Stichting Bargerveen

# The germination of *Typha* species

## Implications for paludiculture

Dr A.J.M. Jansen

GREIFSWALD MIRE CENTRE

Bosgroepen


# The germination of *Typha* species

## Implications for paludiculture

A literature research

Dr A.J.M. Jansen

2021

## Colofon

*Published*: Stichting Bargerveen © 2021



*Photos (unless otherwise stated)*: André Jansen

*Lay-out*: Aukje Gorter

*This publication can be cited as:*
Jansen, A.J.M., 2021. The germination of Typha species – implications for paludiculture. A literature research. Stichting Bargerveen, Nijmegen, The Netherlands. 72 pp.

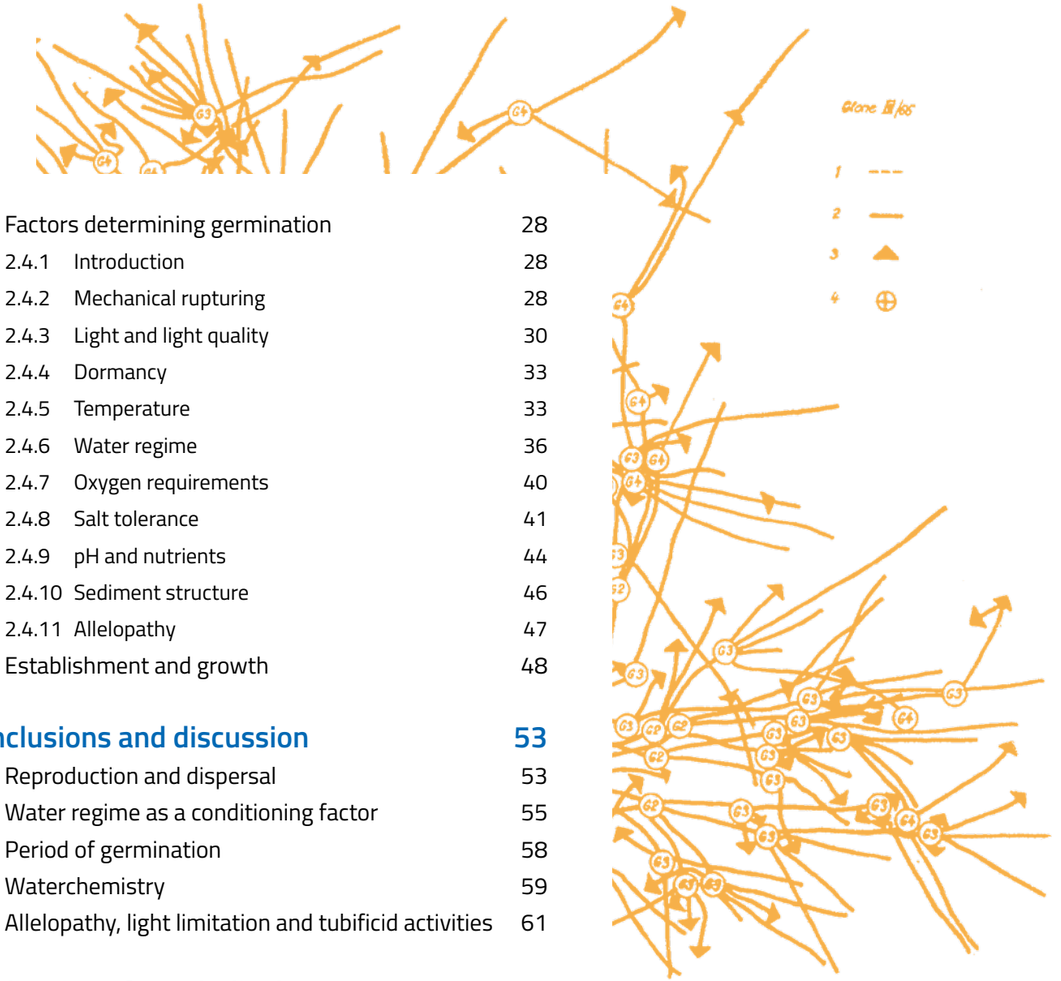
This study was carried out in association with Greifswald Mire Centre and De Bosgroepen.

GREIFSWALD MIRE CENTRE

Bosgroepen

# Table of contents





Lars Soerink/Vildaphoto

# 1 Introduction

## 1.1 Paludiculture

Drainage of wetlands for agriculture and forestry causes many problems, such as loss of biodiversity, peat soil degradation and subsidence, increased greenhouse gas emissions, and catastrophic peat fires (Wichtmann et al., 2016). In west and central Europe almost all natural peatlands have more or less been drained. The water management of these degraded peatlands requires various – often complex – technical measures. This is costly and requires a great deal of fossil energy, which in turn promotes the atmospheric emission of greenhouse gasses. Peat soil degradation and subsidence are typical examples of positive feedbacks.
In order to reverse this ongoing process with its associated negative effects, an increase in water levels is necessary. However, the rewetting of peatlands leads to the loss of productive agricultural land and forests. Therefore, alternative production opportunities are being sought, for economically valuable crops grown on wet soils. Thus, the process of continuous loss of peatlands can be counteracted, and it may even lead to renewed peat accumulation. Such wet agriculture and forestry is known as paludiculture. According to Wichtmann et al. (2016), "Paludiculture is the agricultural and silvicultural use of wet and rewetted peatlands. Paludiculture uses spontaneously grown or cultivated biomass from wet peatlands under conditions in which the peat is conserved or even newly formed."





## 1.2 Typha as a paludiculture crop

The highly productive species of the *Typha* genus belong to the promising plants for paludiculture, in particular T. latifolia and T. angustifolia. Such "paludiculture plants" are wetland plants that produce useful biomass in sufficient quantity and simultaneously contribute to preserving the peat. During harvest, the below-ground biomass generally remains untouched to avoid disturbing the peat body (Wichtmann et al., 2016). The above-ground biomass of the *Typha* species can be used as building material for insulation, for energy generation, and for wastewater treatment in constructed wetlands. Moreover, many parts of the plants are edible (young shoots, base of stem, flower stalks, pollen, and rhizomes), and *Typha* rootstocks and stems offer food for geese and muskrats, whereas *Typha* marshes provide shelter and nesting cover for several bird species (Stevens and Hoag, 2003). T. latifolia's tolerance to heavy metals makes it desirable in reclamation or revegetation efforts (Gucker, 2008a). The use of the *Typha* species by native Americans and early European settlers may inspire a modern, contemporary use of these species. Gucker (2008a) mentions matting and making dolls, baskets and shelters as examples of past use. Seed fluff was used as soundproofing material, insulation material, stuffing material for pillows, mattresses, diapers, and lifejackets, and as tinder for fire starting. Leaves were woven into bedding, kneeling mats, capes, hats, blankets, and bags Medically,

*Typha* was most commonly used as wound dressing. For example, rhizomes were ground into a salve for wounds and used to stop bleeding, and rhizomes were also used to make tea to treat stomach cramps. Fluff from broadleaf cattail seeds was used to make burn dressings. Morton (1975) gives a comprehensive overview of the former use of *Typha* species and suggests that "[t]heir stems and leaves might well be more extensively fashioned into floor coverings and other woven products, and the leaves, suitably processed, might relieve the growing shortage of papermaking substances." In conclusion, *Typha* species are promising as crops in paludiculture.

## 1.3 Aim of the study

Several attempts have been made to breed *Typha* by planting the species (Dubbe et al., 1988; Heinz, 2012; Stevens and Hoag, 2003; Christian Fritz, pers. comm.). However, planting *Typha* is expensive, with costs ranging from €2,500 - €4,500 per hectare (Sabine Wichmann, pers. comm.). Sowing may be a cheaper alternative, leading to higher profits of *Typha* cultivation by paludiculture. The seeds of the *Typha* species are relatively simple to collect in nature, and sowing costs less time than planting young plants, which must also be grown first. After germination, the seedlings rapidly develop into productive clones. However, so far there has been little experience with sowing in the context of cultivation (Georgiev et al., 2013, 2014). According to Dubbe et al. (1988), sowing in the open as an establishment method has obvious advantages, but there are also some problems involved, which are associated with a lack of reliability due to highly variable germination and seedling survival rates. They attribute this high variability to the sensitivity of cattail seed germination and development as well as to certain environmental factors. Hence, knowledge of these factors and the way they affect the germination of *Typha* seeds and their development as seedlings is essential for establishing cattail as an agricultural crop in the future (Müller-Sämann et al., 2003). Subsequently, this knowledge must be converted to practical

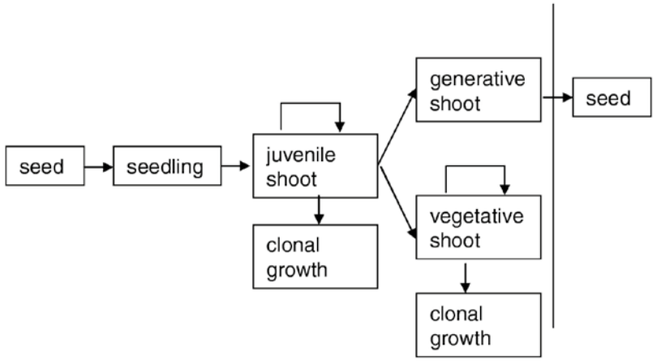



Figure 1: Schematic life cycle of *Typha* (Heinz, 2012).

guidelines for creating the correct seed conditions. This report discusses the existing knowledge of the environmental factors that affect the germination of the *Typha* species based on a comprehensive literature study. Based on the insight gained, the implications of sowing as part of *Typha* paludiculture are discussed.

## 1.4 Approach

Germination and the growth of seedlings to adult plant are part of the *Typha* life cycle (Figure 1). This literature study takes a population-biological approach, which enables the quantification and comparison of the factors that determine the germination and growth of the seedlings (Grace, 1984; Heinz, 2012).
Grace (1984) presented a conceptual model for the environmental factors that affect *Typha*'s germination and establishment (Figure 2), and this model has been used as a starting point and guide in this study.

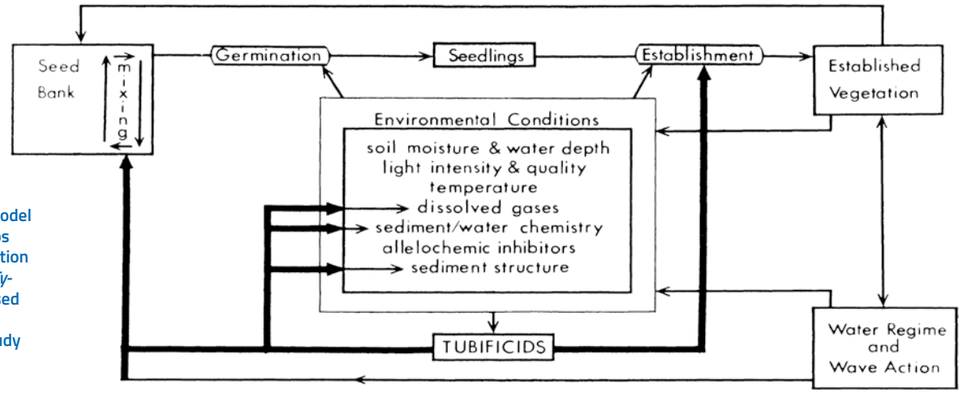



Figure 2: Conceptual model of the interrelationships regulating the germination and establishment of *Typha*, which has been used as a starting point and guide in the current study (Grace, 1984).





## 1.5 Acknowledgements

This study was carried out as part of a sabbatical at the University of Greifswald between February and April 2017. This sabbatical was made possible by my former employer, the *Unie van Bosgroepen* (Federation of Forest Support Groups), as part of my orientation on my further career development. I would like to thank my former employer for this possibility. The sabbatical helped me to make choices about the content of the last phase of my career.
The sabbatical taught me how much interest and commitment I have in mires, how important mires are in combating climate change, and how essential it is to obtain new knowledge and pass on existing knowledge in this respect, particularly to younger ecologists, soil scientists and hydrologists. That is why in 2018 I switched to *Stichting Bargerveen* (Bargerveen Foundation), which has given me the opportunity to put this into practice. In the Landscape Ecology team, we carry out projects aimed at peatland recovery, and we study the interaction between the landscape, vegetation, and fauna of bogs, percolation mires and groundwater-fed forests. For this reason, the Foundation has made funds available to finalise and publish the present report so that its findings can be taken note of. This is another reason that makes it good to work at *Stichting Bargerveen*.
Fulco Teunissen (fulco@twelvetrees.nl) improved my English and made this a good, readable text. He did so quickly and in a pleasant way.

My stay in Greifswald was one of the highlights of my career. First and foremost, this is thanks to Hans Joosten, professor of Peatland Studies and Palaeoecology. I would like to thank Hans for the hospitality of his institute, his never-ending enthusiasm and inspirational erudition, and for the many instructive conversations in the Moor Library, where we worked together for six weeks. Ine Joosten, Hans' wife, organised accommodation for me in the Pfarrer-Wachsmann-Haus, where Benita Geiger took outstanding care of me. I would also like to thank Ine for her good care and for the wonderful trips we made together. We had a great time together!
Hans Joosten leads the Greifswald Mire Centre and the Institute of Botany and Landscape Ecology, where many passionate and expert researchers are working on mires, on their restoration and on paludiculture. I had many excellent and inspiring conversations, excursions and trips with these researchers and learned a great deal from them. In particular, I would like to thank – in alphabetical order – Almut Mrotzek, Anja Prager, Anke Nordt, Balazs Baranyai, Claudia Oehmke, Greta Gaudig, Frederike Wichtmann, Henning Holst, Jenny Schulz, John Couwenberg, Monika Hohlbein, Martin Theuerkauf, Mathias Krebs, Sabine Wichmann, Susanne Abel, Tobias Dahms, and Wendelin Wichtmann.

It was exceedingly enjoyable!

The "Moor-bibiliothek" in Greifswald.

Sabine Wichmann and Claudia Oehmke discuss the species composition of the reeds that are being used as fuel in the biomass plant in Malchin.

> The pilot site for Sphagnum paludiculture (Sphagnum farming) in the peatland 'Hankhauser Moor' (Niedersachsen (Lower Saxony)).

Wendelin Wichtmann

André Jansen, Claudia Oehmke and Felix Reichelt study a soil profile of a Typha latifolia vegetation in Polder Grosse Rosin (Kummenower See; Mecklenburg-Vorpommern).

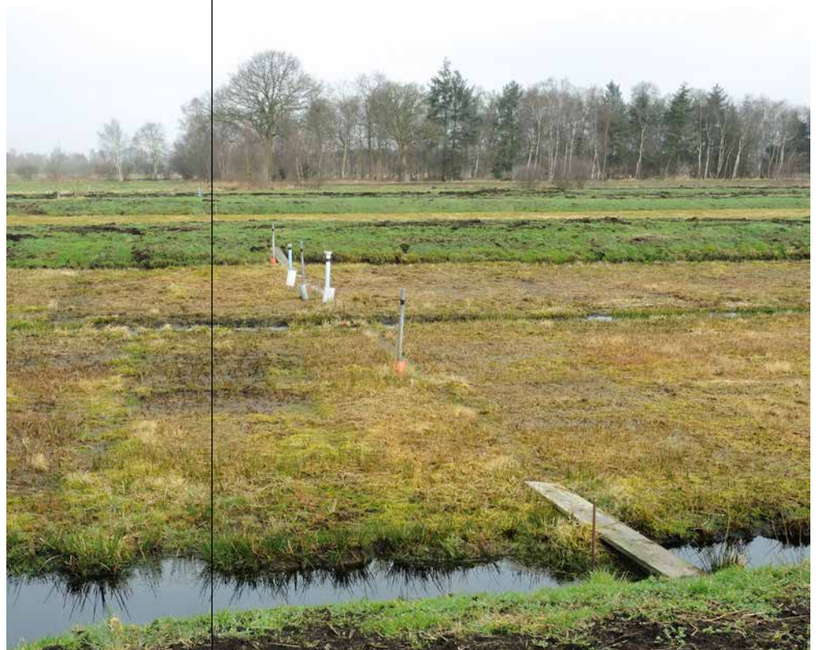





< The manager of the biomass power plant in Malchin (left) with Wendelin Wichtmann.

Hans en Ine Joosten during a boat trip on the Peene.

> Greta Gaudig explains the hydrological functioning of the Hankhausen pilot site.



Matthias Krebs measures the groundwater table in Hankhausen.

# 2 Results

## 2.1 Short introduction to the species

### 2.1.1 Taxonomy

*Typha* is a genus belonging to the subphylum *Angiosperms,* class *Monocotyledonae,* order *Typhales* and family *Typhaceae.* Species belonging to the genus include *Typha angustifolia* L., *T. domingensis* Pers. (Synonym: *T. angustata* Bory and Chaub), *T. elephantina* Roxb., *T. latifolia* L., *T. minima* Funck ex Hoppe, and *T. orientalis* C.Presl.

### 2.1.2 Distribution

*Typha* species are widespread in the temperate to tropical zone, although they are naturally absent from Madagascar, Malaysia, and the warm Americas (Watson and Dallwitz, 1992 onwards).

*T. latifolia* is a cosmopolitan species, with its native range encompassing large regions on all continents, except Antarctica, the major part of Africa and Oceania (Clements, 2010). It is recorded as having been established as a non-native species in six countries (Australia, Indonesia, Malaysia, New Zealand, Papua New Guinea, and the Philippines). The species is also increasingly seen as taking on invasive characteristics in some countries where it is native (Shih and Finkelstein, 2008; Olson and Freeland, 2009).

*T. angustifolia* occurs in at least 56 countries throughout the temperate northern hemisphere (Murphy, 2007). It has been suggested that *T. angustifolia* was first introduced into Atlantic Coastal North America from Europe and then migrated westward (Stuckey and Salamon, 1987).

Furthermore, the hybrid product of *T. latifolia* and *T. angustifolia*, *T. x glauca* tends to be more invasive than *T. latifolia* (Olson and Freeland, 2009).

### 2.1.3 Morphology

According to Heinz (2012), "*Typha latifolia* and *T. angustifolia* [Figures 3 and 4] largely share the same morphology. Both are erect, rhizomatous perennial species (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 and Harrison, 1986)." The flowers are densely packed, and individual flowers can barely be identified. The stems are connected by creeping rhizomes (Figure 5). Dispersal occurs by numerous aerial and floating seeds and stolons. Shoots and rhizomes have a well-developed aerenchyma, providing underground organs with oxygen (Grime et al. 1988).

Clements (2010), Gucker (2008a), Murphy (2007) and Snyder (1993) described the morphology of both species in more detail:

- Narrowleaf cattail (*T. angustifolia*) is an aquatic, emergent plant; a slender, erect, rhizomatous perennial growing to 3 m tall, but usually 1-2 m tall. It has branched creeping rhizomes, 2-4 cm in diameter, commonly 70 cm or even longer, with dense fibrous root masses occurring at the base of stems and at rhizomes. Stems are unbranched and round with long (60-150 cm) linear leaves, which are 3-12 mm wide and deep green. Leaves are strongly planoconvex, numbering <10 per stem, sheathing at the base, and commonly overtopping the inflorescence. The inflorescence is a thin, dense crowded cylindrical spike of male flowers (brown to yellowish) above a similar spike of female flowers (reddish to dark brown), with a gap of approximately 10 mm between the two. The fruits are cigar-shaped and 5-15 cm long. Fruits contain soft, downy seeds (Murphy (2007; Snyder, 1993). According to Dickerman and Wetzel (1985), *T. latifolia* is a highly productive species, whose productivity varies from 430 to 2,250 g dry matter per $m^2$/yr
- Broadleaf cattail (*T. latifolia*) plants are normally 1-3 m tall, reed-like, and extensively clonal. Broadleaf cattail stems are stout, cylindrical, and unbranched. Flowering stem length is typically equal to or somewhat longer than leaf length. Leaves are thick, linear, flat, with a sheath at the base, extending to flowering spikes, and measure 5 to 29 mm wide (Gucker, 2008a; Clements, 2010). *T. latifolia* can be highly productive. "Numerous tiny, unisexual flowers include a pistillate portion below the staminate portion, forming a continuous spike which is 1.8-5 cm thick. Spike goes from green to brown as ripening occurs. Male spikes (the upper, narrower half) and female spikes (the lower half) are rarely separated. A small space of less than 1.5 cm may occur. Spikes are typically 6 times as long as they are thick

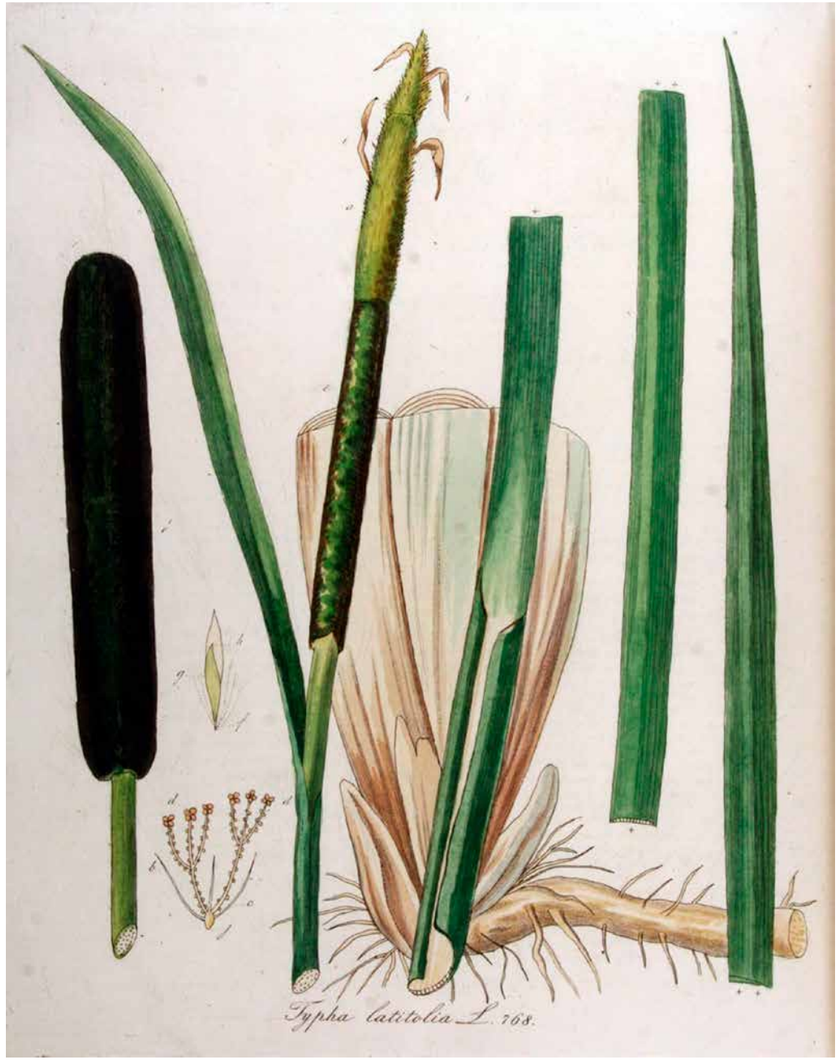



Figure 3 *Typha latifolia* (Kops, J. and Van der Trappen, J.E., 1849, Flora Batava, Part 10 (in https://wilde-planten.nl/grotelisdodde.htm).





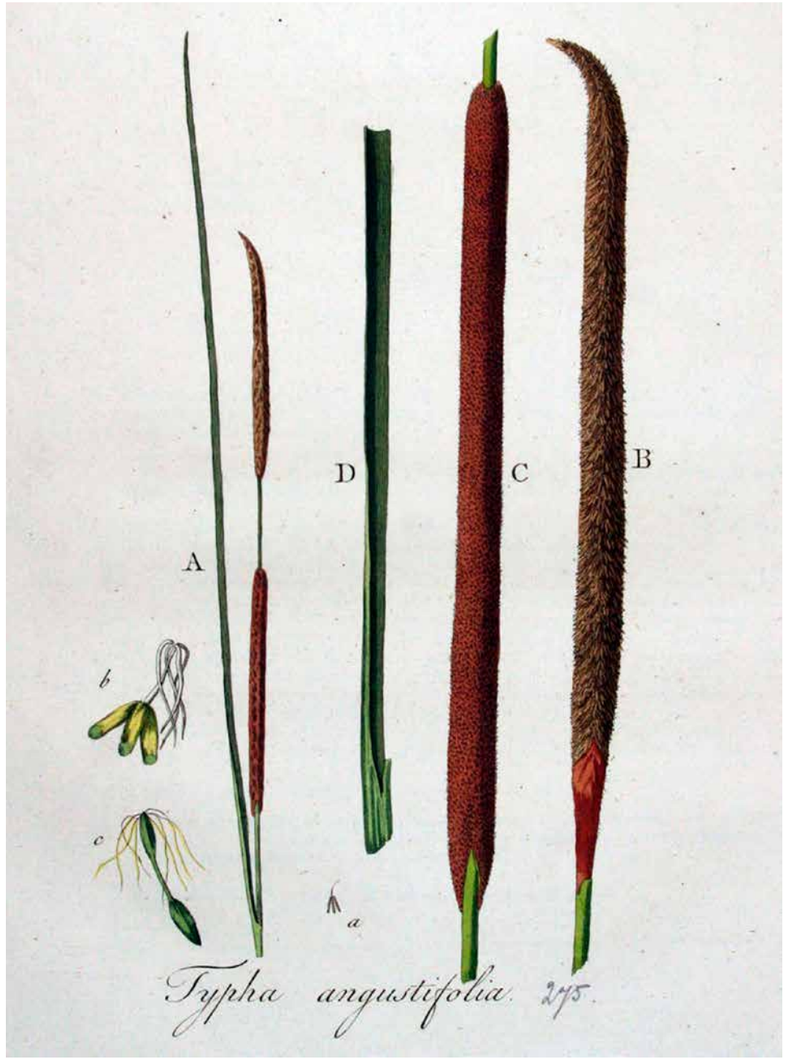



Figure 4 *Typha angustifolia* (Kops, J., 1822. Flora Batava, Part 4 (in https://wilde-planten.nl/kleinelisdodde.htm).

(11-30 cm). Its rhizomes are being described as tough, stout, coarse, and grow horizontally just below the soil surface. They are as long as 70 cm and 0.5-3 cm in diameter." (Gucker, 2008a). Yeo (1968) measured the length of the spikes, which averaged 7 inches (approx. 18 cm).

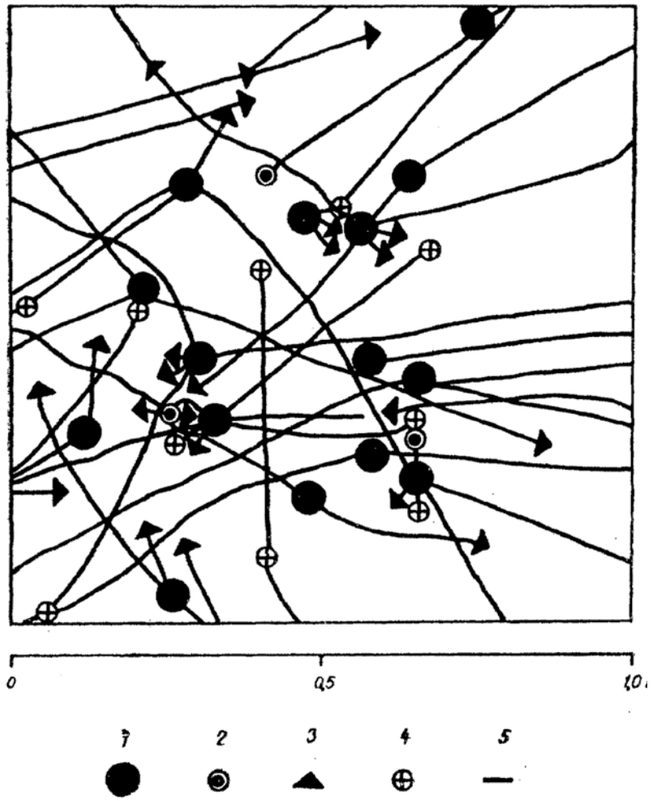



Figure 5: Horizontal projection of the rhizome system of *Typha latifolia* in mature stands: 1-3: living shoots, 1: sterile shoots, 2: fertile shoots, 3: hibernating buds, 4: remnants of old dead shoots, 5: rhizomes (Fiala, 1971).

Grace and Wetzel (1981a) described the differences between the species as follows: "*Typha latifolia* differed from *T. angustifolia* in having shorter leaf height, wider leaves, greater leaf surface area, greater allocation to leaves, greater number of smaller rhizomes, greater allocation to vegetative reproduction, smaller allocation to sexual reproduction, and fewer number of flowering plants. For both species, those plants growing in deeper water had taller leaves, a greater allocation to leaves, and a decreased allocation to sexual and vegetative reproduction."

### 2.1.4 Habitat

Both species are characteristic of a wide variety of wetland habitats. *T. angustifolia* occurs in natural freshwater and wetland systems (lakes, rivers, ponds, topogenous and soligenous mires, fens, and other marsh systems). It also grows in anthropogenic wet habitats such as drainage and irrigation channels, associated reservoir and pond systems, and navigation canals (Murphy, 2007). Because of its clonal growth pattern and high competitive ability, it tends to form monodominant stands in suitable habitats for growth. *T. latifolia* grows in marshes, wet meadows, lakeshores, roadside ditches, seacoast estuaries, pond margins, bogs or fens as well as rice paddies (Grace and Harrison, 1986; Clements, 2010). *T. latifolia* tends to be replaced by *T. angustifolia* in waters more than 15 cm deep (Figure 6) (Grace and Wetzel, 1982; see also Murphy, 2007 and Snyder, 1993). Under normal conditions, neither species survives in water deeper than 60-100 cm (Grace and Wetzel, 1982). This is in contrast to findings by Weeda et al. (1996), who report that plant communities of *T. angustifolia* occur in open waters between 0.5 and 1.5 m deep, and sometimes even deeper. Furthermore, Clements (2010) mentioned that *T. latifolia* may also occupy somewhat drier sites, such as along the edge of





marshy woodlands or among woody shrubs (Grace and Wetzel, 1981b). The only agricultural habitat where *T. latifolia* regularly occurs is in rice paddies (Mitich, 2000). The plants prefer a soil pH of >5.5, and are absent in more acidic soils. However, *T. latifolia* can tolerate acidity (Weeda et al., 1994). Moreover, both *T. latifolia* and *T. angustifolia* are characteristic of eutrophic sites, although *T. angustifolia* can also occur in mesotrophic conditions (Oberdorfer, 1983; Weeda et al., 1994). However, Lieffers (1983) found *Typha latifolia* not only in nutrient-poor sites, namely on floating organic mats in oxbow lakes in the boreal forest zone of Alberta, Canada, but also in more nutrient-rich sites on grounded substrates. He measured peak above-ground biomass ranging from 456 to 848 g/m², dependent on the successional and nutrient status of the oxbow lake. *T. latifolia* had larger stems and greater biomass after sites had returned to an earlier stage of succession due to flooding.

In northwest and central Europe, *T. latifolia* and *T. angustifolia* are part of species-poor plant communities, which belong to the class *Phragmitetea*, alliance *Phragmition* (Oberdorfer, 1983). In Germany, *T. latifolia* is considered the characteristic species (kentaxon) of the association *Typhetum latifoliae* (Oberdorfer, 1983) and *T. angustifolia* as the characteristic species of the *Typhetum angustifoliae* (Oberdorfer, 1983). In the Netherlands, communities of *T. angustifolia* are classified as *Typho-Phragmitetum*, subassociation *typhetosum angustifoliae*, whereas species-poor vegetation types of *T. latifolia* are considered as belonging to a poorly-developed frame community (Weeda et al., 1996). Communities occupied by *T. latifolia* range from early to late successional stages. Although in many wetlands it is a dominant species that forms high densities, in other wetlands it may occur as scattered individuals or clumps (Clements, 2010). Plant communities of *T. angustifolia* belong to the early successional stages of terrestrialisation of open waters, primarily at sites with a thick sapropelium layer (Weeda et al.,1996). Different from *T. latifolia*, *T. angustifolia* is capable of building a floating mat, thanks to its relatively short, stout and longer-lived stolons (Grace and Harrison, 1986). Such floating mats belong to the first stages of succession from open water to reed lands, or from open water to floating sedge communities (quacking mires). The accumulation of above-ground biomass depends on the length of the growing season, precipitation, cumulative degree days, and cumulative pan evaporation (Holm et al., 1997).

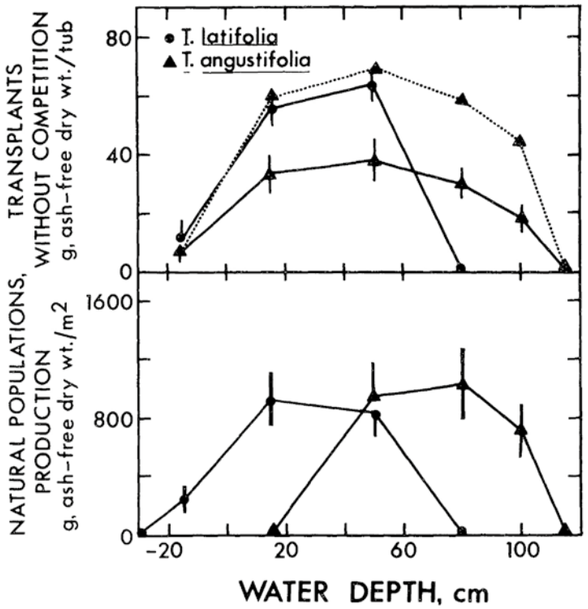



Figure 6: Potential and realised distributions of *Typha* species along a gradient of water depth. Points connected by a broken line in the upper figure represent values adjusted for density for *T. angustifolia*. Error bars represent 95% confidence intervals (Grace and Wetzel, 1981c).

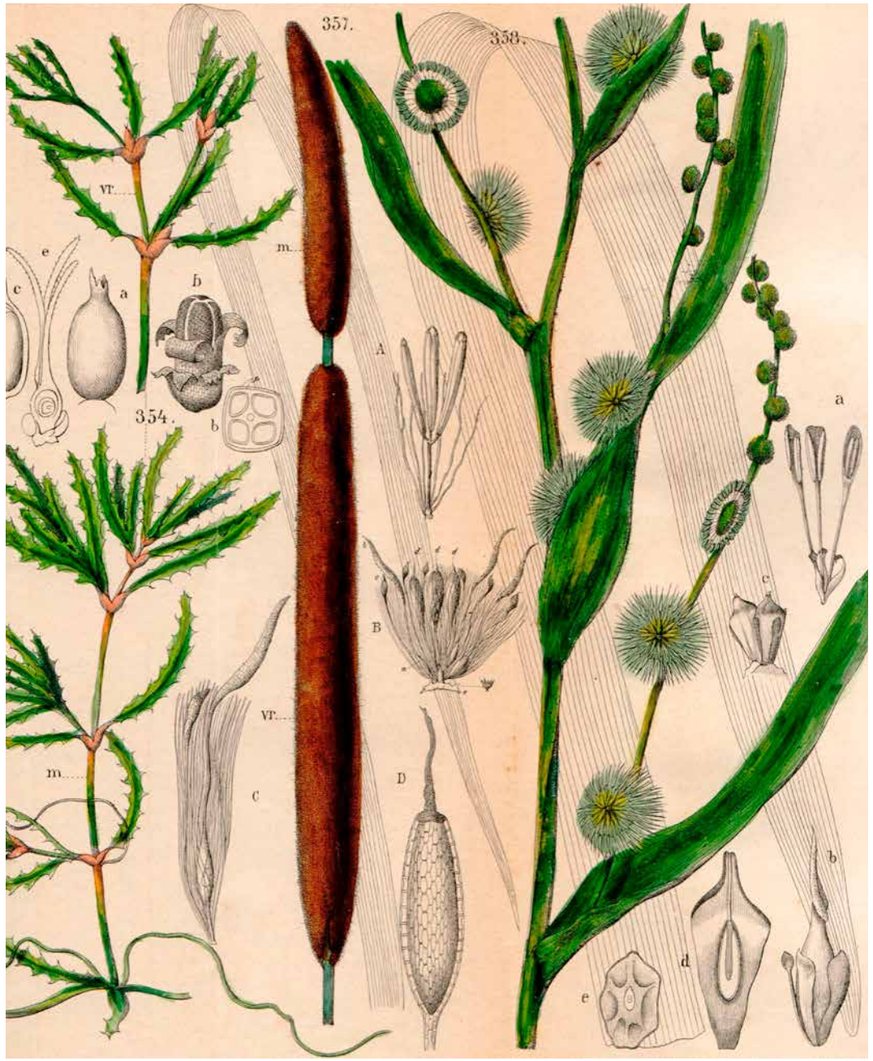



Figure 7: *Typha angustifolia*, with the male flower (m) as the upper part of the inflorescence and the female or pistillate flower (vr) as the lower part.

A = male flower;
B= part of the female flower whorl with three fertile flowers (a = ovary; b = stigma; c = pistillodium; d = infertile flowers); C = fertile flower with pistillodium and a bunch of bristle or gynophore hairs;
D = fruit or achene on a stipe (magnification x30) (Oudemans, 1862).





## 2.2 Fruits and seeds

### 2.2.1 Inflorescence and flower and fruit anatomy

The inflorescence of *Typha* species consists of a single, cylindrical spike with two flower whorls (Figure 7), the upper one with the male flowers (the staminate part) and the lower one with the female flowers (the pistillate portion). The inflorescences of *Typha* are wind-pollinated and bear copious pollen. *T. latifolia* forms 280 to 420 million pollen grains per inflorescence. Pollen is wind-borne, but the plants still have a high degree of self-pollination. Pollen has been shown to remain viable for at least 4 weeks, but it is sensitive to high humidity and temperature extremes (Mitich, 2000).

Both fertile and sterile flowers occur on the spike (Figure 7). The mature fertile flower consists of a persistent style and stigma (Figure 8), a seed surrounded by a thin pericarp (Figure 9), and a stipe with numerous bristle hairs at the base (Figure 10; Yeo, 1964). The pistillodes (rudimentary pistils; Figure 7) are distributed throughout the inflorescence. They regulate the release of fruits (Grace and Harrison, 1986; Figure 11). The fruits are equipped with numerous gynophore hairs (Figures 7, 10, 11, and 12; Grace and Harrison, 1986).
Yeo (1964) described the fertilisation and the subsequent changes of the inflorescence precisely: “Just prior to pollination the pistillate flowers become fully developed. The style elongates and supports a salver-shaped stigma. Bristle hairs at the base of the ovary elongate too, but remain appressed to the floret. Pollination occurred over a 2- to 3-week period. The ovary swells after fertilisation. The apex of the stigma turns brown, changing the overall colour of the spike. Next, the stipe at the base of the ovary elongates and holds the ovary away from the rachis. As a consequence of the elongation of the stipe the maturing pistillate portion of the inflorescence thickens.”

*Typha* seeds are small, from ca. 1 mm (Grace, 1984) up to 1.4 mm in size (Grime et al., 1988). The diaspores are light-weight, single-seeded dry fruits with basal hairs (Grace and Harrison, 1986; Grime et al., 1988). Figure 12 depicts the fruits and seeds of *T. latifolia* and *T. angustifolia* (Cappers et al., 2006). According to Grace (1985) and Grace and Harrison (1986), the seeds of all *Typha* taxa are very small, with those of *T. latifolia* (1.5 mm in length) slightly larger than those of *T. angustifolia* (1.0 mm). Extensive studies by Marsh (1962) showed seed lengths of 0.962-1.776 mm for *T. latifolia* and 0.718-1.358 mm for *T. angustifolia*.
Both *Typha* species produce single-seeded, nutlike achenes, with long slender hairs at the base which allow for wind and water transport of the dehiscent seeds (seeds which do not open at maturity; Pojar and MacKinnon, 1994).

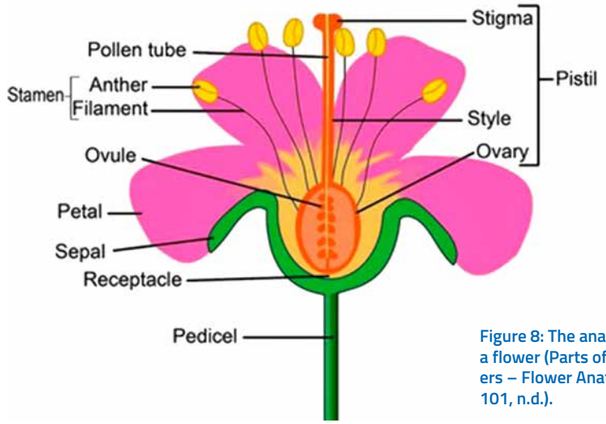



Figure 8: The anatomy of a flower (Parts of Flowers – Flower Anatomy 101, n.d.).


Figure 10: The anatomy of a flower with respect to fruit development. A gynophore is the stalk of certain flowers which supports the gynoecium (the ovule-producing part of a flower), elevating it above the branching points of other floral parts (https://en.wikipedia.org/wiki/Gynophore, 2019, 21 May).

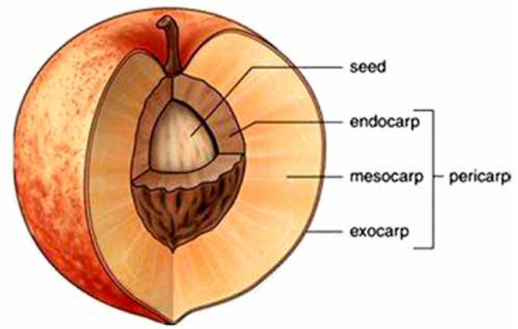



Figure 9: The anatomy of a fruit (walnut). The pericarp is the ripened ovary wall (Lesson 11 Fruit morphology Flashcards, n.d.).

Figure 11: Bursted inflorescences of *Typha latifolia*. Picture taken by the author at Haaksbergerveen (The Netherlands), 16 March 2017.





### 2.2.2 Seed numbers

The seeds weigh 10-13 mg (Mitich, 2000). According to Murphy (2007), *T. angustifolia* produces very large numbers of small pendulous seeds, with a straight, narrow embryo, whereas *T. latifolia* may produce over 1000 flowers on one plant (Clements, 2010). Stewart et al. (1997) stated that both *T. domingensis* and *T. latifolia* produce tens of thousands of seeds. More than 50% of the pollinated flowers set seeds (Yeo 1964). Grace and Harrison (1986), Prunster (1941), Marsh (1962) and Yeo (1964) reported that the *Typha* species produce small single-seeded fruits in great numbers, with estimates for a single inflorescence ranging from 20,000 to 700,000. Yeo (1964) mentioned a production of 117,000 to 268,000 (average 222,000) per cattail spike, Dubbe et al. (1988) reported 200,000 seeds, while Heinz (2012) reported that in each flower spike more than 100,000 diaspores mature. Furthermore, Dubbe et al. (1988) calculated that 0.4 ha - with a density of 50 plants per square meter - can be established by the seeds of a single cattail inflorescence, assuming 100% germination.

### 2.2.3 Seed viability and seed bank

In the pilot study of Stewart et al. (1997), 100% germination occurred under selected conditions for *T. domingensis*, which points to full viability of the seeds of this *Typha* species.
Van der Valk and Davis (1976) examined the seed banks of shallow, glacial prairie marshes in north central Iowa. They defined a seed bank as " the amount of viable seed present in the substrate at any given time". With its presence of 69%, *Typha glauca* was among the seven species that had a presence of 40% or higher in the 16 seed banks that they investigated. *Typha glauca* was also an abundant species in the seed bank: it accounted for 16% of the total number of individuals of all species in the seed banks.Van der Valk and Davis (1976). In addition, they concluded that "the type of vegetation present at any time is primarily a function of water level, while its floristic composition is a function of the makeup of the seed bank." This stresses the importance of the species composition of the seed bank and the numbers of the seeds of the individual species present.

*Typha* species can build up a seed bank with high seed densities. In wetland substrates, which are characterised by high seed densities (Keddy and Reznicek, 1986), they may make up a large portion of the seed bank; for example, Leck and Graveline (1979) reported 25%. *Typha* seeds may remain dormant for long periods (Van der Valk and Davis, 1976; Keddy and Reznicek, 1986). After prolonged high water periods, dense *Typha* vegetation and the wooded areas on lake shores die off. Consequently, open gaps are created, allowing many vegetation types and plant species, such as *Typha* species, to regenerate from buried seeds during low water periods (Keddy and Reznicek, 1986). According to Bakker et al. (1996), *T. latifolia* - with its average of 9,510 seeds per $m^2$ - belongs to the 15 species with the highest average seed densities. As most of the other species with such seed densities, *T. latifolia* has small or very small seeds (Bakker et al., 1996). The longevity of seeds is one of the important factors which determines the species composition of a seed bank. The question is whether the seeds of *Typha* species have a short or a long viability. Literature shows that *Typha* latifolia seeds have a short to a very long lifespan.

Leck and Simpson (1987) and Tu et al. (1980) showed that dense *T. latifolia* seedlings often emerged from sites where broadleaf cattail was abundant. According to Poschlod and Jackel (1993), *Typha* species have a transient (<1 year) or short-

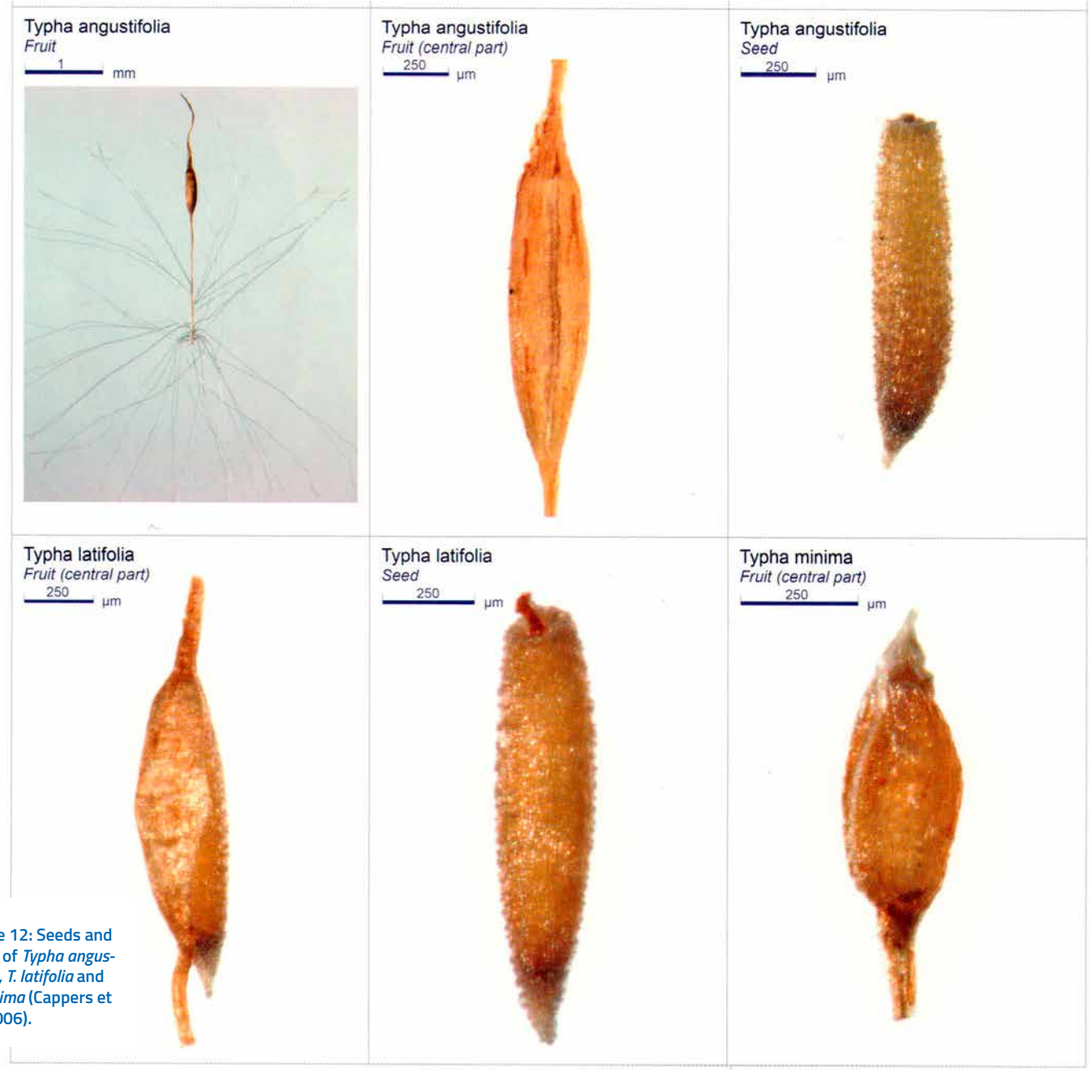



Figure 12: Seeds and fruits of *Typha angustifolia, T. latifolia* and *T. minima* (Cappers et al., 2006).





lived (1-2 years) seed bank, which they have in common with other helophytes, such as *Phaiaris arundinacea* and *Phragmites australis*.

Comes et al. (1978) showed that a small percentage of T. latifolia seeds collected in the field germinated after being stored in water for 60 months. Therefore, it has at least a short-lived seed bank, i.e. seeds with a viability of 1-5 years (Bekker et al., 1998). This is confirmed by Grace (1984), who assumed, based on Crocker (1938), Bedish (1967) and Van der Valk and Davis (1976), that *Typha* seeds can remain viable in the seed bank for long periods when conditions are not suitable for germination. Crocker (1938; in Bedish 1964) found that *T. latifolia* seeds stored air-dry at room temperature gave 78% germination after 4.5 years, 96% after 5.5 years, and no germination after 12.5 years. Bedish (1964) placed fresh and one-year-old *Typha* seeds in water ranging in temperature from 15 to 30°C. The result was that the viability of *Typha* had decreased by more than 50% after one year of dry storage at room temperature (Figure 13). A t-test showed this to be significant at a 99% confidence level. However, several investigations in the USA have suggested long-term persistence or long-distance dispersal. Wienhold and Van der Valk (1989) found *T. angustifolia* in wetland seed banks that had been drained for more than 70 years. Still, according to Stark et al. (2006), the number of soil plots from which the species emerged appeared to be low in late-successional forests in south-central British Columbia, where *T. latifolia* was not part of the existing vegetation and suitable habitats have long been lacking. Comparable results were found by Strickler and Edgerton (1976) in soil collected from 130- to 175-year-old mixed-conifer forests in eastern Oregon's Blue Mountains, where *T. latifolia* was absent, both in the study plots and in adjacent areas, although it emerged from the litter or top

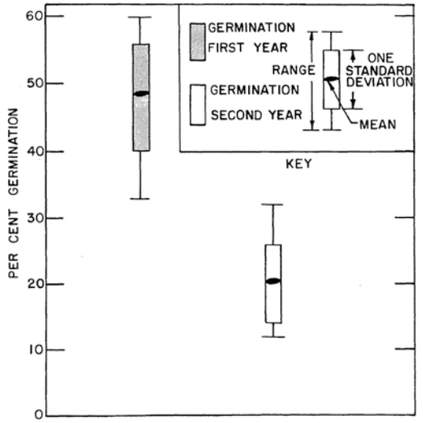



Figure 13: The effect of one year's dry storage on the viability of a sample of cattail seed germinated under 1 inch of water (Bedish, 1964).

soil in low numbers. There were similar findings in soil collected from mature Douglas fir and fir (*Abies* spp.) forests with an average age of 88 years or more in central Idaho (Kramer and Johnson, 1987). Nevertheless, other studies have shown that dense *T. latifolia* seedlings often emerge from sites where broadleaf cattail was prevalent (Leck and Simpson, 1987; Tu et al., 1998). On the basis of their own experiments and those by Van der Valk and Davis (1976), Bonnewell et al. (1983) argued that a certain percentage of *Typha* seeds can survive long periods of imbibition under natural conditions, since seeds from depths of 30-35 cm in marsh soil are still viable.

Jansen (2000) postulated that the differences in longevity of the soil seed bank of the investigated plant communities of wet heathlands and fen meadows in the Netherlands are related to successional stages. As already indicated by Bekker et al. (1998) and Strykstra et al. (1998), species which form more persistent seed bank types

are more common in the soil seed bank of plant communities of pioneer and early successional stages than in those of plant communities of later successional stages. Thomson and Grime (1979), Fenner (1987) and Bernhardt (1993) also argued that pioneer species of secondary succession stages are characterised by a persistent soil seed bank. According to Leck and Graveline (1979), the seed bank profile of freshwater tidal marsh soils is characterised by seeds of species with a prolonged viability and/or prolonged dormancy. Bakker et al. (1996) mentioned *T. angustifolia* as an example of a species that can disperse over long distances (see below), and that can build large persistent seed banks. Both long-distance dispersal as well as persistent seed banks are traits of species that have adapted to  rare environments, which may only provide a short-term opportunity for germination and establishment (Bakker et al., 1986). Such species only germinate on lake bottoms on the rare occasions that these are dry (Ter Heerdt and Drost, 1994). These findings are in accordance with Snyder (1993), who reported that in the field, *T. angustifolia* seeds usually germinate following exposure of mudflats. Nevertheless, *Typha* species produce massive numbers of seeds that are very easily spread by wind and are thus capable of rapidly colonising new, appropriate sites (Bernhardt et al., 2003).

#### 2.2.4 Seed dispersal

Cattails reproduce by seed and rhizomes. Their primary means of colonising is by seed, and once established, colonies are maintained by vegetative reproduction via rhizome growth and fragmentation (Grace and Wetzel, 1981c). Vegetative reproduction provides a mechanism for short-distance dispersal (Grace and Wetzel, 1981a).
Yeo (1964) and Grace and Harrison (1986) described the burst of the female inflorescence and the subsequent release of the fruits. In humid conditions, the pistillodes are swollen and the integrity of the spike is maintained. When conditions are dry, however, the pistillodes shrivel and permit the inflorescence to burst (Grace and Harrison, 1986). Yeo (1964) stated that the drying of the bristle hairs determines the spike burst: “The bristle hairs are appressed to the flowers during the development of the achenes. When the bristle hairs dry and tend to spread, the achenes are being held in place until late maturity. Then, the stipes break free of the pedicels, the stem that attaches a single flower to the inflorescence. Due to the tension formed by the simultaneous spreading of millions of bristle hairs the spike bursts.”

*Typha* species are anemochoreous, i.e. they are dispersed by wind. By anemochory, seeds are easily transportable over long distances (Lombardi et al., 1997; Grace, 1984; Grace and Harrison, 1986; Pojar and MacKinnon,1994; Sculthorpe 1967), and the numerous hairs facilitate wind dispersal of the small and light fruits (Grace, 1984; Grace and Harrison, 1986; Yeo, 1964; Heinz, 2012). Dispersal by wind occurs from October to January (Coops and Van der Velde 1995), and the plumed seeds may have a potential wind-dispersal range of 3,600 m (Soons and Ozinga, 2005).

According to Sculthorpe (1967), the seeds of nearly all aquatic and marsh plants float or are wind-dispersed, including *Typha* species. The long slender hairs at the base allow not only for wind transport but also for water transport of the *T. latifolia* seeds (Grace, 1984; Grace and Harrison, 1986; Hickman, 1993; Pojar and MacKinnon, 1994; Yeo, 1964). When wet, many of the fruits fall close to the parent plant. The numerous hairs allow the fruits to float on water (Pojar and MacKinnon, 1994). Once the fruits come into contact with water, the pericarp (Figure 9) opens rapidly and the seed is released and sinks with the pointed, posterior part downward (Grace and Harrison, 1986). Hickman (1993) reported that the dehiscent achenes split or burst when they come into contact with water. Yeo (1964) described the succession of both dispersal mechanism as follows: “The bristle hairs form parachutes and carry the fruits away in the wind or they fall to the ground in dense mats and remain there to germinate at a later date or are carried away by spring floods or wind.” Next, when a *Typha* fruit comes into contact with the water, the seed is liberated and sinks rapidly (Krattinger, 1975). Furthermore, the small seeds are easily buried during sedimentation and mixing of the sediments.
In addition, Pojar and MacKinnon, (1994) found that *T. latifolia* seeds are also transported by substrate movement. Seeds may be readily transported by birds and livestock through their presence in mud in areas where *T. latifolia* grows (State of Queensland, Department of Agriculture and Fisheries, 2020), and disturbance by animals – creating bare mudflats - may also play a role (Hewitt and Miyanishi, 1997). Finally, Krattinger ( 1975) reported dispersal by fish: the pointed seeds can become embedded in fish skin, resulting in further transport. However, in all likelihood, this will happen only rarely.

Due to a high production of small, wind-dispersed diaspores, new habitats can easily be reached by *Typha* species (Heinz, 2012). Van der Valk and Davis (1976) found that seeds of *Typha glauca* were capable of dispersing to all zones in a marsh. This also suggests that *Typha* species hardly have any dispersal problems.





## 2.3 The germination of the *Typha* species

### 2.3.1 The mechanism of cattail seed germination

The actual mechanics of cattail seed germination are described by Kerner von Marilaun (1895, as cited in Bedish, 1964): “The germination of the Reed-mace *(Typha)* is quite peculiar. The small fruits which are blown off the spike, fall on to the surface of the water and remain floating for some days. Then the pericarp opens and the seed sinks slowly down into the water. The husk of the seed is pointed at one end, and at the other is closed by an extremely pretty trapdoor. While sinking through the water the pointed end is turned downwards, and the covered end upwards. At the bottom the seed lies in the position indicated and germination commences. The cotyledon[1] grows in length, pushes open the trapdoor, and makes its appearance at the mouth of the seed coat. It now describes an arch and the end, in which are concealed the hypocotyl[2] and the bud, reaches the mud. Scarcely has it done so, however, when its epidermal cells elongate and form long tubular structures which penetrate into the slime, and the free end of the cotyledon is thus firmly fixed. Later on rootlets make their appearance, which, proceeding from the hypocotyl, break through the unresisting cotyledon. Meanwhile the reserve food has been sucked up by the apex of the cotyledon which remained in the seed; this apex is now drawn out of the seed-coat, the cotyledon straightens itself, turns green, and functions as a foliage-leaf.”

1 Cotyledon is defined by the Oxford English Dictionary as “[t]he primary leaf in the embryo of the higher plants (Phanerogams); the seed-leaf. Cotyledons are formed during embryogenesis, along with the root and shoot meristems, and are therefore present in the seed prior to germination.”
2 Hypocotyl is the embryonic stem.

The germination of *Typha* is a typical example of epigeal development (Figure 14), i.e. expanding on the germination of the seed, throwing off the seed shell, the cotyledon(s) rising above the ground, and becoming photosynthetic (Cotyledons, 2004, April 18; Mayer and Poljakov-Mayber, 1989). This type of germination is characteristic of small-seeded species that provide the seedling with only few resources, such as the *Typha* species. Therefore, the seedlings need to elongate rapidly and start photosynthesis to support further development (Heinz, 2012).

According to Gucker (2008a), *T. latifolia* seedlings are extremely small when compared to seedlings of associated vegetation. After germination, *T. latifolia* produces 2-4 small leaves or 2-6 floating leaves before producing erect leaves. Flooding and sediment can affect seedling survival and growth. Bernhardt et al., (2003), Lang et al. (2014) and Sharma and Gopal (1978) also reported the development of longer, floating leaves by T. latifolia seedlings when flooded, which are in contrast to the stout and erect leaves of the adult plants (Figures 15 and 16).

### 2.3.2 The speed of germination

*Typha* species, such as *T. latifolia* and *T. domingensis*, are characterised by a rapid germination (Stewart et al., 1997; McNaughton, 1966; Clements, 2010). Stewart et al. (1997) reported a start of germination within three days with a peak on the seventh day, reaching a germination rate of 22-40% in seven days, for both *T. domingensis* and *T. latifolia*. McNaughton (1966) studied possible differences between *T. latifolia* and *T. angustifolia* populations from different habitats in the USA. He revealed that the *T. angustifolia* population of North Dakota reached 50% germination after three days (regardless of previous treatment), whereas *T. latifolia* seed from Texas, Nebraska, and two North Dakota sites also reached 50% germination after 3 days at 24 °C. Ekstam and Forseby (1999) reported more than 50% germination within 1–3 days at favourable temperatures (see also section 3.4.5).

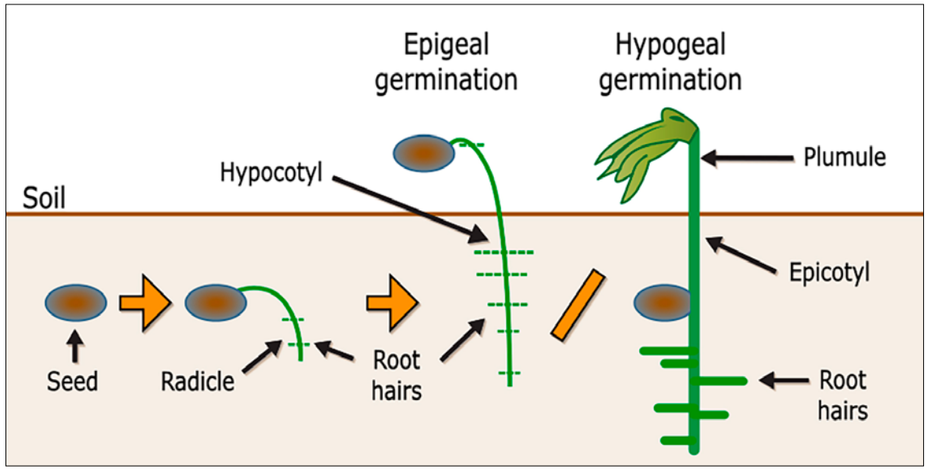



Figure 14: Epigeal and hypogeal germination (Cotyledons, 2004, April 18).





Heinz (2012) investigated whether the origin of *T. latifolia* seeds influenced germination characteristics. In this study, seeds were collected at 15 locations throughout Europe. It emerged that almost all populations germinated faster in the regimes with the highest night and daylight temperatures (Figure 17).

Heinz (2012) also found a correlation between seed mass and germination percentage (at 5/15°C, night and daylight temperature, respectively) and germination time, indicating a positive effect of seed mass on germination speed. However, in her experiments seed mass was primarily correlated to germination speed and germination percentage

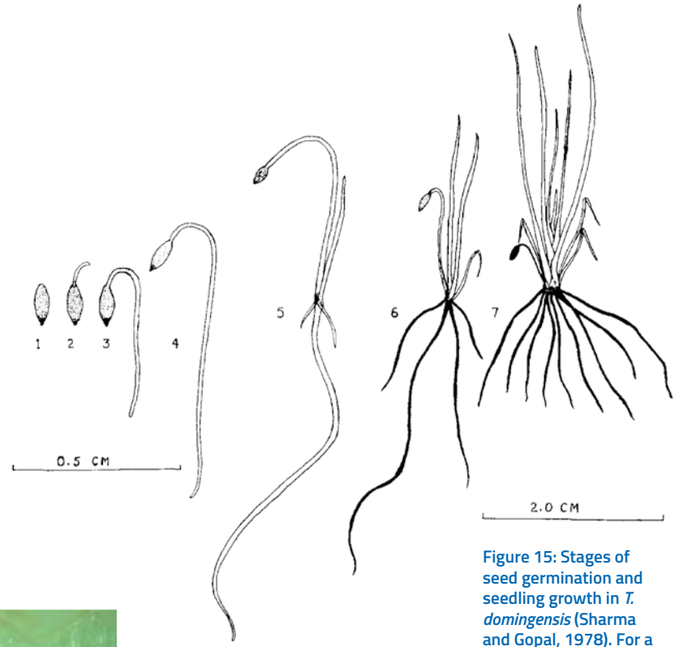



Figure 15: Stages of seed germination and seedling growth in *T. domingensis* (Sharma and Gopal, 1978). For a description of the several stages, see section 2.3.1.


Figure 16: Broad-leafed cattails (*Typha latifolia* L.) after six days under water at 26 (daylight)/18 (night) °C (Lang et al., 2014).

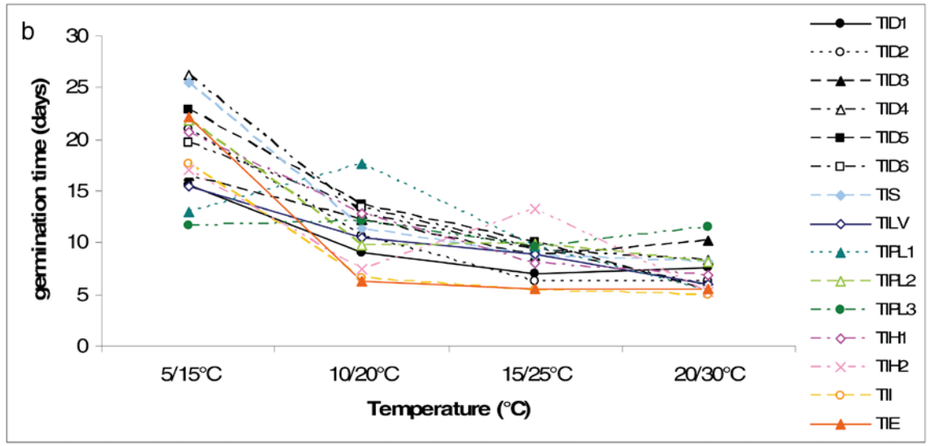



Figure 17: The onset of germination of 15 European populations of *T. latifolia* in different night and daylight regimes (Heinz, 2012).

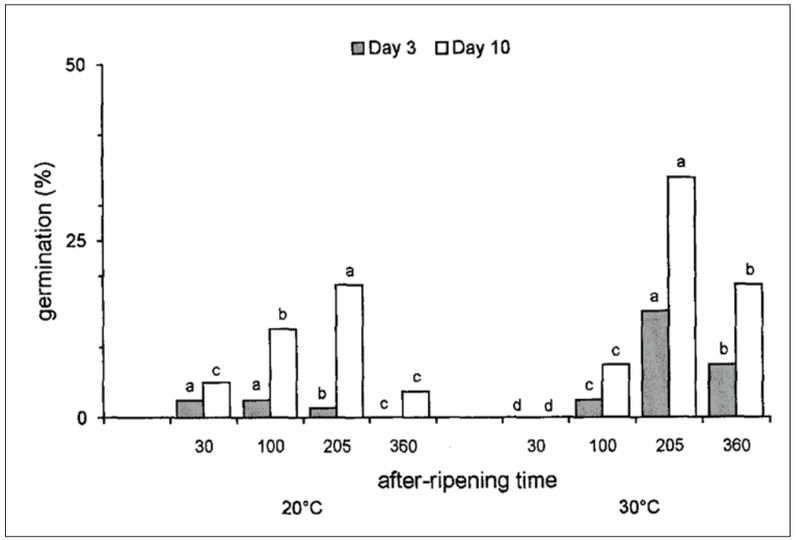



Figure 18: Mean percentage of germination of *T. latifolia* seeds at 20°C and 30°C after 30-360 days of ripening. No germination was observed at 10°C. Different letters within the same day of culture and temperature indicate significant differences at the 0.05 probability level among days after ripening (Lombardi et al., 1997).





at inadequately low temperatures. Hence, it seems obvious that under such adverse conditions only the seeds with the most reserves germinate.

### 2.3.3 Period of germination

Lombardi et al. (1997) found no significant changes in the germination rate and/or capacity during the first year, with the exception of the 20°C trials, in which a germination peak was observed on the tenth day of culture, corresponding with the month of May (205 days of after-ripening; Figure 18). This peak disappeared in the trial at 360 days of after-ripening (Figure 18). Lombardi et al. (1997) explained their observations by the season (in spring) during which *T. latifolia* seeds germinate: "Then, water bodies still have adequate water levels, external temperatures are very mild and hours of daylight are increasing. In such conditions, an endogenous biorhythm could favour seed germination even under non-optimal thermos period conditions (constant 20°C) inasmuch as the photoperiod is markedly favourable (12 h/12 h)." Their results are in agreement with those of Beule (1979), who found that collection time of *T. latifolia* seeds affected their germination. Less than 1% of the seeds collected in November germinated in light and distilled water, in contrast to seeds collected in May, of which 90% germinated. In the field, *T. angustifolia* seeds germinate from May to September (Beule, 1979), usually following exposure of mudflats.

These results are in agreement with Yeo (1964), who planted a seed with ruptured seed coat on April 1 under cultured conditions. He did so in the centre of a metal stock-watering tank with a six-foot diameter, in which "four inches of old manure and loam soils were placed in the bottom of the container and covered with 2 inches of sand. The container was filled with water". The experiment showed a rapid growth of the seedlings after germination; a single seedling developed a network of rhizomes covering an area 10 feet in diameter in 6 months (on November 1).
In contrast to Lombardi et al. (1997) and Yeo (1964), Hayden (1948) believed that late July and August were favourable for the germination of *Typha* seeds when water levels are low.

### 2.3.4 Where do seeds germinate?

*T. latifolia* L. and *T. angustifolia* L. seedlings have only rarely been reported from nature (Smith, 1967; Fiala and Kvet, 1971). The absence of *Typha* species seedlings within *Typha* stands has been attributed to the autotoxic effects of its leaves (McNaughton, 1968). Sharma and Gopal (1978) made extensive field trips in India, during which they observed widespread occurrence of *T. domingensis* and *T. elephantina* seedlings within *Typha* stands and outside on the open waterlogged soils. Within the stands, the seedlings were seen in relatively open spaces and at the margins of the stand. Sharma and Gopal (1978) also found seedlings on mud flats and "millions of freshly germinated seedlings (1-2 leaf stage) on the soil surface, leaf sheaths, and decomposing leaf litter within *a T. elephantina* stand." Van der Valk and Davis (1976) found seedlings on mud flats and in shallow water.

Bedish (1962) only observed germination when the soil was flooded to some degree or had been flooded. This observation is in agreement with Dubbe et al. (1988), who stated that apparently the best scenario for establishing a cattail stand from seed is to apply seed, with hairs intact, onto a flooded site where the water level is allowed to drop slowly. Their advice is based on research by Pratt et al. (1985), who found that germination and survival were superior in flooded paddies which were slowly drawn down to saturated conditions over the course of three weeks, compared to in paddies

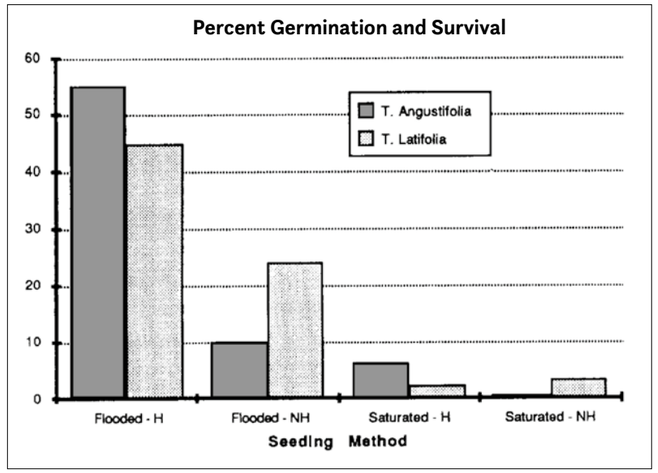



Figure 19: Germination and survival percentages for *Typha latifolia* and *T. angustifolia* seed using four seeding methods. Methods were flooded versus saturated soil applications, and seed hairs present (H) versus seed hairs absent (NH). 2 × 2 × 2 factorial design; 6 replicates per treatment. No significant difference between species; flooded versus saturated and H versus NH different at $\alpha = 0.01$ (Pratt et al., 1985, in Dubbe et al., 1988).

which had no standing water (Figure 19). This was true whether or not the downy seed hairs were removed. Under flooded or saturated conditions, germination and survival was higher when the hairs were left intact. This difference may well be explained by their observation that in both flooded and saturated paddies the hairs prevent the tiny seed from being buried in the mud.

## 2.4 Factors determining germination

### 2.4.1 Introduction

Seed germination and seedling establishment are critical stages in the life history of plants (Fenner, 1985). The survival of these critical stages requires adequate habitat conditions. Moreover, specific environmental conditions function as a trigger to start germination (Heinz, 2012).

Crocker (1907) and Morinaga (1926a, 1926b) were among the first scientists researching the factors that determine the germination of *Typha* seeds. They both found that treatment of the seed coat resulted in much higher germination rates, and Morinaga showed that light, reduced oxygen pressure, alternation of temperature, and nitrate compounds could all be utilised to increase the germination of *T. latifolia* seeds. Other researchers stated that moisture is a prerequisite for germination (Grace and Harrison, 1986). Hence, it is obvious that site factors such as light, temperature, water table, redox status, and nutrient availability are important for *Typha* seed germination.
Some environmental factors control a whole set of physical and/or chemical factors; in other words, these environmental factors are conditional to so-called operational factors (Figure 20; Van Wirdum, 1979). The local water regime determines the redox status, the light penetration (quantity and quality), and the temperature fluctuations at a certain site. In addition, the position of a specific site in the landscape determines the traits and/or ranges of the relevant conditional factors; for example, (i) the water regime of a site is determined by its position in the altitudinal gradient or (ii) the salinity of surface water in tidal marsh depends on the distance to the sea and the altitude.

In this chapter we discuss these factors with a focus on *T. latifolia* and *T. angustifolia*. We start with mechanical rupturing of the seed coat as an artificial treatment that – as we will see - results in very high germination rates; then we continue with a discussion of the natural site factors that are important for *Typha* seed germination.

### 2.4.2 Mechanical rupturing

Crocker (1907) and Morinaga (1926a, 1926b) already found that mechanical rupturing of the seed





coat increased the percentage of seeds germinating. Crocker found that 89% of cattail seeds germinated after the pericarp was ruptured. Morinaga (1926b) showed that the favouring effects of reduced oxygen pressures disappeared when the seed coats were broken. Then, germination proceeded readily in oxygen pressures ranging from 1-90% of the full atmospheric oxygen pressure. This large increase in germination occurred even in darkness and in air at a constant temperature. It removed the necessity for any other treatment (Morinaga, 1926a, 1926b).
Sifton (1959) repeated much of Morinaga's work and found the same results, but also made some additional points: "In complete darkness the inhibition of germination is overcome by removing the caps from the seeds and to a lesser degree by pricking them in the side." In one sample, with seeds intact, he found a germination of 99% in light and 4% in darkness; after removal of the seed caps, the germination in darkness increased to 99%, and with a needle prick in the side the germination in darkness increased to 92%. He also experimented with radiation, passing a blue filter in combination with rupturing the seed coat and a needle prick in the side. This blue filter treatment resulted in an inhibitory effect that was much less affected by the mechanical measures: of the same sample with pricked seeds only 10% germinated, whereas in another sample 81% germinated in unscreened light, 13% in blue light, and 31% in blue light with caps removed.

Stewart et al. (1997) also found higher germination rates after seed treatment. They found a final germination rate of 82% if the seed was separated from the perigonial hairs, stigmas, and bracts, compared to the 30% germination found without this separation.
It seems that Yeo (1964) discovered the reason for the increased germination rates after rupturing of the seed coats. He found that 100% of the seed of common cattail (*Typha latifolia* L.) germinated if the blunt ends of the seed coats were ruptured. The rupture of the seed coat happened after applying pressure, due to which the cells along the transverse edge ruptured and exposed a circular-shaped opening. He observed in all other treatments aimed at an increase in cattail seed germination that if the germinating seed imbibed water, the seed coat dehisced similarly to when it is forced from the seed coat. In such cases, the embryo emerges first. According to Process of Seed Germination: 5 Steps (With Diagram). (2015, October 26) "the first step in (barley) seed germination is imbibition. In this process, water penetrates the seed coat and begins to soften the hard, dry tissues inside. The water

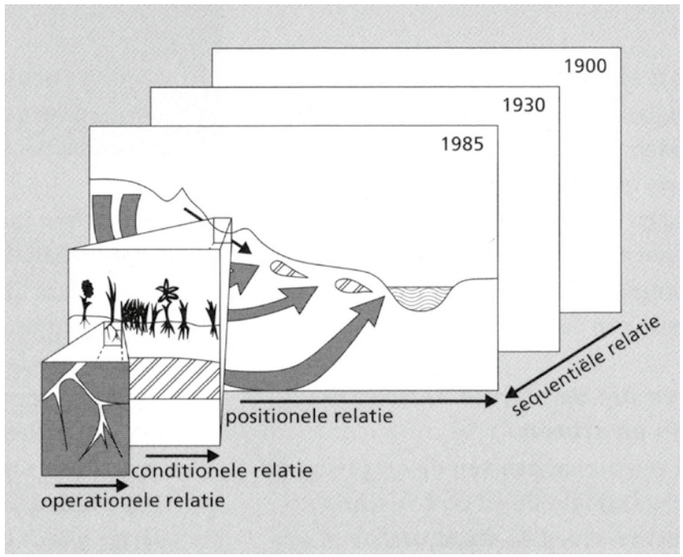



Figure 20: Interrelationship between environmental factors on different scale levels (Van Wirdum, 1979; Jalink and Jansen, 1995). Positional factors (positionele relatie) determine conditional ones (conditionele relatie), which in turn control a whole set of operational factors (operationele relatie). Sequential factors (sequentiële relatie) refer to the state of development of an ecosystem and are associated with succession and consequences of former events.

uptake causes the grain to swell up. The seed/fruit coat usually splits open allowing water to enter even faster. The water begins to activate the biochemistry of the dormant embryo." It is likely that rupturing the seed coat mimics the process of dehiscence of the seed coat, which normally occurs by the imbibition of water and guarantees the swelling of the embryo; in other words, this is germination by resolving potential natural failure factors. Therefore, the rupture of the seed coat results in much higher germination rates than during the natural germination process.

### 2.4.3 Light and light quality

Seeds of many species require light to germinate; the importance of light as a factor in the germination of seeds has long been recognised (Mayer and Poljakov-Mayber, 1989). *Typha* seed germination has long been known to be light-sensitive (Guppy, 1897). Although *Typha* seeds are capable of germination when shed (McNaugthton, 1966), many studies have shown that these seeds require light to germinate (e.g. Bonnewell et al., 1983; Frankland et al., 1987; Guppy, 1897; Lombardi et al., 1997; Morinaga, 1926a, 1926b; Sifton, 1959; Sharma and Gopal, 1979a; and Stewart et al., 1997). For example, in the experiments without light by Sifton (1959), seed germination of *T. latifolia* was 0-10%, whereas with light, seed germination increased to 91-100%. Furthermore, Stewart et al. (1997) showed that seeds placed under subdued light germinated to a lesser extent (55%) than those exposed to full sunlight (76%). Nevertheless, Sifton (1959) and before him Morinaga (1926b) reported satisfactory germination in darkness when rather wide alternations of temperature were employed (30-15°C; 35-15°C; 35-20°C and 30-20°C). Sifton (1959) showed that under such conditions the central vacuoles in the seed were larger and more plentiful than when constant temperatures were employed: "Without doubt the favourable effect of the alternating temperatures on germination was due to vacuole formation." These temperature alternations improve respiration and, consequently, more vigorous growth of the vacuoles. Sifton (1959) also showed that the swelling of the aleurone grains is much more rapid and vigorous in white or yellow light than in darkness or in blue light. He explains the observed increased germination as a consequence of "the more vigorous growth of vacuoles, being sufficient to compensate for the lesser amount of strongly held water in the aleurone grains, and so to bringing about rupture of the coats and germination."

On the basis of field observations and experiments, Sharma and Gopal (1978) concluded that a minimum light intensity is required for the seeds of *T. elephantina* to germinate: "Light intensity at the ground level inside a stand of this species was below 50 lux. After thinning had occurred, seedlings were found in the stand. At this point the light intensity reaching the ground was up to 2000 lux." Sharma and Gopal (1979a) found that *T. domingensis* seedlings do not survive at a light intensity of less than 2,500 lux.

Bonnewell et al. (1983) showed that high percentages of germination of *T. latifolia* seeds could only be obtained by prolonged exposure to light. Seeds appeared to be most sensitive to red light (day light) when exposed for 6-24 hours. At least ten hours of continuous red light (2.5 X $lo^{-8}$ W/$m^2$) was needed for maximum germination. They reported that "when seeds were exposed to light of the same intensity for four 30-minutes periods over a 12-hour span, the effect was nearly the same as 12 hours of continuous light", and, "[a]fter the intermittent irradiation the germination percentage was nine times that produced by a single 2-hour





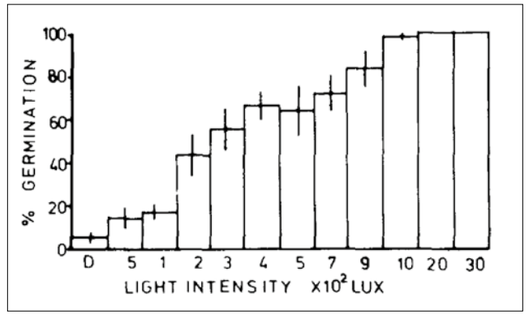



Figure 21: Effect of light intensity on seed germination (%) in *T. domingensis*. Seeds were placed in beakers under a 3 cm water layer. D = dark. Vertical bars indicate ± 1 s.d (Gopal and Shrama, 1983).

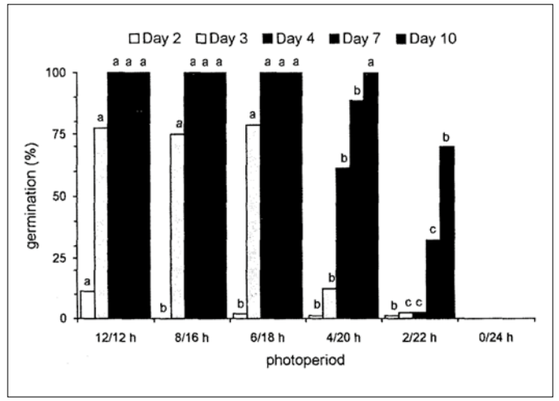



Figure 23. Mean percent germination (%) of *Typha latifolia* L. seeds at different photoperiods and after 2, 3, 4, 7 and 10 days of culture. Different letters within the same day of culture indicate significant differences at the 0.05 probability level among different photoperiods (Lombardi et al., 1997).

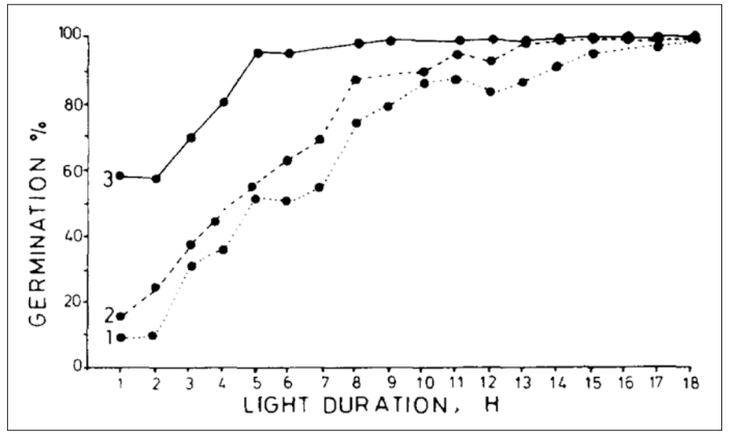



Figure 22: Effect of photoperiod on seed germination. Light intensity: 1500 lux, water depth: 3 cm. 1, 2 and 3 represent the number of cycles in a 24-hour cycle (Gopal and Shrama, 1983).

exposure." They also investigated the effects of the alternation of red (R) and far red (FR) light. They found that "five minutes of far-red light (FR) reversed the germination effect of 6 hours of R to the (very low) level of dark controls. The photoreversible effect of FR was less pronounced for seeds imbibed prior to illumination. When spans of R and FR were alternated (FR-R-FR, R-FR-R, FR-R-FR-R, R-FR-R-FR), repeated reversibility was observed. However, FR was progressively less effective in reversing the effect of R." This experiment showed that for "*Typha* seeds, the energy of FR needed to reverse the germination effect of R was far less than the energy of R which the seeds had received." Bonnewell et al. (1983) concluded that the light requirement for *Typha* seed germination is one of duration as well as energy. This conclusion corresponds with the results of Gopal and Sharma (1983) and Lombardi et al. (1997). The former study found that the seeds of *Typha domingensis* (syn = *T. angustata*) germinated at room temperature (25-27°C) only in the presence of light. Germination rates increased with an increase in both light intensity and duration. 100% germination occurred within 48 hours after an 18-hour photoperiod at 1,000 lux (Figure 21). The latter study found that dark germination of six-month-old *T. latifolia* seeds was almost virtually absent (consistently below 10%) at the end of the 10-day culture period, both for seeds subjected to constant (10°C, 20°C, 30°C) or alternating (10/20°C, 20/30°C, 10/30°C) temperatures. In addition, their trials showed a marked decrease in the germination rate and capacity of the *T. latifolia* seeds when the photoperiod fell below 6 hours a day (Figure 22). However, when the seeds were subjected to a 12/12 h, 8/16 h or 6/18 h (light/dark) photoperiod, they showed a mean germination of roughly 77% on Day 3 (Figure 23). In all cases, 100% germination was achieved by Day 4 (Lombardi et al. (1997). Their results also indicated that germination was dependent on the sum of light hours to which seeds were exposed, and on the cumulative number of dark hours that neutralise the previous light-derived positive impulse. Similar to Bonnewell et al. (1983) and Gopal and Sharma (1983), Lombardi et al. (1997) concluded that not only light intensity but also the number of hours of light regulates seed germination of the *Typha* species.

Therefore, they hypothesised – again similar to Bonnewell et al. (1983) - that the principal mechanism triggering germination of *T. latifolia* is the presence of phytochrome. This plant pigment is involved in the registration of light and acts as a light sensor. It regulates the day and night rhythm of the plant and causes the growth of a plant when it is shaded. Two types of phytochrome can be distinguished: phytochrome B1 and phytochrome B2. The former absorbs the red light of 660 nm, while the latter absorbs the far red light of 730 nm. Daylight consists for a large part of red light, when mainly phytochrome B2 is present. During the night, phytochrome B2 changes into phytochrome B1. Phytochrome B2 counteracts the elongation of the seedlings as germination takes place in the soil and therefore in the dark. When the seedling rises above ground level, the growth by elongation stops (Phytochrome, 2020, December 06).

Phytochrome helps the *Typha* species avoid the risk of light limitation during germination and seedling growth. Therefore, *Typha* seedlings are hardly ever seen in or in the vicinity of dense *Typha* populations from which the seeds themselves are derived (Sharma and Gopal, 1978). Light requirement can thus guarantee seedling viability in spite of low levels of *Typha* seed reserves, which mostly consist of oleic and linoleic acid (Meara, 1957). Indeed, epigeal germination, which is characteristic of the *Typha* family, is initiated with the emergence of the photosynthesising coleoptile[3] (Lang, 1965) and cotyledon (Mayer and Poljakov-Mayber, 1989).





However, not only light in the red and far red spectrum is of importance with respect to seed germination. Sifton (1959) found that the germination of *Typha* seed when wrapped in blue cellophane was invariably low, as he illustrated by two examples of seeds of which the germination was 95% and 98% in clear light, 7% and 10% in darkness, and 7% and 8% in blue light. He further showed that under the blue filter, alternating temperatures produced little or no improvement in germination. Gopal and Sharma (1983) carried out several experiments with *T. domingensis* (*T. angustata*) in which they investigated the influence of the spectral quality of light on the germination of *T. domingensis*. Their most important conclusion was that seed germination is inhibited by blue light.[4] This inhibition can be reversed by exposure to yellow or red light. The longer the exposure to blue light, the longer the duration of yellow or red light that is required to overcome the inhibition. They also found that yellow light is nearly as effective as white light in yielding 100% germination, and that red light is also inhibitory to germination, but longer exposure improves germination, although red light exposure did not completely overcome the inhibition; even after 72 hours there was no 100% germination.

### 2.4.4 Dormancy

According to Baskin and Baskin (2004), a dormant seed is one that is unable to germinate in a specified period of time under a combination of environmental factors that are normally suitable for the germination of the non-dormant seed. Dormancy is a mechanism to prevent germination during unsuitable ecological conditions, when the probability of seedling survival is low (Black et al., 2006). This may be advantageous for the survival of the species (Mayer and Poljakof-Mayber, 1989). A cold period to break seed dormancy is quite common in many species (Fenner, 1985). However, a cold period is not required for germination of *T. latifolia* and *T. angustifolia*, as has been reported by McNaughton (1966). The same author showed that the lowest temperature at which germination of populations of *T. latifolia* and *T. angustifolia* occurred was lower in southern than in northern populations on a north-south transect of the North-American continent. McNaughton (1966) studied seeds from contrasting habitats, which were stored for 2 weeks at 20°C or 21°C and then germinated at 24°C. He thus showed that a cold period was not required for germination. Furthermore, he argued that rather than dormancy, *Typha* species have an alternate system which prevents premature germination. Moreover, Lang et al. (2014) reported that no special treatments were required for the germination of *T. latifolia* seeds.

### 2.4.5 Temperature

*T. latifolia* seed germination requires high temperatures, as appeared from the investigations of Sifton (1959), McNaughton (1966), Bonnewell et al. (1983), Lang et al. (2014) and Lombardi et al. (1997).

According to Sifton (1959; Table 1), "a temperature of 30°C is clearly satisfactory for the germination of these seeds when other conditions are satisfactory. A temperature of 35°C is somewhat too high, and 20°C is clearly too low. The optimum is probably somewhere between 25° and 30°, and nearer the higher temperature. This fact was clearly indicated throughout the investigation."

3 Coleoptile: the pointed protective sheath covering the emerging shoot in monocotyledons such as grasses (Coleoptile, 2020, December 14).

4 Possibly due to the reduced swelling of the aleurone grains (see Sifton, 1959).

Table 1: Germination in light at constant temperatures (Sifton, 1959).

Germination in light at constant temperatures

| Temperature | % germination | |
|---|---|---|
| | Immersed in water | Moist blotters in air |
| 35° C | 81 | 48 |
| 30° C | 89 | 61 |
| 25° C | 86 | 44 |
| 20° C | 69 | 37 |
| 15° C | 24 | 20 |

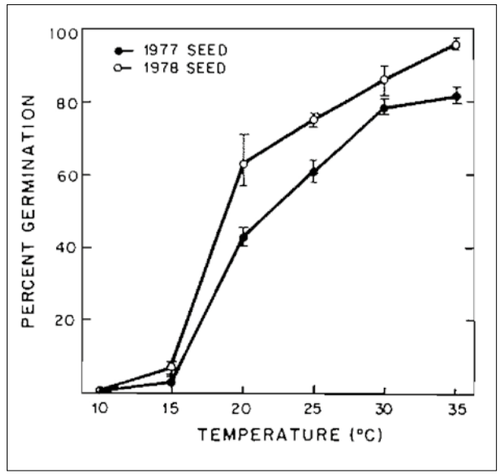



Figure 25. The effect of temperature on germination of *Typha latifolia* in continuous light for 7 days. Each value represents the mean ± 1 standard error of 10 replicates of 50 seeds each for 1977 seed and of 5 replicates for 1978 seed (Bonnewell et al., 1983).

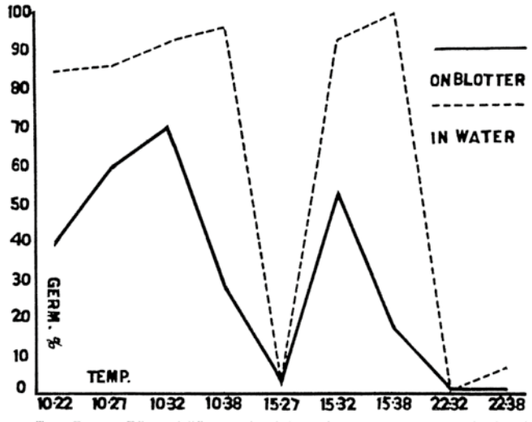



Figure 24: Effects of different pairs of alternating temperatures on germination of seeds of cattail (*Typha latifolia* L.) (Morinaga, 1926b).





Morinaga (1926b) reported considerable germination of *Typha* seeds, as high as 70%, at favourable diurnal alternations (10-32°C and 15-32°C; Figure 24), while at constant temperatures less than 1% germinated. The alternations 15-27°C and 22-32°C were not favourable either and resulted in a maximum germination of 5%. Hence, Morinaga concluded that alternating temperatures were necessary to germinate intact, non-ruptured seeds of *Typha latifolia*. Similar to Morinaga (1926b), Lombardi et al. (1997) observed that alternating day and night temperatures favour germination. Among the three thermoperiods they considered, the two in which a 30°C phase was present (10/30°C and 20/30°C) were more favourable to germination than the one in which a 20°C phase was present (10/20°C). Bonnewell et al. (1983) found that *T. latifolia* seed germination required high temperatures, low $O_2$ concentration, and relatively long exposure to light to induce high percentages of seed germination. More precisely, they observed for submerged seeds a maximum germination at 30°C (Figure 25) when exposed to red light and at a low $O_2$ water concentration (between 2.3 and 4.3 mg/l). Moreover, a larger percentage of seeds germinated at 35°C than at lower temperatures; fewer than 10% of the seeds germinated at 15°C and none at 10°C. These results are in agreement with those of Ekstam and Forseby (1999) as well as with those of Lang et al. (2014), who reported a maximum germination rate of 80% at 26°C for 14 hours during daylight hours and 18°C for 10 hours at night. The latter reported germination of nearly all *T. latifolia* seeds (>95%) in favourable temperature regimes. Mean temperature (range 10–30°C) and amplitude (range 0–20°C) affected their final germination. The germinated proportion of *T. latifolia* had a maximum at around 20°C, above which it decreased, and amplitudes were more stimulating at low than at high levels of mean temperature.

McNaughton (1966) studied possible differences between *T. latifolia*, *T. angustifolia* and *T. domingensis* populations from different habitats in the USA. Of all species, the northern populations showed germination at higher temperatures than those from the south: *T. latifolia* seeds from northern populations did not germinate at temperatures lower than 24°C, those from southern populations did not germinate at temperatures lower than 18°C, whereas the southernmost population failed to germinate at temperatures lower than 13°C. Of two *T. angustifolia* populations, the southern germinated at a lower temperature than the northern. Within *T. domingensis*, the more northern populations germinated at temperatures as low as 18°C, while the southernmost population germinated at 13°C. Bonnewell et al. (1983) interpreted these results as follows: “McNaughton found that the temperature optimum for germination of *Typha* seed varies. Seeds from moderate southern climates have lower temperature optima than seeds from more extreme, northern climates.” Heinz (2012) did not find differences in optimum germination temperatures between *T. latifolia* and *T. angustifolia* populations from different origins (several spots in Germany and one spot in Hungary). Although there are marked differences in germination rates between the populations, they all show a positive germination reaction to the combination of diurnally fluctuating temperatures and flooding; the highest germination percentage was obtained at 10/25°C and flooded conditions for all populations. However, in a second experiment with *T. latifolia* seeds originating from 15 locations (the Mediterranean, central Europe, and eastern Europe), Heinz (2012) found large differences in germination traits between the 15 populations. Germination rates differed by factors of 10 to 100 and germination time by factors of 2 to 3 between populations. Once more, the temperature regime

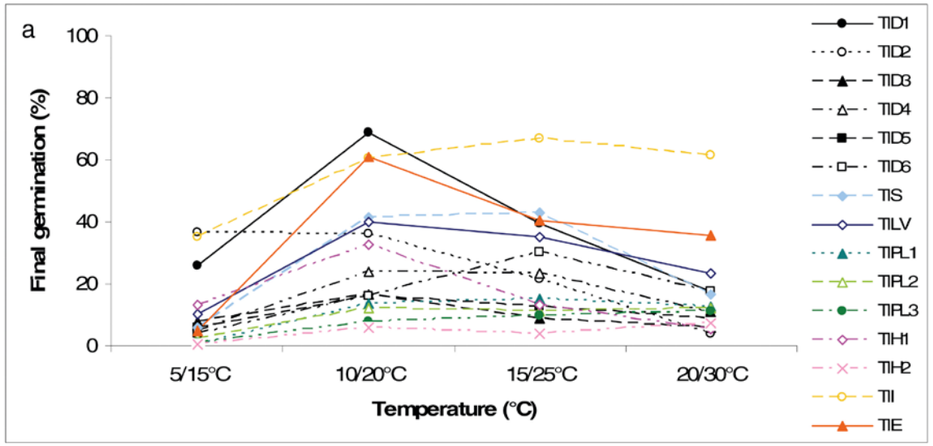



Figure 26: Final percentage of germination at different temperature regimes. Abbreviations refer to populations from different locations in Europe (Heinz, 2012).

with the highest germination rate appeared not to be linked to mean annual temperature. Statistically, the germination rate was most related to mean temperature in winter and precipitation in July. An ordination analysis of germination traits showed that the populations were more or less arranged to climate type. Both Mediterranean populations showed high germination rates (mean 51.6 %) and fast germination. The second highest and fastest were the oceanic populations situated around the Baltic Sea, whereas the lower percentage germination and slower germination were expressed by the sub-continental and continental populations from Germany and Hungary. These showed relatively low percentages of germination at 5/15°C and a pronounced increase in germination with an increase in temperature.
The most surprising element of this part of the study by Heinz is that in almost half of the 15 populations investigated, the highest rates of final germination did not occur at the alternating temperature regimes with the highest daylight temperatures (15-25°C or 20-30°C), but at the relatively low 10-20°C regime (Figure 26). This is in contrast to studies by Lombardi et al. (1997) and Lang et al. (2014), who not only showed that alternating temperatures were necessary for germination, but also that highest germination rates were obtained in the regimes including a much higher daylight temperature (30°C and 28°C, respectively). The experimental design of these studies were almost equal: "seeds were germinated in plastic Petri-dishes in deionised water saturated filter paper and water was added if necessary." (Lang et al. (2014)

### 2.4.6 Water regime

Water levels and their fluctuations have been shown to critically affect seedling survival and growth (Weller, 1975; Sharma and Gopal, 1979b, cited in Grace, 1984). As early as at the beginning of the 20th century, Morinaga (1926b) reported that





*Typha* seeds gave a much higher germination rate under water than on filter paper.

In his PhD thesis, Bedish (1964) gave an overview of what was then known about the germination of *Typha* species in relation to water levels. Several authors reported germination of seeds below the surface water level. Bedish cites Wilson (1955), who found that induced seeds of *T. latifolia*, *T. angustifolia*, *T. domingensis*, and *T. x glauca* germinated in simulated and actual marsh conditions in North Carolina. Moreover, Wilson found that seed germinated on exposed mud and under water depths of 1-2 inches. Seeds placed under 8 inches of water gave poorer results. Germination of *Typha* species after surface waters run dry were reported by Kadlec (1960), Lynch et al. (1947), Hayden (1948) and Summerhayes and Turrill (1948). Kadlec (1960, cited in Bedish, 1964) indicated that cattail seedlings in Michigan established themselves only on very wet soil areas. Lynch et al. (1947) observed germination of *Typha* on floating masses of plant debris and soil which had been lifted from the marsh bottom by decomposition gases. Hayden (1948) found that pond floors and lake beds from which the water had been evacuated were populated with *Typha* seedlings within 2-3 weeks. July and August were especially favourable for germination of amply-seeded soil. Summerhayes and Turrill (1948; cited in Bedish, 1964) observed what they described as the establishment from seed of mature fruiting *Typha* plants on bare mud flats of Lake Binley in England. Kaushik (1963) found that *Typha* seed which was stored dry or frozen prior to germination gave the highest percentage of germination. Seeds stored in mud or water gave poorer germination whether or not they were frozen. Furthermore, he noted more seeds germinating in moist conditions than in flooded conditions.

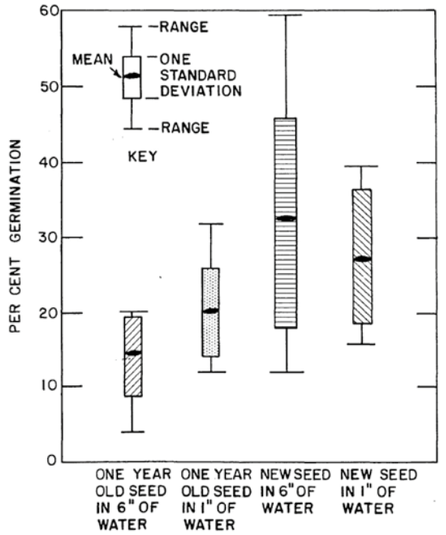



Figure 27: A comparison of germination rates of two ages of cattail seed in 6 inches of water and 1 inch of water (15.2 and 2.5 cm, respectively) (Bedish, 1964).

Bedish (1964) showed that germination occurred only when the soil was or had been flooded to some degree. He concluded that a water depth of 1 inch (2.5 cm) was found to be the optimum moisture condition for seed germination in a greenhouse. However, he stated that "[n]either the 1962 nor the 1963 seed tests showed any significant effect of water depth on per cent germination" (see also Figure 27). Therefore, he qualified his conclusion by stating: "In addition, this study indicates that moisture conditions ranging from saturated soil to 6 inches of water will provide almost equally favourable growing conditions." Bedish (1964) assumed that light penetration is the limiting factor to seed germination rather than water depth, as long as other determining factors are favourable (Mayer

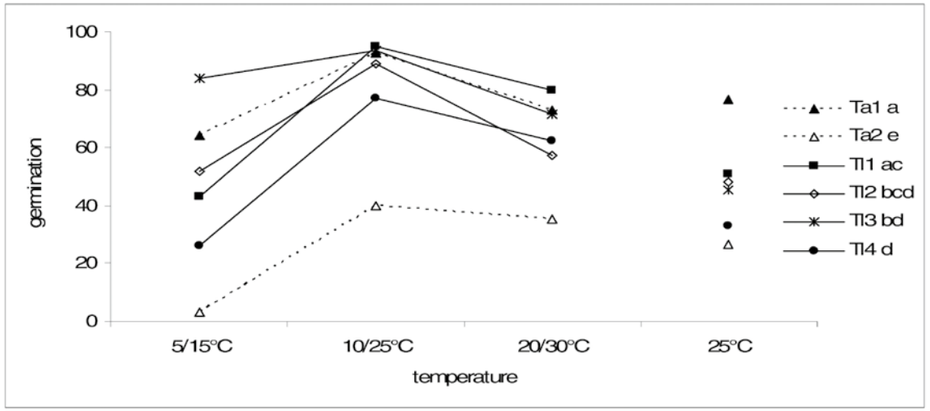



Figure 28: Mean final germination rates of the *T. angustifolia* (Ta) and *T. latifolia* (Tl) populations at different temperature regimes and flooded conditions. Significant differences between populations averaged over all temperature regimes are marked by different characters. Abbreviations indicate the origin of the *T. latifolia* and *T. angustifolia* populations (Heinz, 2012).

and Poljakoff-Mayber, 1989). In his opinion, any references to *Typha* seed germination at the soil surface level (in Kadlec, 1960; Lynch et al., 1947; Hayden, 1948; and Summerhayes and Turrill, 1948) "may well have been the result of field observations of seedlings left growing on mud exposed by natural lowering of water levels."

In addition, Shay and Shay (1986) described *T. latifolia* as tolerant to water fluctuations and that this species spreads both vegetatively and by seed, particularly under drawdown. Sharma and Gopal (1979b) reported that *T. domingensis* seedlings grew best when submerged in 10 cm of water.

Temperature and water depth both had a significant effect on final germination rates in *T. latifolia* and *T. angustifolia* populations from different origins. They differed significantly in the final germination percentage. Heinz (2012) reported that the highest germination percentage was obtained at 10/25°C and flooded conditions (at a water depth of 4 cm) for all populations (Figure 28); a further increase in temperature did not stimulate an increase in germination percentage. Raising the water depth, however, resulted in a significant increase in the germination percentage at every temperature regime. In her trials the applied water depth treatments were 'moist' (soil kept saturated), 'surface' (water depth maintained at the soil surface), and 'flooded' (water depth maintained at 4 cm above the surface). Growth cabinets were set to diurnal fluctuations of 5/15°C, 10/25°C, 20/30°C, and a constant temperature of 25°C. Temperature fluctuations corresponded to a light regime of 16 hours of light (higher temperature) and 8 hours of darkness (lower temperature). Generally, *T. latifolia* obtained higher final germination rates than *T. angustifolia* at all factor combinations except for the constant temperature regime (Figure 29).

Grace (1985) sowed seeds of *Typha latifolia* and *T. domingensis* species along a miniature gradient in water depth, both in monocultures and in mixtures,





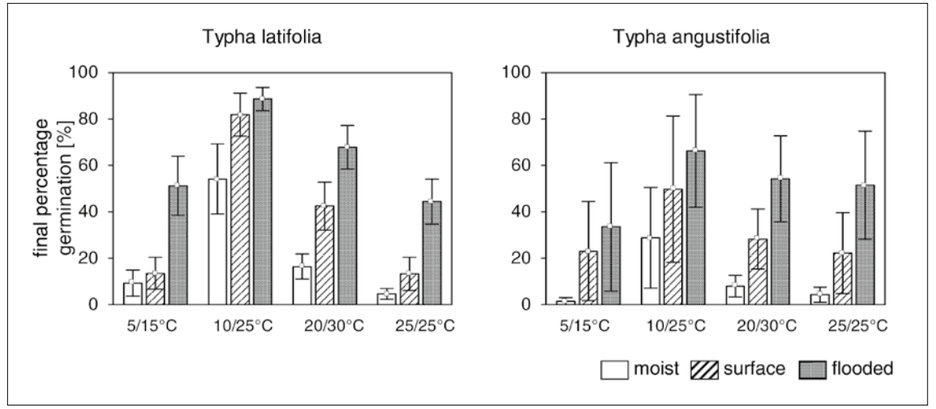



Figure 29: Final percentage of germination (a), onset of germination (b) and T50 (c) of *Typha latifolia* (left) and *T. angustifolia* (right) at different temperatures and water depths. Presented are mean ± 95% confidence limits (Heinz, 2012).

to ascertain the relatively competitive abilities of juveniles. In monoculture (low density gradient), *T. latifolia* was found to germinate and grow better at slightly higher elevations than *T. domingensis*. In mixtures, *T. latifolia* was the better competitor above the water table while *T. domingensis* dominated below the water table. For *T. latifolia*, germination along the low density gradient was zero if the water level was more than 18 cm above the soil surface, but maximal at levels slightly higher than 10 cm above the soil surface. No obvious trends in germination were apparent for either species between -7 and +21 cm water depth (Figure 30). For both species, mortality was low across most of the gradient. *T. latifolia* plant mass showed a more or less unimodal distribution with a peak at a water level of 3 cm above the soil surface (Figure 30). The cause is unknown. For both species, plants that germinated under water developed floating leaves before developing erect leaves.

Last, the results of the laboratory studies by Beule

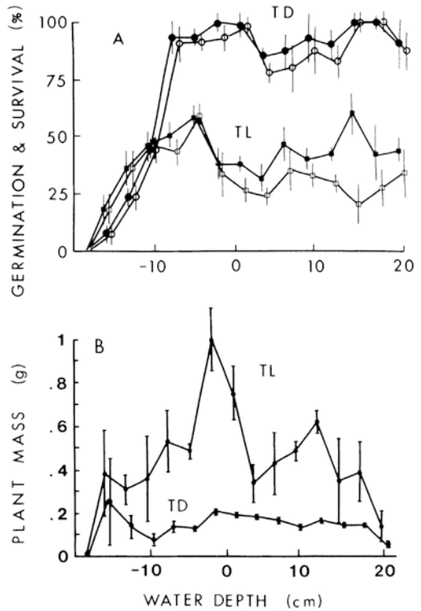



Figure 30: Performance of *T. domingensis* (TD) and *T. latifolia* (TL) sown in monoculture across a miniature water-depth gradient ("Low Density" gradient). Negative depth values are above the water table. (A) Germination and survival. The solid symbol for each species represents the percentage of seeds that germinated, and the open symbol represents the percentage of seeds that germinated and survived, with the difference between the curves representing mortality. (B) Average plant mass per individual. Error bars for both figures are ±1 standard error (Grace, 1985).

(1979), Keddy and Ellis (1985) and Gopal and Sharma (1983) on *T. angustifolia* and *T. domingensis* (*T. angustata*) are briefly discussed. Keddy and Ellis (1985) found no response in seedling recruitment of *T. angustifolia* to a water range depth from 5 cm below the soil surface to 10 cm above the soil surface. In contrast, Beule (1979) showed that *T. angustifolia* seeds germinate best in water of a depth of 1 inch (2.5 cm), but also that they can germinate in water as deep as 16 inches (40 cm). Keddy and Ellis (1985) found a 90% seedling recruitment at all depths, which indicates that their range of water depths was too limited to find the optimal water regime for *T. angustifolia* seed germination. Experiments by Gopal and Sharma (1983) with *T. domingensis* (*T. angustata*) showed that seeds germinated better under water than on moist filter papers (Figure 31).

In summary, based on the literature studied, the range of optimum water levels for the germination of *T. latifolia* varies between a groundwater table around the soil surface and a surface water level that does not exceed 15 cm. Under controlled conditions, maximum germination rates were found at water depths of between 2.5 and 4 cm (Bedish, 1964; Beule, 1979; Grace, 1985; Heinz, 2012). Although germination has been known to occur at surface water depths that exceed 10 cm and groundwater tables lower than 15 cm below the soil surface, seedlings which have germinated under these conditions may be too small to develop into adult plants (Figure 30). The water regime requirements of *T. angustifolia* seed germination are less well-known. Although the adult plants of these species grow in deeper water than those of *T. latifolia*, it may be expected that these species germinate at a water regime corresponding to that of *T. latifolia* as this is suggested by the results of Beule (1979), Dubbe et al. (1988), Heinz (2012) and Keddy and Ellis (1985).

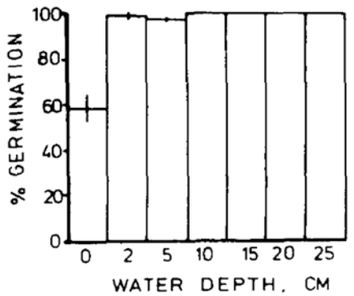



Figure 31. Effect of water depth on seed germination (%) in *Typha domingensis*, under daylight conditions. 0 cm = moist filter paper. Vertical bars indicate ± 1 s.d (Gopal and Sharma, 1983).

### 2.4.7 Oxygen requirements

The germination of the *Typha* species is characterised by low oxygen concentrations. Morinaga (1926b) and Sifton (1959) reported that very little oxygen is required for germination (see also Grace, 1984); however, no germination has been observed in the absence of oxygen (Morinaga, 1926b). According to Bonnewell et al. (1983), the maximum germination of submerged seeds was achieved when the $O_2$ concentration in the water was between 2.3 and 4.3 mg/l, corresponding to 28-52% of the $O_2$ concentration in water equilibrated with air (Figure 32). At both lower and higher $O_2$ concentrations, germination was reduced. Seeds that had failed to germinate at either 1.0 or 7.5 mg/l $O_2$ readily germinated when $O_2$ levels were changed to 3.7 mg/l. Lang et al. (2014) found germination of *T. latifolia* under hypoxic conditions, i.e. in the presence of low oxygen concentrations. We conclude that a small supply of oxygen is necessary for germination.
Anaerobic conditions may already originate less than 2 cm below the surface of lake sediments (Mortimer, 1971). Therefore, it is likely that the required $O_2$ concentrations for optimum germination of *Typha* seeds are likely to occur near the surface of water-saturated soil. This assumption is consistent with the appearance of seedlings on mud flats or in shallow water (Van der Valk and Davis, 1976) and complements Bedish's (1964) finding that flooding provides the reduced oxygen tension required for *Typha* seeds germination. Bedish (1964) stated that *Typha* seeds will probably germinate at any water depth into which light can penetrate, as long as other influential factors are favourable (Meyer and Poljakoff-Mayber, 1963). The fact that they do not germinate in water too deep for light penetration prevents germination in sites where seedlings will not survive.

### 2.4.8 Salt tolerance

The ability of a species to germinate and establish seedlings frequently determines its distribution in nature (Choudhurii, 1968). Salinity may affect germination in two ways: (1) salts in the soil solution may be sufficient to create osmotic pressure, which will seriously retard if not prevent the intake of necessary water, and (2) the constituent salts or ions may be toxic to the embryo or the seedlings.

Fassett and Calhoun (1952) describe the water quality conditions of both *Typha* species as follows: "The edaphic conditions tolerated by *T. latifolia* range from basic to acid waters, while *T. angustifolia* is mostly in basic waters and will tolerate some salinity, as in the salt marshes along the east coast. Where there is an overlap in these habitats, hybrid swarms are found." According to Clements (2010) and Murphy (2007), both species are not very tolerant to salinity. Salinity levels of even 1% cause leaf damage to *T. latifolia*, whereas *T. angustifolia* is slightly more salt-tolerant (Weeda et al., 1994). These observations match the known distribution of the two species in the UK (Grime et al., 1988).

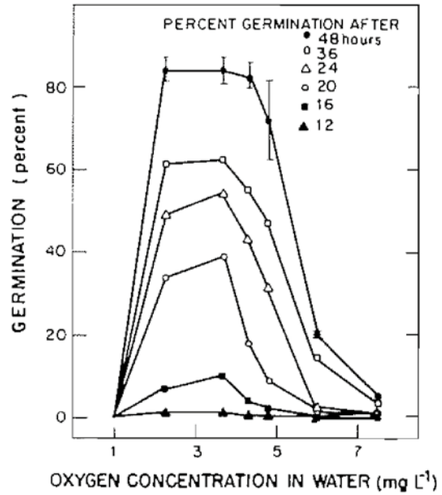



Figure 32: The effect of $O_2$ concentration in the water on the germination of submerged 1977 *Typha* seeds under red light at 32°C. Bars indicate standard error of the mean of triplicates after 48 hours of light (Bonnewell et al., 1983).

*T. angustifolia* tolerates slightly brackish conditions (Crain et al., 2004; Weeda et al., 1994), but fresh waters are clearly its optimum habitat (Crain et al., 2004). In fresh waters *T. angustifolia* becomes a dominant species; in brackish waters this is never the case. There, *T. angustifolia* is "a lone invader from neighbouring zones" (Crain et al., 2004). The maximum biomass markedly decreases with increasing salinity (Figure 33); the same occurs after transplantation (Figure 34; Crain et al., 2004).

Gucker (2008a) stated that *T. latifolia* "tolerates brackish waters, but salinity tolerance may differ with developmental stage." Seed germination rates decreased with increasing salinity; germination of *Typha* seeds was reduced by even 0.5 atmosphere of osmotic pressure in pond water, with no germination above 1 atmosphere. Nevertheless,

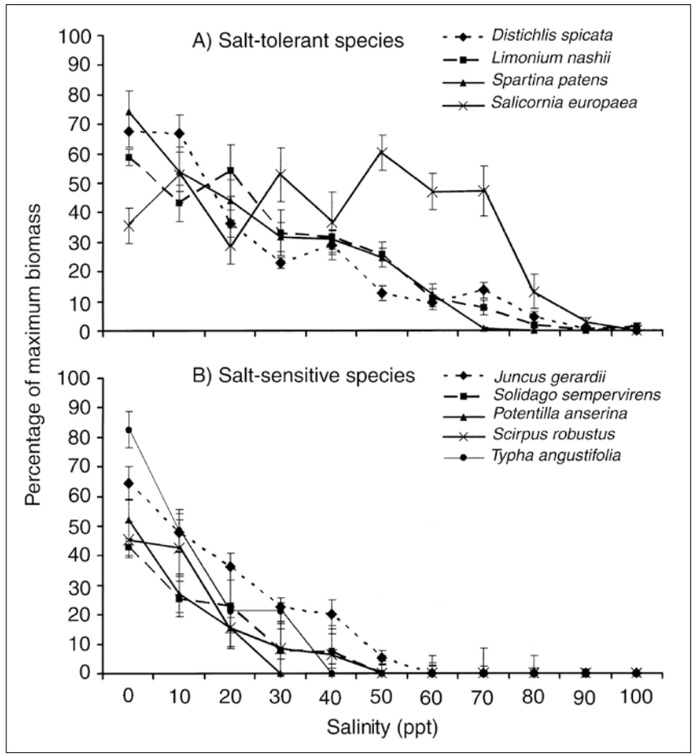



Figure 33: Standardised biomass at varying salinities (parts per thousand; micrograms NaCl per gram water) of common coastal marsh species that are relatively (A) salt-tolerant and (B) salt-sensitive, based on greenhouse performance and field distributions. Data are shown as mean ± 1 standard error for *n* = 8 individuals per species (Crain et al., 2004).

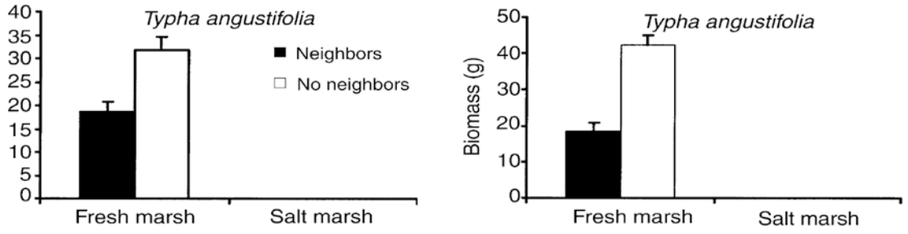



Figure 34: Above-ground biomass harvested after two growing seasons from the central 10 x 10 cm of large turf transplants of five dominant species in salt and freshwater tidal marshes. *T. angustifolia* transplanted to a mid-elevation marsh (left) and a low-elevation marsh (right). Neighbours: with other plant species vegetation; No Neighbours: all other plant species removed. Data are shown as mean ± one standard error for 16 replicates per treatment (Crain et al., 2004).





both adults and seedlings of *T. latifolia* were "quite tolerant" of salinity due to NaCl. The sensitivity to low salinity during germination must prevent the species' colonisation of brackish habitats. Moreover, adverse environmental factors, such as a predominance of $Na_2CO_3$, probably results in a restricted distribution of *T. latifolia*. In the brackish marshes of south-eastern Louisiana (the Bayou), broadleaf cattail rarely occurred at salt levels of up to 1.1%, and then only in low cover (Penfound and Hathaway, 1938). In the boreal forest zone of Alberta, Canada, Lieffers (1983) found *T. latifolia* growing in oxbow lakes with a salinity, measured as water conductivity, of 260 to 1,380 µS/cm. Shay and Shay (1986) describe *T. latifolia* as tolerant of salinity of less than 10,000 µS/cm. *Typha* is adapted to fresh and moderately saline conditions, although under the latter it exhibits "subnormal"[5] development (Millar, 1976, cited in Shay and Shay, 1986).

Lombardi et al. (1997) also investigated the impact of salinity on the germination of *T. latifolia*. NaCl turned out to have a negative effect on germination rates (Figure 35) and seedling growth and development (Table 2); even the lowest NaCl concentration was found to exert an adverse effect, such as shoot tip necrosis. These researchers also found that germination decreased proportionately to increasing NaCl concentration in the presence of alternating temperatures. Analysis of variance showed that shoot length recorded at 10/20°C and 10/30°C differed significantly from lengths obtained at 20/30°C (Table 2). After NaCl was added, the latter temperatures were found to give the greatest seedling lengths. Hence, Lombardi et al. (1997) regarded *T. latifolia* as a glycophilic species (a species attracted to fresh water), with an extreme sensitiv-

5 It was impossible to find the publication on the internet and, therefore the concept "subnormal" remains undefined. We assume that it points to low presence and/or cover of the species.

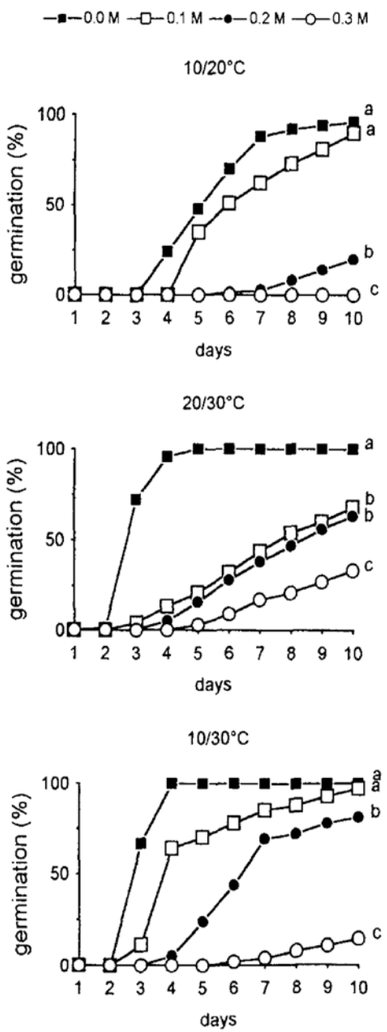



Figure 35: Mean percentage of germination (%) of *Typha latifolia L.* seeds at alternating temperatures during 10 days of culture in NaCl (M). Different letters at 10 days indicate significant differences at the 0.05 probability level among different salinity treatments (Lombardi et al., 1997).

Table 2: Mean length (cm) ± standard error of *T. latifolia* seedlings (shoot + root) on Day 10 in different NaCl solutions and at various alternating temperatures (°C) (Lombardi et al., 1997).

| Temperature (°C) | Length of seedlings (cm) | | | |
|---|---|---|---|---|
| | 0 NaCl | 0.1 M NaCl | 0.2 M NaCl | 0.3 M NaCl |
| 10/20°C | 8.4 ± 1.3 a | 1.5 ± 0.5 c | 1.1 ± 0.1 e | 0.0 ± 0.0 g |
| 10/30°C | 17.1 ± 2.1 b | 1.6 ± 0.1 c | 1.2 ± 0.2 e | 1.0 ± 0.3 h |
| 20/30°C | 15.9 ± 1.2 b | 2.0 ± 0.3 d | 1.5 ± 0.1 f | 1.3 ± 0.4 h |

ity to variations in water body salinity, particularly during germination and early growth. Therefore, they concluded that it is unlikely that this species colonises brackish environments by seed. It seems much more likely to them that the species propagates and establishes itself by vegetative dispersal.

In conclusion, both *Typha* species can occur in slightly brackish conditions, but in low cover, although their germination is strongly inhibited by already low NaCl concentrations. Therefore, we assume that colonisation of slightly brackish habitats mainly occurs through vegetative propagation and through germination during periods with a predominant supply of fresh rainwater or groundwater, but this latter situation will occur only rarely.

### 2.4.9 pH and nutrients

Changes in pH had no effect on *T. latifolia* germination (Lombardi et al., 1997). This underpins the observations that this species can build a species-poor and monotonous vegetation in which the species itself predominates in a wide pH-range from acid to alkaline (Fasset and Calhoun, 1952; Millar, 1976; Weeda et al., 1994). *T. angustifolia* is most abundant in basic waters (Fasset and Calhoun, 1952), but it is able to build a dense, species-poor vegetation in soft-water pools with an average pH-$H_2O$ of 6.5-7.0 (Kieskamp and Jansen, 2017).
Morinaga (1926b) stated that "[c]attail seeds are sensitive to light, nitrogen compounds, and reduced oxygen pressures." However, the impact of reduced oxygen conditions in the germination percentage seems to be of greater importance, as Morinaga reported for *T. latifolia* that "[n]itrates cause a marked increase in the germination of cattail seeds under water (reduced oxygen pressure) at the constant temperature 27°C, but they do not increase the percentage of germination of these seeds on filter papers (full oxygen pressure of the atmosphere) at the same temperature." He substantiated this conclusion with the following results: (i) in Petri dishes with filter paper moistened with nitrate solutions, germination was no better than on filter paper moistened with water, and (ii) after 18 days in darkness, at 27°C immersion of the seeds in nitrate solutions of 0.02 N and 0.01 N $KNO_3$ and in distilled water resulted in germination percentages of 23.5%, 59% and 1.5%, respectively. The latter results show that nitrate enhances the germination of *T. latifolia* seeds only in oxygen-poor conditions.

Stewart et al. (1997) investigated the effects of seed germination of *Typha* species in response to different nutrient levels, focusing on phosphate. In their series II, in which they explored the effects of differences in field-derived nutrients on germination in *T. domingensis* and *T. latifolia*, they used field water collected from three areas of the Everglades (Florida, USA) that had different phosphate





| Location | Impacted | Transitional | Non-impacted |
|---|---|---|---|
| TP[1] (mg P/L) | 0.200 | 0.030 | 0.008 |
| $PO_4$ (mg P/L) | 0.051 | 0.004 | 0.004 |
| TKN[2] (mg N/L) | 2.6 | 2.7 | 2.1 |
| $NH_3$ (mg N/L) | 0.015 | 0.011 | 0.020 |
| $NO_2$ (mg N/L) | 0.004 | 0.004 | 0.004 |
| $NO_2 + NO_3$ (mg N/L) | 0.004 | 0.021 | 0.01 |
| DOC (mg/L) | 46 | 51 | 36 |
| $CaCO_3$ (mg/L) | 299 | 333 | 263 |
| Na (mg/L) | 97 | 46 | 80 |
| K (mg/L) | 6.2 | 3.9 | 6.6 |
| Cl (mg/L) | 150 | 140 | 120 |
| Ca (mg/L) | 84 | 48 | 76 |
| Mg (mg/L) | 24 | 14 | 24 |
| Fe (mg/L) | 40 | 42 | 32 |
| $SiO_2$ (mg/L) | 24 | 20 | 18 |
| $SO_4$ (mg/L) | 62 | 73 | 56 |
| TSS[3] (mg/L) | 16 | 2 | 2 |

[1] TP = Total phosphorus.
[2] TKN = Total Kjeldahl nitrogen.
[3] TSS = Total suspended solids.

Table 3. Nutrient concentrations of the water from three field sites within Water Conservation Area 2A in the Everglades (Florida, USA) (Stewart et al., 1997).

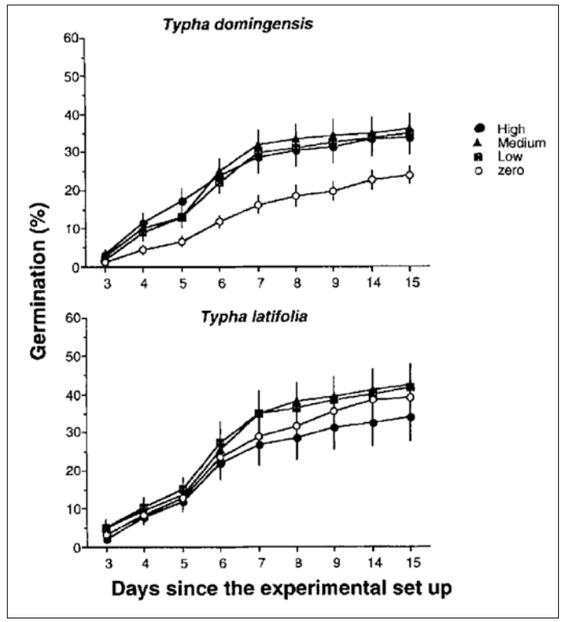



Figure 36: Seed germination of *T. domingensis* and *T. latifolia* over time in four nutrient concentrations of water collected from three sites in Water Conservation Area 2A in the Everglades (Florida, USA). Bars represent one standard error. Each mean represents an average of 18 samples of 50 seeds (in Stewart et al., 1997).

concentrations and represented high, medium, and low nutrient conditions with total phosphate concentrations of 0.200 mg/l (impacted), 0.030 mg/l (transitional) to 0.008 mg/l (non-impacted), respectively (Table 3). Distilled water was used to create a zero nutrient condition. *T. domingensis* and *T. latifolia* seeds were used. There was little difference between either the germination percentage for both species within the medium and low nutrient levels. However, the two species differed in that *T. domingensis* had the lowest percentage of seed germination in zero nutrients, while *T. latifolia* had the lowest in high nutrients (Figure 36). The only significantly different germination rate within species was in the zero nutrient condition for *T. domingensis*.

*Typha* species are known to be characteristic of nutrient-rich sites (see for example Oberdorfer, 1983; Weeda et al., 1994). This leads to the question whether nitrogen or phosphorus limits the growth of *Typha* species.

Köhn (2016) tested the impact of the use of propagation soil and potting soil on the germination on T. latifolia and T. angustifolia. She found much better

Table 4: Means ± S.E. of selected nutrient concentrations of soil samples for reciprocal transplanting (Miao et al., 2000).

| | Sample size | Total P (mg kg$^{-1}$) | Total N (g kg$^{-1}$) | N:P[a] | Total C (g kg$^{-1}$) |
|---|---|---|---|---|---|
| Reciprocal transplanting experiment | | | | | |
| F1 site | 6 | 1572 ± 29 | 26.3 ± 0.4 | 37 | 405 ± 11 |
| U1 site | 6 | 446 ± 8 | 32.1 ± 0.7 | 159 | 483 ± 7 |
| U3 site | 6 | 401 ± 4 | 27.2 ± 0.4 | 150 | 367 ± 2 |

germination in potting soil than in propagation soil, which in her opinion is due to the higher phosphate concentration in the potting soil, although the propagation soil contains more nitrogen. However, over time the number of seedlings in the potting soil decreased, which may be caused by the low nitrate content of the flower soil, which was just one third of that of the propagation soil.

Miao et al. (2000) also provided evidence for the importance of P availability in species expansion in wetland ecosystems. They reciprocally transplanted *T. domingensis* plants originating from seeds collected at a P-enriched site and two unenriched sites (Table 4), and they found that the site had a significant effect: (i) after 7 months, plants (per genet) transplanted to the enriched site exhibited a greater biomass (dry weight) accumulation (152 versus 13 g), higher tissue nutrient concentrations, and more proportional leaf biomass allocation than plants transplanted to the unenriched sites; (ii) each original plant transplanted to the enriched site produced an average of 6.7 new ramets and covered approximately 1.2 m², whereas no ramets were produced at unenriched sites; and (iii) after 2.5 years, the total biomass for plants transplanted at unenriched sites was only about 6% of that of plants at the enriched site measured 2 years prior to this.
Miao et al. (2000) argue that the differences in plant growth between enriched and unenriched sites were largely due to site differences in P availability:

1. Soil analyses show that the major difference between the three sites was P concentration (Table 4). Although site U1 exhibited the greatest soil total N concentration among the three sites, this high N concentration was not associated with enhanced cattail plant growth.
2. In the same area, Craft et al. (1995) demonstrated that P additions but not N additions significantly enhanced cattail biomass accumulation.
3. N:P ratios (based on atomic weights) of plant tissue greater than 16 generally indicate P limitation (see for example Koerselman and Meuleman, 1996). The experiment of Miao et al. (2000) showed that tissue N:P ratios at unenriched sites are clearly P-limited, although at enriched sites this ratio was close to 16.
4. Differences in water depth between the two unenriched sites did not result in different growth rates.

### 2.4.10 Sediment structure

Some researchers mentioned differences in soil type or sediment structure as a cause of differences in germination and/or establishment. According to Van der Valk and Davis (1976), certain substrate samples with high organic matter content (i.e. large amounts of partially decomposed leaves from trees) generally produced fewer seedlings and often had significant seedling mortality rates. Stewart et al. (1997) reported that the use of Everglades Peat had a negative effect on seed germination of *T. latifolia* and *T. domingensis*: "Overall, only 55% of the seeds germinated on the Everglades Peat, while 90% germination occurred on filter paper or paper towels as the substrates."





Grace (1984) investigated the impact of benthos (tubificid worms) on the germination and establishment of *T. latifolia* and *T. domingensis*. He planted seeds into plastic chambers and determined the sedimentation in the chambers arising from organic and inorganic deposition, benthic algal growth, and sediment pushed up through the fabric by tubificid worms. Next, he scored each chamber after the first 30 days as one of the following: 0 = none of the surface area covered by sediment; 1= 25% or less covered; 2 = 26-50% covered; 3 = 51-75% covered, 4 = 76-100% covered by a layer < 3 mm deep; 5 = 100% covered by a layer ≥ 3 mm deep. He observed that only at sedimentation level 5, a significant reduction in germination, survival, and growth had occurred (Figure 37). However, only the *T. domingensis* tubs contained sedimentation values this high, while sedimentation in tubs of *T. latifolia* did not differ significantly from the control tubs, i.e. without tubificids. The cover of the *Typha* seeds with a 3 mm deep layer may cause unfavourable light conditions for germination (see section 3.5.3.). According to Grace (1984), the very small *Typha* seeds (1-1.5 mm long) are easily buried by tubificids. By their burrowing activities, the tubificids mix as much as the upper 15 cm of sediment, which may cause an increase in the redox potential of the upper sediments (Davis 1974). This will negatively influence the germination of *Typha* seeds, which are known to favour low oxygen conditions for germination (see section 3.5.7).

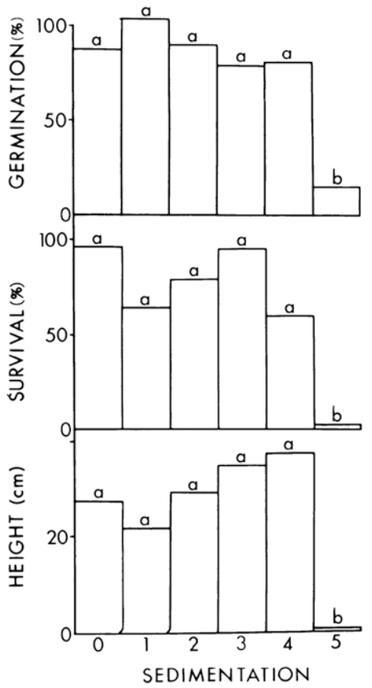



Figure 37: Effects of sedimentation on germination, survival, and height of *T. latifolia* and *T. domingensis* (combined). On the sedimentation scale, 0 = none of the chamber surface covered, and 5 = 100% of surface covered by a layer of 3 mm deep. Bars designated by different letters are significantly different at the 0.05 level based on a Duncan's test (Grace, 1984).

### 2.4.11 Allelopathy

Evenari (1949) listed *Typha* as a plant species producing germination inhibitors. Bedish (1964) subsequently suggested that the leaves of cattail plants produce germination inhibitors and thus inhibited the germination of *Typha* seed in an established cattail stand.
Van der Valk and Davis (1976) hypothesised that the high mortality of seedlings that they observed in the open-water zone of Ventura Marsh with large amounts of partially decomposed leaves from

trees could be due to an allelopathic interaction between the tree leaf litter and certain monocot species (primarily one or more grasses). Normal individuals of dicot species, especially *Urtica dioica*, grew in the same sample, as did some monocots. However, seedlings of *Leersia oryzoides* (a monocot grass species) also survived in high numbers, as did seedlings of *Typha glauca* (Table 1 in Van der Valk and Davis, 1976). Therefore, it is questionable whether an allelopathic interaction is the cause of the high seedling mortality. It seems more likely that decomposition of accumulated layers of leaves resulted in extreme eutrophication and, consequently, in a species composition characteristic of hypertrophic conditions. Van der Valk and Davis (1976) also assumed that the poorer germination of *Typha* in *Typha* stands compared to in open water supports McNaughton's (1968) hypothesis that *Typha* inhibits the germination of its own seed, although they refer to Clambey (1975), who was unable to demonstrate this phenomenon. They concluded with the recommendation that more research is required into the allelopathic properties of marsh plant litter and their influence on vegetation dynamics.

A green leaf extract inhibited germination in the dark only (Rivard and Woodard 1989). Sharma and Gopal (1978) showed that a variety of aqueous extracts, including those from *Typha,* did not affect the seed germination of *T. domingensis*) and *T. elephantine* Roxb. Moreover, the results of inhibition experiments by Grace (1983) indicated that there was no allelopathic inhibition of germination as found by McNaughton (1968). Grace (1983) found inhibitory effects of Typha extracts in liquid culture on seed germination only in concentrations greater than or equal to 3% (dry weight to volume), but these were correlated with the development of water moulds in the cultures. He showed that "prior to the development of water moulds, even 15% extracts were not inhibitory to germination. Further, neither 3% concentrations of senesced leaf pieces nor soil surface water from one year old pots of *T. latifolia* had any detrimental effects on germination. Seeds sown in pots containing established *T. latifolia* germinated as well as seeds sown in control pots." Therefore Grace (1983) concluded that "these results do not support the contention that *T. latifolia* inhibits the germination of its seeds by the release of allelopathic substances."

## 2.5 Establishment and growth

Like many other species of marshes and other aquatic sites, the *Typha* species are characterised by clonal growth (Grime et al., 1988; Figure 38). The following authors reported the following with respect to the growth of *Typha* species:

- Yeo (1964): The growth of the seedlings was rapid. In 6 months a single plant developed a network of rhizomes covering an area 10 feet (3 meter) in diameter. Furthermore, he reported that in a single growing season, a plant grown from seed produced 34 aerial shoots that were 46-61 cm tall, 29 shoots measuring 10-46 cm, 35 shoots measuring 5-10 cm, and 104 lateral buds.
- Wesson and Waring (1969 in Miklovic, 2000): Once germinated, *T. angustifolia* seedlings can achieve high growth rates in full sunlight conditions.
- Grace and Harrison (1976): *Typha latifolia* produces lateral rhizomes of up to 28 inches (70 cm) long, with diameters of 0.2 to 1.2 inches (0.5-3 cm). Shallow fibrous roots are attached to these rhizomes.
- Fiala (1971, 1978): One individual plant (genet) is capable of producing more than 40 new daughter shoots (ramets) during the first growing season, whereas polycorms are capable





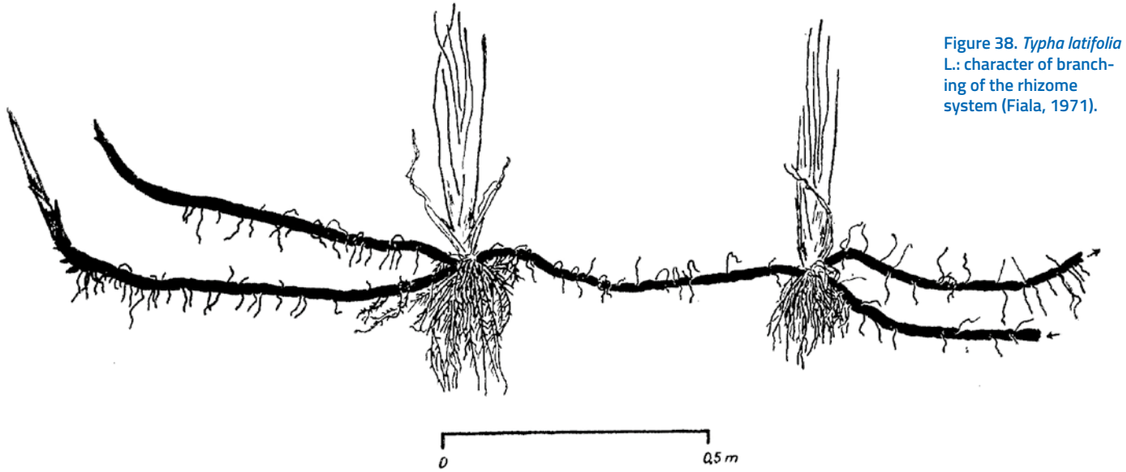



Figure 38. *Typha latifolia* L.: character of branching of the rhizome system (Fiala, 1971).

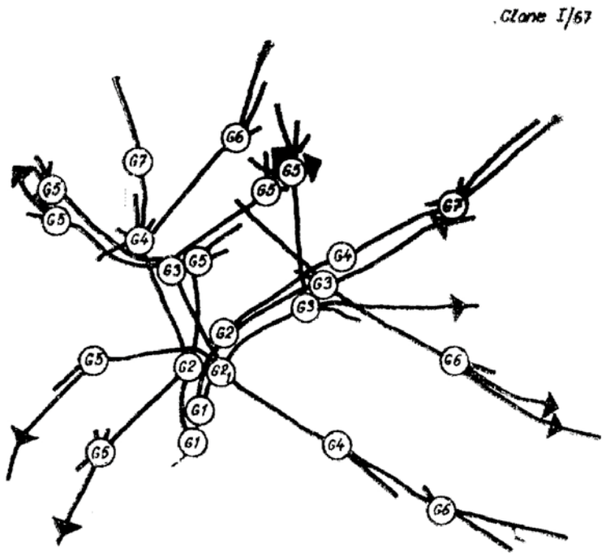



Figure 39: Spreading of the rhizomes in one-year clones of *Typha latifolia* during the 1967 growing season; horizontal projection 1 = rhizomes formed at the end of the preceding year (1966), 2 = rhizomes formed in the course of 1967, 3 = hibernating buds, 4 = remnants of dead shoots remaining from the preceding year; G1 = shoots which emerged at the end of the preceding year, G2 to G7 = shoots which emerged in the course of 1967 (Fiala, 1971).

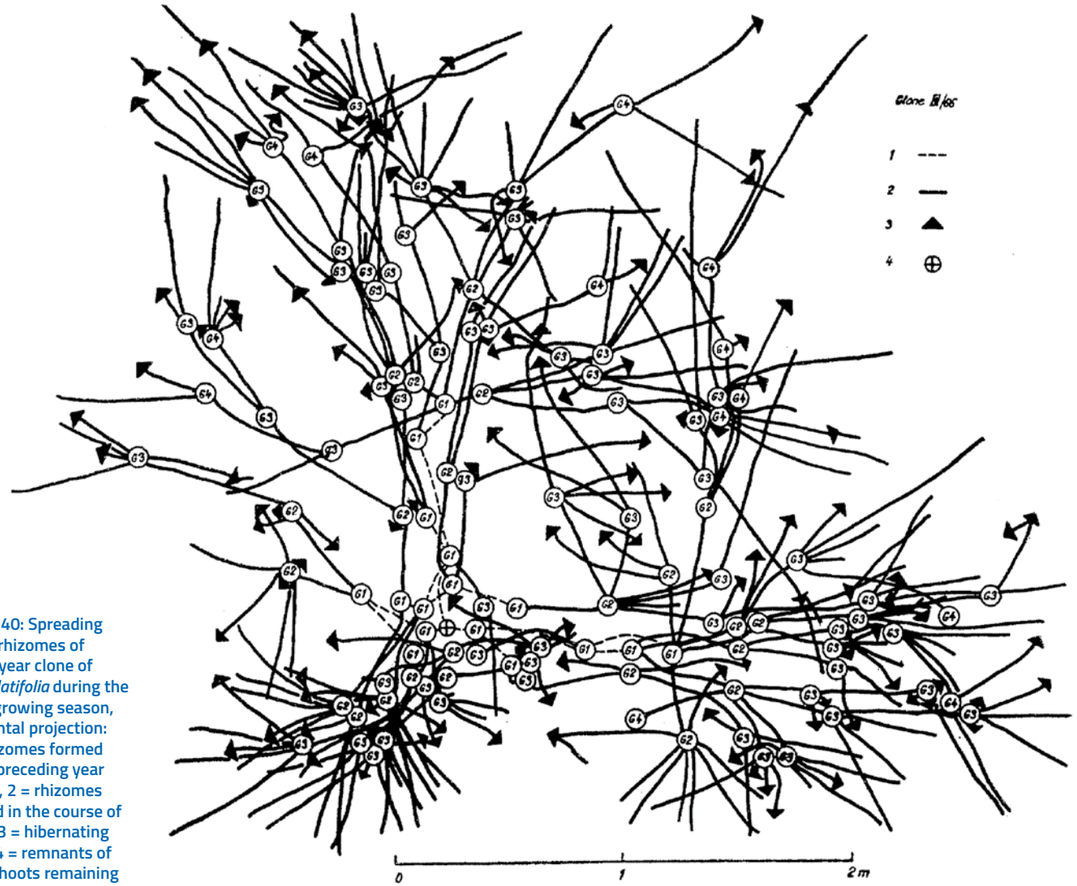



Figure 40: Spreading of the rhizomes of a two-year clone of *Typha latifolia* during the 1966 growing season, horizontal projection: 1 = rhizomes formed in the preceding year (1965), 2 = rhizomes formed in the course of 1966, 3 = hibernating buds, 4 = remnants of dead shoots remaining from the preceding year; G1 = shoots which emerged at the end of the preceding year, G2 to G4 = shoots which emerged in the course of 1966 (Fiala, 1971).





of covering up to 16 m² at the end of the first growing season. However, the highest rate of expansion was observed in two-year clones, in which the annual increment in the colony diameter amounted up to 4 m. He recorded the highest rates of the formation of new shoots during the growing season in the summer (July to early August) and in the autumn (September to October), which corresponds with the two maxima in the increments in rhizome biomass (Figure 39).

- Grace and Wetzel (1981a): Newly established plants rapidly produce large rhizomes from which ramets (rhizomes with emerged leaves and flowering structures) can grow.
- Grace and Wetzel (1981c): Vegetative reproduction occurs by the production of a lateral rhizomes from the meristem at the base of the leaves.
- Holm et al. (1997): Rhizome growth begins once shoots are 14 to 18 inches (35-45 cm) tall. During the first year, rhizomes may spread to 2 m in diameter. After two growing seasons, a single colony of common cattail may cover 54 m² with a total rhizome length of 480 m.

The life cycle of *T. angustifolia* is described concisely by (Apfelbaum, ((1986) and Snyder (1993): *T. angustifolia* leaves emerge in early spring (April), after which new rhizomes and leaves are formed (May and June). Spikes emerge in June, whereas flowering is initiated in early to mid-summer. In July also new basal shoots arise. From August through September maturation of flower head occurs. The greatest clonal growth occurs in the fall. Seeds typically remain on the spikes through the winter and disperse in spring. Aerial shoot growth continues into November or until the first freeze when plants become dormant (Boyd and Hess, 1970). While generative shoots complete their growth with flowering and die after reproduction, some vegetative shoots survive winter and show re-growth in spring (Fiala, 1971; Dickerman and Wetzel, 1985). The latter two studies showed that three shoot emergence pulses occur per year: (i) the first one in early spring, which grows throughout the summer and dies completely in late autumn; (ii) the second one in midsummer, and (iii) in late summer and early autumn, which produces 80-90% of the shoots that will resume growth in spring. Circa ¾ of the midsummer shoot pulse senescences in autumn, while the remainder will resume growth the following spring. These recordings are in agreement with those by Fiala (1971). He found that the total annual production of rhizomes depended to a large extent on both the rate of the development of shoots originating from offshoots formed in the preceding year and on the development of the shoots formed next to these at the beginning of the new growing season. These shoots play an important role in the formation of rhizomes during the whole growing season, and they give rise to a large number of rapidly growing offshoots in the middle of the growing season (Figure 40).

Garver et al. (1988) studied seasonal patterns of biomass and nutrient (nitrogen, phosphorus and potassium) accumulation in *T. latifolia*, *T. angustifolia*. and *T. X glauca* grown in cultivated stands in Minnesota, USA, during the course of two growing seasons and two winters. Their results indicated "that biomass and nutrient accumulation are in a lag phase during the first 4-8 weeks of growth in the spring. The plants then enter a rapid growth phase in which 47-80% of the total seasonal biomass production and nutrient uptake occurs in a 4-8-week period. During this time, *Typha* leaves account for 60-70% of the biomass and represent the major nutrient sink. As the rate of biomass and nutrient accumulation diminishes, translocation

of both nutrients and photoassimilate takes place from leaves to rhizomes, with an estimated 40% of leaf nitrogen, 35-44% of leaf phosphorus and 4-38% of leaf potassium translocated to the rhizomes by 27 October. Over the winter, 75% or more of the rhizome biomass, nitrogen, phosphorus and potassium is preserved." In addition, the results of Miao et al. (2000) need to be mentioned; they found that growth characteristics (rhizome growth and biomass accumulation) and tissue total-P concentrations were greater at an enriched site relative to two unenriched sites (see also section 3.5.9).

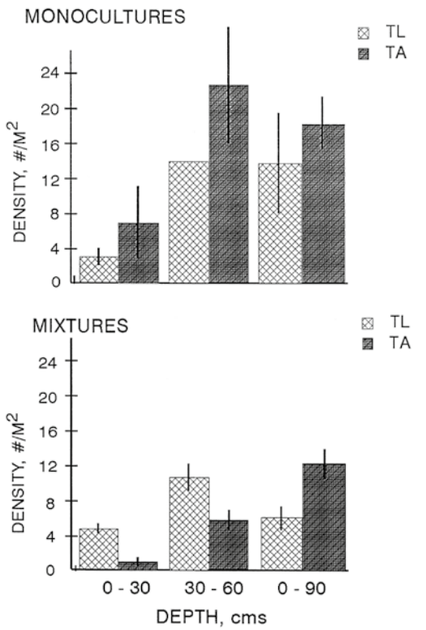



Figure 41: Comparison between natural monocultures and mixtures of *Typha latifolia* (TL) and *Typha angustifolia* (TA) in five experimental ponds that had been undisturbed since their creation and colonisation by *Typha* 23 years before measurement. Values presented are raw densities per 0.4 $m^2$ plot and error bars represent ± one standard error. The water depths for Zones 1-3 were 0-30, 30-60 and 60-90 cm (Grace and Wetzel, 1998).

Grace and Wetzel (1982) showed that the storage of nutrient reserves (carbohydrate) in their rhizomes during their dormant winter period permits the initial growth of spring shoots for both *T. latifolia* and *T. angustifolia*. In addition, it turned out that the size and number of the rhizomes differed between both species: *T. angustifolia* produces a few, large parent rhizomes, whereas *T. latifolia* produces many, small, lateral rhizomes. Therefore, in spring *T. angustifolia* is capable of producing shoots to heights enough to exceed the surface of deeper water. The spring shoots of *T. latifolia* do not exceed a water depth of 50 cm. These differences in size and number of rhizomes determine the position of both species in the water depth gradient as Grace and Wetzel (1998) showed in their study on the interaction between both taxa. They compared mixed and monoculture stands in five experimental ponds that had remained undisturbed for 23 years. They found that the maximum depth of *T. latifolia*, the shallow-water species, was not significantly reduced when growing in the presence of the more flood-tolerant *T. angustifolia* (Figure 41). In contrast, the minimum depth of *T. angustifolia* was reduced from 0 to 37 cm when in the presence of *T. latifolia* (Figure 41). Furthermore, a comparison between the total populations in monoculture and mixed stands revealed that the average density of *T. angustifolia* shoots was 59.4% lower in mixed stands, while the density of *T. latifolia* was 32% lower. *T. angustifolia* was most affected at shallow depths (reduced by 92%) and *T. latifolia* at the deepest depths (reduced by 60%). Hence, Grace and Wetzel (1998) concluded that their long-term observations indicate that competitive displacement between *Typha* taxa has remained stable over time. Therefore, these species hold a separate niche in nature, as is indicated by their stable position in the water depth gradient (see section 3.1.4).



Yves Adams/Vildaphoto

# 3 Conclusions and discussion

## 3.1 Reproduction and dispersal

Cattails reproduce by seed and rhizomes. Their primary means of colonising is by seed, and once established, colonies are maintained by vegetative reproduction via rhizome growth and fragmentation (Grace and Wetzel, 1981a,b,c). *Typha* species produce an enormous number of seeds, with estimates for a single inflorescence ranging from 20,000 to 700,000, with an average of approximately 200,000 (Dubbe et al.,1988; Grace and Harrison,1986; Heinz, 2012; Prunster, 1941; Marsh, 1962; and Yeo, 1964).

*Typha* species are anemochoreous, i.e. they are dispersed by wind. The hairy, small and light seeds facilitate wind dispersal, which happens during autumn and winter. By anemochory the seeds are easily transported over long distances (Coops and Van der Velde 1995; Grace, 1984; Grace and Harrison, 1986; Yeo, 1964; Heinz, 2012; Lombardi et al., 1997; Pojar and MacKinnon,1994; Sculthorpe 1967). Besides being dispersed by wind, *Typha* seeds are transported by water (Sculthorpe, 1967; Grace, 1984; Grace and Harrison, 1986; Hickman, 1993;

Remco Versluijs





Pojar and MacKinnon, 1994; Yeo, 1964). In addition, *Typha* seeds may be transported by substrate movement (Pojar and MacKinnon, 1994), by birds and livestock (State of Queensland, Department of Agriculture and Fisheries, 2020), or by fish (Krattinger, 1975).
As a result of the high production of small diaspores that are easily transported over long distances (of up to 3.6 km, according to Soons and Ozinga, 2005), new habitats are within easy reach (Heinz, 2012; Van der Valk and Davis, 1976). This suggests that there are few dispersal problems.
If the fruits come into contact with water, the pericarp (Figure 9) opens and the seed is released and sinks with the pointed, posterior part downward (Grace and Harrison, 1986; Hickman, 1993; Yeo, 1964; Krattinger, 1975. After a drawdown of the surface water level, *Typha* species germinate very rapidly – within a few days - on mud flats and in shallow water (Stewart et al., 1997; McNaughton, 1966; Clements, 2010).

*T. latifolia* and probably also other *Typha* species build seed banks with very high seed densities (Bakker et al., 1996). It appears that the major part of the soil seed bank of *T. latifolia*, but probably also of other *Typha* species, mainly consists of transient and short-lived seeds (Poschlod and Jackel, 1993), and a minor part of persistent seeds (Van der Valk and Davis, 1976; Keddy and Reznicek, 1986).
*Typha* species germinate after a drawdown of the surface water level on mud flats, open waterlogged soils or in shallow water (Bedish, 1962; Dubbe et al., 1988; Pratt et al., 1985; Sharma and Gopal, 1978; Van der Valk and Davis, 1976; see also section 4.2) or within open *Typha* stands (Sharma and Gopal, 1978). According to Keddy and Reznicek (1986), *Typha* species regenerate from buried seeds in open gaps during low water periods after prolonged high water periods.

After germination, *Typha* species rapidly produce large rhizomes (Yeo, 1964; Grace and Harrison, 1976; Grace and Wetzel, 1981a, 1982; Holm et al., 1997; Wesson and Waring, 1969; Fiala, 1971, 1978). Vegetative reproduction provides a mechanism for short-distance dispersal (Grace and Wetzel, 1981a).

In conclusion, the attendance of persistent seeds and the massive seed production, combined with good dispersal capacities and rapid germination enable *Typha* species to rapidly establish new habitats. Thanks to rapid vegetative reproduction by large rhizomes, *Typha* species colonise large areas within a few years. All in all, the *Typha* species have an enormous colonisation potential.

## 3.2 Water regime as a conditioning factor

Once the *Typha* seedlings have been well established, the plants can tolerate a much broader range of abiotic conditions (McNaughton, 1966; see section 3.1.4). This means that during the *Typha* species life, the range of conditions required during germination is much smaller and therefore determines the occurrence of *T. latifolia* and *T. angustifolia* first and foremost.

However, this leads to the question as to which range of conditions is required for *Typha* species to germinate. Both *T. latifolia* and *T. angustifolia* are pioneer species, which means that they are capable of colonising open areas that are not yet vegetated. Furthermore, both *Typha* species are characteristic of wet sites, which are inundated during a large part of the year. *T. latifolia* occurs in somewhat shallower water than *T. angustifolia*. According to Grace and Wetzel (1982), in North America neither species survives under normal conditions in water deeper than 60-100 cm, and *T. latifolia* tends to be

replaced by *T. angustifolia* in water deeper than 15 cm. In Europe, however, *T. angustifolia* may even occur in open waters of 0.5 to 1.5 m deep, and sometimes even deeper (Weeda et al., 1996).

Although many researchers only experimented with a limited range of water depths, it is obvious that germination of *Typha* species usually only occurs in shallow water, although under controlled conditions germination has been recorded at water levels of up to 40 cm for *T. angustifolia* (Beule, 1979) and up to 20 cm for *T. latifolia* (Wilson, 1955), although germination gave poorer results. The range of optimum water levels for the germination of *T. latifolia* varies between a groundwater table around the soil surface and a surface water level that does not exceed approximately 15 cm. Under controlled conditions, maximum germination rates were found at water depths of between 2.5 and 4 cm (Bedish, 1964; Beule, 1979; Grace, 1985; Heinz, 2012). Although germination is known at surface water depths that exceed 10 cm and groundwater tables lower than 15 cm below the soil surface, seedlings which have germinated under these conditions may well be too small to develop into adult plants (Grace, 1985). The water regime requirements of *T. angustifolia* seed germination are less known. Based on the results of Beule (1979), Dubbe et al. (1988), Heinz (2012) and Keddy and Ellis (1985), it may be expected that this species germinates at a water regime similar to that of *T. latifolia*.

Oxygen-poor conditions – but not anaerobic conditions – are a prerequisite for *Typha* species germination (Morinaga, 1926b; Sifton 1959; Bonnewell et al., 1983; Lang et al., 2014). In nature, a gradual drawdown of the water level to the soil surface often occurs, and it seems to favour germination and/or the growth of the seedlings (Pratt et al., 1985) as long as water-saturated conditions remain. Such conditions ensure the occurrence of the required oxygen-poor conditions. Because anaerobic conditions may already occur less than 2 cm below the surface of lake sediments (Mortimer, 1971) or arise due to prolonged flooding (Bedish, 1964), it is likely that the required low $O_2$ concentrations for the optimum germination of *Typha* seeds occur near the surface of water-saturated soil. This is consistent with the appearance of seedlings on mud flats or in shallow water (Van der Valk and Davis, 1976). Therefore, germination and rejuvenation of *Typha* populations require a drawdown of surface water levels to the soil surface or a few centimetres above it (Bedish, 1964; Dubbe et al., 1988; Pratt et al., 1985). The same is true for other helophytes, such as *Phragmites australis* (Weeda et al., 1994; Remmelzwaal and Verheule, 1999; Gucker, 2008b).

Like other small-seeded species with epigeal germination, due to which the seedling is provided with only few resources, *Typha* seedlings need to elongate rapidly and start photosynthesis to support further development (Mayer and Poljakov-Mayber, 1989). Indeed, the epigeal germination initiates with the emergence of the photosynthesising coleoptile (Lang, 1965) and cotyledon (Mayer and Poljakov-Mayber, 1989).The dependency on a rapid start of photosynthesis for further development means that there must be sufficient light (Meara, 1957). Hence, *Typha* seed germination is light-sensitive as had already been suggested by Guppy (1897), and which has been confirmed by several other researchers (Morinaga, 1926a, 1926b; Sifton, 1959; Bonnewell et al., 1983; Frankland et al., 1987; Lombardi et al., 1997; Stewart et al., 1997). Moreover, Stewart et al. (1997) showed that seeds placed under subdued light germinated to a lesser extent than those exposed to full sun-






photos Koen Brouwer

light. Although *Typha* seedlings can develop small floating leaves when inundated during or shortly after germination (see Figure 16; Lang et al., 2014), germination of *Typha* seeds is presumably prevented in water too deep for light penetration. Then, *Typha* seedlings will not survive because the light intensity, which is almost immediately required for the seedlings to start their photosynthesis, is insufficient. This is in agreement with findings by Sharma and Gopal (1978) and Gopal and Sharma (1983), who concluded that a minimum light intensity is required for the seeds of *T. elephantina* to germinate, and Sifton (1959), who showed that the swelling of the aleurone grains – the first step in germination - is much more rapid and vigorous in white or yellow light than in darkness or in blue light. Therefore, it is likely that the *Typha* species germinate best in shallow open water (with a water depth of up to 15 cm) or on very wet, water-saturated soils (organic and/or open mud flats) after drawdown of the surface water. Under this water regime, the light supply is sufficient and does not limit the development of *Typha* seedlings.

Under such a water regime, water and soil temperatures may easily rise to high levels during the daytime and drop to lower levels during the night. Such an alternating temperature regime has been proved to promote the germination of *Typha* seeds, according to Morinaga (1926b), Lombardi et al. (1997), Heinz (2012) and Lang et al. (2014). The regimes with the highest germination percentage and/or rate mentioned by these researchers range from 10/30°C, 10/32°C, 15/25°C, 15/32°C, 18/26°C and 20/30°C night (first digit) and diurnal temperature. Sifton (1959), McNaughton (1966) and Bonnewell et al. (1983) did not use fluctuating day and night temperatures in their experiments, but showed that germination was favoured by high temperatures in the range of 25-35°C, where 35°C seemed somewhat too high compared to the germination percentages at 25°C and 30°C, but still much better than at lower temperatures of 15°C and 10°C, at which less than 10% of seeds or no seeds germinated, respectively. In deeper water bodies it takes longer or is even impossible to reach such high temperatures and such diurnal temperature alternations.

Ekstam and Forseby (1999) proposed that the above-mentioned thermal requirements provide the non-dormant seeds with a season-sensing mechanism that postpones germination of seeds dispersed during autumn, winter or early spring, until the soil surface is heated by the sun in the spring and sufficiently large diurnal fluctuations of temperature occur. Furthermore, the amplitude requirement implies a strong avoidance mechanism for germination of *Typha* species in sites with small temperature fluctuations, such as below deeper surface water tables.

Therefore, the yearly water regime is a conditional factor in *Typha* seed germination. It regulates the required light, temperature and oxygen conditions for germination.

## 3.3 Period of germination

The next question to answer is during which period of the year the surface water level must drop to the soil surface to promote germination. Lombardi et al. (1997) reported germination in May. Hayden (1948) mentioned late July and August as favourable months for germination. According to Beule, (1979) seeds germinate under good conditions from May to September. Clearly, from late spring until the end of the summer the conditions are favourable: (i) there are high and largely alternating temperatures; (ii) there is prolonged daylight of high intensity (Bonnewell et al., 1983) and (iii) water levels have dropped. Under such conditions, an endogenous biorhythm could favour seed germination, whereas dormancy can be used as a mechanism to prevent germination during unsuitable ecological conditions when the probability of seedling survival is low. This explains the results of McNaughton (1968), who found that the temperature optimum for germination of *Typha* species seed varied in North America; seeds from southern climates had lower temperature optima to germinate than seeds from northern climates. If seeds from northern populations germinated at low temperatures, which prevail during fall, winter and early spring, germination would be highly detrimental to seedling survival. Moreover, a particularly early autumn freeze or late spring freeze would result in the elimination of inadequately established seedlings. Hence, relatively high germination temperatures of seeds from northern populations lead to a delay in germination through the winter, and promote germination and subsequent establishment during the next growing season. The opposite is true for seeds from the southern populations. Their ability to germinate at lower temperatures prevents damage to the seedlings by high temperatures and dry conditions, as the species will have germinated and been established before the most adverse conditions (heat, drought) become predominant in the summer.

The moment of germination is also determined by the time a seedling needs to develop into a plant which is capable of surviving the next winter. If the appropriate water level has been reached, germination occurs very rapidly, within 5-10 days (McNaughton, 1966; Stewart et al., 1997; Ekstam and Forseby, 1999; Heinz, 2012); provided temperatures are favourable, 50% germination within 3 days after the beginning of germination is not uncommon. *Typha* species are characterised by clonal growth. Within a few weeks, once shoots are 35-45 cm tall (Holm et al., 1997), the newly established *Typha* plants start producing large rhizomes from which ramets (rhizomes with emerged leaves and flowering structures) can grow (Grace and Wetzel, 1981a). Within one growing season, the rhizomes may spread from 0.7 to a maximum of 3 m, covering an area of 3 to 16 m² (Yeo, 1964; Fiala, 1971, 1978; Holm et al., 1997). Fiala (1971, 1978) recorded the highest rates of the new shoot formation during the growing season in the summer (July to early August) and in the autumn (September to October), which corresponded with the two maxima in the increments in rhizome biomass (Figure 39). Dickerman and Wetzel (1985) found three shoot emergence pulses during the growing season, namely in early spring, in midsummer, and in late summer/early autumn. The latest pulse produces 80-90% of the shoots that will resume growth in spring. With this in mind, the *Typha* species have the best opportunities to develop into robust plants at sites where water levels drop to near to the soil surface in May. *Typha* seedlings could also develop into robust plants capable of overwintering when they germinate at sites where an appropriate water table has developed by the end of June or the beginning of July at the latest. At such sites, the seedlings can produce shoots and rhizomes twice during the midsummer and late summer/early autumn. It is mainly the shoots formed during the latter period that will continue to grow in the next growing season.

## 3.4 Waterchemistry

*T. latifolia* and *T. angustifolia* occur under a wide range of water chemical conditions. Fresh water is clearly the optimum habitat of both *Typha* species, although they can also tolerate slightly brackish

Yves Adams/Vildaphoto





conditions (Crain et al., 2004; Weeda et al., 1994). In fresh waters, they become the dominant species, whereas in slightly brackish waters, this is never the case (Crain et al., 2004). The absence of *T. latifolia* and the low cover of *T. angustifolia* in slightly brackish waters is a consequence of the sensitivity to low salinity during germination, which prevents the colonisation of brackish habitats (Gucker, 2008a). Lombardi et al. (1997) regarded *T. latifolia* as a glycophilic species (i.e. a species attracted to fresh water), with an extreme sensitivity to variations in water body salinity, particularly during germination and early growth; this was based on their experiments which showed that even the lowest NaCl concentration was found to have an adverse effect on germination and growth. Therefore, they concluded that it is unlikely that the species colonises brackish environments by seed. They stated that it seemed more likely that the species propagates and establishes itself by vegetative dispersal.

With regard to the pH-range, both species can build a very species-poor and monotonous vegetation in a wide pH-range (Fasset and Calhoun, 1952; Millar, 1976; Weeda et al., 1994) from acid to alkaline. *T. angustifolia* is most abundant in basic waters (Fasset and Calhoun, 1952), whereas *T. latifolia* is capable of building a dense plant cover under moderately acidic conditions.

So far not much is known about the impact of different nutrient levels on the germination of *Typha* species. First of all, according to Morinaga (1926a, 1926b), oxygen-poor conditions seem to be of larger importance to the germination percentage than nitrogen levels. However, if oxygen-poor conditions are present during germination – as might be expected under natural conditions - nitrate will enhance the germination of *T. latifolia*. Stewart et al. (1997) showed that *T. latifolia* and *T. domingensis* germinated under a broad range of total phosphorus levels, i.e. showing high percentages of germination and a rapid germination (within a few days). Miao et al. (2000) and Köhn (2016) provided evidence for the importance of total-phosphorus levels on the expansion and germination of *Typha* species, respectively. They showed that under higher phosphate concentrations, *Typha* species exhibited a better growth and a higher germination percentage. Whether or not the nitrate content of the soil is of great importance needs to be further researched. However, this seems unlikely, as *Typha* species require hypoxic conditions for their germination, and under such conditions toxic ammonia predominates nitrate as nitrogen source, and phosphate availability is increased (Patrick and Khalid, 1974). Toxicity of ammonia is reflected in (i) a negative impact on the root growth, (ii) the emergence of chlorosis of leaves, and (iii) the very rapid (within a few hours) reduction of assimilation (Haynes and Goh, 1978; Schenk and Wehrmann, 1979).

## 3.5 Allelopathy, light limitation and tubificid activities

The results of Sharma and Gopal (1978) and Grace (1983) suggest that the non-germinability of seeds in nature in and near a dense vegetation of *Typha* species must be attributed to the absence of ecological conditions favourable to germination, rather than to allelopathic effects. According to Lombardi et al. (1997), seeds thus ”avoid the risk of germination if they are buried or shaded by other vegetation.” The light sensitivity of both the germination process and the seedlings explains this non-germinability of seeds in nature; the light conditions in and near a dense *Typha* vegetation are unsatisfactory (Sharma and Gopal, 1978). Bonnewell et al. (1983) and Lombardi et al. (1977) hypothesised that phytochrome triggers the germination of

*Typha* species. They based their hypothesis on their finding that germination also depended on the sum of light hours to which seeds are exposed, and on the cumulative number of dark hours that neutralise a previous light-derived positive germination impulse. For instance, the plant pigment phytochrome regulates the day and night rhythm (circadian rhythm) of the plant, causing growth to the light as well as elongation of seedlings when the plant becomes shaded. Due to phytochrome functioning, the small-seeded *Typha* species avoid the risks of ongoing elongation, which would cause exhaustion of the seedlings' limited resources under light-limited conditions during germination and seedling growth. This implies that the light requirement for *Typha* seed germination is not only determined by light intensity (the energy) but also by its duration. This confirms the findings of many other studies, which have shown that *Typha* seeds require light to germinate (Frankland et al., 1987; Guppy, 1897, Morinaga, 1926a, 1926b; Sifton, 1959; Stewart et al.,1997).

Furthermore, Gopal and Sharma (1983) hypothesised that blue light inhibition of seed germination might be a survival strategy of *T. domingensis* under unfavourable conditions of submergence of the seeds. The light intensity at ground level in dense *Typha* stands is low (Sharma, 1977; in Gopal and Sharma, 1983), varying between 50 and 200 lux. According to Gopal and Sharma (1983), "in nature the turbidity of water and cover from other vegetation or dead leaves might even further reduce the light intensity. The longer wavelengths of light will be filtered out by the canopy and, therefore, more blue light will penetrate to the ground level. The same appears in open water, in which the deeper layers are rich in blue light, whereas red light is absorbed in the upper layers. This means that the seeds falling on the surface of deeper water bodies and settling down to the sediments will fail to germinate due to blue light inhibition, even if water is clear. When the water level drops, the availability of yellow and red light will allow germination." As at least a part of the seed bank of *Typha* species is persistent, blue light inhibition (and inhibition by darkness) is a strategy of these species to survive lasting unfavourable light conditions in the subaqueous soil layer or in deeper water bodies. Nevertheless, the non-germinability of seeds under dark or strongly shaded conditions contributes to the origin of a (moderately) persistent soil seed bank. A 3 mm deep layer which covers the *Typha* seeds may already cause unfavourable light conditions for germination (Grace, 1984). The burial of the very small *Typha* seeds (1-1.5 mm long) is promoted by tubificid activities (Grace, 1984). They mix as much as the upper 15 cm of sediment, which impedes germination, not only due to a lack of light, but also as a consequence of an increased redox potential of the upper sediments and a deepening of the oxidised layer (> 200 mV; Davis, 1974). The larger impact of oxygen hinders the germination of *Typha* seeds, which require low oxygen conditions for germination.



# 4 Implications for paludiculture

Remco Verkuijs

## 4.1 Points of attention and requirements for sowing

Dubbe et al. (1988) attributed the highly variable germination and seedling survival rates after sowing *Typha* in the open to the sensitivity of cattail seed germination and development to environmental factors. For this reason, this desk study aimed at gaining knowledge of these factors and the way they affect the germination of *Typha* seeds and their establishment. According to the results of this study, the seeding of *Typha* species sets the following preconditions:

1. *Typha latifolia* and *Typha angustifolia* seeds can be easily harvested from large monospecific natural stands with reasonable certainty that no infertile fruits of the hybrid *Typha x glauca* are collected. It is important to harvest the staminate stalks before they dry and blow away (Stevens and Hoag, 2003).
2. No special pre-treatment is required for the germination of *T. latifolia* and *T. angustifolia*

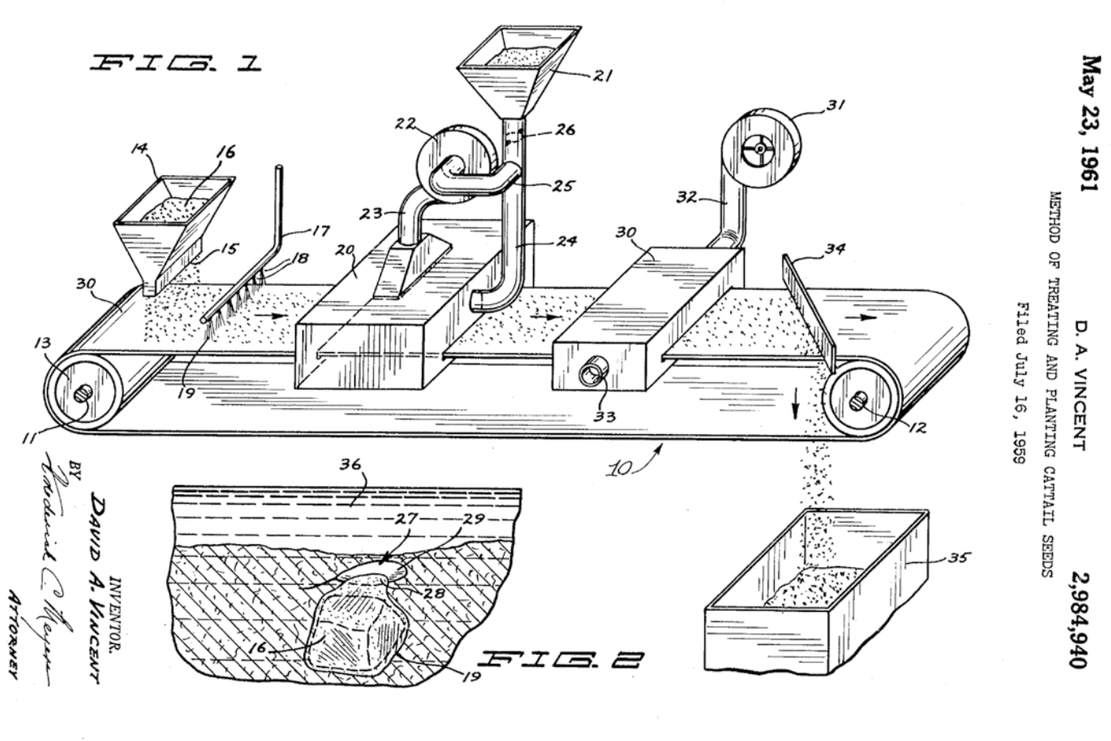



Figure 42. The invention which causes *Typha* seeds to sink without losing their germination capability (Wilton, D., 1951).

seeds. A cold period is not required for germination. Rather than dormancy, *Typha* species have an alternate system which prevents premature germination (McNaughton, 1966).

3. The best time for sowing is in June and July, under conditions of diurnal temperature differences between day (25 °C) and night (10 °C) (Dubbe et al., 1988).
4. Establishing *Typha* stands from seed requires mimicking the field conditions seen in natural marsh drawdown in order to meet the physiological requirements for seed germination and development (Dubbe et al., 1988). The surface water regime largely determines seed germination, both the beginning, the rate and the extent. The surface water regime must be such that at the beginning of June the water level is only a few centimetres above the soil surface. This is the recommended time for sowing. When after approximately three weeks a gradual drop towards the soil surface has occurred, massive germination will appear on the mud flats thus formed. As mudflats only exist for a short time, fast germination gives an essential advantage (Grace, 1987). This water regime provides the required light, temperature and reduced oxygen conditions for germination. Once plants are well established, they can tolerate a much broader range of conditions (McNaughton, 1966; Grace, 1984).
5. *T. angustifolia* grows in deeper waters than *T. latifolia*. Consequently, the drop of the surface water table and the development of mud flats will occur later in the season. The time of sowing must be adjusted accordingly.
6. If an existing water regime is unsatisfactory for the germination and subsequent establishment of *Typha* species, hydrological measures should be carried out aimed at an adequate water regime. Dubbe et al. (1998) advise estimating the water use by *Typha* species of potential *Typha* production sites. At sites where infiltration and evapotranspiration exceed the supply of water by rainfall, seepage, or horizontal water transport, water tables will not stay at or near the soil surface during the summer period. Then, (costly) irrigation will be required to maintain such water tables. It is advisable to calculate the cost of this prior to the beginning of the cultivation of the *Typha* species.
7. Sowing on bare mud flats may be technically easier than in shallow open water, although there is insufficient practical information about the mechanical sowing of *Typha* seeds. The rupture of the seed coat results in much higher germination rates than during the natural germination process (see section 3.4.2). Hence, the sowing of ruptured seeds on water-saturated mud flats may be an alternative to sowing in shallow water.
8. Dubbe et al. (1988) advise keeping the hairs of the seed intact when sowing in flooded or saturated conditions. In such conditions, germination and survival are higher when the hairs are left intact, possibly because the hairs prevent the tiny seed from being buried in the mud. However, due to these hairs, the seeds can continue to float and clog by wind and water movements, which causes spatially uneven germination. As early as in 1959, a way was found to prevent this and to cause them to sink, and this invention was patented in the USA in 1961. (Figure 42; Wilton, 1951).
9. If the very small *Typha* seeds (1-1.5 mm long) are seeded in deeper water, they may easily be buried by tubificids or by sediment movement due to wave action, which causes an increase in the redox potential of the upper sediments. This will negatively influence the germination of *Typha* seeds, which are known to favour low oxygen conditions for germination (see section 3.5.7). Moreover, darker conditions also are unfavourable to their germination (see section 3.4.3).
10. Hydroseeding might give the seedlings an advantage over weed competitors, but once applied, the seedlings must have a narrowly defined environment for continued growth in the following month (Dubbe et al., 1988). Although these conditions have not been properly described, it is clear that permanent water-saturated conditions are necessary during July, August and September. The most important growth occurs during the first growing season. At this time, the winter buds will be formed, from which the plant will sprout next year (see section 3.5). After the shoots have grown high enough (> 0.5 m), a gradual inundation and increase in surface water levels of the mud flats may occur again. To exclude competition with aquatic annuals, drawdowns in early spring and subsequent shallow flooding during summer

should be prevented (Sojda and Soldberg, 1993).

11. *T. latifolia* can be sown in a wide pH-range at sites varying from moderately acidic to alkaline conditions, while seeding of *T. angustifolia* should be restricted to basic waters (sub-neutral to alkaline sites).
12. Both *T. latifolia* and *T. latifolia* are characteristic of eutrophic conditions. Therefore, their seeding and their cultivation should be limited to such environments. Fertilisation before sowing must be discouraged. Although it may increase yields, fertilisation frequently results in extensive algal blooms which have been shown to shade and subsequently kill the young seedlings (Dubbe et al., 1988).
13. *Typha* germination on previously drained and agriculturally used grasslands could be favoured if they were sod cut prior to re-wetting. In this way an open, bare environment will be created, with sufficient light conditions for germination of the *Typha* seeds. However, this is an expensive measure, while the experience in the Anklammer Stadbruch shows that after extensive flooding of such grasslands within a few years a vast vegetation of *T. latifolia* develops (pers. obs.).
14. Established vegetation can inhibit germination and establishment by reducing light intensity, altering light quality, reducing temperature fluctuations (Morinaga, 1926a; Sifton, 1959), and releasing allelochemic inhibitors, although allelopathy appears to be of little significance (see section 3.4.11). Therefore, it is recommended to sow in existing *Typha* vegetation only when large gaps in the existing vegetation have arisen.

Finally, we would like to consider the rapid development of drone techniques. Perhaps these offer alternatives to sowing from land. It is then not necessary to drive on wet land with (heavy) machines. However, it does not alter the fact that seed accumulation due to wind or water movement must be prevented.



# References


Apfelbaum, S.I. 1985. Cattail (Typha spp.) management. Natural Areas Journal 5(3): 9-17.

Bakker, J.P., P. Poschlodt, R.J. Strykstra, R.M. Bekkker & K. Thompson, 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanica Neerlandica 45 (4): 461-490.

Baskin, J.M. & C.C. Baskin, 200). A classification system for seed dormancy. Seed Science Research 14 (1): 1–16.

Bedish, J.W., 1964. Studies of the germination and growth of cattail in relation to marsh management. MSc Thesis. Retrospective Theses and Dissertations. Paper 16857. Iowa State University, Digital Repository @ Iowa State University.

Bedish, J. W. 1967. Cattail moisture requirements and their significance to marsh management. American Midland Naturalist 78:289-300.

Bekker, R.M., J.H.J. Schaminée, J.P, Bakker & K. Thompson, 1998. Seed bank characteristics of Dutch plant communities. Acta Botanica Neerlandica 47: 15-26.

Bernhardt, K.-G., 1993. Untersuchungen zur Besiedlung und Dynamik der Vegetation von Sand- und Schlickpionierstandorten. Dissertationes botanicae 202, Berlin.

Bernhardt, K.-G., M. Koch, M. Spitzer & K.-F. Schreiber, 2003. Untersuchung zur ausbleibenden Makrophytenentwicklung an neuangelegten Flussabschnitten an der Ochtum bei Bremen (Deutschland). Die Bodenkultur 54 (2) : 119-132.

Beule, J.D., 1979. Control and management of cattails in southeastern Wisconsin wetlands. Technical Bulletin No. 112. Department of Natural Resources, Madison, USA.

Black M., J.D. Bewley & P. Halmer, 2006. The Encyclopedia of seeds. Wallingford, CAB International, Oxfordshire.

Bonnewell, V., W.L. Koukkar & D.C. Pratt, 1983. Light, oxygen, and temperature requirements for Typha latifolia seed germination. Canadian Journal of Botany 61: 1330-1336.

Boyd, C.E. & L.W. Hess, 1970. Factors influencing shoot production and mineral nutrient levels in Typha latifolia. Ecology 51(2): 296.

Cappers, R.T.J., R.M. Bekker & J.E.A. Jans, 2006. Ditigal seed atlas of the Netherlands. Groningen Archeological Studies volume 4. Barkhuis Publishing, Eelde.

Choudhurii, G.N., 1968. Effect of soil salinity on germination and survival of some steppe plants in Washington. Ecology 49(3): 465-47.

Clambey, G.K. 1975. A survey of wetland vegetation in north-central Iowa. Ph.D. Thesis, Iowa State University. Ames, Iowa.
Clements, D., 2010. Datasheet Typha latifolia (broadleaf cattail). Available at: http://www.cabi.org/isc/datasheet/54297.
Coleoptile. (2020, December 14). Retrieved December 19, 2020. In Wikipedia. https://en.wikipedia.org/wiki/Coleoptile
Comes, R. D., V. F. Bruns and A. D. Kelley, 1978. Longevity of certain weed and crop seeds in fresh water. Weed Science 26 (4): 336-344.
Coops, H. & G. van der Velde, 1995. Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. Freshwater Biology 34: 13-20.
Cotyledons. (2004, April 18). Retrieved December 19, 2020. In Wikipedia. https://en.wikipedia.org/wiki/Cotyledons
Crain C.M., B.R. Silliman, S.L. Bertness & M.D. Bertness, 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. Ecology 85(9):2539-2549.
Crocker, W. 1907. Germination of seeds of water plants. Botanical Gazette 44:375-380.
Crocker, W., 1938. Life-span of seeds. Botanical Review 4:235-274.
Davis, R. B. 1974. Tubificids alter profiles of redox potential and pH in profundal lake sediment. Limnology and Oceanography 19:342-346.
Dickerman, J.A. & R.G. WetzeL, 1985. Clonal growth in Typha latifolia: Population dynamics and demography of the ramets. Journal of Ecology 73: 535-552.
Dubbe, D. R., E. G. Garver & D. C. Pratt, 1988. Production of Cattail (Typha spp.) Biomass in Minnesota, USA. Biomass 17 (1988): 79-104.
Ekstam, B. & A. Forseby, 1999. Germination response of Phragmites australis and Typha latifolia to diurnal fluctuations in temperature. Seed Science Research 9 (2): 157-163
Evenari, M.l., 1949. Germination inhibitors. Botanical Review 15: 153-194.
Fassett N. & B.M. Calhoun, 1952. Introgression between Typha latifolia and T. angustifolia. Evolution 6:367-379.
Fenner, M., 1985. Seed Ecology. Chapman and Hall, London/New York.
Fenner, M., 1987. Seed characteristics in relation to succession. In: Gray, A. J., M. J. Crawley and P. J. Edwards (Eds.): Colonisation Succession and Stability. Blackwell Scientific Publications, Oxford, p. 103–114.
Fiala, K., 1971. Seasonal changes in the growth of clones of Typha latifolia L. in natural conditions. Folia Geobotanica & Phytotaxonomica Praha 6(3): 255-270.
Fiala, K., 1978. Underground organs of Typha angustifolia and Typha latifolia, their growth, propagation and production. Acta Scientiarum Naturalium (Brno), 12(8): 1-43.
Fiala K. & Květ J. (1971): Dynamic balance between plant species in South Moravian reedswamps.—In: E. Duffey E. & A. S. Watt (ed.): The Scientific Management of Animal and Plant Communities for Conservation. Blackwell Scientific Publications, p. 241–269.
Frankland, B., M.R. Bartley & D.H.N. Spence, 1987. Germination under water. In: R.M.M. CRAWFORD: Plant life in aquatic and amphibious habitats. Vol. 5. Blackwell Scientific Publications, Oxford. 167-177.
Garver, E.G., D.R. Dubbe, & D.C. Pratt, 1988. Seasonal patterns in accumulation and partitioning of biomass and macronutrients in Typha spp. Aquatic Botany 32: 115-127.
Georgiev, G., W. Theuerkorn, M. Krus, R. Kilian and T. Grosskinsky. 2013/2014. The potential role of cattail-reinforced clay plaster in sustainable building. Mires and Peat, Volume 13: 1–13. Available at: http://www.mires-and-peat.net/
Gopal, B. & K.P. Sharma, 1983. Light regulated seed germination in Typha angustata Bory et Chaub. Aquatic Botany, 16: 377-384.
Grace, J. B., 1983. Autotoxic inhibition of seed germination by Typha latifolia: an evaluation. Oecologia (Berlin) 59: 366-369.
Grace, J.B., 1984. Effects of tubificid worms on the germination and establishment of Typha. Ecology 65(5): 1689-1693.
Grace, J.B., 1985. Juvenile vs. adult competitive abilities in plants: size-dependence in cattails (Typha). Ecology 66(5): 1630-1638.
Grace, J.B., 1987. The impact of preemption on the zonation of two Typha species along lakeshores. Ecological Monographs 57: 283-303.
Grace, J.B. & J.S. Harrison, 1986. The biology of Canadian weeds. 73. Typha latifolia L., Typha angustifolia L. and Typha x glauca Godr. Canadian Journal of Plant Science 66: 361-379.
Grace, J.B. & R.G. Wetzel, l98lb. Phenotypic and genotypic components of growth and reproduction in Typha latfolia: experimental studies in marshes of differing successional maturity. Ecology 62: 789-801.
Grace, J.B. & R.G. Wetzel, l98lc: Habitat Partitioning and Competitive Displacement in Cattails (Typha): Experimental Field Studies. The American Naturalist 118 (4): 463-474.





Grace, J.B. & R.G. Wetzel, 1981a. Variations in growth and reproduction within populations of two rhizomatous plant species: Typha latifolia and Typha angustifolia. Oecologia 53:258-263.
Grace, J.B. & R.G. Wetzel, 1982. Niche differentiation between two rhizomatous plant species: Typha latifolia and Typha angustifolia. Canadian Journal of Botany 60: 46-57.
Grace, J.B. & R.G. Wetzel, 1998. Long-term dynamics of Typha populations. Aquatic Botany 61: 137-146
Grime, J.P., J.G. Hodgson & R. Hunt, 1988. Comparative plant ecology. A functional approach to common British species. London, UK: Unwin Hyman Ltd.
Gucker, C.L., 2008a. Typha latifolia. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: https://www.fs.fed.us /database/feis/plants/graminoid/typlat/all.html [2020, December 20].
Gucker, C. L., 2008. Phragmites australis. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: https://www.fs.fed.us /database/feis/plants/graminoid/phraus/all.html [2020, December 20].
Guppy, H.B, 1897. On the postponement of germination of seeds of aquatic plants. Proceedings of the Royal Society of Edinburgh 13: 344-359.
Gynophore, 2019, 21 mei. In: https://en.wikipedia.org/wiki/Gynophore.
Hayden, A., 1948. The status of revegetation of drained lakes in the Ruthven area in the second season of drainage. Iowa State University Cooperative Wildlife Research Unit Quarterly Report for the period of January-March, 1948: 4-7.
Haynes, R.J. & K.M. Goh, 1978. Ammonium and nitrate nutrition of plants. Biological Reviews 53: 465-510.
Heinz, S.I., 2012. Population biology of Typha latifolia L. and Typha angustifolia L.: establishment, growth and reproduction in a constructed wetland. PhD thesis. Technische Universität München.
Hewitt N. & K. Miyanishi, 1997. The role of mammals in maintaining plant species richness in a floating typha marsh in southern Ontario. Biodiversity and Conservation 6:1085-1102.
Hickman, J. C. (ed.), 1993. The Jepson manual: Higher plants of California. University of California Press. Berkeley, CA.
Holm, L.R., J. Doll, J. Holm, J.V. Pancho & J.P. Herberger, 1997. World Weeds: natural histories and distribution. John Wiley, New York.
Jalink, M.H. & A.J.M. Jansen 1996. Indicatorsoorten voor verdroging, verzuring en eutrofiëring van grondwaterafhankelijke beekdalgemeenschappen. Deel 2 uit de serie 'Indicatorsoorten'. Staatsbosbeheer/KNNV Uitgeverij, Driebergen/Zeist.
Jansen, A.J.M., 2000. Hydrology and restoration of wet heathland and fen meadow communities. Thesis, Rijksuniversiteit Groningen.
Kadlec, J.A. 1960. The effect of a drawdown on the ecology of a waterfowl impoundment. Michigan Department of Conservation, Game Division Report 2276.
Kaushik, D.K. 1963. The influence of salinity on the growth and reproduction of marsh plants. Unpublished Ph.D. thesis. Logan, Utah, Library, Utah State University.
Keddy, P.A. & T.H. Ellis, 1985: Seedling recruitment of 11 wetland plant species along a water level gradient: shared or distinct response? Canadian Journal of Botany 63: 1876-1879.
Keddy P.A., & A.A. Reznicek, 1986. Great lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. Journal of Great Lakes Research 12(1):25-36.
Kerner von Marilaun, A., 1895. The natural history of plants. Volume 2. Holt and Company. New York.
Kieskamp, A..A.M. & A.J.M. Jansen, 2017. Inrichtingsplan Grote Rietgat (Boetelerveld). Rapport, Unie van Bosgroepen, Ede.
Koerselman W. & A.F.M. Meuleman, 1996. The Vegetation N:P Ratio: a New Tool to Detect the Nature of Nutrient Limitation. Journal of Applied Ecology 33 (6): 1441-1450.
Köhn, N., 2016. Anzuchtversuch mit Typha latifolia und Typha angustifolia. Forschungspraktikum WS 2015/16. Bericht. University of Greifswald, Greifswald.
Kops, J., 1822. Typha angustifolia. Flora Batava, Part 4. Available at: https://wilde-planten.nl/kleinelisdodde.htm.
Kops, J. & Van der Trappen, J.E. (1849), Flora Batava, Part 10. Available at: https://wilde-planten.nl/grotelisdodde.htm).
Kramer, N. B. & F.D. Johnson. 1987. Mature forest seed banks of three habitat types in central Idaho. Canadian Journal of Botany 65: 1961-1966.
Krattinger, K., 1975. Genetic mobility in Typha. Aquatic Botany 1:57-70.
Lang, A., 1965. Effects of some internal and external conditions on seed germination. In: Encyclopedia of Plant Physiology, Vol. XV(2), Springer Verlag, Berlin, pp. 848-893.
Lang, J., D. Listl, P. Glaab, C. Reisch & P. Poschlod, 2014. Qualität und Keimungseigen-schaften von Saatgut in der Genbank WEL. Handbuch Genbank WEL, Hoppea, Denkschriften der Regensburgischen Botanischen Gesellschaft. Sonderband (2014): 99 – 132.

Leck, M.A. & K.J. Graveline, 1979. The seed bank of a freshwater tidal marsh. American Journal of Botany 66(9):1006-1015.

Leck, M.A. & R.L. Simpson, 1987. Seed bank of a freshwater tidal wetland: turnover and relationship to vegetation change. American Journal of Botany 74(3): 360-370. [66921]

Lesson 11 Fruit morphology Flashcards | Chegg.com. (z.d.). www.chegg.com. Retrieved 21 December 21, 2020. https://www.chegg.com/flashcards/r/1368108.

Lieffers, V.J., 1983. Growth of Typha latifolia in boreal forest habitats, as measured by double sampling. Aquatic Botany 15: 335-348.

Lombardi, T., T. Fochetti, A. Bertacchi, & A. Onnis, 1997. Germination requirements in a population of Typha latifolia. Aquatic Botany 56: 1 – 10.

Lynch, J.J., T. O'Neil and D. W. Lay, 1947. Management significance of damage by geese and muskrats to Gulf Coast marshes. Journal of Wildlife Management 11: 50-76.

Marsh, L, C.1962. Studies in the genusTypha. Ph.D. dissertation. Syracuse University, New York.

Mayer, A. M., and A. Poljakoff-Mayber, 1989. The germination of seeds. Fourth edition. Pergamon, New York, New York, USA.

McNaughton, S. J., 1966. Ecotype function in the Typha community-type. Ecological Monographs, Vol. 36 (4): 297-325.

Meara, M.L., 1957. The fats of higher plants. In: Encyclopedia of Plant Physiology, Vol. VII, Springer Verlag, Berlin, pp. 10-49.

Miao, S.I., S. Newman, F.H. Sklar, 2000. Effects of habitat nutrients and seed sources on growth and expansion of Typha domingensis. Aquatic Botany 68 (2000) 297–311.

Miklovic, Stefanie, 2000. Typha angustifolia Management: Implications for Glacial Marsh Restoration. University of Minnesota, Department of Horticultural Science. Retrieved from the University of Minnesota Digital Conservancy, http://hdl.handle.net/11299/59714.

Millar, J.B., 1976. Wetland classification in Western Canada: A guide to marshes and shallow open water wetlands in the grasslands and parklands of the prairie provinces. Report Series No. 37. Canadian Wildlife Service, Environment Canada, Ottawa, Ontario.

Mitich L.M., 2000. Common cattail, Typha latifolia L. Weed Technology, 14(2):446-450.

Morinaga, Toshito. 1926a. The favorable effect of reduced oxygen upon the germination of seeds. American Journal of Botany 13: 159-165.

Morinaga, Toshito. 1926b. Effect of alternating temperatures upon the germination of seeds. American Journal of Botany 13: 141-158.

Mortimer, C.H. ,1971. Chemical exchanges between sediments and water in the Great Lakes-speculation on probable regulatory mechanisms. Limnology and Oceanography16: 387-404.

Morton, J.F., 1975. Cattails (Typha spp.) - Weed problem or potential crop? Economic Botany 29: 7-29.

Müller-Sämann, K.M., G. Reinhardt, R. Vetter & S. Gärtner, 2003. Anhang zu Nachwachsende Rohstoffe in Baden-Württemberg: Identifizierung vorteilhafter Produktlinien zur stofflichen Nutzung unter besonderer Berücksichtigungumweltgerechter Anbauverfahren. FZKABWPLUS Research Report, Müllheim. Available at: http://www.ifeu.de/index.php?bereich=lan&seite=nawa_bawue.

Murphy, K., 2007. Datasheet Typha angustifolia (lesser bulrush). Available at: http://www.cabi.org/isc/datasheet/54294.

Oberdorfer, E., 1983. Pflanzensociologische Excursionsflora. 5th edition. Verlag Eugen Ulmer, Stuttgart.

Olson A.P.J. & J.R. Freeland, 2009. Habitat preferences of cattail species and hybrids (Typha spp.) in eastern Canada. Aquatic Botany 91 (2): 67-70.

Oudemans, C.A.J.A., 1862. Natuurlijke historie van Nederland. De Flora van Nederland deel III. A.C. Kruseman, Haarlem.

Parts of Flowers - Flower Anatomy 101. (n.d.). Floweraura. Retrieved December 19, 2020. https://www.floweraura.com/blog/parts-of-flowers-flower-anatomy-101

Patrick, W.H.Jr. & Khalid, R.A. 1974. Phosphate release and sorption by soils and sediments: effect of aerobic and anaerobic conditions. Science 186: 53-55.

Penfound, W.T. & E.S. Hathaway, 1938. Plant Communities in the Marshlands of Southeastern Louisiana. Ecological Society of America , Ecological Monographs, Vol. 8 (1): 1-56.

Phytochrome. (2020, December 06). Retrieved December 19, 2020. In Wikipedia. https://en.wikipedia.org/wiki/Phytochrome

Pojar, J. & A. MacKinnon (eds.), 1994. Plants of the Pacific Northwest coast: Washington, Oregon, British Columbia and Alaska. Lone Pine Publishing, Redmond, WA.

Poschlod, P. & A.K. Jackel, 1993. Untersuchungen zur Dynamik von generativen Diasporenbanken von Samenpflanzen in Kalkmagerrasen. I. Jahreszeitliche Dynamik des Diasporenregens und der Diasporenbank auf zwei Kallanagerrasenstandorten der Schwäbischen Alb. Flora 188: 49-71.

Pratt, D.C., D.R. Dubbe, & E.G. Garver, 1985. Wetland biomass production. Energy from Biomass in Minnesota - Part I. Minnesota Department of Energy and Economic Development, 1985, pp. 1-35.





Process of Seed Germination: 5 Steps (With Diagram). (2015, October 26). Retrieved December 19, 2020, from http://www.biologydiscussion.com/seed/germination/process-of-seed-germination-5-steps-with-diagram/15769

Prunster, R.W., 1941. Germination conditions for Typha Muelleri (Bohrbach) and its practical significance in irrigation channel maintenance. Journal of the Council for Scientific and Industrial Research, Australia 14: 129-136.

Remmelzwaal, A.J. & R.S. Verheule, 1999. De vestiging van Riet in de Randmeren. De Levende Natuur 100 (2): 58-61.

Rivard, R.G. & R.M. Woodard, 1989. Light, ash, and pH effects on the germination and seedling growth of Typha latifolia (cattail). Canadian Journal of Botany 67:2783-2787.

Sculthorpe, C.D., 1967. The Biology of Aquatic Vascular Plants. Edward Arnold, London.

Sharma, K.P., 1977. Studies on dry matter production, nutrient turnover and ecology of Typha species with reference to wetland management. Ph.D. Thesis, University of Rajasthan, Jaipur.

Sharma, K.P. & B. Gopal, 1978. Seed germination and occurrence of seedlings of Typha species in nature. Aquatic Botany, 4: 353-358.

Sharma, K.P. & B. Gopal. 1979a. Effect of light intensity on seedling establishment and growth in Typha angustata Bory and Chaub. Polish Archives of Hydrobiology 26: 495- 500.

Sharma, K.P. & B. Gopal. 1979b. Effect of water regime on the growth and establishment of Typha angustata seedlings. International Journal of Ecology and Environmental Science 5: 69-74.

Shay, J.M., & C.T. Shay, 1986. Prairie marshes in western Canada, with specific reference to the ecology of five emergent macrophytes. Canadian Journal of Botany 64: 443 -454.

Schenk, M. & J. Wehrmann, 1979. The influence of ammonia in nutrient solution on growth and metabolism of cucumber plants. Plant and Soil 52(3): 403-414. doi:10.1007/BF02185583

Shih, J.G. & S.A. Finkelstein, 2008. Range dynamics and invasive tendencies in Typha latifolia and Typha angustifolia in eastern North America derived from herbarium and pollen records. Wetlands 28 (1): 1-16

Sifton, H. B. 1959. Germination of light sensitive seeds of Typha latifolia. Canadian Journal of Botany 37: 719-739.

Smith, S.G., 1967. Experimental and natural hybrids in North America Typha (Typhaceae). The American Midland Naturalist 78: 257-287.

Snyder, S. A., 1993. Typha angustifolia. In: Fire Effects Information System, [Online].

U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available at: https://www.fs.fed.us/database/feis/plants/graminoid/typang/all.html.

Sojda, R.S. & , K.L. Solberg, 1993. Management and Control of Cattails. Fish and Wildlife Leaflet 13. United States Department of the Interior, Fish and Wildlife service, Washington, D.C. Available as:: https://www.nwrc.usgs.gov/wdb/pub/wmh/13_4_13.pdf.

Soons, M.B. & W.A. Ozinga, 2005. How important is long-distance seed dispersal for the regional survival of plant species? Diversity and Distributions 11(2):165-172.

Stace, C., 1997. New flora of the British Isles. - Cambridge (Cambridge University Press).

Stark, K. E., A. Arsenault & G.E. Bradfield, 2006. Soil seed banks and plant community assembly following disturbance by fire and logging in interior Douglas-fir forests of south-central British Columbia. Canadian Journal of Botany 84(10): 1548-1560.

State of Queensland, Department of Agriculture and Fisheries, 2020 Cumbungi (bullrush or cat's tail) Typha species factsheet. unpaginated. Available at: www.dpi.qld.gov.au/documents/Biosecurity_EnvironmentalPests/IPA-Cumbungi-PP43.pdf.

Stevens, M. & C. Hoag, 2003. Plant Guide. Broad-leaved cattail Typha latifolia L.

USDA NRCS National Plant Data Centre & Idaho Plant Materials Centre. Available at: https://plants.usda.gov/plantguide/pdf/cs_tyla.pdf.

Stewart, H., S.L. Miao, M. Colbert & C.E. Carraher Jr., 1997. Seed germination of two cattail (Typha) species as a function of Everglades nutrient levels. Wetlands, 17 (I): 116-122.

Strickler, G. S. & P.J. Edgerton, 1976. Emergent seedlings from coniferous litter and soil in eastern Oregon. Ecology 57: 801-807.

Stuckey, R. L. & D. P Salamon, 1987. Typha angustifolia in North America: A foreigner masquerading as a native. Proceedings of the Ohio Academy of Science. Ohio Academy of Science, Columbus USA.

Strykstra, R.J., R.M Bekker & J.P. Bakker, 1998. Assessment of dispersule availability: its practical use in restoration management. Acta Botanica Neerlandica 47: 57-70.

Summerhayes, V.S. & W.B. Turrill, 1948. Vegetation after draining. Nature 161: 421.

Ter Heerdt, G.N.J. & H.J. Drost, 1994. Potential for the development of marsh vegetation from the seedbank after a drawdown. Biological Conservation 67: 1-11.

Thompson K. & Grime J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67: 893–921.

Tu, M., J.H. Titus, S. Tsuyuzaki & R. del Moral, 1998. Composition and dynamics of wetland seed banks on Mount St. Helens, Washington, USA. Folia Geobotanica 32(1): 3-16.

Van der Valk, A. G. & C. B. Davis, 1976. The seed banks of prairie glacial marshes. Canadian Journal of Botany 54: 1832-1838.

Van Wirdum, G. 1979. Trophiegradiënten in een kraggenlandschap. H2O 12(3): 46-57.

Watson, L., & M.J. Dallwitz, 1992 onwards. The families of Flowering Plants: descriptions, illustrations, identification, and information retrieval. Version: 27th November 2020. delta-intkey.com'.

Weeda, E.J., R. Westra, Ch. Westra & T. Westra,1994. Ecologische flora. Wilde Planten en hun relaties 5. IVN, Amsterdam.

Weeda, E.J., J.H.J. Schaminée & R. van 't Veer, 1996. 8. Phragmitetea. In: J.H.J. Schaminée, E.J. Weeda & V. Westhoff: De vegetatie van Nederland 2: wateren, moerassen en natte heiden. Opulus Press, Uppsala/Leiden. p. 161-220.

Weller, M.W. 1975. Studies of Cattail in Relation to Management for Marsh Wildlife. Iowa State Journal of Research 49:383-412.

Wesson, G. & P.F. Waring. 1969. The role of light in germination of naturally occurring populations of buried weed seeds. Journal of Experimental Botany 20: 402-413.

Wichtmann, W., C. Schröder & H. Joosten (eds.), 2016. Paludiculture – productive use of wet peatlands. Climate protection – biodiversity – regional economic benefits. Schweizerbart Science Publishers, Stuttgart.

Wichtmann,. W. & J.H.J. Joosten, 2007. Paludiculture: peat formation and renewable resources from rewetted peatlands. IMCG-Newsletter 2007(3): 24-28.

Wienhold, C.E. & A.G. van der Valk, 1989. The impact of duration of drainage on the seed banks of northern prairie wetlands. Canadian Journal of Botany. 67(6): 1878-1884.

Wilson, K.A., 1955. Experimental marsh management near Currituck, North Carolina. North Carolina Wildlife Resources Commission. Project report W~6-R.

Wilton, D., 1951. US2984940A - Method of treating and planting cattail seeds. Retrieved December 20, 2020, from https://www.google.ch/patents/US2984940

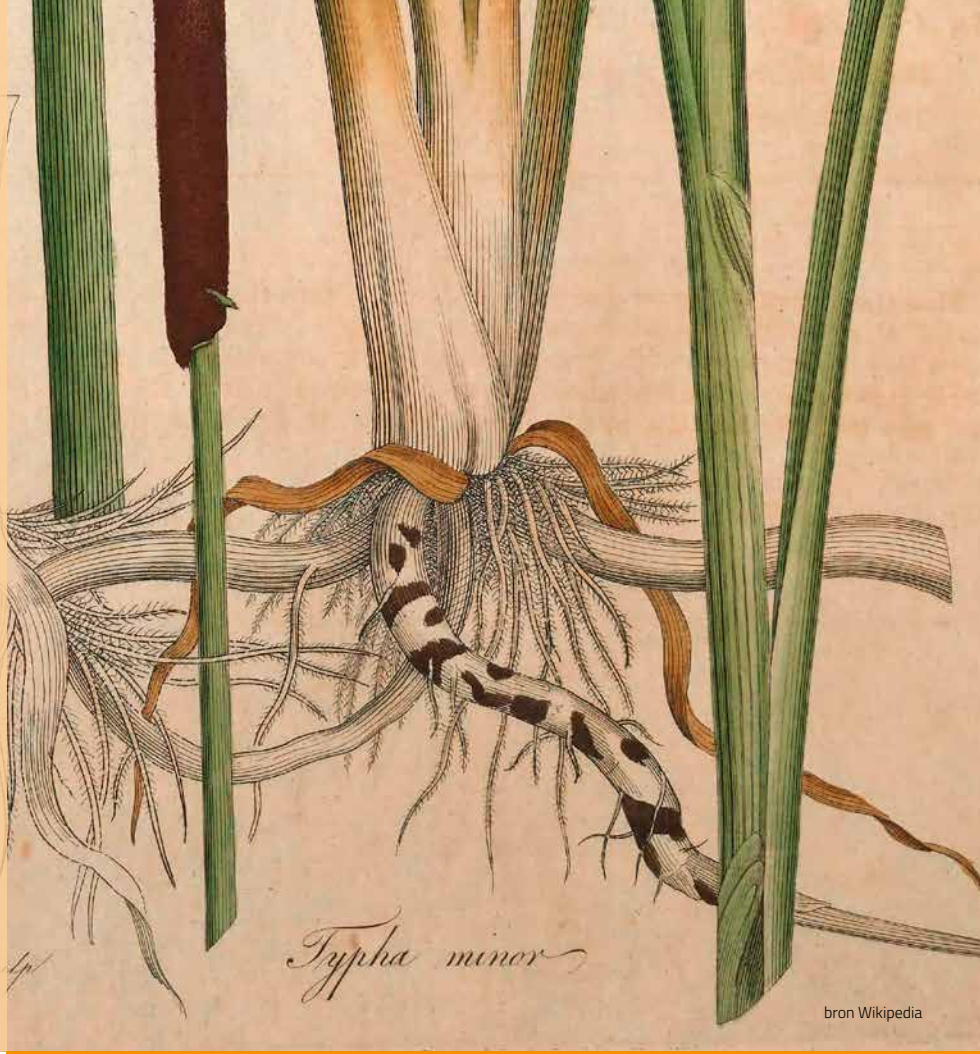
Yeo, R. R., 1964. Life History of Common Cattail. Weeds 12 (4 ): 284-288.



Paludiculture, or the agricultural and silvicultural use of wet and rewetted peatlands, might be an important contribution to climate proof agriculture and forestry. These wetlands can remain productive in an alternative way without the negative effects of drainage such as biodiversity loss, peat soil degradation and subsidence, increased greenhouse gas emissions and catastrophic peat fires. Cattail (Typha) is one of the economically valuable crops that can be cultivated in paludiculture and used, for example, as building material for insulation, for energy generation, and for wastewater treatment in constructed wetlands. Since planting Typha is expensive, sowing is seen as an efficient alternative, but germination and seedling survival rates are highly variable. This book reviews the existing scientific literature on the environmental factors affecting the germination of Typha species and discusses the implications for paludiculture.

**About the author**

Dr. André J.M. Jansen is a landscape ecologist who studies the hydrological processes that determine the occurrence of vegetation at the scale of the landscape. He investigates how wetland ecosystems can be functionally restored under modern conditions. Paludiculture can make an important contribution to this. This book is a result of a study during his sabbatical at the Greifswald Mire Centre.




bron Wikipedia

Stichting Bargerveen
Stichting Bargerveen
Toernooiveld 1
6525 ED Nijmegen
www.stichting-bargerveen.nl

GREIFSWALD MIRE CENTRE
Greifswald Mire Centre
Ellernholzstr. 1/3
17489 Greifswald (Germany)
greifswaldmoor.de

Bosgroepen
Unie van Bosgroepen
Bennekomseweg 43, 6717 LL Ede
Postbus 8187, 6710 AD Ede
bosgroepen.nl