp. While higher temperatures primarily accelerated germination, an increase of water depth had a stronger impact on final germination percentage.

Wetland plants often show a requirement for higher temperatures for an optimum germination (FENNER & THOMPSON 2005). In *Typha* spp. higher temperatures generally resulted in an increase of germination percentage (e.g. BONNEWELL et al. 1983; LOMBARDI et al. 1997; EKSTAM & FORSEBY 1999). In the present study the highest germination percentage was achieved at alternating 10/25 °C. A further increase of temperature did not lead to higher germination success. This effect, that germination percentage was raised by an increase in temperature just to an optimum, was also found by EKSTAM & FORSEBY (1999) who studied a *T. latifolia* population from Sweden and SIFTON (1959), who tested a *T. latifolia* population from Canada. However BONNEWELL et al. (1983) and LOMBARDI et al. (1997) examined the highest germination percentage at the highest tested temperature - at constant 32 °C and fluctuating 20/30 °C respectively - for populations from Minnesota (USA) and Italy.

But as important as absolute temperatures are the amplitudes of temperature fluctuation especially for *T. latifolia* (THOMPSON & GRIME 1983; EKSTAM & FORSEBY 1999), which expressed significantly higher germination percentage at alternating temperatures compared to constant regime with the same mean temperature. Since the temperatures chosen in the present study were based upon the average day- and night-temperatures in April/May and in July in a fen area in southern Germany, not only the mean temperature (10°C and 17,5°C respectively) but also the amplitudes increase from 10°C to 15°C. Therefore the highest germination percentage at 10/25°C may not only be due to the optimum temperature but to the highest temperature amplitude tested.

The time lapse of germination does not show an optimum as in the studies of LOMBARDI et al. (1997) and EKSTAM & FORSEBY (1999). The acceleration of germination up to the highest tested temperature may be partly due to the temperature-dependent process of imbibition, which proceeds more rapidly at higher temperatures (BEWLEY & BLACK 1994).

Water is the other basic requirement for germination. In a study with species from different habitats EVANS & ETHERINGTON (1990) found that none of the wetland species could germinate to any great extent at low soil water potentials (< -1 MPa). As for other wetland species, an elevated water level facilitates germination success in *Typha* (SIFTON 1959; COOPS & VAN DER VELDE 1995; SEABLOOM et al. 1998). However, KEDDY & ELLIS (1985) found *Typha angustifolia* unresponsive to a range of water depth from 5 cm below the soil surface to 10 cm above soil surface. While COOPS & VAN DER VELDE (1995) did not detect an acceleration of germination, EVANS & ETHERINGTON (1990) found a faster onset of germination at higher soil water potentials as in the present study for elevated water levels, even though the effect of water depth on germination speed was minor compared to temperature in the present study.

The water depth does not only have an effect on the availability of water but it interferes with temperature, oxygen and light conditions. The effect on temperature concerns especially the temperature lapse, and it increases with water level (FRANKLAND et al. 1987). Though the generally low water levels in this study with a maximum water depth of 4 cm and small experimental water bodies would not be sufficient for this effect. It was instead simulated by different temperature fluctuations. Studies on the germination of *Typha latifolia* at different oxygen levels (MORINAGA 1926; SIFTON 1959; BONNEWELL et al. 1983) indicate, that the increasing water depth promotes germination by lowering the oxygen level at substrate surface.

Interaction of temperature and water level

Under natural conditions single factors as temperature or hydration never occur isolated, but co-occur and interact with each other. EKSTAM & FORSEBY (1999) found an effect between mean temperature and amplitude for *Typha latifolia*.

In the present study an increase in temperature and in water depth interacted in speeding up the germination of the *Typha* spp. seeds. The positive effect of increasing the water level was more pronounced under unfavourable low or constant temperature conditions than close to the temperature optimum. However, saturated and flooded conditions seemed to be able to substitute to some extent for suboptimal temperature conditions.

Even though germination speed is less often studied than germination percentage it is of essential importance for germination success. Especially in the context of competition the time a seed needs to germinate and establish can be a crucial attribute. The plant that first germinates and becomes established at a site is able to gain an advantage over individuals arriving later (HARPER 1977; GRACE 1987). GRACE (1987) demonstrated that even a protrusion of two days is able to cause a significant competitive advantage between *T. latifolia* and *T. domingensis*. Also in the present study the length of the lag phase and the final percentage germination were negatively correlated.

Because *Typha* spp. as many emergent wetland plants depend on temporal draw-downs for generative reproduction (SHIPLEY et al. 1989; COOPS & VAN DER VELDE 1995; SEABLOOM et al. 1998), germination speed gains further importance, as appropriate conditions are of temporary nature.

When water depth counterbalances to some extent for unfavourable temperatures the interaction of these factors would broaden the niche for seed germination, and would give a strong advantage in competition, especially when not only germination speed but also germination percentage is enhanced as in *T. latifolia*. For managed wetlands this means that the colonisation by *Typha* spp. can be controlled to some extent by an appropriate seasonal water level management.

Differences between species and populations

In a study with both *Typha* species COOPS & VAN DER VELDE (1995) obtained a slightly higher germination percentage for *T. angustifolia* in contrast to the present study. MCNAUGHTON (1966) detected faster germination for *T. latifolia* than *T. angustifolia* whereas species differences were not significant for germination speed in the presented study. A preference for deeper water in *T. angustifolia* was not detected and the spatial distribution of the species in established stands along the water level gradient is probably founded more in competition than in the germination niche (GRACE & WETZEL 1981 a).

All tested populations shared a common response pattern to temperature and water-depth manipulation but the resulting germination percentage differed significantly. In the presented study intra-specific differences between populations exceeded by far inter-specific effects on seed germination. Especially the Hungarian populations stand out by low germination percentage. Differences in seed germination between single populations could be induced by genetically differentiated ecotypes (MCNAUGHTON 1966, LAMOTE et al. 2005, but see: MASHBURN et al. 1978), differences in seed weight or different habitat conditions of the mother plants.

Comparing the optimal germination results of different populations from literature provides different optimal temperatures for different origins. However, differences in the individual study designs impede direct comparison of results. Differences in the germination percentage between populations have been detected between local *T. glauca* and *T. domingensis* populations (BEARE & ZEDLER 1987) and also on a broader scale for populations of *T. latifolia* and *T. angustifolia* on a north-south transect of the north American continent (MCNAUGHTON 1966). The effect described by MCNAUGHTON (1966) that populations originated from the northern US started germination at higher temperatures than population from habitats in the south could not be found in this study nor when the results of SIFTON (1959) , BONNWELL ET AL. (1983) and EKSTAM & FORSEBY (1999) (see above) are compared.

4 Variation in germination requirements among European *Typha* populations

Introduction

Species of wide geographical distribution frequently show local variation in morphological and physiological characters (TURESSON 1922). Also germination requirements differ between populations of different origins (BASKIN & BASKIN 1998; QIU et al. 2010). The differences between populations can be interpreted as adaptation to the specific habitat properties. Selection is expected to favour appropriate responses to local environmental cues that synchronise germination with periods optimal for seedling survival. Some studies on wider climatic gradients show a trend to higher temperature requirements for northern species and populations respectively than for species from milder climates (MCNAUGHTON 1966; PROBERT 2000; SCHMUTHS et al. 2006). However, in other cases no consistent geographical patterns were found, that could be related to environmental conditions (MCKEE & RICHARDS 1996; TRUDGILL et al. 2000).

Among populations of *Typha* spp. variations in germination (MCNAUGHTON 1966), in allocation, productivity, sexual reproduction (MCNAUGHTON 1966; GRACE & WETZEL 1981 a; MIAO et al. 2000) and reactions to pollutant status (KEANE et al. 1999) were observed in North America. While studies on isoenzymes (MASHBURN et al. 1978) and some studies on different DNA markers (KEANE et al. 1999; ZHANG et al. 2008) discovered only minor or no differences between populations, LAMOTE et al. (2005) and TSYUSKO et al. (2005) detected genetic differences between European *Typha spp.* populations in Flanders and the Ukraine respectively using DNA.

Typha spp. are perennial emergent aquatic plants with a north-hemispherical distribution from the boreal zone to the subtropics. Throughout their range, they typically form monodominant stands in the littoral zone of lakes, along rivers and ditches and in marshlands. Even though vegetative regeneration is the main mechanism in *Typha* (GRACE & HARRISON 1986; GRACE & WETZEL 1981 a) sexual reproduction plays a major role in colonisation of new habitats or in re-colonisation after disturbance (SHIPLEY et al. 1989). Small single-seeded fruits with hairs are produced in great numbers and dispersed by wind (GRACE & HARRISON 1986). Seeds are capable of germination when shed (MCNAUGTHTON 1966) but require light (e.g. LOMBARDI et al. 1997), sufficient moisture and temperature (COOPS & VAN DER

VELDE 1995; LOMBARDI et al.1997). Elevated and fluctuating temperatures further germination (LOMBARDI et al.1997; EKSTAM & FORSEBY 1999).

Due to predicted shifts in species distributions under climate change (SEBASTIÁ et al. 2008) and increasing human impact on wetlands, colonisation processes will gain relevance for the maintenance of species populations. *Typha,* as a frequent species in nutrient rich wetlands, on one the hand plays an important role in nutrient cycling and as wildlife habitat. On the other hand the intense vegetative spread after colonisation could make alien populations a thread to local populations and to the plant community (SALTONSTALL 2002; BOERS et al. 2007; KETTENRING et al 2010).

To quantify population differentiation in germination traits seeds of 15 European *T. latifolia* populations from different climatic regions were subjected to five different alternating temperature regimes. As EKSTAM & FORSEBY (1999) proved a significant effect not only of mean temperature but of temperature amplitude, two different amplitudes were tested on the mean temperature of 15°C. In addition to germination success (final percentage germination) the time lapse measured as time to germination onset and germination rate have been investigated as important traits for successful seedling establishment (GRACE 1987).

The objectives of this study were (1) to investigate the dependence of germination success and time lapse on temperature, (2) to test if different European populations of *Typha latifolia* differ in germination percentage and time, and (3) to explore the correlations between site characteristics of the populations and germination requirements.

Methods

Study material

Spikes with ripe seeds of *Typha latifolia* were collected in winter (from November to January) by local scientists from 15 European origins (Fig. 4-1, Table 4-1). All seeds were stored at room temperature until the start of the experiment in May. The seeds were separated from adhering structures (pericarp, gynophore and hairs) by blending them in water and a small amount of a detergent (cp. BONNEWELL et al. 1983). The seeds settling to the bottom were placed on filter paper, washed in deionizied water and dried in an oven at 22°C. Seeds from several spikes per population were combined and thoroughly mixed.

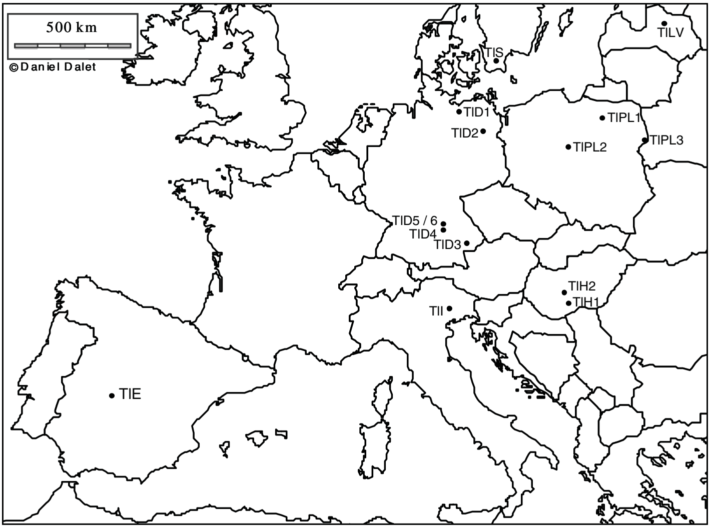

Figure 4-1: Geographic location of 15 *T. latifolia* populations across Europe. Population abbreviations see Table 4-1.
(Map: http://histgeo.ac-aix-marseille.fr/webphp/carte).

Five samples of about 200 seeds of each population were weighed and the exact number of seeds counted to calculate the mean seed mass (Table 4-1).

Mean annual temperature and precipitation of the site of every tested *Typha*-population were adopted from the nearest station from the Climate Diagram World Atlas (LIETH et al. 1999, Table 4-1).

Table 4-1: Origin and seed weight of *T. latifolia* seeds from different populations used in the experiment.
Climate (WALTER 1984): O - Oceanic, SO - Sub-oceanic, C - Continental, SC - Sub-continental, M - Mediterranean. MAT - mean annual temperature, Jan - mean annual temperature in January, MAP - mean annual precipitation, % July - % of annual precipitation in July.

Population (label)	Climate	latitude	longitude	MAT (°C)	Jan (°C)	MAP (mm)	% July	seed mass [mg]
Groß Rolübbe (TlD1)	O	54°14'N	10°41'E	8.6	0.7	762	10.7	0.0615
Beetz (TlD2)	SO	52°49'N	13°01'E	8.6	-0.7	589.6	11.1	*
Linden (TlD3)	SC	48°25'N	12°49'E	8.5	-1.5	1198.9	14.4	0.0499
Karlskron (TlD4)	SC	48°41'N	11°25'E	8.4	-1.3	823	13.4	0.0425
Donaumoos 1 (TlD5)	SC	48°40'N	11°25'E	8.4	-1.3	823	13.4	0.0449
Donaumoos 2 (TlD6)	SC	48°40'N	11°25'E	8.4	-1.3	823	13.4	0.0440
Lund (TlS)	O	55°40'N	13°13'E	7.6	-0.6	733.3	9.4	0.0522
Aumeistezi (TlLV)	O	57°31'N	26°11'E	6	-4.9	567.7	12.7	0.0486
Mragowo (TlPL1)	C	53°49'N	21°16'E	6.8	-4.1	585.6	13.4	*
Lubien Kujawski (TlPL2)	SC	52°24'N	19°11'E	7.8	-3.2	445.2	15.3	*
Bialowieza (TlPL3)	SC	52°42'N	23°52'E	6.8	-4.1	585.6	13.4	*
Lakitelek (TlH1)	C	46°52'N	20°00'E	11.5	-1.4	707.5	11.2	0.0473
Szeremle (TlH2)	C	46°09'N	18°53'E	10.4	-1.5	515.7	11.5	*
Treviso (TlI)	M	45°35'E	12°11'N	12.7	3	1331.8	6.3	0.0558
Escalona (TlE)	M	40°10'N	4°24'W	14.2	5.4	441.8	2.1	0.0439

*seed mass not calculated

Experimental design

Seeds were germinated in plastic Petri-dishes (90 mm diameter) with a lid on water saturated filter paper at five different temperature regimes: 5/15°C, 10/20°C, 15/25°C, 20/30°C and 7/23°C. The diurnally temperature fluctuations corresponded to a light regime of 16 h light (higher temperature) and 8 h darkness (lower temperature). Six replicates of 50 seeds each evenly distributed were used for each of the 15 *T. latifolia* populations. Germinated seeds were counted every day for the first 14 days after sowing, from day 15 on every second day till the end of the experiment on day 35. A seed was considered to have germinated when the seed coat was broken and parts of the hypocotyl appeared. All seedlings were removed from the Petri-dishes and water was added if necessary.

Calculated parameters and data analysis

Beside the final percentage germination, the onset of germination and the germination rate were determined to differentiate between germination success and the time lapse of germination. The onset of germination refers to the number of days elapsed between sowing and the onset of germination.

The germination rate was estimated as a weighted mean according to the formula:

$$r_{ij}=\Sigma_j(p_{ij}\ {*}j)$$

where p_{ij} is the proportion of all seeds of species i germinating on day j, relative to the total number of seeds of species i germinating during the experiment (SHIPLEY et al. 1989).

The effects of population and temperature regime on the response variables were analysed by two-factorial ANOVA. For multiple comparisons of the means the Tukey (HSD) test was used. Proportion data was arcsin-square-root transformed before analysis.

In order to test for the effect of temperature amplitude, germination percentage, onset and germination rate at 10/20°C and 7/23°C with the same mean temperature were compared directly with ANOVA.

Differences among populations in seed mass were analysed by one-way ANOVA. Correlations between the response variables, seed mass, geographic position and climate of sites were investigated by Spearman rank correlation. All tests of significance were done at a predetermined level of significance of $p<0.05$ if not explicitly stated otherwise.

The relationships between germination percentage, mean germination percentage over all temperature regimes, onset, seed mass, geographic (altitude, latitude, longitude) and climatic (mean annual temperature, mean annual precipitation and % precipitation in January and July) variables were plotted using principal component analysis (PCA) in PC-Ord (MCCUNE & MEFFORD 1999). A distance based two-dimensional biplot overlay graph of the variables allowed for an examination of correlations and ordinate axis. The length of the variable arrow indicates its relative importance, the direction indicates correlation with the axis and the angle of one arrow relative to the other indicates the relative correlation between variables. Variable arrows with $r<0.5$ were not plotted.

Results

Temperature regimes

Differences in germination percentages between the seed populations and between temperature regimes were highly significant (Table 4-2). The tested populations showed a distinct germination response (Fig. 4-2). Germination percentage increased in most populations just until a certain point, and decreased above the optimum. Most populations achieved the highest germination percentage at 10/20°C, but the highest germination in the population “Groß Rolübbe” (TlD1) occurred at 5/15°C, and for the populations “Bialowiza” (TlPL3), “Magrowo” (TlPL1) and “Szeremele” (TlH2) at 20/30°C. Overall germination percentages between 1 % and 67 % were obtained. The populations from Poland and the population “Szeremele” (TlH2) achieved only 7 % to 15 % as a maximum.

The differences in germination rate between the seed populations were significant (Table 4-2). Germination rate showed a marginal negative correlation to the germination percentage (Sperman´s r=-0.32) and a positive correlation to time till onset (Sperman´s r=0.8). The temperature regime affected the germination rate and onset significantly. The effect of population was significant but only small. Increasing temperatures accelerated germination generally (Fig. 4-2). But in four populations (TlPL1, TlPL3, TlH2, TlD3) an increase in mean temperature delayed germination.

The interaction of population and temperature was significant and was responsible for the significant difference between populations. When the factor population was tested on its own (data not shown) no significant difference could be detected.

Table 4-2: Result of the analysis of variance (ANOVA) testing the effects of temperature regime (temp) and population (pop) on the final percentage germination, the onset of germination and the germination rate. *** p <0.001.

		F		
	d.f.	Final percentage germination	Onset of germination	Germination rate
temp	3	63.7 ***	90.9 ***	106.4 ***
pop	14	35.8 ***	5.1 ***	3.2 ***
temp x pop	42	4.5 ***	2.5 ***	2.5***

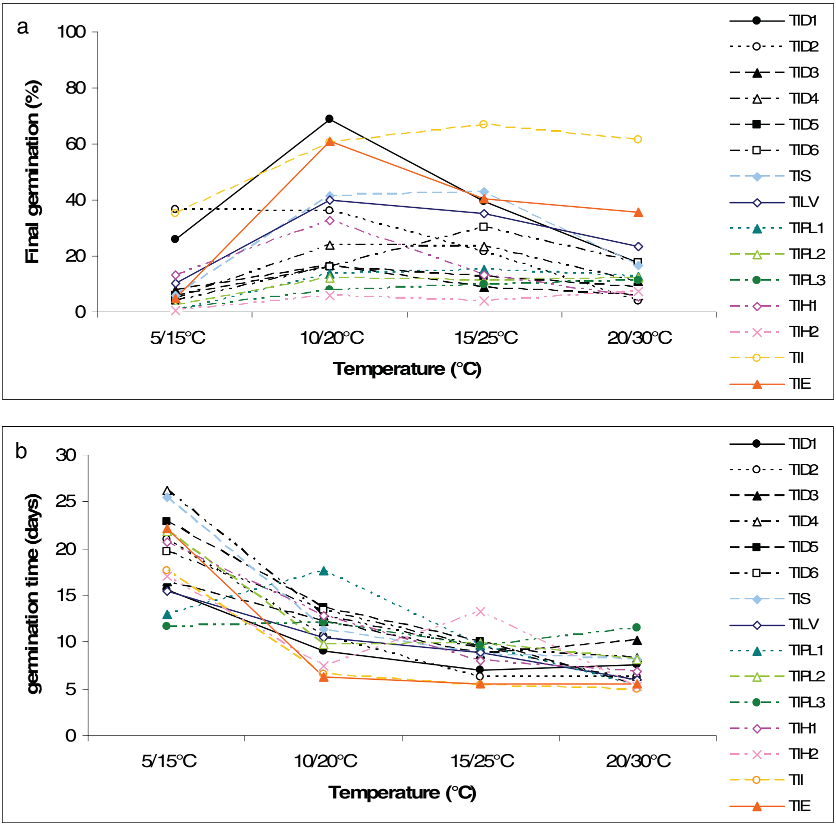

Figure 4-2: Final percentage germination (a) and germination rate (b) at different temperature regimes. Population abbreviations see Table 4-1.

Amplitude

Direct comparison of all measured parameters showed significant differences between populations and temperature regimes indeed (Table 4-3). But post-hoc tests revealed that temperature amplitude was significant only for two populations (TlD3, TlH2) for germination onset and for three populations (TlD3, TlD5, TlPL1) for germination rate. The increase in temperature amplitude from 10°C to 16°C resulted in an increase of final percentage germination. In seven populations this increase proved significant (Fig. 4-3).

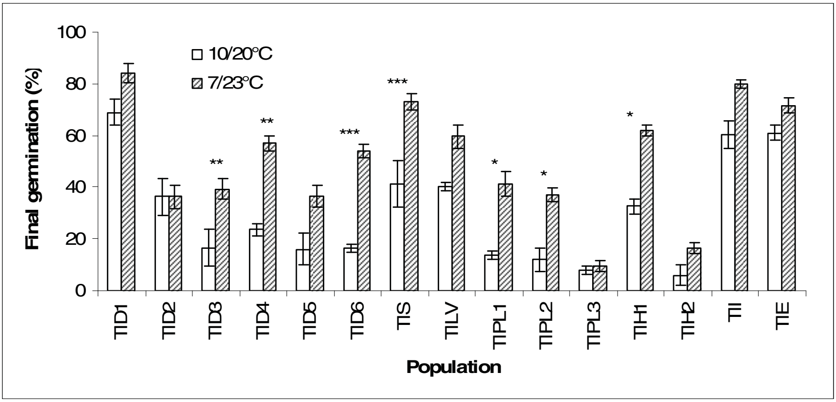

Figure 4-3: Comparison of final percentage germination (+/- 1 SE) of 15 populations of *T. latifolia* at alternating 10/20°C and 7/23°C. Population abbreviations see Table 4-1. Significant differences are marked * p <0.05, ** p <0.01, *** p <0.001.

Table 4-3: Result of the analysis of variance (ANOVA) testing the effects of different temperature amplitude at a mean temperature of 15°C (temp) and population (pop) on the final percentage germination, the onset of germination and the germination rate. *** p <0.001.

	d.f.	F Final percentage germination	Onset of germination	Germination rate
temp	1	141.8 ***	27.6 ***	89.5 ***
pop	14	36.7 ***	2.7 ***	10.6 ***
temp x pop	14	2.5 ***	2.6 ***	2.8 ***

Seed mass

The seed mass of the investigated *Typha latifolia* populations averaged between 0.04 mg/seed (± 0.0008 SE) for “Karlskron” and 0.06 mg/seed (± 0.0072 SE) for “Groß Rolübbe”. Post hoc testing proved significant differences only between the populations “Groß Rolübbe”, “Treviso”, “Linden” and “Lund”.

Interrelation of seed germination and origin

Geographical positions of the populations (latitude, longitude) were not correlated to any of the measured germination traits. Only altitude showed a weak correlation with germination onset (Tab. 4-4). Seed mass was not associated with any of the geographic or climatic variables, but was correlated to percentage germination at 5/15°C and onset of germination at different temperature regimes. Final germination percentage showed positive correlation to mean temperature and mean precipitation in January, and negative correlation to precipitation percentage in July. Germination onset at 7/23°C was negatively correlated to mean annual temperature, positively to temperatures in January. Onset at 10/20°C and 7/23°C showed a correlation to precipitation proportion in July. Germination rate showed some negative correlations to mean annual temperature, temperature and precipitation in January. Germination rate at the lowest temperature (5/15°C) was positively correlated with temperature in January and germination rates at 10/20°C and 15/25°C with precipitation percentage in July.

Table 4-4: Correlation coefficients (r, Spearman Rank) between germination variables and geographic and climatic variables and seed mass.
MAT - mean annual temperature, Jan °C - mean temperature in January, mm Jan – mean precipitation in January, % July - % of annual precipitation in July. n.s. - not significant.

Germination variable		Altitude	MAT	Jan °C	mm Jan	% July	Seed mass*
Percentage germination	5/15°C	n.s.	n.s.	n.s.	0.53	n.s.	0.83
	10/20°C	n.s.	n.s.	0.70	0.59	-0.71	n.s.
	15/25°C	n.s.	n.s.	0.66	0.54	-0.66	n.s.
	7/23°C	n.s.	n.s.	0.57	0.57	-0.57	n.s.
	Ø	n.s.	n.s.	0.70	0.56	-0.75	n.s.
onset	5/15°C	n.s.	n.s.	n.s.	n.s.	n.s.	-0.73
	10/20°C	n.s.	n.s.	n.s.	n.s.	0.54	n.s.
	15/25°C	0.57	n.s.	n.s.	n.s.	n.s.	n.s.
	7/23°C	n.s.	-0.58	0.65	n.s.	0.62	-0.65
	Ø	n.s.	n.s.	n.s.	n.s.	n.s.	-0.65
Germination rate	5/15°C	n.s.	n.s.	0.54	n.s.	n.s.	n.s.
	10/20°C	n.s.	n.s.	n.s.	n.s.	0.60	n.s.
	15/25°C	n.s.	-0.55	-0.65	-0.55	0.68	n.s.
	7/23°C	n.s.	-0.66	-0.65.	n.s.	n.s.	n.s.

*only populations with calculated seed mass included (see table 4-1)

The first two axes of the ordination biplot explained a total of 61.2 % of the variation in all variables among the 15 *T. latifolia* populations (Fig. 4-4). Axis 1 of the ordination accounted for 49.7 % of the variation, whereas 18.5 % of the variation was attributed to axis 2. Mean final germination percentage (r^2=0.95), germination percentage at various temperature regimes and germination rate at 15/25°C (r^2=0.72) were strongly correlated to the axis 1. The highest correlations with axis 2 showed onset at 20/30°C (r^2=0.81). The ordination arranged the populations corresponding approximately with the climate types. Longitude had the strongest correlation with axis 1 (r^2=0.16) and axis 3 (r^2=0.20) of all tested geographical variables.

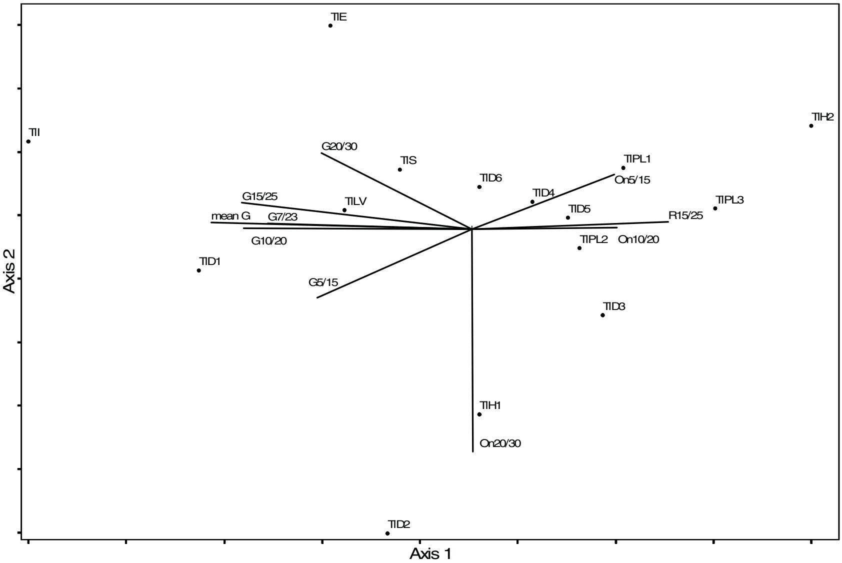

Figure 4-4: Biplot showing association of seed attributes and seed germination characteristics based on principal components analysis (PCA). Population abbreviations see Table 4-1.
G - final percentage germination, R - germination rate, On - germination onset at the respective temperature, mean G - mean percentage germination over all temperature regimes.

Discussion

Temperature requirements

In seasonal climates temperature is a good indicator for time of year (FENNER & THOMPSON 2005) and is employed in triggering germination in times and places where conditions for seedling establishment are favourable.

Typha latifolia seeds were able to germinate at all tested temperature regimes, even though germination percentage overall was low (7/23°C: 48.2 % ± 2.3 SE) compared to other studies (BONNEWELL et al. 1983; LOMBARDI et al. 1997). Germination percentage and germination time were differently affected by temperature regime.

An increase in temperature increases percentage germination (BONNEWELL et al. 1983; LOMBARDI et al. 1997, EKSTAM & FORSEBY 1999). The increase in mean temperature from 10 to 15°C triples the germination percentage. In accordance with this study EKSTAM & FORSEBY (1999) described an increase in percentage germination just until a certain optimal temperature and a decrease at higher temperatures. In contrast BONNEWELL et al. (1983) and LOMBARDI et al. (1997) examined the highest percentage germination at the highest tested temperature.

A fast germination and establishment of seedlings may give a competitive advantage and enables to colonise mudflats during temporal draw-downs (GRACE 1987; SHIPLEY et al 1989). The first *Typha* seeds germinate within one to two days at suitable temperatures (LOMBARDI et al. 1997; EKSTAM & FORSEBY 1999). In contrast to percentage germination germination time showed a linear increase with temperature in this study. An optimum, as QIU et al. (2010) detected for Canadian populations of *Festuca hallii*, was not obtained within the tested temperature range.

In many wetland species alternating temperatures promote germination (FENNER & THOMPSON 2005). Diurnally alternating temperatures will indicate low water levels and will therefore serve as depth sensing (THOMSON & GRIME 1983) and season sensing (FENNER & THOMPSON 2005) mechanisms. Increasing amplitude from 10 to 16°C at a mean temperature of 15°C increased the germination percentage significantly. EKSTAM & FORSEY (1999) showed that the effect of amplitude is more pronounced in low mean temperatures than in high (>20°C). The influence of temperature amplitude on germination time was small but significant. Consistently with the results of EKSTAM & FORSEBY (1999) onset of germination was accelerated about 4 days at 16°C amplitude.

Population origin

Large differences in germination traits were found between the 15 populations of *Typha latifolia*. Germination percentage differed by factors 10 to 100, germination time by factors 2 to 3 between populations. Similar or smaller differences between populations of different species were found by MCNAUGHTON (1966), GREIPSSON & DAVY (1995), MCKEE & RICHARDS (1996) and BISCHOFF et al (2006). QIU (2010) discovered only minor differences in percentage germination of *Festuca hallii* but a larger variation in germination time. The largest differences in percentage germination in *Typha* occurred in the lowest temperature regime tested, an effect also detected by SCHMUTHS et al. 2006 for the germination of *Arabidopsis thaliana*.

The different ranking of the populations across various temperature regimes indicates an adaptation in germination traits to specific habitat conditions. A link between germination requirements and habitat was found in different studies. In a study on *Typha latifolia* on a north-south transect in North America MCNAUGTHON (1966) observed that seeds from populations from milder climates germinated at lower temperatures. QIU et al. (2010) found an adaptation to local environment along a west-east precipitation gradient in Canada for *Festuca hallii*. On the other hand MCKEE et al. (1996) were not able to detect a correlation between seed set or germination and local climate for European *Phragmites australis* populations.

As for *Phragmites* (MCKEE et al. 1996) this study showed only a partial correlation of the tested climate parameters to germination traits of *T. latifolia*. Mean annual temperature showed only a correlation to germination rate at 15/25°C, temperatures in January were correlated to different germination traits. The temperature regime with the highest percentage germination was not linked to mean annual temperature as stated for populations in North America (MCNAUGHTON 1966). But the ordination analysis of germination traits arranges population approximately to climate type. The Mediterranean populations, “Treviso” (TlI) and “Escalona” (TlE), showed both high germination percentage (mean 51.6 %) and fast germination. The second highest and fastest are the oceanic populations situated around the Baltic Sea (“Lund” TlS, “Aumeistezi” TlLV, “Groß Rolübbe” TlD1). Lower percentage germination and slower germination were expressed by the sub-continental and continental populations. These show relatively low percentage germination at 5/15°C and a pronounced increase in germination with an increase in temperature. The sub-oceanic population “Beetz” (TlD2) does not fit into the pattern with the fastest germination at all temperature regimes (mean onset day 7) and a high germination percentage at 5/15°C (36.6 %).

The distance between populations does not affect the extent of variation between populations in *Typha* as found for other species (KELLER & KOLLMANN 1999). Populations “Donaumoos 1” (TlD5) and “Donaumoos 2” (TlD6), only 200 m apart, are as different in germination as populations from origins more than 2000 km apart. Probably microclimate, nutrient supply (MIAO et al. 2000) or founder effects play a more important role than regional climate.

The linkage of germination traits and habitat conditions can rely on genetic as on non-genetic (maternal effects) sources of variation. Studies on isoenzyme patterns and DNA markers of *Typha* discovered a low genetic variability within and between populations in North America (MASHBURN et al. 1978; SHARITZ et al. 1980; KEANE et al. 1999; ZHANG et al 2008). However, KEANE et al. (1999) was able to link genetic variation to environmental pollution and examined higher genetic heterogeneity at polluted sites. For European *Typha* populations LAMOTE et al. (2005) detected differences in DNA-marker frequencies between different river basins in Flanders. Among Ukrainian populations TSYUSKO et al. (2005) found distinct genetic differences and even proved a weak correlation between genetic and geographic distance of *T. latifolia* using DNA microsatellite techniques. For *Phragmites australis*, another clonal emergent wetland plant with similar habitat requirements and wide distribution LAMBERTINI et al. (2008) postulated a possible continent wide ´single meta-population´ in Europe on the base of extensive AFLP analysis. As *Phragmites Typha* produces small, wind dispersed seeds and is wind pollinated which could enable long-distance genetic exchange.

Different environmental maternal effects on seed germination have been discovered (GUTTERMAN 2000). Seed mass is known to be largely effected by the maternal environment and studies proved a positive correlation between seed mass and germination percentage (GREIPSSON & DAVY 1995). The correlation between seed mass and percentage germination (at 5/15°C) and germination time indicates a positive effect of seed mass on germination speed. But seed masses of the tested populations showed only low variability. The correlation of site temperature to germination traits and especially the fact that both Mediterranean populations showed high germination percentage suggests an effect of environmental temperatures at seed maturation on the mother plant on germination percentage (BASKIN & BASKIN 1998). To determine whether the variation in germination responses found is due to genetic or maternal effects, F1 seeds produced under homogenous conditions have to be used (BASKIN & BASKIN 1998; BISCHOFF et al.2006).

Conclusions

This study demonstrates that temperature requirements for the germination of *Typha latifolia* differ considerably between European populations. The big difference between close neighbouring populations assumes a great influence of habitat conditions and microclimate on germination traits. Percentage germination is affiliated to mean temperature in winter and precipitation in July. Seed mass primarily is correlated to germination speed and germination percentage at inadequately low temperatures. An increase in temperature as predicted for the future decades would improve germination of *T. latifolia* and a potential shift in population distribution may unbalance plant communities by enhancing colonisation by *Typha*. Especially alien populations when facilitated to colonise new habitats may become invasive (SALTONSTALL 2002; KETTENRING et al. 2010). On the other hand the predicted increase in extreme climate events in combination with increasing temperatures will affect water levels and frequency of draw-downs and increase the frequency of colonisation events of *Typha* sp. in wetlands.

Acknowledgments

Thanks are due to Solvita Jermacane, John Strand, P. Cantó, Dóra Steták, Torsten Seeger, Francesco Scaraton, Iwona Paszek and Werner Theuerkorn for collecting seeds.

5 Seedling growth in the macrophyte species *Typha latifolia* and *Typha angustifolia*

Introduction

\`Recruitment´ describes the development from a resilient seed to an established, reproductive individual including germination and the seedling stage (GRUBB 1977). Microhabitats exploited by juveniles may be quite different from those experienced by adult plants (GRIME & HILLIER 1992). GRUBB (1977) established the concept of the regeneration niche, focussing on the factors influencing the development from seed to recruit. In some plant communities recruitment is widely limited to exceptional conditions as created by fire in grasslands (e.g. ZIMMERMANN et al. 2008) or draw-downs in aquatic systems (e.g. GALINATO & VAN DER VALK 1986; SEABLOOM et al. 1998). Thus adult and regenerative niches are uncoupled to some extent (GRUBB 1977; SHIPLEY et al. 1989). In aquatic plant communities water-level is a key factor structuring not only vegetation zonation (COOPS & VAN DER VELDE 1995; LENSSEN et al. 1998; SEABLOOM & VAN DER VALK 2003), but controlling invasions of wetlands by supporting or hindering seedling establishment (WEI & CHOW-FRASER 2006; BOERS et al. 2007).

Typha latifolia L. and *T. angustifolia* L. are emergent wetland plants native to Europe with a distribution in the temperate northern hemisphere. They are tall erect perennials with long linear leaves and flower spikes (GRACE & HARRISON 1986). Their habitat ranges from temporary floodplains, ditches, ponds and lakes to slow flowing rivers. Because of their extensive distribution and commonness *Typha* communities form an important and widespread wetland type under more eutrophic conditions. *Typha* species colonize new sites by seed dispersal (GRACE & HARRISON 1986). Due to a high production of small, wind dispersed diaspores new habitats can easily be reached. Established plants spread rapidly by rhizomes over large areas (FIALA 1978) to form dense mono- or oligo-specific populations.

Germination of *Typha* sp. is furthered by moderately increased water levels (COOPS & VAN DER VELDE 1995; cp. chapter 3), and water-level fluctuations with prolonged flooding caused Typha x glauca dominated wetlands in North America (BOERS et al. 2007). In the adult phase GRACE & WETZEL (1981 a, 1998) observed *T. angustifolia* being displaced into deeper water by *T. latifolia* along a water level gradient. In an experiment with *T. latifolia* and *T. domingensis* seedlings GRACE (1985) detected a higher biomass production in mono-cultures in *T. latifolia* in deeper water.

Competitive success of the species at different water levels differed between the seedling phase, where *T. latifolia* was superior, and adult phase (GRACE 1985).

In a greenhouse experiment the effect of three different water-levels on seedling growth was tested (1) to investigate differences in shoot height and biomass development, and (2) to examine variations in the establishment capacity of *T. latifolia* and *T. angustifolia*.

Methods

Ripe spikes of *Typha latifolia* and *T. angustifolia* were collected at maturity (December and January) in a fen area in southern Germany (48°42´N; 11°11´E). The air dry spikes were stored at room temperature till the start of the experiment in March.

Three-week-old seedlings raised from seeds incubated in containers filled with unfertilised breeding substrate where planted individually in 8 x 8 x 8 cm³ PVC pots filled with the same substrate. Three water depth treatments were applied: moist (soil kept saturated), surface (water depth maintained at soil surface) and flooded (water depth maintained 12 cm above soil surface). Seven pots per species were randomly placed in twelve containers and the containers were arranged in blocks in the greenhouse (minimal 20 °C day/10°C night). Every water depth treatment was replicated twice. Extra light was provided for 16 hours daily by Philips SON-T Agro 400 W tubes situated 140 cm above the soil surface. Two days after transplanting the seedlings, water levels were gradually raised over three days until the designated water depth was reached. During these five days dead plants were replaced. Water was circulated continuously by aquarium pumps and changed completely once a week. After the second week containers were refilled with a diluted (1:10) nutrient solution with 21.2 mg l^{-1} N, 3.2 mg l^{-1} P, 23.4 mg l^{-1} K and 0.1 mg l^{-1} Fe (HOAGLAND No 2).

Survival of the seedlings and the length of the plant from the shoot base to the tip of the longest leaf were measured every second week. After 11 weeks all plants were harvested and dry weight biomasses of above-ground and below-ground parts were determined after drying at 85 °C. The effect of water level and species on survival, shoot height after 11 weeks and biomass per plant was tested by a two-factorial Analysis of Variance (ANOVA). No significant block effects were revealed in the experiment, wherefore they were neglected in the computations.

Results

In the flooded treatment the whole seedlings became submersed and developed fragile, floating leaves. Under exposed conditions (saturated and surface) the seedlings produced erect leaves. Differences in the capacities of the *Typha* species to grow at different water depth treatments were demonstrated by the development of shoot length (Fig. 5-1). While shoot growth increased in *T. angustifolia* with increasing water depth, seedling growth of *T. latifolia* decelerated after week four under flooded conditions and at the end of the experiment seedlings grown with the water level at the soil surface were taller than seedlings from the flooded treatments. Pooled over all treatments *T. latifolia* attained a higher shoot length (30.3 cm) than *T. angustifolia* (26.9 cm), but only water level had a significant effect on shoot height at the end of the experiment (Tab. 5-2).

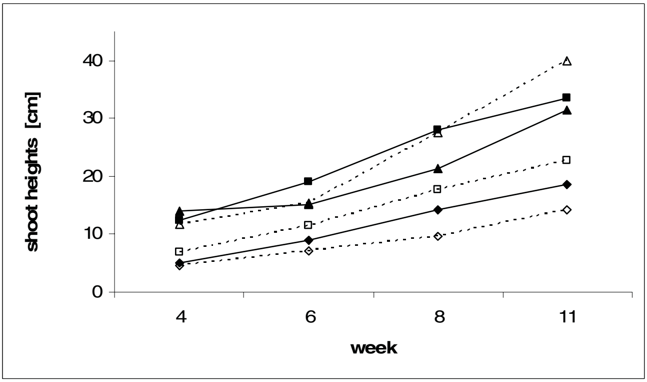

Figure 5-1: Development of shoot height of *T. latifolia* (solid symbols) and *T. angustifolia* (open symbols) at different water level treatments. Moist – diamante, surface – square, flooded – triangle.

The species differed significantly in the number of surviving plants (Tab. 5-2). While in *T. latifolia* twelve to thirteen seedlings were able to establish, the mortality was higher in *T. angustifolia* seedlings and only nine to ten survived (Tab. 5-1). Differences between water-level treatments were only minor and proved not significant.

Table 5-1: Number of established *T. latifolia* and *T. angustifolia* plants after 11 weeks of 14 planted seedlings.

	moist	surface	flooded
T. latifolia	13	13	12
T. angustifolia	10	10	9

The final biomasses differed between the water levels and the species (Tab. 5-2). *T. angustifolia* and *T. latifolia* produced the highest total biomass with the water level at the surface. A further increase of water level reduced biomass production (Fig. 5-2). The proportion of below-ground biomass after eleven weeks decreased with increasing water levels.

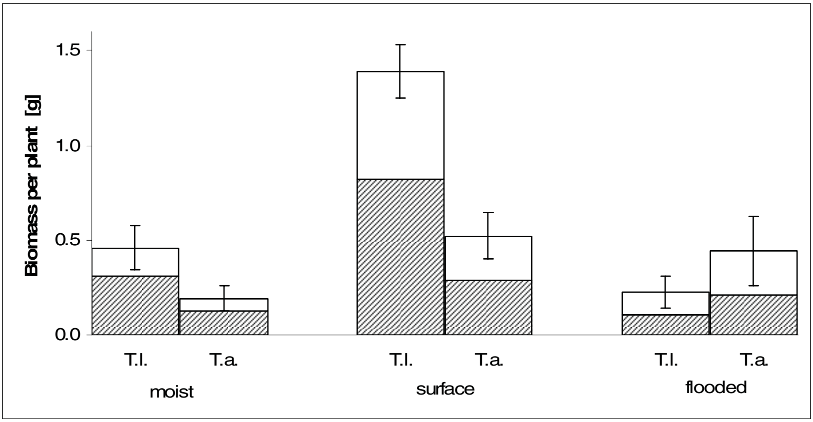

Figure 5-2: Total biomass per plant (± 1 SE) divided in below- (hatched) and above-ground (white) proportion of *T.latifolia* (T.l.) and *T. angustifolia* (T.a.) at different water level treatments.

Table 5-2: Results of the Analyses of Variance (ANOVA) on the effect of species and water level (Wl) on shoot height after 11 weeks, total biomass per plant and seedling survival. * $p< 0.05$

	df	Shoot height (week 11) F	Biomass F	Survival F
Water level	2	31.3 *	16.9 *	0.6
Species	1	1.2	8.7 *	11.6 *
Wl*Species	2	8.4 *	9.5 *	0.0

Discussion

Environmental requirements for germination and seedling establishment can differ conspicuously in scale from the requirements of an adult plant (HARPER 1977). Differences between wetland plant species concerning these early life-history components may contribute to the zonation of helophyte vegetation over the water depth gradient along water bodies (GALINATO & VAN DER VALK 1986; COOPS & VAN DER VELDE 1995; LENSSEN et al. 1998) and influence long-term population development by the pre-emption of competitors (GRACE 1987; BOERS et al. 2007).

The shoot heights and the biomass of *T. latifolia* and *T. angustifolia* were affected by the water depth treatment, while survival showed no significant difference between water depths. Water depth can constrain plant growth by limiting the availability of atmospheric carbon and oxygen. Emergent macrophytes adjust to water depth through elongation of the shoot to maintain an emergent canopy (GRACE 1989; BLANCH et al. 1999). *T. latifolia* and *T. angustifolia* reacted with an increase of shoot heights and the production of fragile floating leaves to the increase in water depth. But while *T. angustifolia* was able to develop higher shoots in the flooded treatment, the growth of *T. latifolia* decreased under flooded conditions at the height of the water level in week six and only attained the height of the shoots in the saturated treatment at the end of the experiment. The long submerged leaves are sensitive to desiccation and would not survive drainage (BEDISH 1967; COOPS & VAN DER VELDE 1995). COOPS & VAN DER VELDE (1995) detected in seedlings of both species the longest leaves in the permanently flooded treatment (10 cm), though their experiment ended after six weeks.

Parallel to shoot height, the biomass production was increased by the surface water level treatment, but species differ significantly in their reaction. While *T. latifolia* showed a distinct peak of biomass at the surface treatment and the lowest biomass under flooded conditions, *T. angustifolia* produced nearly the same amount of biomass at the surface and flooded treatment. Comparable results were achieved by COOPS & VAN DER VELDE (1995). In *T. angustifolia* the above-ground seedling biomass was higher under flooded than under exposed conditions, while *T. latifolia* developed a higher biomass in the exposed treatment (COOPS & VAN DER VELDE 1995). Comparing the species, as in the present study, biomass production of *T. latifolia* was higher in the exposed, the biomass of *T. angustifolia* in the flooded conditions (COOPS & VAN DER VELDE 1995). In a competition experiment with native and invasive wetland plants HAGER (2004) also measured higher biomass production in *T. latifolia* compared to *T. angustifolia*. *T. latifolia* even exceeded the biomass production of *Lythrum salicaria*, and in consequence was less suppressed by the existing vegetation and had a higher success in establishment than *T. angustifolia* (HAGER 2004). The water level had no effect on the number of surviving seedlings. KEDDY & ELLIS (1985) found different recruitment responses to a water level gradient reaching from 5 cm below soil surface to 10 cm above soil surface in eleven wetland species. While six species were influenced in germination and seedling growth by the water level according to their adult niche, the other species, among them *T. angustifolia,* showed a mainly equal recruitment rate over all treatments (KEDDY & ELLIS 1985).

Generally, species from the upper shoreline prefer low water levels for recruitment, while emergent species tolerate higher water levels (KEDDY & ELLIS 1985; COOPS & VAN DER VELDE 1995; LENSSEN et al. 1998). Especially in small seeded species providing the seedling only with few resources, as *Typha* sp., seedlings need to elongate rapidly and start photosynthesis to support further development. In deep water seed resources would be exhausted before water surface is reached. Germination is therefore triggered by alternating temperatures, which indicate low water levels (FENNER & THOMPSON 2005, cp. chapter 3). Critical for recruitment success is the absolute water depth. While a water level at the soil surface provides continuous water supply for the seedlings, higher water levels impede development (WEI & CHOW-FRASER 2006; cp. chapter 7). While the growth of *T. latifolia* seedlings was already constrained by a flooding of 12 cm, *T. angustifolia* seedlings tolerated flooding. Under competitive conditions water level probably would be a key factor determining recruitment success between *T. latifolia* and *T. angustifolia*.

6 Growth dynamics and demography of shoots of the clonal macrophytes *Typha latifolia* and *Typha angustifolia*

Introduction

Vegetative reproduction occurs in the majority of herbaceous perennial plants. Especially aquatic, forest floor and grassland plant communities are dominated by clonal plant species (GRIME et al. 1988). In many species sexual reproduction and seed dispersal mainly plays a role in the colonisation of new habitats or for re-colonisation after disturbance (SHIPLEY et al. 1989). After the establishment the area is colonised by vigorous vegetative growth, often forming extensive virtually pure stands with a high level of stability (HUTCHINGS 1979). Especially among competitive, dominant and alien invasive species extensive clonal growth prevails (ZEDLER & KERCHER 2004; LIU et al. 2006; XU et al. 2010).

Clonal plants possess the capacity to share resources such as water, photosynthates and nutrients among individual subunits (ALPERT 1996; HUTCHINGS et al. 2000). Thus clonal integration may facilitate the colonisation and growth of ramets in habitats with low resource availability or adverse conditions and promote recovery after biomass loss (AMSBERRY et al. 2000; Liu et al. 2006). The degree of physiological integration differs between clonal species and between life stages (SCHMID & BAZZAZ 1987; HARA et al. 1993; XU et al. 2010). An individual clonal plant (genet), derived from a single seed, produces several vegetative progeny (ramets) connected by runners, rhizomes etc. (HARPER 1977; COOK 1985). The ramets form functional sub-units, becoming independent after the connections to the mother plant decayed. The underlying identity of genets in natural populations is usually unknown (Cook 1985). Studies on the genetic variation of clonal stands provide some evidence of clone size and genet frequency (LAMOTE et al. 2005; KETTENRING et al. 2010), but the complete mapping of individuals based on DNA-analysis is only possible in small scale investigations (ARAKI et al. 2009). Employing the concept of the ´plant as population of parts´ (HARPER 1977), investigating rather the dynamic of the constructional modules than the whole individual, the demography of ramets in terms of birth and death rate and age structure could be studied keeping in mind differences caused by clonal integration and genetic stand structure.

After the first phase of colonisation with an almost exponentially growth rate, populations become denser and competition increases (HARPER 1977, DEKROON 1993). The course of shoot competition is experienced differently by non-clonal and clonal plants. While in non-clonal plants high population densities result in asymmetric competition, with size dependent mortality (self-thinning), growth in clonal plants is regulated by clonal integration (HARPER 1977; COOK 1985). The physiological integration effects a reduction of the production of new shoots as density increases (density dependent natality), prevents over-production (DEKROON 1993), and would ideally regulate the development of new shoots to shoot densities close to the carrying capacity of the environment (HUTCHINGS 1979). Besides mortality and natality, the biomass allocation to the production of daughter ramets and sexual reproduction could be density dependent (OGDEN 1974; VAN KLEUNEN et al. 2001).

In this study the growth and demography of shoots of the clonal wetland plants *Typha latifolia* and *T. angustifolia* is addressed, focussing on the colonisation and early stand development in a new habitat. *Typha* communities form an important and widespread wetland type under more eutrophic conditions. *Typha latifolia* and *T. angustifolia* are native to Europe with a distribution in the temperate northern hemisphere (GRACE & HARRISON 1986). Both are erect, rhizomatous perennials (STACE 1997), forming mono-dominant stands. In summer numerous small, wind-dispersed diaspores develop. Established plants spread rapidly by lateral rhizomes produced at the base of the leaves. One individual plant (genet) of *T. latifolia* can produce up to 46 new daughter shoots (ramets) in the first growing season (FIALA 1978). Polycormones can cover up to 16 m² at the end of the first growing season (FIALA 1978). In autumn nutrients are stored in the underground rhizome (GARVER et al. 1988). While generative shoots complete their growth with flowering and die after reproduction, some vegetative shoots survive winter and show re-growth in spring (DICKERMAN & WETZEL 1985).

Population development of *T. latifolia* and *T. angustifolia* were studied in a constructed wetland in southern Germany. By marking every shoot individually according to its date of emergence and monitoring its developmental state, the stand age and state structure were investigated, under comparable soil and water conditions and virtually excluding inter-specific competition. This way the stand-structure and the demography can be investigated from the perspective of the development of the individual shoot, as well as in terms of proportion of shoots in the stand.

The objectives of the study were (1) to investigate the velocity of the colonisation of a new habitat by *T. latifolia* and *T. angustifolia*, (2) to examine the stand-structure and demography of both species and (3) to test whether the fate of a shoot to become generative depends on population traits as stand density or heights and can be predicted from them.

Methods

Study site

Populations of *T. latifolia* and *T. angustifolia* were investigated in a constructed wetland in the Donaumoos, an extensive fen area 80 km north of Munich (Germany, 48°42´N, 11°11´E). The study site was one of three basins established to investigate the cultivation of *Typha* sp. as a renewable resource in degraded fen areas. The experimental basin was built by removing the top-soil and creating a dyke with the material. The area of 22.000 m² was planted with *T. latifolia* (approx. 18000 m²) and *T. angustifolia* (approx. 4000 m²) at a density of two shoots/m² in June 1998. The basin was supplied by nutrient rich water from a drainage ditch with a permanent flow rate of 10 l/s, the water level was fixed to 0.4 m (cp. chapter 7).

Aerial biomass was harvested in late winter 1999/2000 for the first time. Due to not permanently frozen soil and heavy harvest machinery with caterpillar drive, soil and plant rhizomes were damaged especially at gateways and turning radii. *T. latifolia* stands were affected more seriously because of the spatial distribution of the experimental sites. The second harvest in winter 2000/2001 was conducted with light-weight machinery with balloon tyre on completely frozen soil and caused minor to no damage to soil and plants.

Population development

In the planted stands of *Typha latifolia* and *T. angustifolia* 36 plots of 1 x 1 m² were installed. *Typha* shoots (ramets) were counted and individually marked with a coloured label in August and October 1998 and in monthly intervals during the vegetation seasons (April to October) 1999 and 2000. In 2001 the censuses were conducted only in April, May and August. The shoot cohorts were labelled according to their month of emergence. Additionally to the number of shoots of every colour labelled cohort, the developmental state of the shoot as vegetative, generative or dead and the mean heights of each cohort was recorded at every census date.

Shoot height was measured from the soil floor to the tip of the standing leaves. All shoots without colour label were classified as members of the cohort of the respective census date (new shoots). To follow the individual fate of a shoot all shoots on a 0.25 m² sub-plot of every 1 m² were labelled additionally with a numbered tag and the individual developmental state and height was recorded at every census date.

Data analysis

Differences between the species in stand density, growth rate, stand heights and percentage of generative and dead shoots in the different years were analysed separately with one-way analysis of variance (ANOVA). Differences in shoot height between states, census dates and species were tested by factorial ANOVA. Post hoc testing was done by the Tukey (HSD) test.

The relationships between the population traits, shoot density in May, the number of new shoots produced from May to October, the shoot height in May, the shoot heights increment from May to August, the probability of shoots to become generative till the end of the season and the probability of shoots to die till August were tested for each species individually by the Spearman-Rank Correlation.

Multiple regression was used to test the effects of shoot density and shoot height in May, the number of new shoots per year and the shoot heights increment from May to August on the probability of shoots to become generative till the end of the season.

All tests of significance were done at a predetermined level of significance of $p<0.05$.

Results

Stand development

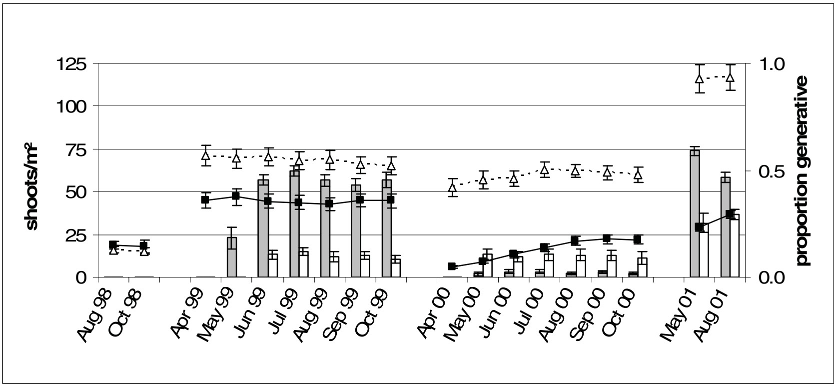

Figure 6-1: Development of shoot density (shoots/m²) and proportion of generative shoots (columns, right axis) of *Typha latifolia* (squares / grey columns) and *T. angustifolia* (triangles / white columns) three seasons after stand establishment in June 1998. Means ± 1SE.

The plantlets of *Typha latifolia* and *T. angustifolia* displayed fast clonal growth and colonized the surface rapidly. Within three months a dense stand with 16 to 19 shoots/m² had developed (Fig 6-1, 6-2). In the following spring stands were built up by re-grown shoots from the first year and newly emerged shoots (Table 6-2). One year after stand establishment *T. angustifolia* developed stand densities of up to 68 shoots/m². *T. latifolia* showed a significantly lower shoot density (42 shoots/m²; Tab. 6-1), but started flowering by the end of May. While 50 % of *T. latifolia* shoots became generative till July 1999, only 12 % of the *T. angustifolia* shoots flowered in 1999 (Fig. 6-1).

Table 6-1: Result of the analysis of variance (ANOVA F) testing the differences between *T. latifolia* and *T. angustifolia* in shoot density in May and August, the relative growth rate, shoot heights in August and the proportion of generative and dead shoots in the stand.
n.s. - not significant, * - p< 0.05, ** - p < 0.01, *** - p < 0.001.

	1998	1999	2000	2001
Shoots/m² in May	-	6.9 *	147.9 ***	191.2 ***
Shoots/m² in August	n.s.	13.7 **	73.4 ***	174.5 ***
Relative Growth rate	n.s.	25.4 ***	5.6 *	n.s.
Shoot heights in August	-	22.5 ***	46.0 ***	234.9 ***
% generative shoots	-	73.2 ***	18.9 ***	17.7 ***
% dead shoots	-	n.s.	6.2 *	4.3 *

Because of rhizome-damages by the first harvest of the stand in late winter 1999/2000 the re-establishment in 2000 was delayed especially in *T. latifolia*. Starting from only 6 shoot/m² in April, shoot numbers more than tripled until autumn (22 shoots/m²), but could not gain the densities of the first season till the summer of 2001 (37 shoots/m²). While only few shoots of *T. latifolia* flowered in summer 2000 (3 %), the proportion of generative shoots increased in 2001 (57 %). Suffering less damage by harvest in winter 1999/2000 *T. angustifolia* obtained shoot densities of 63 shoots/m² in summer 2000, increasing to 117 shoots/m² in summer 2001. In 2001, the third season after establishment, even the proportion of generative shoots showed a significant increase in *T. angustifolia* (29 %) (Tab. 6-1).

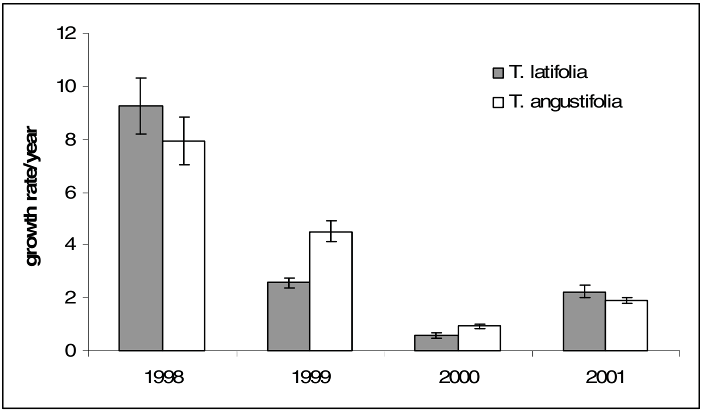

Figure 6- 2: Development of the yearly relative growth rate (Nt+1/Nt) of *Typha latifolia* and *T. angustifolia* from the establishment of the stand in 1998 to the year 2001. Means ± 1SE.

Development of individual shoots

In the 0.25 m² sub-plots altogether 1055 *T. latifolia* and 644 *T. angustifolia* shoots were marked in the years 1998, 1999 and 2000.

In *T. latifolia* the shoot height of individual shoots differed according to shoot fate. Shoots becoming generative in the course of the season showed a greater height already in May than shoots staying vegetative throughout the season (Fig. 6-3). In 1999 shoot height did not increase from May to August. Shoots dying before autumn were always the smallest. The shoots of *T. angustifolia* were higher than the *T. latifolia* shoots. Shoot height in May did not differ between shoots becoming generative or staying vegetative. While generative shoots showed no increase in shoot height from May to August 1999, the vegetative shoots grew in size.

The life span of the individually marked shoots varied widely from shoots classified dead at the date of emergence to 426 days. Because of the overall low emergence of *T. angustifolia* shoots in the cohorts succeeding April 1999 (Tab. 6-2, Fig. 6-4), no shoots emerged in the 0.25 m² sub-plots. The cohorts differed in life span. The shoots which emerged in the first month of colonisation had the longest life expectancy, in the following years life expectancy decreased in the course of the year (Fig. 6-4).

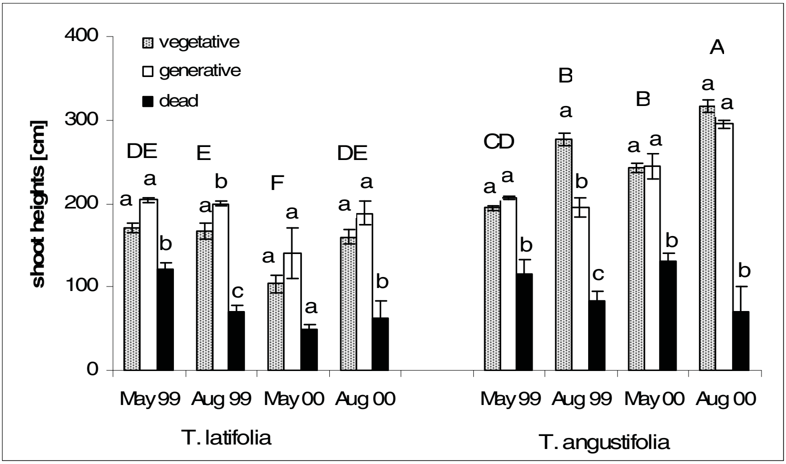

Figure 6-3: Shoot heights (cm) of individual shoots of *Typha latifolia* and *T. angustifolia* in May and August of two successive seasons after stand establishment classed by the fate of the shoot (state) in August of the respective year. Small letters indicate significant differences between states at the same census in *T. latifolia* or *T. angustifolia* respectively. Capital letters indicate different mean height between census and species. Means ± 1SE.

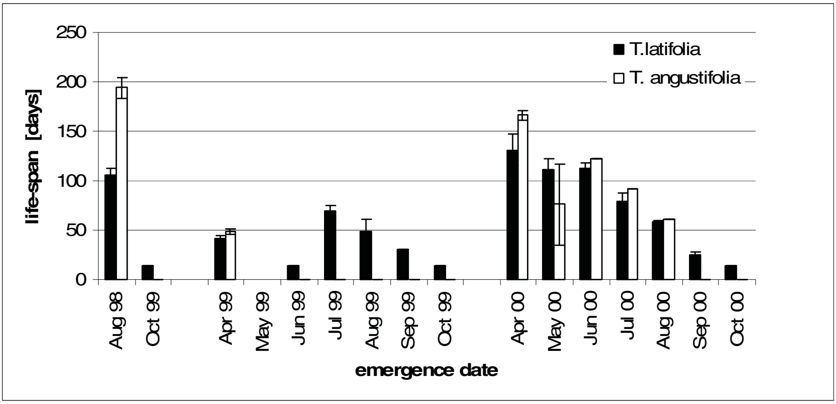

Figure 6-4: Mean life span (days) of different shoot-cohorts of *Typha latifolia* and *T. angustifolia* from stand establishment in 1998 to the year 2000. Means ± 1SE.

Shoot emergence

Most shoots of the years 1999 and 2000 emerged in the month April (Fig. 6-5). All following months showed only a very low shoot emergence in 1999 with a maximum of three new-shoots/m² per month. While shoot emergence of *T. angustifolia* in both years followed the same pattern, the shoot emergence of *T. latifolia* varied between the years. In April 1999 30 new-shoots emerged, but in 2000 only 5 new-shoots/m² developed. In the year 2000 the emergence of 3 to 4 new shoots per month continued till October when the development of new shoots ceased.

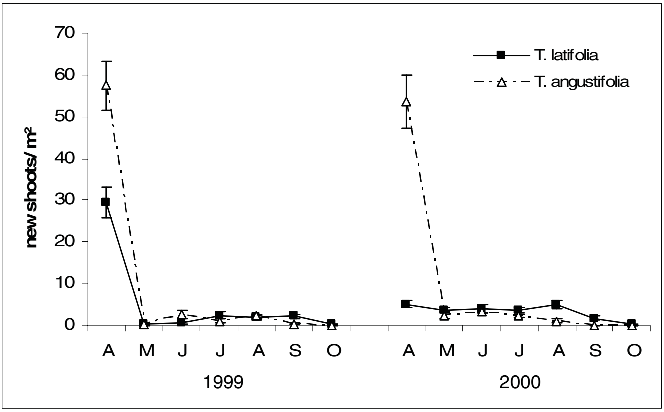

Figure 6-5: Mean number of new shoots per m² per month of *T. latifolia* and *T. angustifolia* from April 1999 to October 2000. Means ± 1SE.

Age structure and shoot fate

Shoots emerged in April formed the majority of the shoots of one year, followed by shoots re-grown from the year before (Table 6-2). Because of the harvest beneath the water level in winter 1999/2000 any re-growth could not be discriminated from new shoots in spring 2000 and all shoots were assigned to the April cohort. While in *T. angustifolia* only 7 to 14 % of the shoots resulted from cohorts later than April, these cohorts had a share of 16 to 82 % in *T. latifolia*.

Whereas in general the shoot-age is related to shoot-fate, both species showed differences in the proportion of generative and dead shoots in the different cohorts.

In *T. angustifolia* only re-grown shoots and shoots from the April cohort had a chance to become generative. In *T. latifolia* even shoots just emerged in July started to flower.

Also the proportion of dead shoots in the end of the year differed between the species. While in *T. latifolia* only shoots of the May to October cohorts stayed vegetative and alive to a greater proportion, in *T. angustifolia* 70 to 80 % of the April and even some of the re-grown shoots were alive in October.

Table 6- 2: Age structure of *T. latifolia* and *T. angustifolia* stands in autumn and developmental state composition of each cohort in the years 1999 and 2000. The row ´total´ presents the cohort composition of the stand in the end of the year. The columns show the proportions of vegetative, generative and dead shoots in the respective cohort.

cohorte			regrowth	Apr	May	June	July	Aug	Sep	Oct
T. latifolia	1999	total	0.24	0.60	0.00	0.01	0.05	0.04	0.05	0.01
		vegetative	0.01	0.23	1	0.67	0.4	1	1	1
		generative	0.45	0.52	0	0	0.31	0	0	0
		dead	0.54	0.25	0	0.33	0.29	0	0	0
	2000	total	0	0.18	0.15	0.19	0.18	0.22	0.06	0.01
		vegetative		0.21	0.52	0.85	0.98	0.97	1	1
		generative		0.11	0	0	0	0	0	0
		dead		0.68	0.48	0.15	0.02	0.03	0	0
T. angustifolia	1999	total	0.15	0.78	0.00	0.03	0.01	0.02	0.01	0
		vegetative	0.26	0.80	1	0.82	1	1	1	
		generative	0.20	0.08	0	0	0	0	0	
		dead	0.54	0.12	0	0.18	0	0	0	
	2000	total	0	0.86	0.03	0.05	0.04	0.02	0	0
		vegetative		0.71	0.91	0.95	0.93	1		
		generative		0.14	0	0	0	0		
		dead		0.14	0.09	0.05	0.07	0		

Predictors of shoot-fate

The proportion of generative shoots showed different relations in the populations of *T. latifolia* and *T. angustifolia* (Tab. 6-3, Fig. 6-6). While shoot density showed a negative relation to shoot height increment in *T. latifolia*, the variables were unrelated in *T. angustifolia.* Shoot density correlated positively to shoot height as well as percentage generative and percentage dead shoots in both species. The number of new-shoots and the shoot heights increment showed a significant negative relation to the proportion of generative shoots in *T. latifolia* (Tab. 6-3). *T. angustifolia* in contrast showed a positive correlation between percentage generative shoots and shoot height increment.

Table 6-3: Spearman-Rank Correlation (r) between shoot density in May, the number of new shoots produced from May to October, the shoot height in May, the shoot heights increment from May to August, the probability of shoots to become generative till the end of the season and the probability of shoots to die till August in *T. latifolia* and *T. angustifolia*. $p < 0.05$, n.s.– not significant.

	T. latifolia					T. angustifolia				
	(2)	(3)	(4)	(5)	(6)	(2)	(3)	(4)	(5)	(6)
N shoots/m² in May (1)	n.s.	0.77	-0.37	0.62	0.47	n.s.	0.56	n.s.	0.77	0.68
N new-shoots/m² (2)		n.s.	0.39	- 0.50.	n.s.		n.s.	n.s.	n.s.	n.s.
Shoot heights in May (3)			n.s.	0.69	0.57			0.43	0.45	n.s.
Shoot height increment (4)				-0.34	n.s.				0.56	0.42
% generative shoots (5)					0.45					0.43
% dead shoots (6)										

While shoot height in May was the best predictor of shoot fate in *T. latifolia* in the multiple regression, the shoot density in May had a Beta of 0.74 in *T. angustifolia* and none of the other traits added significantly to the result when shoot density in May was included in the analysis (Table 6-4).

Table 6-4: Multiple regression on the effects of shoot density and shoot height in May, the number of new shoots per year and the shoot heights increment from May to August on the probability of shoots to become generative till the end of the season in *T. latifolia* and *T. angustifolia*. n.s. – not significant

	Typha latifolia		*Typha angustifolia*	
R^2	0.71 (p<0.0001)		0.81 (p<0.0001)	
	Beta	p	Beta	p
N shoots/m² in May	0.15	n.s.	0.74	<0.0001
N new-shoots/m²	-0.37	0.01	-0.09	n.s.
Shoot heights in May	0.61	0.0001	0.19	n.s.
Shoot height increment	-0.45	0.0002	-0.06	n.s.

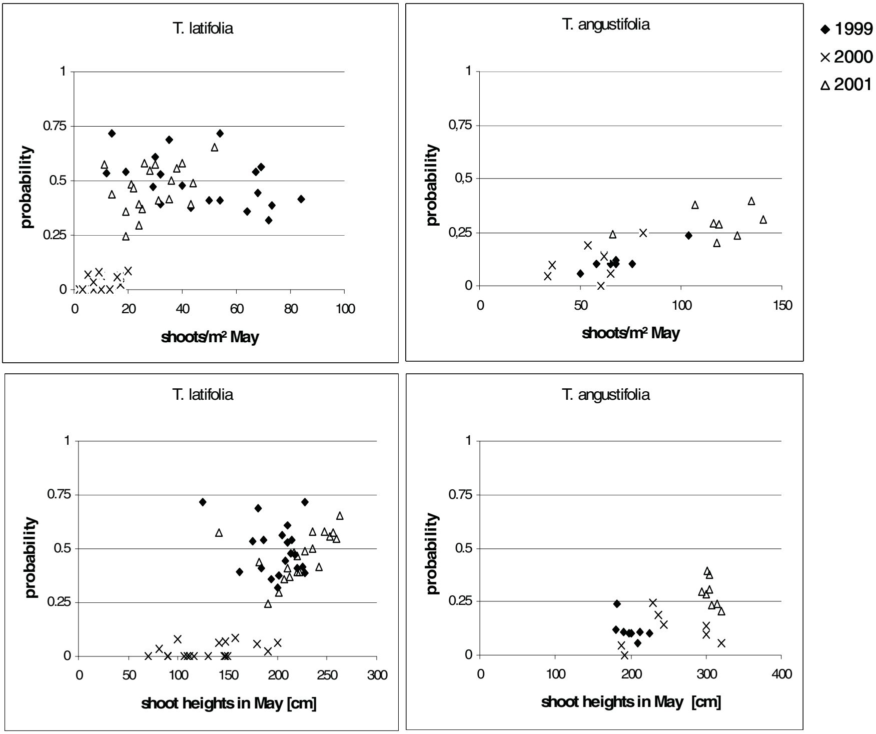

Figure6-6: Effect of shoot density (shoots/m²) and shoot heights (cm) in May on the probability of shoots to become generative till the end of the season in *T. latifolia* and *T. angustifolia* in three successive years after planting.

Discussion

Colonisation of new habitats

The colonisation of a new habitat is the first phase of population development. With little or no competition populations grow exponentially (Harper 1977; DeKroon 1993). The velocity and vigour of growth in this phase determines plant community composition (Weiher & Keddy 1995). Especially in habitats undergoing periodical disturbance as aquatic systems, which are often prone to episodes of flooding and low-water, colonisation and re-colonisation are important (Zedler & Kercher 2004).

Typha latifolia and *T. angustifolia* colonised the constructed wetland rapidly by clonal growth and established a close stand within three months. A high growth-rate is characteristic for *Typha* sp. in the first phase of colonisation. Grace & Wetzel (1981 b) found growth-rates of 13.6 shoots/year and 9.2 shoots/year for *T. latifolia* and *T.*

angustifolia respectively in a semi-natural stand in Michigan (USA). Without competition single shoots of *T.latifolia* and *T. angustifolia* can produce up to 46.2 and 13.6 daughter-ramets in the first year covering up to 16 m² and 9 m² respectively (FIALA 1978). This fast colonisation effectually excludes competitors (HAGER 2004) and makes *Typha* sp. and other wetland plants successful invaders (ZEDLER & KERCHER 2004). After colonising the open space the growth rate of *T. latifolia* and *T. angustifolia* declines. This could be interpreted as a density dependent reduction of shoot production (DEKROON 1993). In an experiment over two years with different initial shoot densities of the rhizomatous graminoids *Brachypodium pinnatum* and *Carex flacca*. DEKROON & KWANT (1991) observed the highest production of shoots at the lowest density level. In the second year shoot densities in both treatments reached similar values.

The investigated *Typha* species differ gradually in their colonisation performance. While *T. latifolia* shows slightly faster growth in the first month after planting, *T. angustifolia* develops higher shoot densities in the following seasons. Comparative studies investigating semi-natural or experimental stands of *T. latifolia* and *T. angustifolia* always detected a higher shoot-density for *T. angustifolia* compared to *T. latifolia* (GRACE & WETZEL 1981a; 1982, WEISNER 1993; HAGER 2004, SELBO & SNOW 2004). The densities detected in the basin in southern Germany fit as well into the range found in an eutrophic lake in Sweden (WEISNER 1993:, *T.latifolia* 20, *T.angustifolia* 50 shoots/m²) as for one-year old mesocosms (HAGER 2004: *T.latifolia* 75, *T.angustifolia* 91 shoots/m²). But the increase in shoot density in *T. angustifolia* in 2001 suggested, that at least *T. angustifolia* has not obtained maximum density. Even shoot densities of more than 100 shoots/m² are described for *T. angustifolia* (MASON & BRYANT 1975: 100.2 ± 5 shoots/m²) and *T. domingensis* (GRACE 1989: 170 shoots/m²) in North America. Because of the extensive damage in the second winter the population development of *T. latifolia* relapsed and population development in the year 2000 iterated widely the colonisation after planting in 1998. The denser stands of *T. angustifolia* also result from the production of shorter rhizomes between mother and daughter ramet and the re-sprouting from the last year rhizome in spring (FIALA 1978; GRACE & WETZEL 1982). FIALA (1978) especially observed the production of short daughter-ramets in *T. angustifolia* at the end of season, while *T. latifolia* produced a greater number of ramets on long rhizomes in spring.

The constructed wetland was exclusively colonised by clonal growth. Although seeds were present in the seed-bank (personal observation) and parts of the basin were only sparsely populated in May 2000 (Minimum 4 shoot/m²) no seedlings were able to establish in this basin (but cp. chapter 7). In natural stands seedlings are rarely found and GRACE (1983) detected auto-toxic inhibition of germination in dense stands. But presumably the water level of 0.4 m in the basin impedes successful establishment (FENNER & THOMPSON 2005, cp. chapter 5).

Development of stand-structure

Even though most shoots of *Typha* sp. die at the end of the season and only the underground rhizome outlasts winter, some shoots survive winter and re-grow in spring, causing an overlap of shoot-generations (DICKERMAN & WETZEL 1985). Especially shoots developed late in the season with shoot heights below 50 cm have a chance to survive winter (GRACE & WETZEL 1981 b; WILD et al. 2002). Because of the harvest in the second winter and the affiliated loss of shoot marks, over-wintering was only investigated in the season 1998/1999 in the present study. The re-growth of shoots resumes early growth in spring and may support shooting of the first cohort in spring (GARVER ET AL.1988; DICKERMAN & WETZEL 1985). In *T. latifolia* nearly all the over-wintering shoots died in the following season. But 45 % of them flowered and set seed before. In *T. angustifolia* re-grown shoots have the greatest share in the generative shoots. 54 % of the re-growth dies without flowering, 24 % stayed vegetative to the end of the season possibly surviving a second winter, thus making the shoot cohort of August 1998, the year of stand establishment, the shoots with the longest life-span (*T. angustifolia* > 200 days).

The *Typha* stands developed a clear age-structure with an intense pulse of growth in spring, when most shoots emerged (April/May). This clear seasonality in shoot emergence was also detected in a natural *T. latifolia* stand in Michigan (USA) (DICKERMAN & WETZEL 1985). The spring shoot cohort development is mainly triggered by nutrients from the rhizome rather than by photosynthesis (GARVER et al. 1988; ROCHA & GOULDEN 2009). This synchronized shoot emergence effectuates the development of a nearly even-aged stand (HUTCHINGS 1979; DEKROON 1993). Shoots of later cohorts had only a short life expectancy. Established populations of clonal plants are generally characterised by a high shoot turn-over compared to a remarkably constant number of living shoots (see review by COOK 1985). After the colonisation phase in 1998, population density was kept nearly constant during the vegetation season from May to October. Shoot mortality was balanced by the production of new shoots. DICKERMAN & WETZEL (1985) observed increasing shoot densities throughout the season in the first year - comparable with the year 2000 in the present study - and constant densities maintained by shoot turn-over in the second year in *T. latifolia*.

In *T. angustifolia* shoot fate is nearly exclusively determinated by shoot age. Hence, beside the re-growth the April shoot-cohort was the only one to become generative. In *T. latifolia* even shoots from the July cohort had a chance to develop inflorescences. Additionally both investigated species differ in the time lapse and proportion of generative reproduction. While *T. latifolia* developed inflorescences in the end of May and produced over 50 % generative shoots in the first season (1999), *T. angustifolia* started flowering in June and produced only 12 % flowering shoots in the first and second and only 29 % generative shoots in the third season. The difference in time lapse and proportion of generative reproduction could be interpreted as a differentiation in development strategy between the species, with *T. latifolia* showing a more short-lived strategy with fast colonisation and early reproduction. Based on the shoot development MCNAUGHTON (1975) suggests *T. latifolia* to be more r-selected, because of the high number but lower investment per ramet, and positioned *T. angustifolia* on the more K-selected side of the gradient. Data on the rate of flowering shoots is rare and fluctuates extremely. While GRACE (1985) and DICKERMAN & WETZEL (1985) found only single inflorescences in the investigated stands of *T. latifolia*, GRACE & WETZEL (1981 b) detected 44.8 % flowering shoots of *T. latifolia* in a natural marsh which fits the range found in the experimental basin in southern Germany. Comparing *T. latifolia* to *T. domingensis* the latter species developed the higher number of inflorescences (GRACE 1985, 1989).

The main proportion of shoot death is synchronised by the course of the year, too. While shoots emerge in spring, senescence started shortly after the growth peak in summer and in autumn all generative shoots and most vegetative shoots senescence and die (GRACE & HARRISON 1986; DICKERMAN & WETZEL 1985). Such seasonality as main factor influencing the shoot life cycle is characteristic in temperate regions (HUTCHINGS 1979; DICKERMAN & WETZEL 1985; DEKROON 1993; HARA 1997) and was detected in *Juncus effuses* even though the investigated *Juncus* population in sub-temperate Alabama (USA) grows permanently (WETZEL & HOWE 1999). Irrespective the seasonality of shoot death some mortality was present throughout the summer. Especially small shoots and young as well as very old shoots had an increased risk of death. DICKERMAN & WETZEL (1985) observed an especially high mortality (up to 50 %) directly after shoot emergence in *T. latifolia*. Shoot mortality rates up to 30 percent per growing season are not uncommon (COOK 1985; DEKROON 1993).

Density dependence of growth and shoot fate

Population growth is limited by competition for resources as space, nutrients or light (HARPER 1977). In clonal plants physiological integration decreases competition by reducing the production of new shoots as density increases (density dependent natality), preventing over-production (DEKROON 1993), and ideally regulating the development of new shoots to shoot densities close to the carrying capacity of the environment (HUTCHINGS 1979). Shoot density can control the biomass allocation to the production of daughter ramets as well as to sexual reproduction (OGDEN 1974; VAN KLEUNEN et al. 2001).

While shoot density in spring was not related to the production of new shoots in *T. latifolia* and *T. angustifolia* in the three seasons after establishment, density showed a positive correlation to the percentage of generative shoots. Thus a density dependent reduction of production of new shoots is not effective. DICKERMAN & WETZEL (1985) detected a reduction of shoot emergence in the later cohorts in the second year studied, but not in the first cohort. In the present study the pronounced seasonality of shoot emergence, especially in *T. angustifolia*, may prevent any density effects on shoot production (DEKROON 1993). The reduced life span of shoots emerging in summer could be interpreted in both directions: as a density dependent mortality or as an effect of season. Denser stands produce and store more resources to support the production of inflorescences (COOK 1985; VAN KLEUNEN et al. 2001). GRACE & WETZEL (1981 b) and GRACE (1985) observed an influence of the age and successional state of the stand on the production of inflorescences. As in the investigated stands biomass production (see chapter 7) and shoot density (especially in *T. angustifolia*) increased with stand age the accession in the proportion of generative shoots at least in *T. angustifolia* may be particularly an effect of the rise in stand age.

The positive correlation of shoot height in May to the percentage of flowering shoots is expressed by both species, but more pronounced in *T. latifolia*. This difference originates from a different growth development of generative and vegetative shoots in the species. While in *T. latifolia* the fate of an individual shoot depends on its height early in the season and only the highest shoots flower, the fate of *T. angustifolia* shoot cannot be predicted by their heights in May.

The multiple regression analyses suggests a strong dependence of proportion of generative shoots on shoot density in *T. angustifolia*, while in *T. latifolia* the percentage of generative shoots was predicted best by mean stand height in May. The negative beta for shoot heights increment and the number of new shoots in *T. latifolia* indicate in the direction of a trade off between generative reproduction and growth (e.g. SCHMID & HARPER 1985; VAN KLEUNEN et al. 2001). In contrast, OGDEN (1974) found no severe effect of density in seed production in *Tussilago farfara*, but observed a density dependent decrease in vegetative reproduction. VAN KLEUNEN et al. (2001) connected different biomass allocation to the production of daughter ramets and sexual reproduction to different growth strategies (sensu LOVETT DOUST 1981). Reviewing different studies they found species with guerrilla growth type to allocate more biomass into sexual reproduction when population density increased and no change in allocation in phalanx growth types (VAN KLEUNEN et al. 2001). Hence, *T. latifolia* would express more the guerrilla growth type, with shoots more spreading out, while *T. angustifolia* grows more compact, which was demonstrated by FIALA (1978) and GRACE & WETZEL (1982). Overall *T. latifolia* showed strong adaptations to the colonisation of habitats, while *T. angustifolia* developed extremely dense stands.

7 Etablierung und Ernte künstlicher Bestände von Breitblättrigem Rohrkolben (*Typha latifolia* L.) und Schmalblättrigem Rohrkolben (*Typha angustifolia* L.)

Einleitung

Künstliche Feuchtgebiete werden vielfältig genutzt: Sie dienen der Wasserreinigung (CIRIA et al. 2005; MANDER & MITSCH 2009), dem Hochwasserschutz (CAMPBELL & OGDEN 1999), werden aber auch für Erholung und Naturschutz (CAMPBELL & OGDEN 1999; ANDERSON et al. 2002) eingesetzt und stellen eine Möglichkeit der nachhaltigen Nutzung von degradierten Niedermoorstandorten dar (PFADENHAUER & GROOTJANS 1999; TIMMERMANN et al. 2003). Oft werden auch verschiedene Ziele gemeinsam verfolgt (VYMAZAL et al. 1998) z.B. Hochwasser- und Naturschutz (CAMPBELL & OGDEN 1999; ANDERSON et al. 2002), Rohstoffproduktion und nachhaltige Nutzung von Torfböden bzw. Gewässerschutz (KOPPITZ et al. 1998; WILD et al. 2001; SCHÄTZL et al. 2006). Auf degradierten Niedermoorstandorten dient die Vernässung dem Boden- und dem Klimaschutz gleichermaßen, da der oxidative Torfabbau gestoppt wird und nach der Vernässung weniger klimaschädliche Spurengase freigesetzt werden (SUCCOW & JOOSTEN 2001). Gerade in intensiv genutzten Landschaften kann auch ein künstliches Feuchtgebiet ein wertvolles Habitat für zahlreiche Arten darstellen (ANDERSON et al. 2002).

Neben Schilf (*Phragmites australis*; KOPPITZ et al. 1998) bietet sich Rohrkolben (*Typha* spp.) zur Kultur in künstlichen Feuchtgebieten an. Rohrkolben ist einheimisch, erträgt auch hohe Nährstoffbelastungen, hat eine hervorragende Reinigungsleistung speziell auch für Schwermetallbelastungen (SAYGDEGER et al. 2004; CIRIA et al. 2005), emittiert wenig Methan (KAO-KNIFFIN et al. 2010) und bildet geschlossene Bestände mit einer hohen Biomasseproduktion (GARVER et al.1988).

Ein Rohrkolbenbestand kann bis zu 83% der Ammonium- bzw. 86% der Nitrat- und bis zu 74% der Phosphatfracht aus dem Wasser aufnehmen und einen wesentlichen Beitrag zur Wasserreinigung leisten (LENZ & WILD 2000). Daneben eignen sich die trockenen Blätter zur Herstellung von Isoliermaterial (WILD et al. 2002). Sowohl Spross als auch Rhizom sind mit einem Luftleitsystem durchzogen (Aerenchym), das die untergetauchten Pflanzenteile mit Sauerstoff versorgt. Das Aerenchym des Rohrkolbens ist in Form kleiner kommunizierender Kammern ausgebildet, die durch ein Festigungsgewebe (Sklerenchym) ausgesteift werden (KRATTINGER 1978). Da die Struktur auch im getrockneten und geschnittenen Zustand erhalten bleibt, hat das Rohrkolbenmaterial hervorragende Wärmedämmeigenschaften (SCHÄTZL et al. 2006).

Nach der Besiedlung eines Habitats durch Samen und Keimlinge vermehrt sich *Typha* sp. vor allem durch ein weitläufiges unterirdisches Rhizom, aus dem neue Sprosse hervorgehen (FIALA 1978). Die Sprosse bestehen aus ineinander geschobenen Blättern und erreichen Höhen von bis zu 3m. Im Juni/Juli bildet ein Teil der Sprosse einen Stängel mit einem endständigen Blütenstand aus (KRATTINGER 1978). Im Herbst vergilben die Blätter und die Nährstoffe werden in das Rhizom verlagert (GARVER et al.1988).

Im Projekt „Rohrkolbenanbau in Niedermooren“ wurde im Donaumoos, einem Niedermoorgebiet in Süddeutschland, der Anbau von Rohrkolben in gefluteten Poldern untersucht. Die Rohstoffgewinnung in Form von trockener Biomasse wurde dabei mit Wasserreinigung, Hochwasser- und Moorschutz zu einem nachhaltigen Nutzungskonzept kombiniert (WILD et al. 2001). Zusätzlich wurde die Emission klimaschädlicher Spurengase gemessen und die Ansiedlung von Wirbellosen und Vögeln beobachtet (KAMP 1998; WILD et al. 2002).

Der feldmäßige Anbau von Rohrkolben als Monokultur in gefluteten Poldern wirft zahlreiche Fragen in Bezug auf die Etablierungsmöglichkeiten, die Bestandesentwicklung und die Ernte dieser einheimischen Röhrichtpflanze auf. Die schnelle Etablierung eines dichten Bestandes ist wichtig, einerseits um möglichst schnell Biomasse ernten bzw. die angestrebte Reinigungsleistung der Anlage erreichen zu können, aber auch um die Besiedlung mit Konkurrenzarten zu verhindern. Sowohl die Etablierung durch Pflanzung als auch die Aussaat wurden in Hinsicht auf die Sprossdichte des Bestandes und die Entwicklung der Populationsstruktur untersucht. Um einen mehrjährigen Bestand nachhaltig zu bewirtschaften, darf durch die Ernte das Wachstum im Folgejahr nicht beeinträchtigt werden. Deshalb wurden in den ersten zwei Wintern Ernteversuche in verschiedenen Schnitthöhen durchgeführt und die Entwicklung im folgenden Jahr beobachtet.

Ziel dieses Projektes war es,

(1) die Etablierung eines Rohrkolbenbestandes durch Pflanzung und Aussaat zu testen und Unterschiede in der Entwicklung des Bestandes zu untersuchen,

(2) die im Winter von Breitblättrigem Rohrkolben (*Typha latifolia* L.) und Schmalblättrigem Rohrkolben (*Typha angustifolia* L.) erntbare Biomasse zu ermitteln und

(3) eine geeignete Schnitthöhe für die Ernte zu erproben, die einen möglichst hohen Biomasseertrag erzielt, ohne das Wachstum des Bestandes im Folgejahr zu beeinträchtigen.

Methoden

Versuchsflächen

Die Versuchsflächen wurden im Frühjahr 1998 im Donaumoos bei Ingolstadt (48°42´N, 11°11´E), dem größten Niedermoorgebiet Süddeutschlands, auf entwässerten und intensiv genutzten Dauergrünlandflächen eingerichtet. Drei Becken mit einer Gesamtfläche von 6,2 ha wurden ausgehoben, mit dem Aushub umwallt und von 1998 bis 2001 mit nährstoffbelastetem Wasser als Durchflusssystem betrieben (Abb. 7-1). Fläche 1 wird aus dem Längenmühlbach mit 6 ls^{-1} gespeist (Wasserstand 20 cm). Fläche 2 (40 cm Wasserstand) und Fläche 3 (20 cm) sind in Reihe geschaltet. Wasser (10 ls^{-1}) aus dem Graben Nr. 242 wird in Fläche 2 gepumpt und fließt von dort in Fläche 3 (Abb. 7-1, Tab. 7-1) (vgl. WILD et al. 2001). Durch die Reihenschaltung war der Stickstoff- und auch der Phosphatgehalt des Zuflusses zu Fläche 3 deutlich geringer als bei den anderen beiden Flächen (Tab. 7-1).

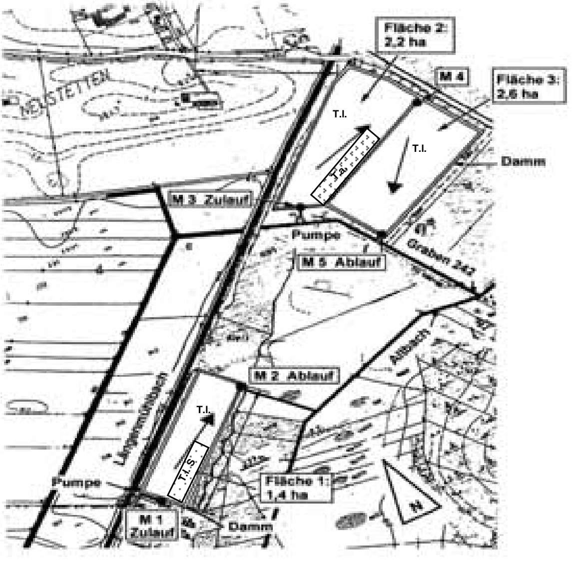

Abb. 7-1: Lageplan der Flächen 1 bis 3 im Donaumoos bei Ingolstadt. T.l.- *T. latifolia* gepflanzt, T.l. S – *T. latifolia* angesäht, T.a. - *T. angustifolia*. Lageplan: Ingenieurbüro Lenz.

Im Juni 1998 wurden Fläche 2 und 3 gleichmäßig mit 2 Pflanzen pro m^2 bepflanzt. Gepflanzt wurde Breitblättriger Rohrkolben (*Typha latifolia*) und in Fläche 2 auch Schmalblättriger Rohrkolben (*T. angustifolia*) (Abb. 7-1). Von beiden Arten wurde eine Samenherkunft aus dem Donaumoos und eine Samenherkunft aus Ungarn verwendet. Die Auswertungen beziehen sich allgemein auf die Bestände aus einheimischem Samenmaterial.

Ein Viertel der Fläche 1 wurde nicht bepflanzt und im April 1999 mit *T. latifolia* eingesät. Zur einfacheren Handhabung der sehr kleinen flugfähigen Samen wurden diese vor der Aussaat mit Lehm vermischt, getrocknet und als Lehmgranulat ausgebracht. Der Wasserstand wurde bis Juli auf wenige Zentimeter abgesenkt.

Tabelle 7-1: Mittlerer Stickstoff (N ges) und Phosphatgehalt (P ges) im Zulauf der Flächen 1, 2 und 3 in der Vegetationsperiode (April bis Oktober) 1999. Mittelwert ± Standardabweichung.

	Fläche 1	Fläche 2	Fläche 3
N ges [mg/l]	7,11 ± 1,67	7,41 ± 1,38	2,42 ± 1,69
P ges [mg/l]	0,34 ± 0,12	0,34 ± 0,13	0,11 ± 0,09

Bestandesentwicklung

Um die Bestandesentwicklung zu untersuchen, wurden in Fläche 2 und 3 Untersuchungsflächen von 5 m x 5 m eingerichtet und mit Magneten dauerhaft markiert. In je vier Flächen von 1 m² wurde 1998 im August und September, 1999 und 2000 monatlich in der Vegetationsperiode die Sprosszahl und der Anteil der Sprosse an den Entwicklungsstadien Keimling, juvenil, vegetativ, generativ und tot ermittelt (vgl. GATSUK et al. 1980). Jungpflanzen wurden bis zur Entwicklung des dritten Blattes als Keimlinge eingestuft. Nach der Entwicklung des dritten Blattes wurden alle Triebe als juvenile Sprosse bewertet, da ab diesem Entwicklungsstadium die Unterscheidung zwischen etablierten Keimlingen und vegetativ entstandenen Sprossen ohne Beschädigung der Pflanzen nicht mehr sicher möglich war. In den Beständen von *T. latifolia* wurden je fünf Untersuchungsflächen (insgesamt: 5 x 4 m² = 20), im Bestand von *T. angustifolia* je zwei (2 x 4 m² = 8) eingerichtet. Monatlich wurden auch alle anderen Arten in den 1 m² Flächen erhoben.

In der Ansaatfläche in Fläche 1 wurden 36 Untersuchungsquadrate von 1 m² Fläche eingerichtet und monatlich Sprossdichte und Entwicklungsstadien aller Sprosse aufgezeichnet. Dazu wurden Wasserstand und Konkurrenzarten notiert.

Um die Entwicklung der gepflanzten Bestände (Pflanzung 1998) und des ein Jahr später gesäten Bestandes (1999) gemeinsam darstellen zu können, wird die Entwicklung relativ zum Zeitpunkt der Etablierung dargestellt. Die auf die Etablierung folgenden Jahre werden als ´1. Jahr´ und ´2. Jahr´ bezeichnet.

Biomasseentwicklung

Zweimal jährlich - zum Höchststand der Vegetation im Juli/August und im Winter vor der Ernte - wurde in jeder Untersuchungsfläche in Becken 2 und 3 auf je zwei Quadratmetern die gesamte oberirdische Biomasse geerntet und die Frisch- und Trockenmasse bestimmt. Die Trocknung und Bestimmung der Trockenmasse wurde durch die Labore der Bayerischen Landesanstalt für Bodenkultur und Pflanzenbau (LBP, heutige Landesanstalt für Landwirtschaft) durchgeführt. Die unterirdische Biomasse wurde im März 2001 in Becken 2 für *Typha latifolia* und *T. angustifolia* auf je 10 Flächen von 18 cm x 20 cm Größe bis zu einer Tiefe von 40 cm beprobt. Die Proben wurden ausgewaschen und getrocknet.

Ernteversuch

Im Winter 1998/1999 wurden in Becken 2 und 3 kleinflächige Ernteversuche (je 1 m² Flächen) durchgeführt. Zum gleichen Zeitpunkt wie die Biomasseprobe (gesamte oberirdische Biomasse – g) wurden zwei verschiedene Schnitthöhen getestet. In jeweils 10 (*T. latifolia*) bzw. 6 (*T. angustifolia*) Wiederholungen wurden die Sprosse in Höhe des Wasserspiegels (w), so dass Wasser in die abgeschnittenen Schäfte eindringen kann, und ca. 5 cm über dem Wasserspiegel (o) geerntet. Dabei wurde die jeweils erntbare Biomasse festgestellt und die Anzahl der Sprosse gezählt. Im Winter 1999/2000 wurde das Schnittmanagement auf den gleichen Flächen wiederholt und zusätzlich auf je fünf bisher nicht geernteten Flächen (1 m²) durchgeführt, um Auswirkungen einer wiederholten Ernte zu untersuchen.

Statistik

Vergleiche zwischen den Sprossdichten, der Biomasse und der Biomasse je Spross zwischen den einzelnen Versuchsvarianten wurden mit Hilfe der Varianzanalyse untersucht (einfaktorielle ANOVA). Signifikante Unterschiede zwischen den einzelnen Faktorstufen (z.B. Schnittvarianten: gesamt, in Höhe des Wasserspiegels, oberhalb des Wasserspiegels) wurden mit dem Tukey HSB Verfahren untersucht. Der Zusammenhang zwischen Wasserstand, Algenbedeckung und der Anzahl der Sprosse und Keimlinge zu verschiedenen Zeitpunkten in der Ansaatfläche wurde nach dem Spearman Rank Verfahren ermittelt. Als signifikant wurden in allen statistischen Tests Ergebnisse mit einer Irrtumswahrscheinlichkeit von $p<0{,}05$ gewertet.

Ergebnisse

Etablierung und Entwicklung eines Rohrkolbenbestandes

Die Etablierung von Rohrkolben (*Typha* spp.) durch Pflanzung führte innerhalb weniger Monate zum Aufbau eines dichten Bestandes. Die gesetzten Jungpflanzen kolonisierten die Fläche schnell durch Rhizomausläufer. Von Juli bis September wurden bis zu 10 Tochtersprosse je Pflanze gebildet. So wurde bereits im September eine Sprossdichte von bis zu 20 Sprossen je Quadratmeter (*T. latifolia*) erreicht. Später im Jahr verlangsamte sich der Zuwachs (Abb. 7-2).

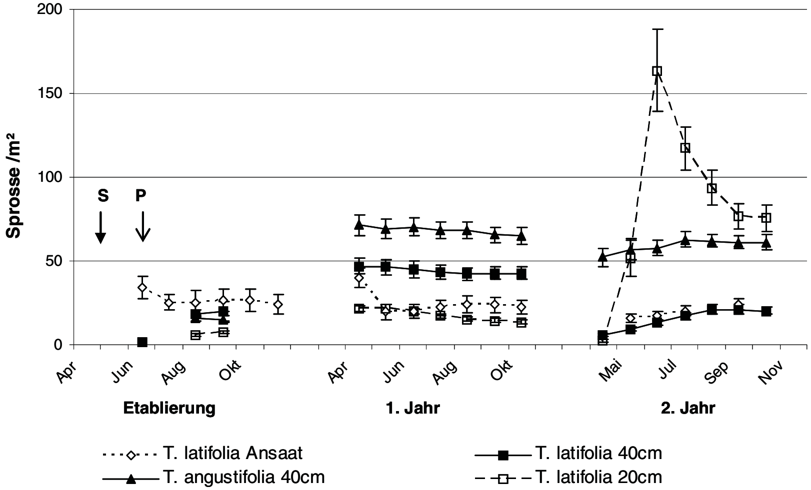

Abb. 7-2: Entwicklung der Sprosszahl (Sprosse m^{-2}) gepflanzter Bestände von *Typha latifolia* und *T. angustifolia* bei 40 cm bzw. 20 cm Wasserstand im Vergleich mit einem angesäten *T. latifolia* Bestand in den ersten zwei Jahren nach der Etablierung.
Mittelwert ± Stdf., S- Zeitpunkt der Aussaat, P- Zeitpunkt der Pflanzung.

Der im Mai angesäte Bestand entwickelte sich sehr ungleichmäßig. Waren die Keimlinge zunächst noch über die gesamte Ansaatfläche verteilt, wenn auch in unterschiedlichen Dichten, bildeten sich innerhalb der ersten Monate einerseits dichte Bestände mit über 100 Keimlingen/m², aber auch große Bestandeslücken heraus. Nach einer deutlichen Abnahme der Sprosszahl bis Juni, stabilisierte sich die Anzahl bei ca. 25 Sprossen/m² (Abb. 7-2). Die Etablierung der Keimlinge wurde im Sommer auch durch die Bildung dichter Algenmatten mit bis zu 100% Deckung behindert, die den Grund beschatteten.

Während die Bedeckung der Wasseroberfläche mit Algen im Juni eine negative Korrelation mit der Anzahl aller Sprosse (Keimlinge und Juvenile) und auch mit der Anzahl der Keimlinge zeigt, hat sie keinen signifikanten Einfluss auf die Sprossdichte im September (Tab. 7-2). Der Wasserstand im Juni, der zwischen 5 cm und 14 cm lag, ist dagegen auch mit der Sprosszahl im September negativ korreliert.

Tabelle 7-2: Korrelation zwischen der Bedeckung der Wasseroberfläche im Juni mit Algen bzw. dem Wasserstand im Juni und der Anzahl der Keimlinge bzw. aller Sprosse im Juni und im September des Etablierungsjahres im angesäten *T. latifolia* Bestand.
r^2 - Spearmans Rangkorrrelation, $p<0{,}05$, n.s. – nicht signifikant.

	N Sprosse Juni	N Keimlinge Juni	N Sprosse September
Algen (%) Juni	-0,541	-0,446	n.s.
Wasserstand Juni	-0,432	n.s.	-0,660

Im Etablierungsjahr unterschieden sich die Sprosszahlen auch auf Grund der großen Schwankungen nicht signifikant (Tab. 7-3). In den folgenden Jahren zeigten sich sowohl zwischen den beiden Rohrkolben-Arten, zwischen den verschiedenen Flächen (Wasserstand 40 cm bzw. 20 cm) und auch zwischen dem gepflanzten und dem gesäten Bestand deutliche Unterschiede. Im ersten Jahr erreichte *T. angustifolia* die höchste Sprossdichte (68 Sprosse/m² im August), während *T. latifolia* in Fläche 2 (40 cm Wasserstand) 42 Sprosse/m² und in Fläche 3 (20 cm) nur 15 Sprosse/m² ausbildete (Tab. 7-2). Die Sprossdichten der drei gepflanzten Bestände unterschieden sich signifikant ($p<0{,}05$) von einander und mit Ausnahme von *T. latifolia* in Fläche 3 auch von der Sprossdichte des gesäten Bestandes (Tab. 7-3). Im Verlauf der Vegetationsperiode blieb die Sprossdichte im ersten Bestandesjahr sehr konstant. Die Anzahl der neuen Sprosse entsprach etwa der Zahl der absterbenden.

Tabelle 7-3: Vergleich der Sprossdichte pro Quadratmeter von gepflanzten Beständen von *Typha latifolia* und *T. angustifolia* bei 40 cm bzw. 20 cm Wasserstand und einem angesäten *T. latifolia* Bestand im Sommer der ersten zwei Jahre nach der Etablierung.
Unterschiedliche Buchstaben zeigen signifikante Unterschiede der Sprossdichte zwischen den Arten, Wasserständen und Etablierungsmethoden zu einem Zeitpunkt an.

	T. latifolia			*T. angustifolia*
	Ansaat	Pflanzung 20 cm	Pflanzung 40 cm	Pflanzung 40 cm
Aug Etablierung	25,1±7,1 (a)	6,0±0,6 (a)	18,5±2,1 (a)	15,9±1,8 (a)
Aug 1. Jahr	24,1±4,9 (c)	15,2±1,3 (c)	42,3±3,7 (b)	68,4±5,3 (a)
Juli 2. Jahr	20,2±3,0 (c)	117,3±12,7 (a)	17,4±2,2 (c)	62,8±4,5 (b)

Während der Bestand im ersten Winter ungemäht blieb, wurde im folgenden Winter (1./2. Standjahr) auf den Flächen 2 und 3 der gesamte Bestand gemäht. Die Mahd fand erst im März statt und führte an einigen Stellen (Wendekreise, Einfahrt des Gerätes) zu starken Schäden auch an den Rhizomen der Pflanzen, so dass die Sprosszahl im Frühjahr des zweiten Bestandesjahres deutlich unter der des Vorjahres lag. Im Bereich von *T. angustifolia* entstanden nur geringe Schäden und der Bestand erreichte hier schon im April eine Dichte von 52 Sprossen /m^2. *T. latifolia* entwickelte in Fläche 2 im Laufe des zweiten Bestandesjahres fortlaufend neue Triebe, so dass sich die Sprosszahl bis zum Jahresende mehr als verdreifachte. In Fläche 3 (20 cm) starben bereits im Sommer des ersten Jahres zahlreiche Triebe in Folge einer Pilzinfektion und es entstanden größere Bestandeslücken. Im folgenden Frühjahr besiedelten zahlreiche Keimlinge die offenen Flächen und führten zu Bestandesdichten von 160 Sprosse/m^2 (Abb. 7-2). Im Juli des 2. Bestandesjahres unterschieden sich die Sprossdichten des gesäten und des gepflanzten Bestandes (Fläche 2) nicht mehr (Tab. 7-3).

Auch in der Populationsstruktur unterschieden sich gepflanzter und gesäter Bestand und die beiden Rohrkolbenarten deutlich (Abb. 7-3). In den gepflanzten Beständen entwickelte sich bereits im August des Etablierungsjahres ein großer Anteil vegetativer Triebe als im gesäten Bestand. Im ersten Bestandesjahr verzögerte sich die Bildung von generativen Trieben im gesäten Bestand bis zum Sommer, während der gepflanzte Bestand von *T. latifolia* bereits im Mai begann Blütenstände zu bilden. *T. latifolia* bildete im ersten Bestandesjahr einen größeren Anteil generative Sprosse aus als *T. angustifolia*.

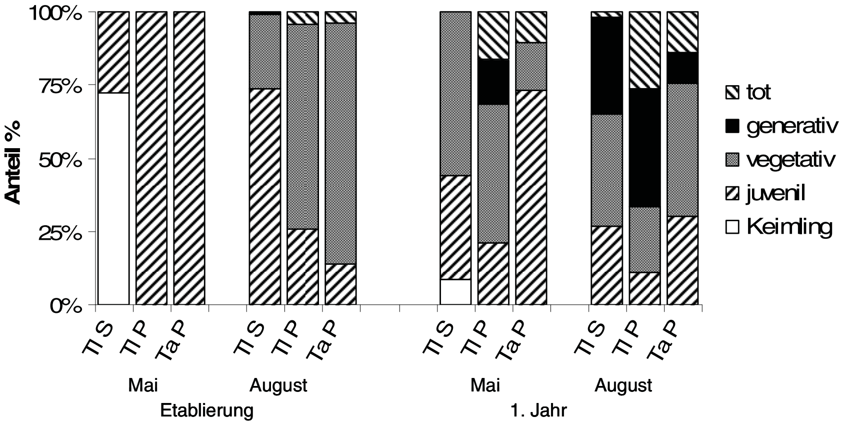

Abb. 7-3: Populationsstruktur von *Typha latifolia* (gesät TlS und gepflanzt, Fläche 2 TlP) und *T. angustifolia* (gepflanzt Fläche 2 TaP) im Etablierungsjahr und im 1. Bestandesjahr.

Biomassentwicklung

Seit der Anlage der Becken zeigte sich ein ständiger Zuwachs der erntbaren Biomasse im Winter (Abb. 7-4). Die höchsten Erträge erzielten die gepflanzten Bestände von *Typha angustifolia* gefolgt von *T. latifolia* in Fläche 2 (40 cm Wasserstand). Die Ernte im Winter 99/00 erfolgte erst sehr spät, so dass ein Sturm zuvor die Sprosse geknickt hatte. Der Ertrag blieb deshalb hinter dem Wert von Winter 00/01 zurück. In Fläche 3 (*T. latifolia,* 20 cm Wasserstand) wurde stets auf Grund der niedrigen Sprossdichte bzw. Größe der Pflanzen ein geringer Ertrag erzielt.

Nachdem die Biomasse im Sommer vom Jahr der Etablierung zum 1. Bestandesjahr stark anstieg, blieb sie für *T. angustifolia* im 2. Bestandesjahr gleich und sank für *T. latifolia* stark ab.

Die von der Bayerischen Landesanstalt für Bodenkultur und Pflanzenbau (LBP) durchgeführten Biomasseproben in der Ansaatfläche ergaben 1999 (Etablierungsjahr) 585 g/m² und im Jahr 2000 (1. Bestandesjahr) 1889 g/m² Trockenmasse.

Die im März des dritten Bestandesjahres (2001) durchgeführte Beprobung der unterirdischen Biomasse ergab für *T. latifolia* 3332,6 ±476,3 g/m² und *T. angustifolia* 3326,8±368,4 g/m².

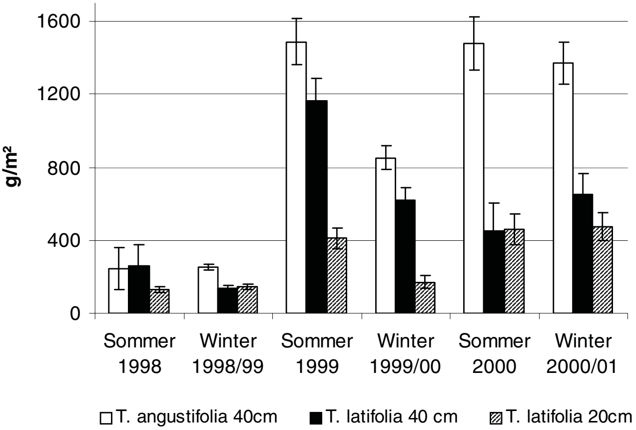

Abb. 7-4: Entwicklung der Trockenmasse (g/m²) von *Typha latifolia* und *T. angustifolia* bei 40cm bzw. 20 cm Wasserstand vom Etablierungsjahr (Sommer 1998) bis zum Winter zwei Jahre nach der Bestandesetablierung (Winter 2000/01). Mittelwert ± Stdf.

Ernte

Insgesamt war der Biomasseertrag im Ernteversuch im Etablierungsjahr gering. Auffällig waren die großen Unterschiede zwischen den einzelnen Stichproben, die sich in einer großen Standardabweichung widerspiegelten (Abb. 7-5a).

Den höchsten Trockenmasseertrag erbrachte zwar jeweils der Schnitt direkt an der Bodenoberfläche, statistisch signifikant war der Unterschied zwischen den verschiedenen Schnittvarianten - gesamte oberirdische Biomasse (g), in Höhe des Wasserspiegels (w), 5 cm oberhalb des Wasserspiegels (o) – allerdings nur in Fläche 3.

Bezieht man die Trockenmasse auf die Anzahl der geernteten Sprosse (Abb. 7-5b), zeigt sich, dass, wie erwartet, der größte Ertrag bei einer Ernte direkt an der Bodenoberfläche zu erzielen war. Zwischen dem Schnitt in Höhe des Wasserspiegels und 5 cm oberhalb des Wasserspiegels konnte weder in der Trockenmasse pro m², noch in der Trockenmasse je Spross ein signifikanter Unterschied festgestellt werden (Abb. 7-5a & b).

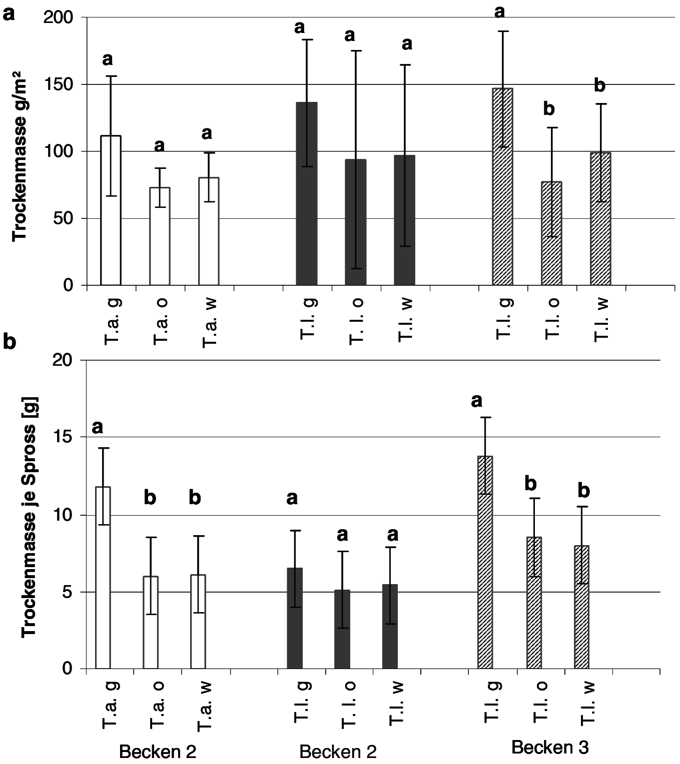

Abb. 7-5: Trockenmasse je Quadratmeter (g/m²) (a) und Trockenmasse je Spross (g) (b) im Winter des Etablierungsjahres (1998/99).
T. a. - *Typha angustifolia*, T.l. - *Typha latifolia*, Schnittvarianten: g- Schnitt an der Bodenoberfläche, o - Schnitt 5 cm oberhalb des Wasserspiegels, w - Schnitt in Höhe des Wasserspiegels.
Mittelwert ±Standardabweichung. Unterschiedliche Buchstaben zeigen signifikante Unterschiede der Trockenmasse zwischen den Schnittvarianten an.

Die Wiederholung der Ernte im Winter 99/00 zeigte für alle Varianten in Fläche 2 eine Zunahme der Erntemenge im Vergleich zum Vorjahr (Abb. 7-5a & 7-6). Die wiederholte Ernte der gesamten oberirdischen Biomasse (gg) führte zum geringsten Ertrag, die erstmalige Ernte in Höhe der Bodenoberfläche (ng) zum höchsten (Abb. 7-6).

Bei den Schnittvarianten in Höhe des Wasserspiegels oder oberhalb des Wasserspiegels unterschied sich die Erntemenge der zum zweiten Mal geernteten (oo bzw. ww) und erstmals geernteten (no bzw. nw) Flächen nur geringfügig und niemals signifikant (Abb. 7-6). Wie bereits bei der ersten Ernte unterschied sich die erntbare Biomasse zwischen einem Schnitt in Höhe des Wasserstandes und oberhalb des Wasserspiegels nicht signifikant (Abb. 7-6).

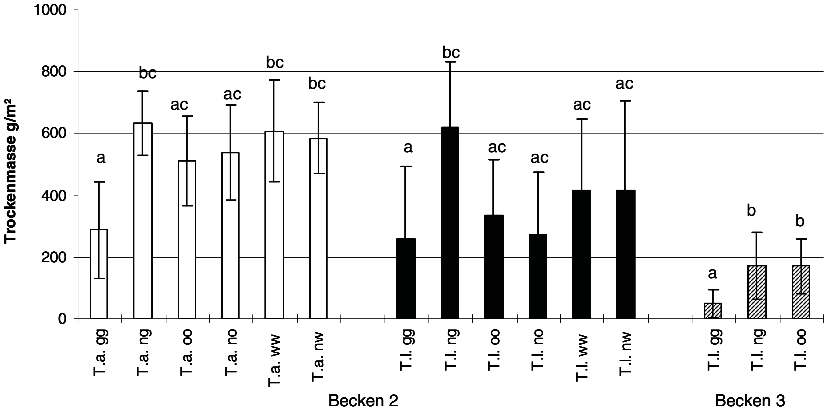

Abb. 7-6: Trockenmasse (g/m²) im Winter 1999/2000 - Vergleich der zum zweiten Mal gemähten Flächen mit erstmals gemähten in verschiedenen Schnitthöhen. (Abkürzungen vgl. Abb. 7-5, erster Buchstabe steht für Behandlung im Winter 1998/99, zweiter für Behandlung im Winter 1999/00, n - ohne Behandlung). Mittelwert ±Standardabweichung. Unterschiedliche Buchstaben zeigen signifikante Unterschiede der Trockenmasse zwischen den Schnittvarianten an.

Diskussion

Etablierungsverhalten und Bestandesentwicklung

Rohrkolbenbestände lassen sich im Gegensatz zu Schilfbeständen (VYMAZAL et al. 1998) sowohl durch Pflanzung als auch durch Aussaat etablieren. Durch die Vorkultur von Sämlingen und Pflanzung von Hand ist die Pflanzung deutlich aufwendiger (SCHÄTZL et al. 2006), führt allerdings auch schneller zur Ausbildung eines geschlossenen Bestandes. Der Etablierungserfolg nach einer Aussaat hängt stärker von äußeren Faktoren wie Wasserstand, Temperatur und Konkurrenzdruck ab.

Rohrkolben kann unter geeigneten Bedingungen Keimraten von bis zu 100 % erreichen (z.B. LOMBARDI et al. 1997). Entscheidende Umweltfaktoren für die

Keimung sind Temperatur und Wasserstand (COOPS & VAN DER VELDE 1995; LOMBARDI et al. 1997). Samen von *T. angustifolia* und *T. latifolia* aus dem Donaumoos zeigen die höchsten Keimerfolge bei wechselnden Temperaturen von 10/25°C, was den mittleren Minimal- und Maximal- Temperaturen im Juni/Juli im Donaumoos entspricht (vgl. Kapitel 2 und 3; WILD et al. 2002). Andere Samenpopulationen erreichen die höchste Keimrate allerdings bei höheren Temperaturen (z.B. LOMBARDI et al. 1997). Ein leichter Wasserüberstau fördert die Keimung (COOPS & VAN DER VELDE 1995, WILD et al. 2002), während ein zu hoher Wasserstand die Etablierung der Keimlinge erschwert (GRACE 1985). Schon geringe Unterschiede im Wasserstand von 10 cm im Frühjahr beeinflussten den Besiedlungserfolg in Fläche 1 langfristig. Beschattung der Samen und Keimlinge durch Konkurrenzarten wie die Algen in Fläche 1 oder auch Konkurrenz der eigenen Art (GRACE 1983) beeinträchtigen die Keimung und auch den Etablierungserfolg (HAGER 2004) deutlich. Die Wiederbesiedelung der Fläche 2 im Frühjahr des zweiten Bestandesjahres deutet darauf hin, dass autotoxische Prozesse, wie sie von GRACE (1983) beschrieben werden, nur in einem dichten Bestand wirksam werden und die Keimung behindern. Sowohl in der Ansaatfläche, wie auch im zweiten Bestandesjahr in Fläche 3 nach dem teilweisen Zusammenbruch des Bestandes, bildete sich im Frühjahr zunächst ein sehr dichter Keimlingsbestand mit über 100 Keimling/m². Durch Prozesse der Selbstauslichtung (Selfthinning vgl. SILVERTOWN 1982) nimmt die Dichte des Bestandes im Sommer (Juni - September) wieder ab. Dieser Absterbevorgang ist zeitlich mit dem Übergang der Keimlinge zum vegetativen Wachstum gekoppelt und bildet sich auch in der Populationsstruktur ab. Während sich einige Keimlinge etablieren konnten und ins juvenile Stadium übergingen, starben zahlreiche andere Keimlinge ab und die Sprossdichte je Quadratmeter sank (vgl. Abb. 7-3 und 7-2).

Durch die Pflanzung von Jungpflanzen wird die sensible Phase der Keimung und Etablierung der Keimlinge im Freiland, die mit einer hohen Mortalität verbunden ist (HARPER 1977), umgangen und die Bestandesetablierung beschleunigt. Die Kolonisierung des Habitats erfolgt durch die Bildung vegetativer Tochtersprosse am Ende unterirdischer Rhizome (GRACE & HARRISON 1986). Eine hohe Wachstumsrate wie in Fläche 2 (10,3 Sprosse/a) in der Kolonisationsphase ist typisch für *T. latifolia*. GRACE & WETZEL (1981 c) beobachteten für *T. latifolia* bis zu 13,6 Sprosse/a und für *T. angustifolia* 9,2 Sprosse/a in einem halbnatürlichen Bestand in Michigan (USA). Ohne Konkurrenz konnte FIALA (1978) eine Produktion von bis zu 46,2 bzw. 13,6

Sprosse/a im ersten Jahr für *T. latifolia* bzw. *T. angustifolia* messen. Die starke Produktion von neuen Sprossen bei der Neu-Besiedelung oder auch nach der Beschädigung des Rhizoms (Fläche 2, 2. Jahr) vermindert allerdings die Bildung von Blütenständen (GRACE & WETZEL 1982).

FIALA (1978) zeigte, dass eine einzelne Pflanze von *T. latifolia* in der Lage ist, eine Fläche von bis zu 16 m² im ersten Jahr zu besiedeln, für *T. angustifolia* beträgt die Fläche 9 m². Beide Arten unterscheiden sich dabei in der Sprossanatomie leicht. *T. latifolia* bildet längere Rhizome, an deren Ende ein Tochterspross entsteht. Die Rhizome von *T. angustifolia* sind etwas kürzer (28 cm *T. latifolia*, 13 cm *T. angustifolia*; GRACE & WETZEL 1982). Im Vergleich bildet *T. angustifolia* stets dichtere Bestände aus als *T. latifolia* (GRACE & WETZEL 1981 a; 1982; WEISNER 1993; HAGER 2004; SELBO & SNOW 2004). Die Sprossdichten in Fläche 2 im ersten Bestandesjahr liegen im gleichen Bereich wie sie von WEISNER (1993) in Schweden (*T.l.* 20, *T.a.* 50 Sprosse/m²) oder von HAGER (2004) in einjährigen Versuchsbecken (*T.l.* 75, *T.a.* 91 Sprosse/m²) gefunden wurden. Die Sprossdichte hängt neben dem Wasserstand (GRACE & WETZEL 1981 a) auch von der Nährstoffversorgung (LORENZEN et al. 2001) ab. Welcher der beiden Faktoren für die unterschiedliche Entwicklung der Sprossdichten von *T. latifolia* in Fläche 2 und 3 verantwortlich ist, lässt sich anhand der Flächen im Donaumoos nicht trennen. GRACE & WETZEL (1981 a) zeigen allerdings, dass *T. latifolia* gerade flachere Wasserstände bevorzugt und hier konkurrenzstärker ist als *T. angustifolia*, so dass die schlechtere Entwicklung von *T. latifolia* in Becken 3 vermutlich vor allem durch die deutlich schlechtere Versorgung mit Nährstoffen bedingt ist (vgl. Tab. 7-1), die den Bestand auch anfälliger für Parasiten und Krankheiten machte. Der niedrige Wasserstand begünstigte hier nach dem Bestandeszusammenbruch die Wiederbesiedlung mit Keimlingen.

Biomasseproduktion und Ernte

Feuchtgebiete gehören zu den produktivsten Biotopen der Erde (ESSER et al. 2000). Überlegungen zur Nutzung von Rohrkolbenbeständen zur Wasserreinigung und Erzeugung von Bio-Energie wurden bereits in den achziger Jahren angestellt (GARVER et al. 1988). Neben der nachhaltigen Nutzung nasser Standorte durch künstliche Bestände (WILD et al. 2002, TIMMERMANN et al. 2003; SCHÄTZL et al. 2006) steht heute der Hochwasserschutz und die kostengünstige Wasserreinigung (CIRIA et al. 2005; MANDER & MITSCH 2009) im Vordergrund bei der Nutzung von Feuchtgebieten.

Die Biomasseerträge im Donaumoos sind mit Angaben von GRACE & WETZEL (1981 a) für ältere halbnatürliche Bestände und DICKERMANN & WETZEL (1985) für natürliche Bestände in Michigan (USA) vergleichbar. GARVER et al. (1988) konnten im Oktober des zweiten Jahres allerdings mit 818 g/m² bzw. 484 g/m² für *T. latifolia* und *T. angustifolia* nur deutlich geringere Erträge messen. Ein Unterschied in der Biomasseproduktion zwischen den beiden Arten mit höheren Erträgen von *T. angustifolia*, wie er in diesem Projekt festgestellt wurde, findet sich in der Literatur nicht. Die Biomasserträge von Rohrkolbenbeständen hängen stark von der Nährstoffversorgung ab (GRACE 1988). Mit Hilfe eines Modells konnten TANAKA et al. (2004) sowohl Zusammenhänge mit der Nährstoffversorgung, als auch mit der geographischen Breite des Standortes feststellen.

Soll der Bestand nachhaltig genutzt werden, darf die Ernte den Fortbestand der Population nicht gefährden. Das über zwei Jahre durchgeführte Schnittexperiment zeigt, dass eine Ernte generell nicht die Biomasseproduktion verringert. Wichtig ist allerdings die Schnitthöhe.

Während ein Schnitt im Sommer unterhalb der Wasseroberfläche den Bestand schädigt und daher empfohlen wird, um Rohrkolbenbestände zu kontrollieren (BOERS et al. 2007; DAS & TANAKA 2007), hat der Schnitt im Winter keine negativen Auswirkungen, wie der Vergleich eines Schnittes oberhalb und in Höhe des Wasserstandes zeigt. Im Sommer werden durch eine Mahd unterhalb der Wasseroberfläche einerseits die wachsenden Rhizome von der Sauerstoffversorgung abgeschnitten und durch anaerobe Prozesse geschädigt (SALE & WETZEL 1983), außerdem werden Nährstoffe aus dem Bestand entfernt, die im Herbst ins Rhizom verlagert würden, um den Wiederaustrieb im Frühjahr zu fördern (GARVER et al. 1988; DAS & TANAKA 2007).

Durch eine Mahd direkt an der Bodenoberfläche wird zwar der höchste Ertrag erzielt, sie vermindert allerdings die Biomasseentwicklung im Folgejahr und ist deshalb für eine dauerhafte Nutzung nicht zu empfehlen. Ein Schnitt an der Bodenoberfläche entfernt auch kleine Triebe, die für die Regeneration des Bestandes von Bedeutung sind (DICKERMANN & WETZEL 1985). WILD et al. (2002) konnten zeigen, dass die Regeneration des Bestandes nach dem Winter zwar vor allem durch die Bildung neuer Tochtersprosse erfolgt, der Wiederaustrieb vorhandener Sprosse entsprach jedoch einem Anteil von ca. 30 %. Vor allem Sprosse, die im Herbst noch sehr klein waren (Höhe <100 cm), hatten eine hohe Überlebenswahrscheinlichkeit. Sprosse ab einer Größe von 100 cm haben eine Überlebenswahrscheinlichkeit von unter 50 %. Werden die jüngsten Triebe geschont, wie bei den Schnittvarianten in Höhe des Wasserspiegels bzw. oberhalb des Wasserspiegels, wird der Ertrag im folgenden Jahr nicht vermindert.

Auf der Grundlage dieser Ergebnisse ist ein Schnitt ca. 10 bis 20 cm über dem Boden für die Ernte zu empfehlen, da hier bei jährlich wiederholter Ernte die höchsten Erträge erzielt werden können. Durch die Ernte wird die in natürlichen Rohrkolbenbeständen oft angehäufte tote Biomasse entfernt und eine Verjüngung des Bestandes herbeigeführt. Neben der Schnitthöhe ist für die weitere Bestandesentwicklung besonders eine Schonung der Rhizome wichtig. Als besonders günstig hat sich dazu die Ernte auf gefrorenem Boden mit einem leichten Fahrzeug erwiesen, wie sie im Winter 2000/01 durchgeführt wurde. Starke Rückgänge in der Bestandesdichte wie im Winter 1999/00 konnten dadurch vermieden werden.

8 Conclusions

The presented studies investigated the population biology of *Typha latifolia* and *T. angustifolia* following the life cycle of the plants from germination, to establishment, growth and vegetative and generative reproduction by performing different experiments and by observing the development of a planted stand in a constructed wetland. High germination percentage and successful establishment of seedlings associated with a vigorous clonal growth with up to twenty new shoots per square metre within three months and the first generative reproduction in the season after stand establishment enables both investigated *Typha* species to colonise new habitats successfully within short time. While chapter three to seven cover the different phases of the life cycle of *T. latifolia* and *T. angustifolia* largely independently here in chapter eight the different results on population development will be combined and possible effects on natural and constructed wetlands as well as for the cultivation of *Typha* will be discussed. A focus will be set on the shared and distinct responses of the species. Table 8-1 reviews the results of the investigated generative and vegetative traits of the species.

Initially the collected data on the different phases of the life cycle will be combined to a simple model to quantify the colonisation potential of the species. In a second step the question if both species differ in their growth and reproductive strategies will be addressed. Terminally recommendations for the cultivation of *Typha* spp. will be deduced.

8.1 Colonisation potential of T. latifolia and T. angustifolia

The colonisation of a new habitat is the first phase in the development of a new population. Especially in habitats undergoing periodical disturbance as aquatic systems, which are often prone to episodes of flooding and low-water, colonisation and re-colonisation are important (ZEDLER & KERCHER 2004). The colonisation of a new habitat can be divided into several phases (HARPER 1977). When these phases are arranged in their temporal order, it is possible to follow the life cycle of the species: From an established stand over the development of inflorescences, to the number of seeds and seedlings and in the end the number of possible plants in a new habitat (cp. Fig. 8-1).

Table 8-1: Comparison of generative and vegetative traits of *T. latifolia* and *T. angustifolia.* + higher value compared to the other species; = no difference between species; (+) superiority under certain environmental conditions; N – Number.

trait	response	*T. latifolia*	*T. angustifolia*
Generative traits			
Chapter 3 and 4			
Final percentage germination	Increased by alternating temperatures (10/25°C optimum) and higher water level (3 cm)	+	
Germination speed	Increased by higher temperatures	=	=
Seedling growth			
Chapter 5			
Biomass	Depends on water level; low to medium water level – *T. latifolia* higher biomass; flooded conditions *T. angustifolia* higher biomass production	(+)	
N established	*T.latifolia* higher proportion of seedlings established, no effect of water level	+	
Chapter 6			
N generative shoots/m²	*T. latifolia* fast reproduction 40-50 %; *T. angustifolia* 29 % in the third year	+	
Vegetative traits			
Chapter 6 and 7			
Shoot density	*T. latifolia* about 50 shoots/m²; *T. angustifolia* up to 117 shoots/m²		+
Growth rate	Decreases after colonisation	=	=
Biomass production	*T. angustifolia* about 1300 g/m² in the third winter; *T. latifolia* about 700 g/m²		+
Below-Ground biomass	About 3300 g/m² in the third season for both species	=	=
Sensibility to harvest	Harvest at 10 to 20 cm above the soil tolerated	=	=

Between the different steps the probability to reach the next one functions as a sieve. These `sieves´ are determined by the physiological properties of the species and the environmental conditions as for example adequate temperatures for germination or water supply during seedling growth. By combining the individual steps of colonisation a simple model can be derived to estimate the colonisation potential. Using data from experiments conducted under standardised conditions provokes an overestimation of the colonisation potential because adverse effects, for example predation or shortages in nutrient supply are ignored. Nevertheless, the calculation enables a comparison of the colonisation potential of different species under optimal conditions. The model deduced from the data of the studies facilitates to calculate minimal and maximal reproductive output of both Typha species under different input requirements and to detect the most vulnerable steps in the life-cycle.

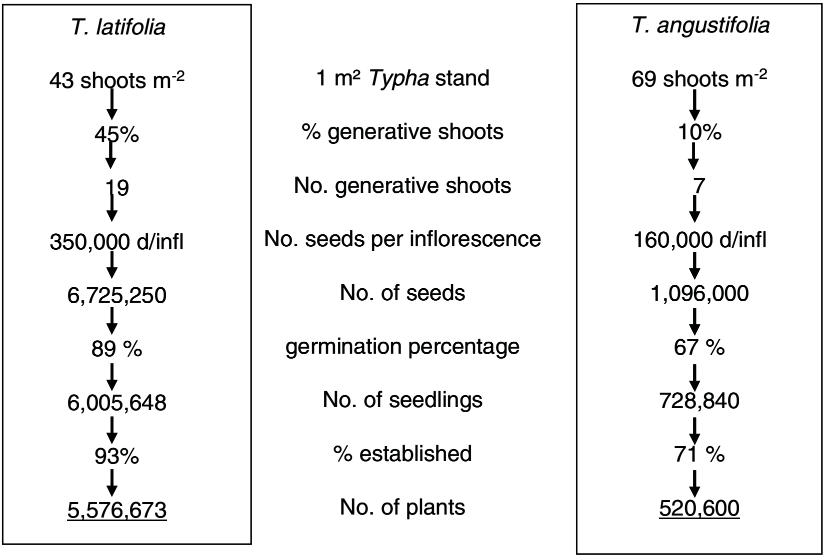

Figure 8-1: Schematic life cycle of *T. latifolia* and *T. angustifolia* calculating a maximal number of offspring produced by one square metre stand in the year 1999 (first season, cp. Tab. 8-2 scenario 1).

Despite the similarities of *Typha latifolia* and *T. angustifolia* in morphology and their co-occurrence the studied populations of the two species differed in shoot density, production of generative shoots, percentage germination and establishment (Table 8-1). Comparative studies investigating semi-natural or experimental stands of *T. latifolia* and *T. angustifolia* always detected a higher shoot-density for *T. angustifolia* compared to *T. latifolia* (GRACE & WETZEL 1981a; 1982; WEISNER 1993; HAGER 2004, SELBO & SNOW 2004) as in the constructed wetland in southern Germany. While *T. angustifolia* increased shoot densities every season and had its maximum shoot density in 2001 (116.6 shoots/m²), *T. latifolia* reached the maximum measured shoot density in the first season after establishment (1999: 47.0 shoots/m², cp. chapter 6). However, *T. latifolia* produced the higher proportion of generative shoots (*T. latifolia* 59 %; *T. angustifolia* 29 %). In each inflorescence several 100,000 diaspores develop. The diaspore numbers used in the model are derived from COOPS & VAN DER VELDE (1995), who counted them in natural stands in the Netherlands.

The tested *Typha* species attained maximum germination at 10/25°C, but differed markedly in final percentage germination (cp. chapter 3). *T. latifolia* shows greater germination percentage at every temperature treatment. At 10/20°C and flooded conditions 89.3 % and 66.5 % final percentage germination are achieved by *T. latifolia* and *T. angustifolia* respectively. Studies comparing both species detected different performance of the species but while MCNAUGHTON (1966) observed faster germination of *T. latifolia*, COOPS & VAN DER VELDE (1985) found higher percentage germination for *T. angustifolia*. In a greenhouse experiment over eleven weeks 93 % of the *T. latifolia* seedlings survived under moist conditions and with the water level at the soil surface. In *T. angustifolia* under the same conditions 71 % of the seedlings were able to survive.

Inserting these results into a simple model (Fig. 8-1) and connecting the phases in life-cycle using the obtained data one square metre *T. latifolia* stand is able to produce 5.6 millions of offspring, while *T. angustifolia* produces 500,000 new plants in the first year after establishment. Because the data was derived from individual experiments and the treatment with the most positive result for each step was used, the calculation overestimates the colonisation potential under field conditions by far, but it is able to show the tendencies: *T. latifolia* expresses a much higher colonisation potential than *T. angustifolia*.

Comparing the different steps in life cycle the greatest differences between species can be detected in the proportion of generative shoots (*T.latifolia/T.angustifolia* = 4.5). The germination percentage and the percentage of seedling survival differ both by the factor 1.3 (Table 8-2). Using the germination percentage observed by COOPS & VAN DER VELDE (1985) with a higher germination percentage for *T. angustifolia* instead, diminishes the difference between species, but does not reverse the order of species (Table 8-2, scenario 3). The model can be easily re-calculated, testing different scenarios. The number of generative shoots per square metre was a key factor for the colonisation potential. Therefore, the increase in shoot density and in the proportion of generative shoots in *T. angustifolia* has changed the offspring out-put considerably even within the investigated seasons. Using the stand data of the year 2001 *T. latifolia* produced only double the number of offspring than *T. angustifolia* (Table 8-2, scenario 2).

Generally the model shows that both investigated *Typha* species have a high potential to colonise new habitats. *Typha latifolia* and *T. angustifolia* differ in their reproductive success. Especially in the phase shortly after stand establishment *Typha latifolia* expressed a considerably higher colonisation potential than *T. angustifolia* producing a ten-fold higher number of offspring under optimal conditions (Table 8-2, scenario 1).

Table 8-2: Different scenarios calculated by the colonisation model (Fig. 8-1) of *T. latifolia* (T.l.) and *T. angustifolia* (T.a.). Data input differing from scenario 1 are printed in bold letters. f – Factor T.l./T.a.

	Scenario 1: early colonisation (1999)			Scenario 2: third year after stand establishment (2001)			Scenario 3: = scenario 1 but germination data from Coops & Van der Velde (1995)		
	T.l..	T.a.	f	T.l..	T.a.	f	T.l..	T.a.	f
Shoots/m²	42.7	68.5	0.6	**36.5**	**116.6**	0.3	42.7	68.5	0.6
% generative shoots	45	10	4.5	**47**	**29**	1.6	45	10	4.5
generative shoots/m²	19.2	6.9	2.8	17.2	33.8	0.5	19.2	6.85	2.8
seeds per inflorescence	350000	160000	2.2	350000	160000	2.2	350000	160000	2.2
No. of seeds	6.7 mio	1.1 mio	6.1	6.0 mio	5.4 mio	1.1	6.7 mio	1.1 mio	6.1
% germination	89.3	66.5	1.3	89.3	66.5	1.3	**71.2**	**94.2**	0.8
No. of seedlings	6.0 mio	728840	8.2	5.3 mio	3.6 mio	1.5	4.8 mio	1032432	4.6
% established	92.9	71.4	1.3	92.9	71.4	1.3	92.9	71.4	1.3
No. of plants	5.6 mio	520'600	10.7	5.0 mio	2.6 mio	1.9	4.4 mio	737'451	6.0
T. l/T. a.	10.7			1.9			6.0		

8.2 Growth and reproductive strategies of *Typha latifolia* and *Typha angustifolia*

The environmental conditions of a habitat effect the adaptation of plant species in different vegetative and generative traits. The complex of these co-evolved adaptive traits can be interpreted as life-strategy (Stearns 1976). The concept of r- and K-selection by McArthur & Wilson (1969) (modified by Gadgil & Solbrig 1972) divides species according to habitat stability. R-selected plant species settle in instable habitats, are short-lived and produce high numbers of offspring. On the other end of the gradient the K-selected species live in stable habitats, produce high amounts of biomass, are long-lived and reproduce only seldom (Gadgil & Solbrig 1972). In

GRIME´s (1974) C-S-R-model plant species are placed according to their adaptations to competitiveness (C), stress-tolerance (S) and reaction to disturbance (ruderal strategy - R) in a three-dimensional space.

The investigated *Typha latifolia* and *T. angustifolia* are both perennial macrophyte species producing a high number of offspring to colonise new habitats or to re-colonise the habitat after disturbance (see above). Both *Typha* species are common and widespread in Europe, but different distribution patterns can be recognized comparing the distributions on geographical grid maps (e.g. Germany, British Isles). The geographical range of both species is comparable, but *T. latifolia* occurs at nearly every grid point, while *T. angustifolia* occurs scattered (NBN 2004; BUNDESAMT FÜR NATURSCHUTZ 2006). The different abundances can, beside other reasons, be caused by different niche widths of the species (GRACE & WETZEL 1981; COOPS & VAN DER VELDE 1995), competitive displacement or differentiations in colonisation and life strategy (GRACE & WETZEL 1981 a, 1998). Generally both species express a similar life strategy with adaptations to generative dispersal and fast clonal colonisation of the habitat. But on the fine scale *T. latifolia* and *T. angustifolia* differ in their population biology (e.g. MCNAUGHTON 1966; GRACE & WETZEL 1981 a, c, 1998; present study).

The life strategies of the species were assessed differently by different studies. Based on the shoot development MCNAUGHTON (1975) suggests *T. latifolia* to be more r-selected, because of the high number but lower investment per ramet, and positioned *T. angustifolia* on the more K-selected side of the gradient. GRACE & WETZEL (1982) on the other hand denoted *T. angustifolia* as ´fugitive´ and *T. latifolia* as the more competitive species. Their classification was mainly based upon the higher investment in sexual reproduction and ramet production of *T. angustifolia* (GRACE & WETZEL 1982). However, GRACE & WETZEL (1981 a) observed a higher rhizome storage in *T. angustifolia* and attested *T. latifolia* a wider niche in relation to water-level compared to *T. angustifolia*.

In contrast to the present study MCNAUGHTON (1975) and GRACE & WETZEL (1981 a, 1982) investigated long established stands. In these stands *T. latifolia* produced a smaller number of inflorescences than *T. angustifolia* (GRACE & WETZEL 1982). Also, DICKERMAN & WETZEL (1985) investigating a natural stand of *T. latifolia* detected only low numbers of inflorescences. In the present study covering only the first three seasons after stand establishment *T. latfolia* produced a high number of inflorescences, expressed higher germination percentage and seedling survival. Compared to *T. angustifolia* it developed less dense stands but starts generative reproduction earlier and with a higher number of inflorescences. The difference in time lapse and proportion of generative reproduction could be interpreted as a differentiation in development strategy between the species, with *T. latifolia* showing a more short-lived strategy with fast colonisation and early reproduction.

Also the vegetative growth and the development of daughter ramets point at a differentiation between both investigated *Typha* species. VAN KLEUNEN et al. (2001) connected different allocation to production of daughter ramets and sexual reproduction to different growth strategies (sensu LOVETT DOUST 1981). Reviewing different studies they found species with guerrilla growth type to allocate more biomass into sexual reproduction when population density increased and no change in allocation in phalanx growth types (VAN KLEUNEN et al. 2001). Hence, *T. latifolia* would express more the guerrilla growth type, with shoots more spreading out, while *T. angustifolia* grows more compact, which was also demonstrated by FIALA (1978) and GRACE & WETZEL (1982). Overall *T. latifolia* showed strong adaptations to the colonisation of habitats, while *T. angustifolia* developed extremely dense stands.

As the stand density and the proportion of flowering shoots increased in *T. angustifolia* in the seasons following the establishment the relation between the species may shift in long established stands and *T. angustifolia* may produce more offspring than *T. latifolia*.

Concluding the presented studies on population development, *T. angustifolia* will build up dense, stable, long-lived and more competitive populations, while the populations of *T. latifolia* will be more flexible, they may invade new habitats, colonise them and start generative reproduction the first season. Transferred to a landscape scale the stands of *T. angustifolia* should be long-lived, while *T. latifolia* would frequently colonise new habitats and stands would be short-lived. In a study in Finland in 54 small lakes near Tampere TOIVONEN (1980) compared frequency and abundance data of both species from 1947-1951 with data from 1975-79 and detected population developments according to the assumptions based on population data: While *T. angustifolia* occurred in a smaller number of lakes (7), the stands being still existent after 30 years, *T. latifolia* was found in 27 of the investigated lakes in 1947-1951 and had colonised 39 lakes thirty years later and showed higher fluctuation in abundance (TOIVONEN 1980). Even the different distribution patterns of both species on grid-maps (cp. NBN 2004; BUNDESAMT FÜR NATURSCHUTZ 2006) could at least in part be due to the different life-strategies of *Typha latifolia* and *T. angustifolia* with *Typha latifolia* expressing the characteristics of a pioneer with a very efficient generative reproduction, while *T. angustifolia* is adapted to a more competitive strategy.

The great colonisation potential could even convert *Typha* species into invasive species especially when environmental conditions as hydrology and nutrient supply are modified by human intervention in the natural wetland dynamics or by climate change. In terms of invasiveness reproductive traits seem to be of particular importance for species abundance (MURRAY et al. 2002; PYŠEK & RICHARDSON 2007). Commonness or invasiveness shows the most reliable relations to a higher fecundity, a longer flower period and an earlier or better germination on a wider range of conditions (MURRAY et al. 2002; PYŠEK & RICHARDSON 2007). While HODGSON (1986) found no rare – common difference in lateral vegetative spread, PYŠEK & RICHARDSON (2007) detected a more vigorous spatial growth as a reliable trait of invasive species in their review. In the corollary of the population date *T. latifolia* would show more potential to become invasive at least in Europe. Especially the dispersal of alien populations with divergent traits could increase the risk of an invasion (cp. SALTONSTALL 2002).

8.3 Recommendations for the cultivation of Typha spp.

- *Typha* spp. stands are suitable for water treatment, retention and as a renewable ressource. Especially sites under intense agricultural use or degraded fens can be improved by *Typha* cultivation, when a year round water supply is guaranteed.
- *Typha* stands can be established as well by planting as by sowing. The favourable method of establishment depends on site conditions (control of water supply, competition). If water depth can be regulated to constant low levels (< 20 cm) during germination and seedling phase and competition by existing vegetation is low, stand establishment by sowing will be successful. To improve and accelerate germination higher temperatures as in the months June and July are preferable for sowing. When the foremost objective is a fast and complete colonisation of the site planting pre-cultivated seedlings is recommended. The establishment of the planted seedlings is furthered by constant low water levels, supplying the plantlets with water without inundation of the whole shoot. Shoot densities of 2 plantlets/m² and less will be sufficient (e.g. 0.5 or 0.25 plantlets/m²) because of the vigorous clonal growth of the species in the colonisation phase.
  A combination of sowing and later planting of single seedlings in possible gaps the following season would be a low-priced and safe alternative for the establishment of a *Typha* stand.
- Biomass could be harvested in winter on frozen soil with light-weight machinery. To remove nutrients from the habitat stands should be harvested as early in winter as possible. While a cutting height of 10 to 20 cm above the surface is recommended, to spare small, new shoots at the soil surface improving growth the following spring, the relation of cutting height in winter and water level is irrelevant for stand development. Rhizomes survive inundation of the cutting height and re-sprout in spring.
- *T. angustifolia* produces higher leave biomass with long closed sheets suitable for the production of insulation material. For the production of inflorescences T. latifolia is preferable. Yields of up to 650 to 1400 g/m² dry-mass (equates: 6.5 - 14 t/ha) could be harvested.
- A sufficent nutrient supply is inevitable for the development of stable and long-lived stands. Up to 83 % and 86 % of the ammonia- and nitrate-load respectively, and up to 74% of the phosphate could be absorbed by a *Typha* basin.

Empfehlungen für den Anbau von Rohrkolben (Typha spp.)

- Der Anbau von Rohrkolben ist besonders auf bisher intensiv genutzten Flächen sowohl für die Wasserreinigung, Wasserrückhaltung und auch als nachwachsender Rohstoff geeignet. Möglichkeiten für eine ganzjährige Vernässung sollten gegeben sein.
- Die Etablierung des Bestandes kann sowohl durch Aussaat als auch durch Pflanzung erfolgen. Die Wahl der Etablierungsmethode hängt von den Umweltbedingungen (Regulierbarkeit des Wasserstandes, Konkurrenzdruck), aber auch vom geplanten Zeitrahmen ab. Besteht die Möglichkeit, den Wasserstand zu kontrollieren und während der Keimung und Etablierung gleichmäßig niedrige Wasserstände (< 20 cm) zu erreichen und ist nur wenig Konkurrenz vorhanden, ist eine Etablierung durch Aussaat Erfolg versprechend. Um eine sichere und zügige Keimung zu fördern, sind die Monate Juni und Juli für die Aussaat besonders günstig. Steht eine schnelle, dichte Besiedelung der Fläche im Vordergrund, ist die Vorkultur und Pflanzung von Jungpflanzen zu empfehlen. Auch das Anwachsen der Jungpflanzen wird durch gleichmäßig niedrige Wasserstände gefördert. Auf Grund des schnellen Wachstums sind auch Pflanzdichten von weniger als 2 Pflanzen m^{-2} möglich (z.B. 0,5 oder 0,25 Pflanzen m^{-2}).

  Eine Kombination aus Aussaat und, wenn notwendig, Bepflanzung der Lücken im Folgejahr könnte eine kostengünstige und sichere Alternative darstellen.
- Die Ernte der oberirdischen Biomasse im Winter sollte mit leichtem Gerät auf gefrorenem Boden erfolgen. Um einen möglichst hohen Ertrag zu erzielen bzw. möglichst viele Nährstoffe aus dem System zu entfernen, sollte die Ernte im Winter so früh wie möglich stattfinden. Der Schnitt sollte mindestens 10 bis 20 cm über der Bodenoberfläche durchgeführt werden, um junge Sprosse nahe am Boden zu schonen, die für die Regeneration des Bestandes im Frühjahr sorgen. Die Höhe des Wasserstandes im Verhältnis zur Schnitthöhe hat keine Bedeutung. Ein Überstau der Schnittflächen nach einer Wintermahd beeinträchtigt den Austrieb aus dem Rhizom nicht.
- Steht die Produktion von Blattmasse im Vordergrund, erweist sich *T. angustifolia* für die Rohstoffgewinnung als vorteilhaft, da neben dem hohen Biomasseertrag die Blattmasse zur Weiterverarbeitung besonders geeignet ist. Allerdings werden von *T. angustifolia* nur wenige Samenstände gebildet. Für die Gewinnung der Samenwolle

ist deshalb *T. latifolia* besser geeignet. Erträge von 650 bis 1400 g/m² Trockenmasse (entspricht 6,5 - 14 t/ha) können erzielt werden.

- Entscheidend für einen dauerhaften Bestand ist eine gute Nährstoffversorgung. Ein Rohrkolbenbestand kann bis zu 83 % der Ammonium- bzw. 86 % der Nitrat- und bis zu 74% der Phosphatfracht aus dem Wasser aufnehmen und einen wesentlichen Beitrag zur Wasserreinigung leisten.

Summary

Typha latifolia L. and *T. angustifolia* L. are closely related emergent wetland plants native to Europe with a distribution in the temperate northern hemisphere. They are tall erect perennials with long linear leaves and flower spikes. Both *Typha* species are common and widespread in Europe and often build mono-dominant stands characterised by low plant species diversity. Because of their extensive distribution and commonness *Typha* communities form an important and widespread wetland type under more eutrophic conditions.

This study investigated the establishment, growth and reproduction of *T. latifolia* and *T. angustifolia* by performing different experiments and by observing the development of a planted stand in a constructed wetland. It was integrated in the project "Cultivation of *Typha* in a degraded fen area – integration of raw-material production, water purification and soil protection into a sustainable landuse concept" (Rohrkolbenanbau in Niedermooren – Integration von Rohstoffgewinnung, Wasserreinigung und Moorschutz zu einem nachhaltigen Nutzungskonzept). The population biology approach enables not only to study the effect of environmental factors but also to quantify them and to compare the dimension different factors have on growth and reproduction. *Typha* was studied following the plant´s life cycle from germination, over seedling establishment and growth to reproduction and death. The focus was set on the colonisation of new habitats, the population establishment and the first years of population development.

Chapter 3 examinated the effect of temperature and water level on seed germination. Water depth and temperature had a significant effect on the germination percentage as well as on germination speed. Both factors interacted in accelerating germination. *T. latifolia* additionally showed a significant interaction between water depth and temperature for all measured parameters. Thereby water depth had a more pronounced effect on percentage germination, while temperature affected the time lapse of germination. Comparing constant and fluctuating temperatures showed a clear preference of fluctuating temperatures. Populations differed in germination success. Over all treatments *T. latifolia* achieved a higher germination percentage than *T. angustifolia*, even though no difference in germination onset was detected.

In **Chapter 4** variations in the germination response of fifteen European *Typha latifolia* populations from different climatic regions were investigated. Large differences in final germination percentage and time lapse of germination were found

between populations and between temperature regimes. An increase in temperature increased germination percentage, but even more accelerated germination while an increase in amplitude augmented primarily germination percentage. Populations showed a distinct germination response. The different ranking of the populations across various temperature regimes indicated an adaptation in germination traits to specific habitat conditions. Optimal germination temperatures were not linked to mean temperature of population site, but the ordination analysis of germination traits arranged populations approximately along a climate gradient. Mediterranean populations showed both high germination percentage and fast germination, followed by populations with oceanic and sub-continental or continental origin. Predicted increasing temperatures especially in winter could further germination of *T. latifolia* and a potential shift in population distribution may unbalance plant communities by enhancing colonisation by *Typha*.

Chapter 5 investigated the effect of different water-levels on the seedling growth of *T. latifolia* and *T. angustifolia*. Both species reacted with an increase of shoot heights and the production of fragile floating leaves to the increase in water depth. But while *T. angustifolia* was able to develop higher shoots in the flooded treatment, the growth of *T. latifolia* was constrained by a flooding of 12 cm. Parallel to shoot height, the biomass production was increased by the surface water level treatment, but species differ significantly in their reaction. While *T. latifolia* showed a distinct peak of biomass in the surface treatment and the lowest biomass under flooded conditions, *T. angustifolia* produced nearly the same amount of biomass in the surface and flooded treatment. Under competitive conditions water level probably would be a key factor determining recruitment success between *T. latifolia* and *T. angustifolia*.

The development of planted stands of *T. latifolia* and *T. angustifolia* in a constructed wetland was investigated in **Chapter 6**. The plantlets of *Typha latifolia* and *T. angustifolia* displayed a fast clonal growth and colonised the surface rapidly. While 50 % of the *T. latifolia* shoots became generative till July, only 12 % of the *T. angustifolia* shoots flowered in the first season. In the following seasons shoot density and the proportion of generative shoots increased in *T. angustifolia*. The regression analyses suggested a strong dependence of proportion of generative shoots on shoot density in *T. angustifolia*, while in *T. latifolia* the percentage of generative shoots was predicted best by mean stand height in May. The negative beta for shoot heights increment and the number of new shoots in *T. latifolia* indicated in the direction of a trade off between generative reproduction and growth. Overall *T. latifolia* showed strong adaptations to the colonisation of habitats, while *T. angustifolia* developed extremely dense stands.

Cultivating wetland plants as raw-material instead of traditional cultures provides a sustainable land use concept for degraded fen soils**. Chapter 7** addressed the establishment and biomass yield of *Typha* sp. in constructed wetlands. Cattail stands can be established in constructed wetlands by planting or sowing. Establishment by planting is the faster but more costly method. Closed stands can be achieved within one year by planting less than two seedlings per square meter. As germination is furthered by higher, alternating temperatures, sowing in early summer is recommended. A constant, low water-depth below 10 cm is crucial for a successful establishment of the seedlings. *Typha* spp. produced 800 to 1200 g dry-mass m^{-2} at harvest-time in winter. Harvesting with light machinery on frozen grounds at a cutting level of 10 to 20 cm is convenient, to preserve small young shoots which accelerate recruitment in spring. The harvest in winter does not impact re-growth and biomass production the following year.

Chapter 8 concluded the results by combining the collected data on the different phases of the life cycle to a simple model to quantify the colonisation potential of the species. In a second step the question if both species differ in their growth and reproductive strategies was addressed. Finally the effects derived from population biology of *T. latifolia* and *T. angustifolia* for natural and constructed wetlands were discussed and recommendations for the cultivation of *Typha* sp. deduced. The colonisation model showes that *Typha latifolia* and *T. angustifolia* differ in their reproductive success, and *Typha latifolia* produces a ten-fold higher number of offspring under optimal conditions in the first season after establishment. Generally *Typha latifolia* expresses the characteristics of a pioneer with a very efficient generative reproduction, while *T. angustifolia* is adapted to a more competitive strategy. The observed strategies of the species fit into their distribution pattern with *T. latifolia* being the more frequent species.

Zusammenfassung

Breitblättriger Rohrkolben (*Typha latifolia* L.) und Schmalblättriger Rohrkolben (*Typha angustifolia* L.) sind einheimische Röhrichtarten mit einer Verbreitung in der temperaten Zone der Nordhemisphäre. Beide sind mehrjährig, kommen häufig vor und haben eine weite Verbreitung. Oft bilden die hochwüchsigen Arten artenarme Dominanzbestände. Durch ihr großes Verbreitungsgebiet und das häufige Vorkommen stellen Rohrkolben-Röhrichte einen wichtigen Vegetationstyp in Feuchtgebieten dar.

In dieser Arbeit wird die Etablierung, das Wachstum und die Reproduktion von *T. latifolia* und *T. angustifolia* mit Hilfe verschiedener Experimente und durch die Beobachtung eines gepflanzten Bestandes in künstlich angelegten Becken in Süddeutschland untersucht. Sie wurde im Rahmen des Projektes „Rohrkolbenanbau in Niedermooren – Integration von Rohstoffgewinnung, Wasserreinigung und Moorschutz zu einem nachhaltigen Nutzungskonzept“ durchgeführt. Der populationsbiologische Ansatz der Untersuchungen ermöglicht es, die Wirkung von verschiedenen Umweltfaktoren zu erkennen und auch die Auswirkungen auf das Wachstum und die Reproduktion der Arten zu quantifizieren. Die Arbeit folgt dabei dem Lebenszyklus des Rohrkolbens von der Keimung der Samen, über die Etablierung der Keimlinge, die Bildung von Tochtersprossen bis zur generativen Reproduktion der Pflanzen. Der Schwerpunkt wurde dabei auf die Phase der Besiedlung eines neuen Lebensraumes und die Entwicklung des Bestandes in den ersten Jahren gelegt.

Kapitel 3 untersucht die Wirkung von verschiedenen Temperatur- und Wasserstandsbedin-gungen auf die Keimung. Beide Faktoren haben einen signifikanten Einfluss und können gemeinsam die Keimung beschleunigen und bei *T. latifolia* auch den Keimerfolg steigern. Ein Anstieg des Wasserstandes allein erhöht vor allem den Anteil der gekeimten Samen, während die Erhöhung der Temperatur die Keimung vor allem beschleunigt. Im Vergleich zu konstanten Temperaturen wird die Keimfähigkeit durch wechselnde Tag- und Nachttemperaturen gefördert. Insgesamt erreicht *T. latifolia* einen höheren Anteil gekeimter Samen als *T. angustifolia*. Im zeitlichen Verlauf der Keimung unterscheiden sich die Arten nicht.

In einem weiteren Keimversuch wurden Samen des Breitblättrigen Rohrkolbens (*T. latifolia*) von Populationen aus verschiedenen klimatischen Gebieten Europas getestet (**Kapitel 4**). Sowohl im Keimerfolg, als auch in der Geschwindigkeit der Keimung zeigen sich deutliche Unterschiede zwischen den Populationen. Ansteigende Temperaturen vergrößern allgemein den Keimerfolg und beschleunigen die Keimung.

Die unterschiedlichen Temperaturoptima der Populationen deuten auf eine Anpassung an die Standortbedingungen hin, zeigen aber keine direkte Verbindung zu den Temperaturbedingungen am Standort. In einem Ordinationsdiagramm werden die verschiedenen Samenherkünfte jedoch in etwa entlang eines klimatischen Gradienten angeordnet. Die beiden Populationen aus dem Mittelmeergebiet haben die höchste Keimrate und keimen sehr schnell. Danach folgen die Populationen aus der ozeanischen, der sub-kontinentalen und kontinentalen Zone. Ansteigende Temperaturen im Zuge des Klimawandels könnten die Keimung von Rohrkolben fördern und das räumliche Gefüge der an den Standort angepassten Populationen stören.

Kapitel 5 untersucht die Auswirkung verschiedener Wasserstände auf das Wachstum von Keimlingen von *T. latifolia* und *T. angustifolia*. Das Anheben des Wasserstandes führt bei beiden Arten zu einer Höhenzunahme. Das komplette Untertauchen der Keimlinge bei überstauten Bedingungen verlangsamt bei *T. latifolia* das Wachstum und auch die Bildung von Biomasse. Es werden flexible schwimmende Blätter ausgebildet. Während *T. latifolia* die höchste Biomasse bei einem Wasserstand an der Bodenoberfläche bildet und die Biomasseproduktion bei Überstau sinkt, unterscheidet sich bei *T. angustifolia* die Biomasseproduktion zwischen den beiden Wasserständen nicht. Bei überstauten Bedingungen erreicht *T. angustifolia* sogar eine höhere Biomasse als *T. latifolia*. Unter Konkurrenzbedingungen könnte der Wasserstand entscheiden, welche Art sich etablieren kann.

Die Entwicklung eines gepflanzten Bestandes von *T. latifolia* und *T. angustifolia* in künstlichen Becken wird in **Kapitel 6** untersucht. Die Pflanzen bildeten zahlreiche Tochtersprosse und kolonisierten die Fläche. Bereits nach drei Monaten bildete sich ein geschlossener Bestand und die Wachstumsrate verlangsamte sich. Ab der ersten Vegetationsperiode entwickelte *T. angustifolia* dichtere Bestände als *T. latifolia* und die Bestandsdichte nahm im Laufe der Jahre weiter zu. Bei *T. latifolia* entwickelten allerdings bereits in der ersten Vegetationsperiode etwa 50 % der Sprosse einen Blütenstand, während bei *T. angustifolia* nur 12 % der Sprosse das generative Stadium erreichten. In den folgenden Jahren stieg dieser Anteil bei *T. angustifolia* allerdings auf 39 % an. Die Regressionsanalyse zeigt, dass bei *T. angustifolia* die Bildung von generativen Sprossen vor allem von der Bestandesdichte abhängt, während sich der Anteil generativer Sprosse bei *T. latifolia* besser aus der Sprosshöhe im Frühjahr vorhersagen lässt. Für *T. latifolia* lässt sich auch eine Verringerung der

Höhenzunahme und der Bildung neuer Sprosse zugunsten der Entwicklung von blühenden Sprossen beobachten.

Der Anbau von Röhrichtpflanzen zur Produktion eines nachwachsenden Rohstoffes ist eine nachhaltige Alternative zum Anbau traditioneller Kulturen in degradierten Niedermooren. **Kapitel 7** stellt Möglichkeiten der Bestandesetablierung vor und untersucht Auswirkungen der Ernte auf die Bestandesentwicklung in den folgenden Jahren. Rohrkolbenbestände können sowohl durch Pflanzung als auch durch Aussaat etabliert werden. Die Etablierung durch Pflanzung bietet eine sehr sichere und schnelle, allerdings auch kostenintensive Methode der Bestandesgründung. Das schnelle Wachstum ermöglicht auch Pflanzdichten von weniger als 2 Pflanzen je Quadratmeter. Für die Etablierung durch Aussaat bieten sich die Monate Juni und Juli auf Grund der günstigen Temperaturen an. Kritisch ist die erste Zeit der Keimlingsentwicklung, in der ein gleichmäßig niedriger Wasserstand von wenigen Zentimetern erforderlich ist. Für die Bestandesentwicklung ist zudem eine ausreichende Nährstoffversorgung wichtig. Die Ernte sollte im Winter bei gefrorenem Boden durchgeführt werden, um Schäden am Boden und an den Pflanzen zu vermeiden. Eine Schnitthöhe von 10-20 cm schont bereits gebildete junge Sprosse, die im Frühjahr für einen schnellen Bestandesaufbau sorgen. Langsames Anheben des Wasserstandes im Frühjahr ermöglicht es Keimlingen, Bestandeslücken zu füllen. Jährlich wiederholtes Ernten führt im zweiten Jahr zu keiner Verminderung der Erntemenge. Im Vergleich zeigt *Typha angustifolia* durch eine höhere Bestandesdichte, lange geschlossene Blattscheiden, eine große Höhe und einen hohen Biomasseertrag günstigere Eigenschaften für die Verarbeitung zu Dämmstoffplatten als *Typha latifolia*. Für die Gewinnung von Samenhaaren eignet sich jedoch letztere besser, da ein höherer Anteil generativer Triebe gebildet wird.

In **Kapitel 8** werden die Ergebnisse der verschiedenen Experimente und Untersuchungen zunächst zu einem einfachen Modell zusammengesetzt, um das Besiedelungs-Potential von *T. latifolia* und *T. angustifolia* unter optimalen Bedingungen zu vergleichen. Dabei zeigt sich, dass besonders auf Grund der höheren Anzahl von Blütenständen und der höheren Keimrate ein Bestand von *T. latifolia* theoretisch eine zehnfach größere Anzahl an Nachkommen produzieren kann als *T. angustifolia*. In einem zweiten Schritt werden die Wachstums- und Reproduktionsstrategien beider Arten verglichen. Insgesamt zeigt *T. latifolia* vermehrt Eigenschaften einer Pionier-Art mit einer schnellen Besiedlung und einer frühen und zahlreichen Reproduktion. Dagegen scheint *T. angustifolia* mit sehr dichten hochwüchsigen Beständen und einer später einsetzenden generativen Reproduktion stärker an Konkurrenzbedingungen angepasst zu sein. Diese Ergebnisse passen auch zum unterschiedlichen Verbreitungsmuster der Arten. Beide haben etwa das gleiche Verbreitungsgebiet, jedoch kommt *T. latifolia* deutlich häufiger vor als *T. angustifolia*.

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Lebenslauf

Persönliche Angaben

Sabine Isabell Heinz

Geboren am 24.10.1971 in Berlin

Schul- und Hochschulbildung

Juli 1991	Abitur, Albert-Schweitzer Oberschule (Gymnasium), Berlin
Oktober 1991 – April 1997	Biologiestudium an der Freien Universität Berlin
	Diplomprüfung in den Fächern: Morphologie und Systematik der Pflanzen, Pflanzengeographie und Ökologie
Diplomarbeit	Teucrium montani-Seslerietum albicantis - Lebensstrategien in Blaugrasrasen des unteren Unstruttals (Sachsen-Anhalt)
Promotion	Lehrstuhl für Vegetationsökologie, Department für Ökologie, Technische Universität München (TUM)
1.11.1998 – 31.10.2001	Stipendium der Deutsche Bundesstiftung Umwelt
1.11.2001 – 31.10.2002	Stipendium des Hochschulsonderprogramms der TUM

Tätigkeiten

1.1.03-31.03.2003	redaktionelle Bearbeitung der Veröffentlichung „Renaturierung von Kalkmagerrasen. Zehn Jahre Sicherung und Entwicklung der Heiden im Norden von München“ - Angewandte Landschaftsökologie 55 (2003) an der TUM.
15.5.03-15.11.2003	redaktionelle Bearbeitung und Mitherausgabe des Bandes „Renaturierung von niedermoortypischen Lebensräumen – 10 Jahre Niedermoormanagement im Donaumoos“ Naturschutz und Biologische Vielfalt 9 (2004) an der TUM.
seit 1.8.2005	Bayerische Landesanstalt für Landwirtschaft (LfL) Institut für Agrarökologie, Arbeitgruppe Vegetationskunde