Germination Ecology of *Carex* (Cyperaceae): Effects of light, stratification, and soil moisture

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Abstract

Congeneric species occupying different habitats might be expected to have different seed dormancy strategies and germination requirements while those growing in the same habitats may be more similar. I tested this hypothesis with a broad survey of the germination of 51 *Carex* species from mesic deciduous forests, wet deciduous forests, and wetland or seasonally flooded areas in response to different controlled environmental conditions. A canonical discriminant analysis based on the responses of 29 species to various treatments showed clear differences among seeds from each habitat with respect to germination behaviour. Germination of seeds from mesic deciduous forest species was generally faster after moist stratification than after either submersion or dry storage. In seeds from most wet areas of deciduous forest, wetland, or seasonally flooded habitats, germination was similar or greater after submerged as compared to moist stratification. Total germination was significantly increased by light in all species except *Carex pedunculata*, an ant-dispersed species. Germination was not significantly different on a poorly drained peat soil than on a well-drained sandy loam. Seeds of most species were at least physiologically dormant at maturity and germination of fresh seeds was generally low. Spring germination was similar among species from all habitats and generally began in late May or early June, at fairly high temperatures (min 7°C, max 17°C), which is unusual for forest species but consistent among *Carex* species.

Résumé

Les espèces congenères qui proviennent de différents habitats pourraient différer en tant que stratégies de dormance de leurs graines et d'exigences en tant de germination plus que celles qui proviennent d'habitats semblables. Cette hypothèse a été vérifié en examinant la germination de 51 espèces de *Carex* provenant des forêts à feuilles caduques mésoïques et hydriques et d'habitats ouverts et hydriques sous plusieures conditions environnementales. Une analyse canonique de fonction discriminante basée sur les réactions à plusieurs traitements de 29 espéces démontra des différences précises entre les graines de différents habitat par rapport à leur germination. La germination de graines d'espèces des forêts à feuilles caduques mésoïques était généralement plus vite après une periode de stratification humide qu'après la stratification inondée ou l'entreposage sec. Pour les graines de la plupart des espèces qui proviennent des forêts caduques humides, des zones aquatiques, ou des zones inondables en saison, la germination était semblable ou supérieure après la stratification inondée à comparé à la stratification humide. La lumière a eu des effets positifs sur la germination de toutes les espèces sauf *Carex pedunculata*, une espèce dispersée par les fourmis. La germination sur un sol tourbeux inondé n'a pas différé d'une manière significative á celle sur un sol sablonneux. L'humidité du sol n'a pas eu d'effet. Les graines fraîches de la plupart des espèces ont germé très peu et très lentement. La germination printannière a été semblable à travers les espèces de tous habitats et en général a commencé à la fin mai ou tôt en juin à des températures assez élevées (min. 7°C, max. 17°C), ce qui est peu commun pour les espèces de forêts mais plus commun pour les espèces de *Carex*.

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Literature Review

It is widely accepted that successful seedling establishment depends on a seed's ability to germinate when its likelihood of survival is greatest (Angevine and Chabot, 1979; Fenner, 1985; Baskin and Baskin, 1998). The 'best' period for germination is often defined by the hazards or restrictions associated with a given habitat. The nature of these hazards and restrictions is reflected in the environmental cues that alter states of dormancy and promote or inhibit germination in seeds from that habitat. (A dormant seed is defined as unable to germinate under any conditions, a non-dormant seed will germinate under the widest range of conditions (i.e., of temperature, light, etc.) possible for that seed, and a conditionally dormant seed will germinate under a more restricted set of conditions than when it is nondormant (Baskin and Baskin, 1998).) This influence is particularly evident in seeds from deciduous forests and wetlands (Baskin and Baskin, 1988).

In northern deciduous forests, seeds of most species germinate in the brief period in the spring when the snow has melted but the canopy cover is still undeveloped (Roberts, 1986; Baskin and Baskin, 1988). Seeds of these species usually require cold-stratification to break dormancy but will germinate at fairly low temperatures once stratified (Baskin and Baskin, 1988, 1998). In neighbouring wetlands, germination usually coincides with the drawdown of spring flood waters (Harris and Marshall, 1963; Meeks, 1969; Schneider, 1994). Stratification differs here because it often occurs under flooded conditions, and while dormancy release in other habitats is generally an aerobic process (Bewley and Black, 1994), in some wetland or shoreline species such as *Carex comosa* (Baskin et al., 1996) and *Saponaria officinalis* (Lubke and Cavers, 1969), dormancy loss occurs under anaerobic conditions. Light requirements are also more frequent among wetland seeds (Baskin and Baskin, 1998) and may work in conjunction with fluctuating temperature requirements as a soil/water depth-sensing mechanism (Thompson et al., 1977; Thompson and Grime, 1983; Bliss and Smith, 1985; Pons and Schröder, 1986). Finally, seed germination may also be influenced by soil water potential, and threshold levels of imbibition for germination are species-specific (Manohar and Heydecker, 1964; Dasberg and Mendel, 1971). Some species of dry habitats, such as *Rumex crispus*, are more tolerant of low water potentials during germination than wetland species (Evans and Etherington, 1990). Submerged conditions often promote germination in seeds of many wetland species but this has been attributed to the anaerobic environment rather than to a particularly wet one (Moringa, 1926; Esashi and Ohhara, 1977; Pons and Schroeder, 1986).

On the basis of these findings, seeds from north-temperate wetlands and forests may be expected to behave quite differently with regard to stratification, light, temperature, and soil moisture. However, germination strategies are not solely influenced by habitat. Aspects of seed size (Grime et al., 1981; Venable and Brown, 1988; Pons, 1992), seed dispersal mechanism (Rees, 1993; Rees, 1996), plant phenology (Baskin and Baskin, 1988), plant lifespan (Shipley and Parent, 1991; Rees, 1996), phylogeny (Mirov, 1936; Baskin and Baskin, 1998), life history (Whitmore, 1989), and maternal environment (Gutterman and Heydecker, 1973; Orozco-Segovia et al., 1993), among others, also play a role. Therefore, cross-habitat comparisons are difficult when species with various lifespans, seed dispersal mechanisms, etc. are studied together.

In an attempt to minimize the effects of at least some of these other influences, certain researchers have focused on the germination syndromes of several populations of a single species, such as *Danthonia sericea* (Lindauer and Quinn, 1972), *Chenopodium bonus-henricus* (Dorne, 1981), *Carex lyngbyei* (Hutchinson and Smythe, 1986), *Linum perenne* (Meyer and Kitchen, 1994) and *Bromus tectorum* (Beckstead et al., 1996), or several species within one genus, such as *Dioscorea* (Okagami and Kawai, 1982) and *Penstemon* (Meyer et al., 1995), or family, such as the Caryophyllaceae (Thompson, 1968) growing in different habitats. In these examples, phylogenetic, life-history, lifespan, and/or seed-dispersal influences were minimized. While studies by Naylor and Abdalla (1982), Meyer and Kitchen (1994), and Meyer et al. (1995), included 18, 21, and 135 collections, respectively, those of Thompson (1968) and Okagami and Kawai

(1982) included only 9 and 6 collections, respectively. Because the factors which influence germination are numerous, conclusions based on so few collections are uncertain. Furthermore, Thompson's (1968) work is based on a collection of both annuals, biennials, and perennials that could have potentially confused or created the patterns observed. A comparison of germination behaviours across habitats therefore, would ideally include several populations of one species or several species in one genus that span a wide range of habitats. If several species are used, they should be ecologically similar within their respective habitats to minimize differences in growth form, life history, and lifespan.

The *Carex* genus is particularly well suited to such a congeneric cross-habitat survey of germination behaviour because it includes more than 2000 species worldwide, all of which are herbaceous and perennial, and the genus is an important component of the flora in several habitats (Bernard, 1990). Therefore, aspects of phylogeny, growth form, and lifespan are minimized.

The germination responses of approximately 60-70 *Carex* species have been studied, most of which are European. Dormancy at dispersal is common among species tested and is usually removed by dry storage or stratification (Grime et al., 1981; Schütz, 1997a, 1998, 1999). Seeds of almost all species are positively photoblastic (Amen and Bonde, 1964; Georges and Lazarre, 1983; Haggas et al., 1987). Temperature requirements are frequently high (Grime et al., 1981; Kibe and Masuzawa, 1994; Schütz, 1998) and germination (especially dark germination) is stimulated by fluctuating temperatures (McDonough, 1970; Schütz 1997a, b, 1998, 1999). There are also reports of scarification requirements (e.g., *Carex albonigra* (Amen and Bonde, 1964), *C. kobomugi* (Ishikawa et al., 1993), and *C. raynoldsii* (Johnson et al., 1965)) but these are less common.

Introduction

Despite the shared hazards faced by species of a given habitat, rarely can that habitat be characterized by a specific germination syndrome (Mirov, 1936; Bliss, 1958; Grime et al., 1981; Keddy and Ellis, 1984; Baskin and Baskin, 1988; Van Tooren and Pons, 1988; Washitani and Masuda, 1990; Pons, 1991b; Shipley and Parent, 1991; Leishman and Westoby, 1992). Other factors, such as seed size (Grime et al., 1981; Venable and Brown, 1988; Pons, 1992) or plant phenology (Baskin and Baskin, 1988), may influence the likelihood of seedling survival and therefore the seed's responses to various stimuli. Other factors not directly related to seed survival, such as phylogeny, may also play a role (Mirov, 1936; Baskin and Baskin, 1998). Consequently, detecting the influence of habitat on seed germination behaviour requires that the variation in other factors be minimized. The most logical approach is therefore to study several populations of one species or several species in one genus that range widely in habitat. As previously mentioned, the genus *Carex* is particularly well suited to such a comparison as it is the most species-rich genus in North America, is composed exclusively of perennial herbs, and occurs in a wide range of habitats (Bernard, 1990).

The overall objective of my project was to test the hypothesis that *Carex* species occupying different habitats have different seed dormancy strategies and germination requirements while those growing in the same habitat are more similar. I tested this hypothesis with a broad survey of the responses of 51 *Carex* species from deciduous forest and periodically flooded or wetland habitats to different controlled environmental conditions.

Most seeds were collected from locations in southern Québec, with additional sites in Alaska, Yukon, and Nova Scotia (see Materials and Methods). Habitats included mesic deciduous forests, wet deciduous forests, and wetland or seasonally flooded areas, such as shorelines. As previously mentioned, deciduous forests and wetlands are particularly good examples of habitats that can be characterized by some general germination behaviours. These behaviours may be expected to contrast on the basis of responses to stratification, light, temperature, and soil moisture.

The first objective of my project was to compare the effects of dry storage, moist stratification, and submerged (flooded) stratification on *Carex* germination. My hypotheses were that 1) seeds of wetland *Carex* species are able to undergo dormancy loss under submerged (i.e., anaerobic) conditions but those of mesic habitats require the aerobic conditions of moist stratificaiton, and 2) the afterripening effects of dry storage observed in seeds of other *Carex* species are also present in North American *Carex* species. Afterripening is defined as metabolic changes that result in loss of dormancy, specifically in this instance at room temperature. I also tested the effects of light and soil moisture on germination. Response to light was not expected to vary since germination of all *Carex* species previously studied, but one (*Carex flacca*: Taylor, 1956), were reported to be promoted by light (Baskin and Baskin, 1998). With respect to soil moisture, I tested the hypothesis that seeds of species from wetland habitats have greater and faster germination on a wet, peat substrate than on a well-drained sandy loam substrate. Also, the seasonality of germination outdoors was observed in fresh and overwintered seeds. Freshly ripened (non-stratified) seeds were not expected to germinate in the year of dispersal. Overwintered (stratified) seeds of species from forested habitats were expected to germinate before those from wetland habitats because of a lower temperature threshold for germination. Given the number of species required for this cross-habitat comparison, aspects of temperature could not be directly addressed. A separate experiment, in which seeds were planted in Pro-mix (often used in the germination of garden seeds) and kept under good conditions in a greenhouse, was conducted to test the germinability of seeds after 3-5 months of dry storage. The responses of the studied species to this array of stimuli should reveal any differences in dormancy and germination among carices from different habitats.

Materials and Methods

Seed collections. *Carex* diaspores, hereafter referred to as seeds, are trigonous or lenticular single-seeded nutlets surrounded by a perigynium (≈bract). Seeds were collected over two growing seasons:

Year 1: Seeds of 51 *Carex* species (Table 1) were collected in the field between June 01, 1996 and September 02, 1996 in southwestern Québec, Alaska, Yukon, and Nova Scotia (Table 2). I stored all seeds air-dry in paper envelopes at room temperature (20 ± 6°C) until planting. These seeds were used in the Overwintered Lath House, Dormancy Check Greenhouse, and Main experiments described below. However, because of varying amounts of available seed, not all species were included in the Main experiment (Table 3).

Year 2: Seeds of 33 *Carex* species (Tables 1 and 2) were collected in the field in southwestern Québec between June 01, 1997 and September 11, 1997. I stored the seeds for an average of 5-6 days next to, but not touching, a wet sponge in an opaque green tupperware container until planting. The second year's collections represent a subset of the first year's and I used the same collection sites except for *Carex debilis* (Table 2). I used the second year's seeds in the Fresh Seed Greenhouse and Fresh Seed Lath House experiments described below, except *Carex lupulina* which was not included in the latter experiment (Table 3).

I deposited voucher specimens of the source plant and/or a seedling grown during these experiments in the McGill University Herbarium except for *Carex backii*, *C. debilis* (from Ste-Agathe, Québec), *C. michauxiana*, and *C. plantaginea*. The seedlings of these plants died before the plants were large enough to make voucher specimens.

Terminology. In all experiments, I defined germination as protrusion of the *coleoptile* because all seeds were germinated on soil (or a peat-based medium) therefore making it difficult to observe protrusion of the coleorhiza consistently. I defined the time from planting until onset of germination, hereafter termed *lag*, as the period of time from planting until halfway between the census time when the first germinant was observed and the previous census time. I defined the period

Table 1. *Carex* species name with authority, taxonomic section, and typical habitat for all species used in the experiment. Typical habitat is based on Gleason and Cronquist (1991) and Fernald (1950).

***Carex* species**	**Section**	**Typical Habitat**
C. albursina Sheldon	*Laxiflorae*	Rich woods, especially calcareous
C. appalachica J.M. Webber & P. Ball	*Phaestoglochin*	Well-drained open forest and forest margins
C. aquatilis Wahlenb.	*Phacocystis*	Shallow water, wet soil
C. arctata W. Boott	*Hymenochlaenae*	Moist, rich woods
C. aurea Nutt.	*Bicolores*	Moist or wet places
C. backii F. Boott	*Phyllostachys*	Woods and thickets
C. bebbii (L. H. Bailey) Fern.	*Ovales*	Wet meadows and shores
C. bromoides Willd.	*Deweyanae*	Wet woods, swamps, and bogs
C. canescens L.	*Glareosae*	Swamps and bogs
C. capitata L.	*Capitatae*	Swamps and bogs
C. cephaloidea (Dewey) Dewey	*Phaestoglochin*	Dry woods and thickets
C. communis L. H. Bailey	*Acrocystis*	Deciduous woods
C. crinita Lam.	*Phacocystis*	Wet woods and swales
C. debilis Michx.	*Hymenochlaenae*	Moist, rich woods
C. deweyana Schwein.	*Deweyanae*	Open forest, streambanks, clearings
C. disperma Dewey	*Dispermae*	Bogs, wet woods, shade
C. echinata Murray	*Stellulatae*	Swamps, bogs, and wet places
C. flava L.	*Ceratocystis*	Bogs and wet meadows
C. gracillima Schwein.	*Hymenochlaenae*	Woods
C. gynandra Schwein.	*Phacocystis*	Woods and swales
C. hirtifolia Mackenzie	*Halleranae*	Woods

Table 1 cont'd.

***Carex* species**	**Section**	**Typical Habitat**
C. incurva Lightf.	*Foetidae*	Lakeshore
C. intumescens Rudge	*Lupulinae*	Moist/wet woods
C. kelloggii W.Boott.	*Phacocystis*	Shallow water, wet soil
C. laxiflora Lam.	*Laxiflorae*	Dry to mesic woods
C. leptalea Wahlenb.	*Polytrichoidae*	Bogs and wet soil
C. lupulina Muhl.	*Lupulinae*	Moist to wet woods, meadows, and marshes
C. lurida Wahlenb.	*Vesicariae*	Swamps, wet meadows and woods
C. michauxiana Boeckeler	*Folliculatae*	Bogs and wet meadows
C. normalis Mackenzie	*Ovales*	Open swamps and wet meadows
C. norvegica Retz.	*Atratae*	Streambanks, seepage areas, moist meadows
C. novae-angliae Schwein.	*Acrocystis*	Moist woods
C. pauciflora Lightf.	*Leucoglochin*	Sphagnum bogs
C. paupercula Michx.	*Limosae*	Acid swamps and sphagnum bogs
C. pedunculata Muhl.	*Clandestinae*	Rich woods, usually calcareous soil
C. plantaginea Lam.	*Careyanae*	Rich moist woods
C. platyphylla Carey	*Careyanae*	Woods
C. prasina Wahlenb.	*Hymenochlaenae*	Moist, wet woods and streambanks
C. projecta Mackenzie	*Ovales*	Wet woods and meadows
C. rosea Schk.	*Phaestoglochin*	Mesic to wet woods
C. rugosperma Mackenzie	*Acrocystis*	Dry to moist soil in shade or sun
C. saxatilis L.	*Vesicariae*	Fens, wet meadows

Table 1 cont'd.

***Carex* species**	**Section**	**Typical Habitat**
C. scabrata Schwein.	*Anomalae*	Moist shaded ground and swamps
C. scoparia Schk.	*Ovales*	Open swamps, wet meadows and shores
C. sitchensis Prescott	*Phacocystis*	Fens, swamps, marshes, wet meadows, lakeshores
C. sprengelii Dewey	*Hymenochlaenae*	Open woods, meadows
C. stipata Muhl.	*Vulpinae*	Wet, low ground
C. tenera Dewey	*Ovales*	Moist or wet soil, meadows, and thickets
C. tribuloides Wahlenb.	*Ovales*	Wet woods and meadows
C. trisperma Dewey	*Glareosae*	Sphagnum bogs, wood edges
C. vulpinoidea Michx.	*Multiflorae*	Marshes and wet low places

Table 2. *Carex* seed collections sorted by collection site: collection dates for 1996 and 1997; dry seed weights (perigynium removed, average of 58-300 seeds) for 1996 seeds except where only 1997 collections were made; co-ordinates in latitude and longitude; and collection locations and habitats. Seeds from the Gault Estate species were collected from various places on the mountain and bulked so dates and co-ordinates are approximate. n.a.= not available.

Gault Estate: Mont St-Hilaire, Québec					
***Carex* species**	**1996 coll'n**	**1997 coll'n**	**Sd Wt (mg)**	**Co-ordinates**	**Collection location / habitat**
C. albursina	Jun 27	Jun 30	2.550	45°33'N 73°10'W	SW slope of Burned Hill Peak. Slopes, moist forest.
C. appalachica	Jul 20	Jul 15	0.388	45°33'N 73°09'W-45°35'N 73°11'W	On the trails to Sunrise, Dieppe, and East Hill Peaks. Open forest, path edges.
C. arctata	Jun 23	Jun 25	1.188	45°32'N 73°09'W	Along road to Gault House.
C. backii	Jul 11	Jul 09	5.125	45°33'N 73°10'W	Unnamed trail branching left off trail to Burned Hill Peak. Dry steep slopes often associated with *Pinus* sp.
C. bromoides	Jun 22	Jul 01	0.330	45°32'N 73°09'W	Behind the dormitories. Wet woods.
C. cephaloidea	Jun 26	Jul 14	0.688	45°32'N 73°10'W	Next to the chlorination station in a roadside thicket.
C. communis	Jun 26	Jun 16	1.400	45°32'N 73°09'W	Behind the Research Station Building. Deciduous forest.
C. crinita	Jul 20	Jul 16	0.613	45°34'N 73°10'W	Pond on trail before Dieppe Peak. Wet open sites.
C. deweyana	Jul 03	Jul 16	0.975	45°32'N 73°09'W-45°35'N 73°10'W	Trail to Rocky Peak, trail to Burned Hill, trail to Dieppe, and Lake Hill Peaks. Open forest, clearings.
C. gracillima	Jun 30	Jun 24	0.763	45°32'N 73°09'W	Gault House Road. Roadsides.
C. gynandra	Jul 09	Jul 23	0.725	45°32'N 73°09'W-45°33'N 73°10'W	Trail on W side of Lac Hertel and along Gault House Road. Edge of water, ditches.
C. hirtifolia	Jun 25	Jul 01	n.a.	45°32'N 73°10'W	Near the Nature Centre. Moist, rich woods.
C. laxiflora	Jul 03	Jul 01	n.a.	45°32'N 73°09'W-45°33'N 73°10'W	Road to the research buillding and on the trail connecting the trails to Rocky and Sunrise Peaks. Woods.
C. pedunculata	Jun 01	Jun 11	1.213	45°33'N 73°10'W	Around the western portion of Lac Hertel. Moist rich maple woods.

Table 2 cont'd.

Gault Estate. Mont St-Hilaire, Québec cont'd					
***Carex* species**	**1996 coll'n**	**1997 coll'n**	**Sd Wt (mg)**	**Co-ordinates**	**Collection location / habitat**
C. plantaginea	Jun 08	Jun 17	1.925	45°32'N 73°10'W- 45°35'N 73°11'W	On the trail to Sunrise Peak near the junction with the trail to Rocky Peak. At the junction of the trail to Dieppe Peak with the one connecting to the Pain-de-Sucre Peak trail. SW of Burned Hill Peak. Rich moist maple-beech woods.
C. platyphylla	Jun 28	Jun 26	1.913	45°32'N 73°10'W	Unnamed trail branching left off trail to Burned Hill Peak. Dry gravel slopes, woods.
C. prasina	Jul 05	Jul 07	0.556	45°35'N 73°09'W	Along North Creek. Streambanks.
C. rosea	Jun 30	Jul 16	0.600	45°33'N 73°10'W	Along Gault House Road and at the Casse-Croûte. Mesic woods.
C. rugosperma	Jun 19	Jun 12	1.050	45°32'N 73°09'W	Behind the Research Station Building. Dry rocky, sunny.
C. scabrata	Jul 29	.	1.190	45°33'N 73°10'W	Botany Bay (embayment at W edge of Lake Hertel). Pond and lake edges.
C. sprengelii	Jun 20	Jun 30	1.563	45°33'N 73°10'W	Burned Hill Peak. Rock outcrops.
C. stipata	Jun 28	Jun 30	0.530	45°32'N 73°09'W	In the orchard NE of the Research Station Building. Wet roadsides and disturbed sites.

Hudson, Québec					
***Carex* species**	**1996 coll'n**	**1997 coll'n**	**Sd Wt (mg)**	**Co-ordinates**	**Collection location / habitat**
C. bebbii	Aug 30	.	0.155	45°27'N 74°09'W	End of Beach Rd. Moist to wet thicket.
C. lupulina	Aug 30	Sept 11	5.713	45°27'N 74°09'W	End of Beach Rd. Moist to wet thicket.
C. projecta	Aug 30	Sept 05	0.193	45°27'N 74°09'W	End of Beach Rd. Moist to wet thicket.
C. scoparia	Aug 30	.	0.187	45°27'N 74°09'W	End of Beach Rd. Moist to wet thicket.
C. tenera	Aug 30	Sept 05	0.207	45°27'N 74°09'W	End of Beach Rd. Moist to wet thicket.
C. tribuloides	Aug 30	.	0.213	45°27'N 74°09'W	End of Beach Rd. Moist to wet thicket.
C. vulpinoidea	Aug 30	Sept 05	0.230	45°27'N 74°09'W	End of Beach Rd. Moist to wet thicket.
C. normalis	Aug 30	Sept 05	0.181	45°27'N 74°09'W	End of Beach Rd. Moist to wet thicket.

Table 2 cont'd.

St-Lazare, Québec

Carex species	1996 coll'n	1997 coll'n	Sd Wt (mg)	Co-ordinates	Collection location / habitat
C. lurida	Aug 30	Sept 05	1.200	45°24'N 74°08'W	ca. 1km from Hwy 40, exit 22. Drainage ditch at end of Yearling Drive.

Parc du Mont-Tremblant, Québec.

Carex species	1996 coll'n	1997 coll'n	Sd Wt (mg)	Co-ordinates	Collection location / habitat
C. canescens	Jul 14	.	0.369	46°16'N 74°31'W	Two km inside secteur La Diable. Open wet forest/fen.
C. debilis	Jul 11	.	1.155	46°16'N 74°31'W	Just inside secteur La Diable. Along La Diable riverbank.
C. disperma	Jul 23	Aug 05	0.744	46°30'N 74°10'W	Hwy 3 close to lac des Cyprès. Wet cedar/fir forest with Sphagnum.
C. echinata	Jul 11	Aug 04	0.428	46°26'N 74°25'W	Hwy 2 east. Fen.
C. gynandra	.	Aug 04	0.938	46°16'N 74°31'W	Two km inside secteur La Diable. Roadside ditch with standing water.
C. intumescens	Jul 29	.	12.763	46°16'N 74°30'W	Just inside secteur La Diable. Bank of a small unnamed pond off of La Diable. Sandy soil.
C. leptalea	Jul 23	.	n.a.	46°30'N 74°10'W	Hwy 3 close to lac des Cyprès. Wet cedar/fir forest with sphagnum.
C. michauxiana	Jul 23	Aug 04	2.463	46°26'N 74°25'W	Hwy 2 east. Fen.
C. novae-angliae	Jul 17	.	0.507	46°16'N 74°31'W	Just inside secteur La Diable. In a meadow.
C. paupercula	Jul 11	.	0.953	46°26'N 74°25'W	Hwy 2 east. Fen.

Ste-Agathe-des-Monts, Québec

Carex species	1996 coll'n	1997 coll'n	Sd Wt (mg)	Co-ordinates	Collection location / habitat
C. debilis	.	Aug 15	n.a.	46°03'N 74°17'W	40th Avenue, 16km N on Hwy 329 from Ste-Agathe-des-Monts. Roadside and trailside in thicket.
C. trisperma	Aug 29	.	0.943	46°03'N 74°17'W	40th Avenue, 16km N on Hwy 329 from Ste-Agathe-des-Monts. Spruce forest-bog edge.

Table 2 cont'd.

Alaska

Carex species	1996 coll'n	1997 coll'n	Sd Wt (mg)	Co-ordinates	Collection location / habitat
C. aquatilis	Jul 16	.	0.256	59°16'N 135°34'W	Haines Hwy, 6.7 km N of Tesoro Gas station, Haines, Alaska. Marsh edge .
C. kelloggii	Jul 16	.	0.435	59°16'N 135°34'W	Haines Hwy., 6.7km N of Tesoro Gas station, Haines, Alaska. Marsh edge.
C. leptalea	Jul 16	.	0.969	59°17'N 135°41'W	Haines Hwy, 14.2 km N of Haines, Alaska. Drier edge of open, wet meadow.
C. norvegica	Jul 13	.	n.a.	63°40'N 141°04'W	31.9km NW of Beaver Creek bridge on Alaska Hwy km 2072.7. Edge of small pond.
C. pauciflora	Jul 24	.	0.573	58°24'N 134°38'W	Juneau, Alaska. Side road 0.5 km from Mendenhall Loop Rd., 0.8 km from Glacier Highway N of Juneau. Fen.
C. saxatlis	Jul 16	.	1.055	59°17'N 135°41'W	Haines Hwy, 14.2 km N of Haines, Alaska. Small embayment of Chilkat River.
C. sitchensis	Jul 20	.	0.353	56°35'N 132°45'W	Petersburg, Mitkof Island, Alaska. Ohmer Creek Trail, 37 km south of Petersburg. Marsh.

Yukon

Carex species	1996 coll'n	1997 coll'n	Sd Wt (mg)	Co-ordinates	Collection location / habitat
C. aurea	Jul 11	.	0.420	64°59'N 138°13' W	ca. 60 km N of Stewart Crossing on the Dempster Highway, Yukon. Gravel edge of small stream.
C. capitata	Jul 07	.	n.a.	63°55'N 135°49'W	Mount Haldane, Yukon. South McQuestern Rd. Small lake on N side of mountain. Edge of fen.
C. incurva	Jul 14	.	1.433	61°10'N 138°35'W	Kluane Lake, Yukon. Gravel bank on west shore.

Nova Scotia

Carex species	1996 coll'n	1997 coll'n	Sd Wt (mg)	Co-ordinates	Collection location / habitat
C. flava	Aug 28	.	n.a.	46°06'N 60°33W	New Harris Road, Victoria County, Nova Scotia. In roadside ditch and meadow adjacent to ditch.

Table 3. *Carex* species included in the following experiments: Overwintered Lath House (OLH), Dormancy Check Greenhouse (DCGH), Main, Fresh Seed Lath House (FSLH), and Fresh Seed Greenhouse (FSGH). Some species were subject to a subset of treatments (see text) because of lack of seed (√*). *Carex debilis* was collected in two different locations: Mont-Tremblant Park (1996) and Sainte-Agathe (1997).

Species	OLH	DCGH	MAIN	FSLH	FSGH
C. albursina	√	√	√*	√	√
C. appalachica	√	√	√	√	√
C. aquatilis	√	√	√		
C. arctata	√	√	√	√	√
C. aurea	√	√	√		
C. backii	√	√		√	√
C. bebbii	√	√	√*		
C. bromoides	√	√	√	√	√
C. canescens	√	√	√	√	√
C. capitata	√	√	√*		
C. cephaloidea	√	√	√	√	√
C. communis	√	√	√	√	√
C. crinita	√	√	√	√	√
C. debilis$_{MT}$	√	√	√		
C. debilis$_{SA}$				√	√
C. deweyana	√	√	√	√	√
C. disperma	√	√		√	√
C. echinata	√	√	√	√	√
C. flava	√	√			
C. gracillima	√	√	√	√	√
C. gynandra	√	√	√	√	√
C. hirtifolia	√	√	√*	√	√
C. incurva	√	√	√		

Table 3 cont'd.

Species	OLH	DCGH	MAIN	FSLH	FSGH
C. intumescens	√	√		√	√
C. kelloggii	√	√	√		
C. laxiflora	√	√	√	√	√
C. leptalea	√	√			
C. lupulina	√	√	√		√
C. lurida	√	√	√	√	√
C. michauxiana	√	√	√	√	√
C. normalis	√	√		√	√
C. norvegica	√	√			
C. novae-angliae	√	√	√•		
C. pauciflora	√	√	√		
C. paupercula	√	√	√		
C. pedunculata	√	√	√	√	√
C. plantaginea	√	√	√	√	√
C. platyphylla	√	√	√•	√	√
C. prasina	√	√	√	√	√
C. projecta	√	√	√	√	√
C. rosea	√	√	√	√	√
C. rugosperma	√	√		√	√
C. saxatilis	√	√	√•		
C. scabrata	√	√	√•	√	
C. scoparia	√	√	√		
C. sitchensis	√	√	√		
C. sprengelii	√	√	√	√	√
C. stipata	√	√	√	√	√
C. tenera	√	√	√	√	√
C. tribuloides	√	√	√•		
C. trisperma	√	√	√•		
C. vulpinoidea	√	√	√	√	√
TOTAL	**51**	**51**	**43**	**33**	**34**

during which germination lasted, hereafter termed *range*, as T_{90} - Lag, where T_{90} was the time from planting until 90% of total germination achieved was reached. I measured lags and ranges in days and degree-days, the latter being the mean of the minimum and maximum daily temperatures minus 5 (when the mean was greater than 5°C, otherwise no degree-days). Measurements in days and degree-days were used in outdoor experiments while those in days were used in the (temperature-controlled) greenhouse. In all experiments, the sample size was 50 seeds per pot.

Temperature. In the Main and Dormancy Check Greenhouse experiments (see below), air temperatures were set to 20/16°C (day/night) for approximately 1.5 months and then to 25/20°C (day/night) for the remainders of the experiments. While the thermoperiod in the Main experiment followed a 14hour/10hour cycle (similar to late spring and summer daylengths at this latitude), that of the Dormancy Check experiment was matched to that of a neighbouring greenhouse chamber (16hours/8hours) to minimize light gradients among blocks. During the Fresh Seed Greenhouse experiment (see below), air temperatures were 25/20°C (14hours/10hours) because the experiment was begun while the Main experiment was still running. I chose to have small temperature fluctuations of 4 or 5°C rather than none at all (continuous temperature) or large ones (10°C) because in seeds of many species, 1) there is a germination requirement for or improvement in percent germination with fluctuations in temperature (Thompson, 1973; Thompson and Grime, 1983) but 2) the fluctuations may widen the range of environmental conditions under which they will germinate, thereby masking treatment effects (e.g., red-light-requiring seeds of *Nicotiana Tabacum* germinated under far-red light given a thermoperiod of 30/20°C (Toole et al., 1955)). Though some species may require larger fluctuations, the moderate fluctuations were deemed a compromise. Soil temperatures were measured for some experiments and are available in an electronic appendix available from Marcia J. Waterway (Plant Science Dept.) or Martin J. Lechowicz (Biology Dept.). These temperatures were not included in the thesis as they were single readings measured at variable times rather than daily maxima and minima and could not be used to calculate degree-days.

Main Experiment (Greenhouse). I included 43 species in the Main experiment, ten (Table 3) of which underwent only a subset (Table 4) of treatments due to limited amounts of seed. The experiment was a randomized complete block design (Tables 5, 6) with three blocks (Fig.1) and one replicate per block. The blocks were slightly asymmetrical because some pots had to be moved away from dripping misting rods. I applied two classes of treatments: storage and immediate germination conditions (light and soil moisture).

Storage. I stratified seeds for 0, 2, or 4 months: 4- and 2-month stratification treatments began on November 28, 1996 and January 28, 1997, respectively. Non-stratified (0-month) seeds were stored air-dry at room temperature in paper packets until planting. For stratified treatments, I placed sets of 50 seeds in fine nylon mesh bags that were then loosely packed in plastic mesh bags. Stratification was then applied in either of two ways:

1) Moist stratification: Mesh bags (seeds) were laid between layers of heat-sterilized, moist sand (Fig.2) in opaque plastic containers maintained at 4 ± 3°C. All seeds remained in the dark throughout stratification except when containers were opened (under a dim green safelight) to add to the seeds for the the 2-month stratification treatment.

2) Submerged stratification: I treated and handled seeds as above except that I submerged the mesh bags in demineralized water (no sand) for the stratification period (Fig.2). Quartz stones were used to keep the mesh bags submerged throughout the stratification period.

Immediate germination conditions. I planted seeds on two substrates, a well-drained forest soil and a poorly drained wetland soil, and subjected them to either continuous darkness or natural light. These treatments are described below. I assigned blocks randomly to one of three consecutive planting days: Block A on April 09, Block B on April 11, and Block C on April 10, 1997. On each of these days, I removed all seeds from a given block of stratification containers (one

Table 4. Treatments applied in the Main experiment to 43 seed collections. Ten of these were not subjected to 2M, 2S, and 4S due to lack of seed (cf. Table 3). The design is a randomized complete block design with three blocks and one replicate per block.

Factor	**Level**	**Description**
Storage	0X	dry-stored, no stratification
	2M	two months moist stratification
	2S	two months submerged stratification
	4M	four months moist stratification
	4S	four months submerged stratification
Light	D	continuous darkness
	L	natural daylight (13-15 hr photoperiod)
Soil moisture regime	F	forest soil, low water level
	W	wetland soil, high water level

Table 5. Effects, associated degrees of freedom, and the MS_{ERROR} terms used to test particular effects in the Main experiment. This table is for the 33 species undergoing all treatments. Main effects include Block, Storage (Stor), Light, and Soil moisture regime (Soil). Contrasts are described in Table 7.

	Effect	df	MS_{ERROR}
	Block	2	Block*Stor*Soil*Light
	Stor	4	Block*Stor
	Light	1	Block*Light
	Soil	1	Block*Soil
	Block*Light	2	Block*Stor*Soil*Light
	Block*Soil	2	Block*Stor*Soil*Light
	Block*Stor	8	Block*Stor*Soil*Light
	Stor*Light	4	Block*Stor*Soil*Light
	Stor*Soil	4	Block*Stor*Soil
	Light*Soil	1	Block*Light*Soil
	Block*Light*Soil	2	Block*Stor*Soil*Light
	Block*Stor*Light	8	Block*Stor*Soil*Light
	Block*Stor*Soil	8	Block*Stor*Soil*Light
	Block*Stor*Soil*Light	8	.
Contrast	Strat	1	Block*Stor
Contrast	4vs2	1	Block*Stor
Contrast	SvsM	1	Block*Stor

Table 6. Effects, associated degrees of freedom, and the MS_{ERROR} terms used to test particular effects in the Main experiment. This table is for the ten species undergoing only a subset of treatments due to lack of seed (cf. Table 3); contrasts therefore do not apply.

Effect	**df**	**MS_{ERROR}**
Blocks	2	Block*Stor*Soil*Light
Stor	1	Block* Stor
Light	1	Block*Light
Soil	1	Block*Soil
Block*Light	2	Block*Stor*Soil*Light
Block*Soil	2	Block*Stor*Soil*Light
Block* Stor	2	Block*Stor*Soil*Light
Stor *Light	1	Block* Stor *Light
Stor *Soil	1	Block* Stor *Soil
Light*Soil	1	Block*Light*Soil
Block*Light*Soil	2	Block*Stor*Soil*Light
Block* Stor *Light	2	Block*Stor*Soil*Light
Block* Stor *Soil	2	Block*Stor*Soil*Light
Block* Stor *Soil*Light	2	.

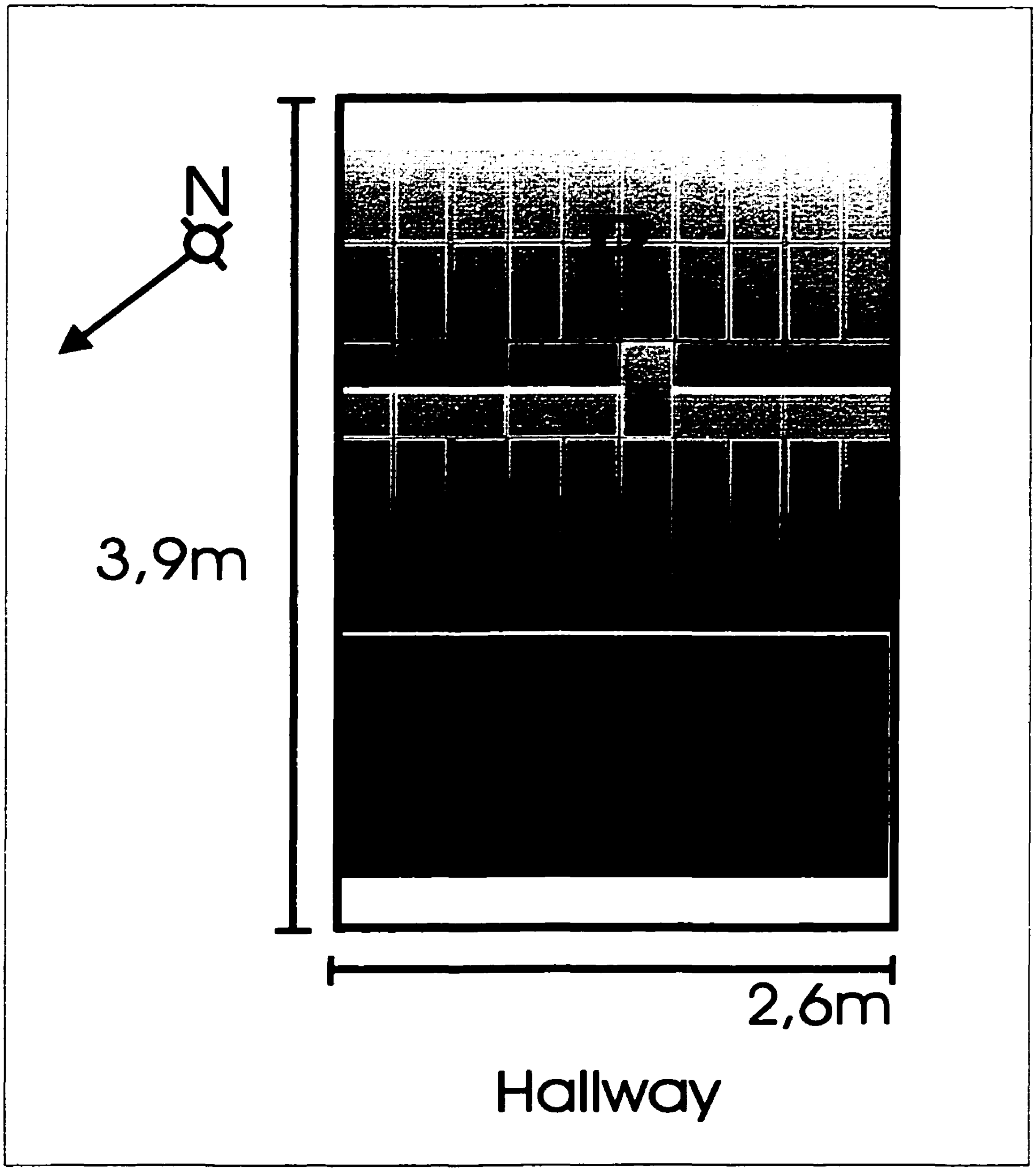


Fig.1. Blocking patterns for the Main experiment. Trays are outlined in white.

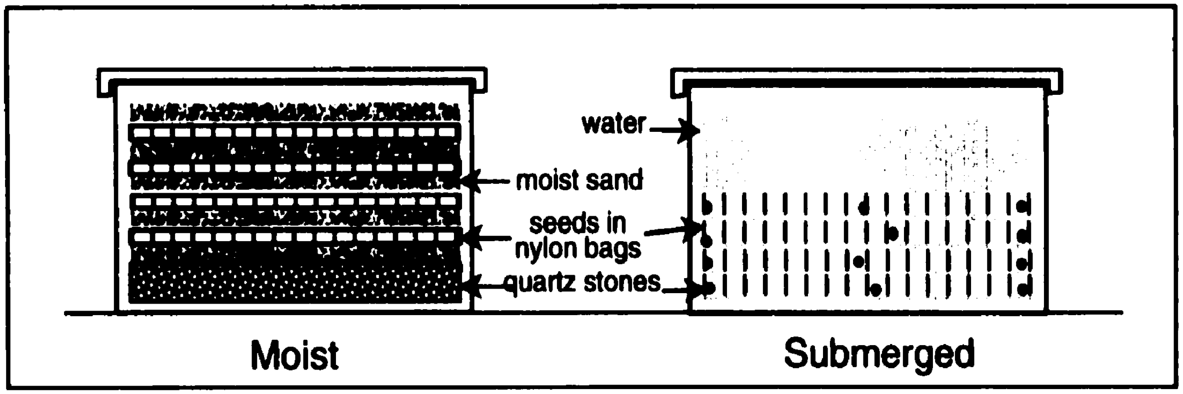


Fig. 2. Stratification containers: seeds are placed between layers of moist sand (underlain with quartz stones for drainage) or submerged in water (with quartz stones to keep them submerged).

moist, one submerged). Seeds intended for light treatments were transferred to a lighted potting room while those intended for dark treatments remained in the darkroom for planting under the safelight. In both cases, seeds were spread on the soil surface. For dark treatments, I added opaque lids to the planting units (see below), capped by aluminum foil cups.

The planting unit is shown in Fig.3. A 55mm diam. tapered, round plastic pot, hereafter termed the inner container (IC), was nested in a 58mm plastic cylindrical container, hereafter termed the outer container (OC) (see Fig.3). The sides of the OC were pierced with two opposite 6mm holes at a height of either 6mm (forest) or 35 mm (wetland) from the base. I added heat-sterilized quartz stones to the bottom of the OC's to stabilize them. The IC's were filled with either a forest loam (1:1, sand: topsoil) or wetland peat (1:1:1, black earth: peat: topsoil) soil mix. Thirty-two planting units were placed in each standard unperforated tray. When the trays were flooded every 3-7days (as needed, when forest soil surfaces began to dry out), water passed through the holes in the OC's and the soil was moistened from below. I made 2-3 small (7mm X 2mm) drainage holes in the trays so that the water would drain out within 5-10 minutes after flooding. The OC's then acted as water reservoirs and essentially set water levels. This created two soil-moisture environments: sandy loam soil with a low water table (forest) and peat wetland soil with a high water table (wetland). I fitted the OC's with an opaque screw-top lid for dark treatments, capped with aluminum foil to reflect light and decrease heat load. Light treatments were left uncapped.

Trays of planting units were placed in the greenhouse of the McGill University Phytotron. Soil moisture was maintained using automatic misting: five second bursts every 10-15 minutes during the day (every 10 min. on sunny days or whenever the soil surface was particularly dry) and hourly at night. Air temperature was maintained at 20°C/16°C (14/10) until May 29, 1997 (average of 49 days: recall planting was staggered over three days) when it was increased to 25°C/20°C until July 25, 1997. I did not supplement the lighting and therefore the seeds in the light treatment were subjected to natural photoperiods ranging from 13 to 15 hours of light per 24-hour cycle. Blocks were arranged as

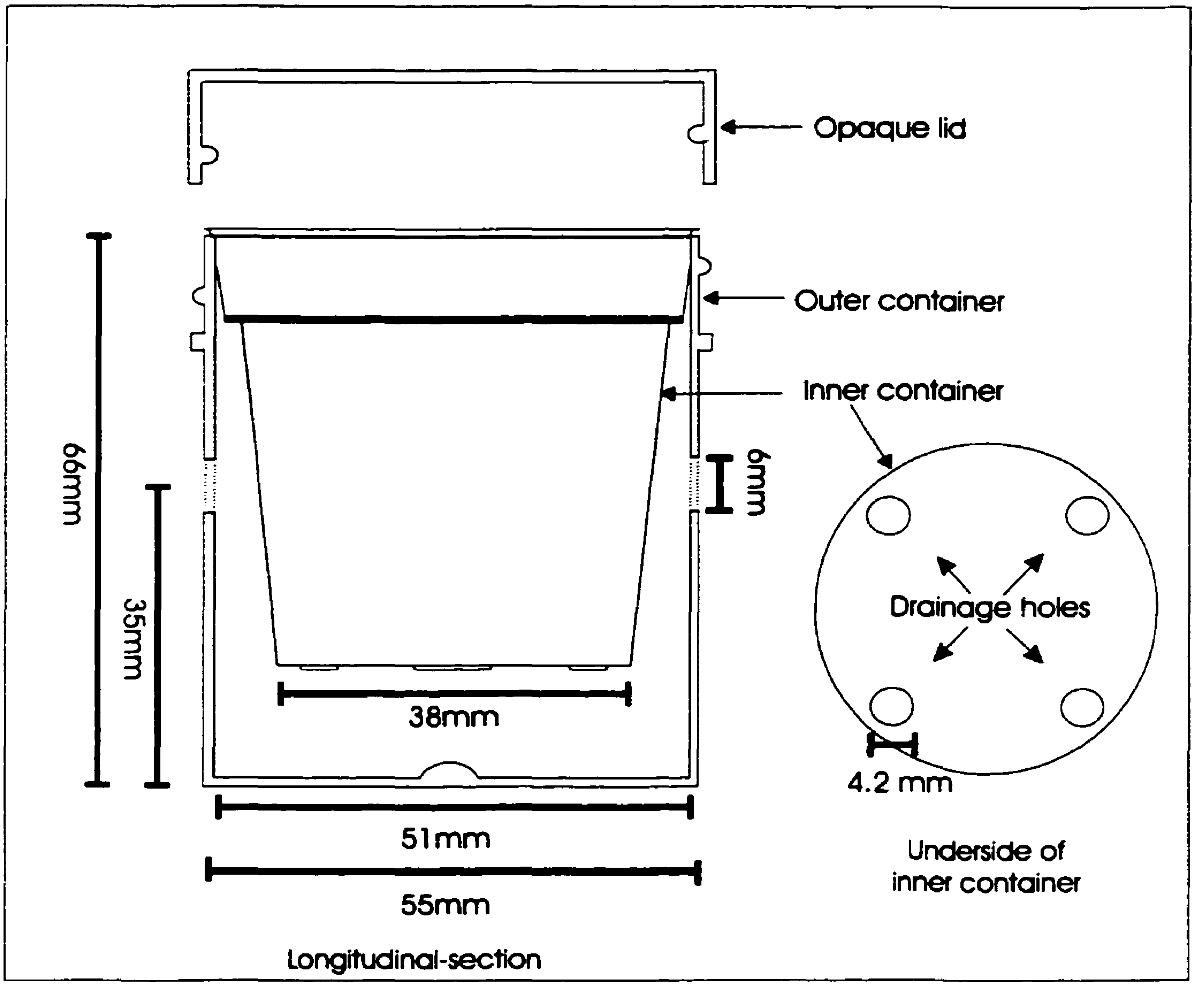


Fig. 3. Planting unit (wetland) for the Main experiment: inner container (IC) nested within the outer container (OC), the latter acting as a water reservoir for the former.

in Fig.1 to account for the lighting and temperature gradient. The greenhouse chamber ceiling and the windows facing outside were covered in 50% thermal and 50% shade cloth, respectively.

Scoring. Germinants were recorded from the greenhouse bench for light treatments and in the dark room (with a dim green safelight) for dark treatments. I monitored the seeds until the first germinant appeared (day 8) and then scored each block in turn on the same stagger as the planting. Although the first cycle was a three-day cycle, I increased the length to four days for all subsequent censuses. After 91 days, I removed the lids from the OC's (outer containers) and scored the dark pots one and two weeks after that.

Overwintered Lath House Experiment. On October 09,1996, I planted seeds of 51 *Carex* species (Table 3) in six randomized complete blocks on the surface of FAFARD topsoil in 8.9 cm-square pots sunk in the sandy soil of an outdoor lath house at the Mont St-Hilaire Research Station, Mont St-Hilaire, Québec. These were watered on sowing and then left undisturbed. Beginning on May 13, 1997 (germination began on May 15, 1997), pots were scored daily for germination until June 22, 1997 when new germinants levelled off and scoring was reduced to a frequency of 3-4 days. Scoring continued until August 08, 1997 and one additional scoring was made on May 30, 1998 after a second winter. I removed the seedlings periodically. Seeds were subject to ambient weather conditions throughout the entire monitoring period with supplemental morning watering during June, July, and August.

Dormancy Check Greenhouse Experiment. On November 22, 1996, I planted seeds of 51 *Carex* species (Table 3) in three randomized complete blocks on the surface of heat-sterilized Pro-mix (peat-based soil-less growing medium) in 6.35 cm-square cell trays with drainage holes. I maintained soil moisture with automatic misting: 2 second bursts applied every 10-30 minutes during the day (changed as needed to maintain moisture on soil surface but discourage algae) and hourly at night. Air temperature was maintained at 23°C days and 16°C nights for 45 days and then increased to 25°C days and 20°C nights until the end of the experiment, on March 27, 1997. I recorded soil temperatures each census morning in ten randomly chosen cells and these were, on average, 19.8°C for the first 45 days and 21.9°C thereafter. I scored germination on a daily basis (except between Dec. 21 and Jan. 04 where scoring was every 3-4 days) until February 13 when the frequency was reduced to every 3-4 days. On February 27, I further reduced the scoring frequency to every 7 days until the end of the experiment.

Scoring was not always performed by me in this experiment but I asked that seedlings not be removed by my assistant because if the seed was not entirely removed from the soil, the basal meristem produced a new shoot looking very much like a new germinated seed. However, this resulted in a few slight inconsistencies (drops of 1 germinant) from one day to the next. Therefore, after calculating cumulative germination, I followed the following rules:

1) If the drop was flanked on either side by the same number (e.g., 7, 7, 6, 7, 7) then the problem was treated as a missed count and only the low number was corrected (e.g., 7, 7, 7, 7, 7).
2) In other instances, numbers increased before or after the drop (e.g., 2, 3, 4, 4, 3, 3 and 1, 4, 7, 6, 8, 10) and the germinants were treated as lost (e.g., 2, 3, 4, 4, 4, 4 and 1, 4, 7, 7, 9, 11).

The second rule my have led to an overestimation of germination but the other obvious solution to the 1, 4, 7, 6, 8, 10 set (1, 4, 7, 7, 8, 10) would lead to underestimations. There is no other option than to use one rule consistently.

Fresh Seed Lath House experiment. A total of 33 species (Table 3) were used in this experiment. I sunk six replicate blocks of 72 plastic pots (8.9 cm-square) filled with BOTANIX topsoil in the sandy soil of a lath house at the Mont St-Hilaire Research Station, Mont St-Hilaire, Québec. The lip of each pot protruded from the soil by about 1 to 2cm. As seeds ripened for each species throughout the summer of 1997, they were harvested and surface-sown, 50 to a pot, in random positions within each of the six blocks. I placed a mesh screen mounted on a wooden frame directly over each block to reduce seed movement caused by rainsplash. I checked pots twice-weekly for seedling emergence until mid August and then scored weekly until October 01, 1997. I scored the pots once more on May 30, 1998. Seeds were subject to ambient weather conditions throughout the entire monitoring period with supplemental morning watering during June, July, and August.

Fresh Seed Greenhouse experiment. A total of 33 species (Table 3) were used in this experiment. I filled 144 potting units (IC + OC with low holes, see main experiment) in each of three replicate blocks with a heat-sterilized 1:1 sand:topsoil mix (equivalent to the Forest soil in the main experiment) and placed them in unperforated trays. As seeds ripened throughout the summer of 1997, they were harvested and surface-sown, 50 to a pot, in random positions within each block. I applied both light (open planting unit) and dark (covered planting unit: see main experiment) treatments to the seeds. Soil moisture was maintained by misting with a 5 second burst every 10 minutes during the day and hourly at night. Natural light (10-15 hours light/14-9 hours dark) was not supplemented. Ambient air temperatures remained at 25°C/20°C (14 hours/10 hours) throughout the experiment. I blocked the pots along the moisture gradient resulting from the position of the misting rods. Pots were scored twice-weekly for seedling emergence until October 27, 1997.

ANALYSES.

All data were analyzed using the Statistical Analysis System (SAS), version 6.12; SAS Institute, Cary, North Carolina, USA.

Main Experiment. Total germination was arcsine-square-root transformed and lag and range were reciprocally transformed, both standard practices for percentage and time measurements, respectively. Recall that *lag* is the time to onset of germination and *range* is the period over which 90% of total germination occurred. Reciprocally transformed lag and range are hereafter referred to as inverse lag and inverse range, respectively. Where no germination occurred, I set inverse lag to zero (i.e., onset of germination was infinitely slow) and defined inverse range as 'missing'. Effects and interactions of treatments were tested (ANOVA) for each of these three variables (transformed total germination, lag and range) with Block as a random factor (for model see Tables 5 and 6). All tests were performed on each species separately. In addition, I used orthogonal contrasts to compare storage treatments: stratified vs. non-stratified, four vs. two months, and submerged vs. moist (Table 7). Positive effects were defined as a significant increase in germination with light (vs. dark), wetland soil-moisture regime (vs. forest), stratification (vs. none), four months stratification (vs. two), and submerged stratification (vs. moist), while negative effects were the opposite: significantly higher germination for dark vs. light, etc. Because range data was frequently missing in dark treatments, I did not included this portion of the data in the analysis. Effects, interactions, and contrasts of (inverse) range are reported on the basis of type IV Sums of Squares because of missing data.

Canonical Discriminant Analysis. This analysis was performed using SAS PROC CANDISC. I chose to discriminate on the basis of habitat and phylogenetic group. The first choice was to address my central hypothesis that the influence of storage, light, and soil moisture would influence germination of seeds from species occupying different habitats differently than those occupying similar habitats. The second was to determine whether there was a phylogenetic basis to the difference. Habitat consisted of three classes: mesic deciduous

Table 7. Weights for orthogonal contrasts to test the effects of stratification (Strat), four months vs. two months of stratification (4vs2), and submersion versus moist stratification (SvsM) in the Main experiment. Storage consisted of 0, 2, or 4 months of stratification applied in Moist or Submerged conditions (cf. Table 4).

Contrast	**0X**	**2M**	**2S**	**4M**	**4S**
Strat	-4	1	1	1	1
4vs2	0	-1	-1	1	1
SvsM	0	-1	1	-1	1

forest, wet areas of deciduous forest, and wetland or seasonally flooded habitats. The last of these contained species from periodically flooded (e.g., lakeshores) to permanently flooded (e.g., marshes and bogs) areas. Phylogenetic groups (Table 8) were based on suggestions from Waterway (personal communication) based on the phylogenetic analysis of DNA sequences where possible (subgenus *Carex*) resulting from the work of Waterway et al. (1997), Waterway and Olmstead (1998), and Yen and Olmstead (1996, 1997) and otherwise on traditional morphological groupings (subgenus *Vignea*).

Fourteen numerical variables were chosen for the canonical discriminant analyses (CDA) based on the results from the Main and side experiments. Variables were chosen to capture the maximum amount of variation in the data. Eleven variables represent data from the Main experiment: six are related to germination and five to inverse lag (onset of germination). They include germination in the dark after no stratification (G0XD) or moist stratification (GMD), germination in the light after no stratification (GOXL), moist stratification (GML), two months of submerged stratification (G2SL) or four months of submerged stratification (G4SL), and inverse lag in the light after no stratification (GOXL), two months of moist stratification (G2ML), four months of moist stratification (G4ML), two months of submerged stratification (G2SL) or four months of submerged stratification (G4SL). Three additional variables represent data from two side-experiments: total germination and inverse lag in the Dormancy Check Greenhouse experiment (GDCGH, LDCGH) and total germination Overwintered Lath House experiment (GOLH). No variables represent data from the Fresh Seed experiments. A total of 29 species were used in this analysis.

Principal Components Analysis. A CDA weights variables to maximize the differences among groups and minimize the differences within groups, while a principal components analysis (PCA) maximizes differences among all individuals. Therefore, the constraints placed on the CDA in this study may have produced results that represented only a small proportion of the variation in the

Table 8. Phylogenetic groups used in the canonical discriminant analysis. Groups with labels ending in C are from the subgenus *Carex* and those ending in V are from the subgenus *Vignea*.

Phylogenetic Group	**Label**
Acrocystis, Hymenochlaenae, Laxiflorae, Careyanae, Halleranae	HC
Anomalae, Bicolores, Phacocysits	IC
Clandestinae, Folliculatae, Limosae, Lupulinae, Vesicariae	JC
Ovales	KV
Multiflorae, Vulpinae	LV
Phaestoglochin, Foetidae	MV
Deweyanae, Glareosae, Stellulatae	NV

data. I performed a PCA using SAS PROC PRINCOMP on the 14 CDA variables. Bi-plots of the principal components labelled by habitat or section were used to determine whether the groupings observed in the CDA were robust and still apparent when these constraints were not applied.

Contingency Table. While I chose to discriminate on the basis of habitat or phylogeny in the CDA's, these classifications may not have been independent. I therefore used the χ^2 test in SAS PROC FREQ to determine whether this was the case.

RESULTS

Main experiment. Total germination across all species and treatments ranged from 0 to 88%. In five species, less than 10% (5 seeds) of the seeds germinated in any treatment and were therefore excluded from all analyses: *Carex bromoides, C. capitata, C. debilis, C. pauciflora,* and *C. plantaginea.*

Germination (Tables 9, 10 and 11). There were significant Block effects in about one third of species, all of which were from wet habitats except for *Carex arctata, C. gracillima, and C. appalachica* which were found in mesic deciduous forests. Average germination was 6% greater in the block closest to the outside window of the greenhouse chamber (Fig. 4) compared with the other two blocks, suggesting a light or temperature gradient. Block soil temperatures, averaged over 19 census days between May 30 and July 10, 1997, were, from hallway to outer window, 25.3°C, 25.8°C, and 27.7°C. Also, in eight of nine instances where there was a significant Block*Light interaction, there was also a significant Block effect.

Storage significantly affected total germination in 2/3 of species and the other third only included species growing in wet habitats, including four from the Ovales section: *Carex bebbii, C. projecta, C. scoparia,* and *C. tribuloides.* Stratification of any kind (Strat contrast) improved germination in 14 of 38 species but decreased germination in *C. pedunculata* and *C. communis.* For seeds of both *C. pedunculata* and *C. communis*, germination was similar after moist stratification and dry storage (no stratification) but submersion during stratification reduced germination dramatically. Fewer species (1/4) were significantly affected by the duration of stratification (4vs2 contrast). *C. incurva* was the only species with significantly higher germination after two months of stratification instead of four. Submerged as opposed to moist stratification decreased seed germination of all upland forest and some wet-habitat species, had no effect on a group of exclusively wet-habitat species, and increased germination of *C. lurida, C. tenera,* and *C. vulpinoidea* seeds, all from wet habitats. Despite the non-significant effects of submersion, some of these wet-habitat species showed improved (not

Table 9. ANOVA results (*p* values) for total germination in the Main experiment: effects, interactions, and contrasts. Percent germination was arcsine-square-root transformed. Contrasts are in the last three columns: stratification of any kind vs. none (Strat), 4 months vs. 2 months (4vs2) of stratification, and submersion vs moist (SvsM) stratification. Positive effects ($p \leq 0.05$) are in **bold** and negative effects are also **underlined** for light, soil and the contrasts. Positive effects refer to germination that was increased by light (vs. dark), wetland (vs. forest) soil, stratification (vs. no stratification), four (vs. two) months stratification, and submerged (vs. moist) stratification. In other columns, significant results are in bold. Significance at the $0.05 < p < 0.100$ level is *italicized.* While there are 38 species shown here, only 29 were included in the contrasts because the others did not have enough seed for some treatments (see text). The table is divided into three categories based on total germination in the light after four months of moist stratification: >50%, 25%-50%, <25%, and then sorted alphabetically by species. Block*Stor*Soil interactions are not shown as they were not significant for any species. *P* values of 0.000 refer to values less than 0.0005.

Germination >50%		Main Effects			Interactions									Orthogonal Contrasts		
Species	**Block**	**Stor**	**Light**	**Soil**	**B*L**	**B*So**	**B*St**	**St*L**	**St*So**	**L*So**	**B*L*So**	**B*St*L**	**St*L*So**	**Strat**	**4vs2**	**SvsM**
C. aquatilis	**0.028**	0.330	**0.020**	0.329	0.272	0.172	0.104	0.560	**0.018**	0.958	0.565	*0.059*	0.614	0.107	0.255	0.540
C. arctata	**0.046**	**0.000**	**0.008**	0.565	0.107	0.773	0.529	**0.029**	0.338	0.167	0.273	0.432	0.987	0.659	**0.000**	**0.000**
C. aurea	*0.079*	**0.000**	*0.076*	0.120	0.134	0.542	0.819	0.687	0.103	*0.053*	0.462	0.329	0.405	**0.000**	**0.013**	**0.000**
C. bebbii	0.672	0.822	**0.000**	0.369	0.991	0.802	0.755	0.461	0.508	**0.045**	0.944	0.633	0.688	.	.	.
C. canescens	0.576	**0.006**	**0.013**	0.410	0.331	0.861	0.759	**0.044**	0.947	0.844	0.435	0.879	0.400	**0.046**	0.991	**0.002**
C. cephaloidea	0.616	**0.001**	**0.014**	0.880	0.266	0.196	0.507	**0.035**	0.627	0.133	0.776	0.647	0.543	**0.002**	**0.007**	**0.000**
C. communis	0.734	**0.002**	**0.006**	0.260	0.785	0.253	0.489	*0.062*	0.716	0.596	0.604	0.929	0.439	**0.007**	0.107	**0.001**
C. deweyana	0.064	**0.002**	*0.062*	0.777	0.141	0.549	0.553	0.836	0.655	0.258	0.433	0.116	0.258	0.290	**0.026**	**0.001**
C. gracillima	**0.001**	**0.001**	**0.016**	0.873	**0.006**	0.281	**0.037**	**0.018**	0.528	0.356	0.226	**0.014**	**0.043**	**0.006**	0.111	**0.000**
C. incurva	**0.002**	**0.006**	**0.003**	0.181	0.635	0.210	0.233	0.562	0.092	0.404	0.928	0.105	0.401	**0.002**	**0.014**	*0.080*
C. kelloggii	*0.079*	*0.081*	*0.054*	0.160	*0.060*	0.483	0.667	*0.067*	**0.045**	0.530	0.552	0.622	0.700	**0.014**	0.244	0.600
C. lurida	**0.023**	**0.001**	**0.050**	0.286	**0.013**	0.479	0.780	0.808	0.853	0.101	0.600	0.111	0.417	**0.000**	0.556	**0.008**
C. novae-angliae	0.910	0.059	**0.003**	*0.068*	0.874	0.862	0.921	0.356	0.188	0.120	0.795	0.886	0.485	.	.	.
C. paupercula	0.415	**0.017**	0.071	0.700	0.614	0.421	0.293	*0.069*	0.865	0.748	0.696	0.742	0.612	**0.008**	0.622	**0.016**
C. prasina	**0.005**	*0.087*	**0.051**	0.706	**0.027**	0.151	0.211	*0.091*	*0.091*	0.586	0.643	0.296	0.407	0.542	0.414	**0.012**
C. projecta	0.529	0.861	**0.004**	**0.046**	0.348	0.962	0.507	**0.027**	0.356	0.775	0.155	0.974	0.598	0.866	0.481	0.465
C. scabrata	**0.031**	**0.015**	**0.013**	**0.048**	*0.071*	0.866	0.324	0.601	0.238	0.601	0.169	**0.012**	0.111	.	.	.
C. sprengelii	0.394	**0.000**	**0.009**	0.115	0.245	0.948	0.820	0.716	**0.040**	0.204	0.758	0.593	0.593	0.202	0.077	**0.000**
C. trisperma	0.252	**0.009**	**0.006**	0.596	0.431	0.183	0.368	0.168	0.453	0.406	0.204	*0.056*	0.156	.	.	.
C. vulpinoidea	*0.082*	**0.000**	**0.026**	0.834	*0.075*	0.515	0.840	**0.001**	0.437	0.807	0.424	0.748	0.389	**0.000**	*0.099*	**0.000**
Proportion significant	**7/20**	**14/20**	**16/20**	**2/20**	**3/20**	**0/20**	**1/20**	**6/20**	**3/20**	**1/20**	**0/20**	**2/20**	**1/20**	**10/16**	**5/16**	**12/16**

Germination 25-50%		Main Effects			Interactions									Orthogonal Contrasts		
Species	**Block**	**Stor**	**Light**	**Soil**	**B*L**	**B*So**	**B*St**	**St*L**	**St*So**	**L*So**	**B*L*So**	**B*St*L**	**St*L*So**	**Strat**	**4vs2**	**SvsM**
C. albursina	0.323	**0.029**	**0.043**	0.985	0.136	0.133	0.257	**0.016**	0.169	0.718	0.318	0.577	0.975	.	.	.
C. appalachica	**0.016**	**0.000**	**0.007**	0.628	0.193	*0.091*	0.106	0.103	**0.009**	0.486	**0.016**	**0.017**	**0.048**	**0.003**	**0.008**	**0.000**
C. crinita	**0.000**	**0.000**	**0.045**	*0.052*	**0.000**	0.384	0.593	**0.000**	*0.065*	0.390	0.292	0.739	0.093	*0.075*	**0.000**	0.891
C. echinata	**0.030**	**0.000**	**0.037**	0.828	**0.049**	0.717	0.458	**0.050**	0.779	0.365	0.845	0.161	0.744	**0.001**	**0.004**	**0.000**
C. gynandra	0.548	0.542	**0.009**	0.136	0.915	0.186	0.371	0.666	0.641	0.164	0.975	0.127	0.406	0.852	0.130	0.584
C. pedunculata	0.680	**0.000**	0.639	**0.007**	0.358	0.997	0.932	0.259	0.637	0.214	0.604	0.789	0.877	**0.000**	0.408	**0.000**
C. saxatilis	0.102	0.147	*0.092*	0.224	0.564	0.439	0.296	0.300	*0.090*	**0.044**	0.909	0.522	0.359	.	.	.
C. scoparia	**0.038**	0.762	**0.011**	0.620	**0.014**	0.068	**0.025**	0.441	0.554	0.561	**0.025**	*0.069*	0.272	0.337	0.830	0.640
C. sitchensis	*0.058*	0.368	**0.005**	0.164	0.584	0.304	0.181	0.174	0.908	**0.013**	0.976	0.320	0.340	*0.059*	0.983	0.814
C. stipata	**0.012**	0.294	**0.007**	0.975	0.206	0.232	0.358	*0.089*	**0.039**	0.233	0.376	0.785	0.732	0.479	0.116	0.724
C. tribuloides	0.565	0.903	**0.017**	*0.055*	0.706	0.999	0.433	0.948	0.142	0.917	0.538	0.613	0.833	.	.	.
Proportion significant	**5/11**	**5/11**	**9/11**	**1/11**	**3/11**	**0/11**	**1/11**	**3/11**	**2/11**	**2/11**	**2/11**	**1/11**	**1/11**	**3/8**	**3/8**	**3/8**

Germination <25%		Main Effects			Interactions									Orthogonal Contrasts		
Species	**Block**	**Stor**	**Light**	**Soil**	**B*L**	**B*So**	**B*St**	**St*L**	**St*So**	**L*So**	**B*L*So**	**B*St*L**	**St*L*So**	**Strat**	**4vs2**	**SvsM**
C. hirtifolia	*0.064*	**0.047**	0.204	0.438	**0.024**	**0.050**	0.152	0.184	*0.090*	0.620	**0.032**	**0.042**	0.500	.	.	.
C. laxiflora	*0.094*	**0.004**	*0.053*	0.497	0.212	0.900	0.928	0.858	0.444	0.552	0.846	0.652	0.545	*0.071*	**0.029**	**0.011**
C. lupulina	**0.000**	0.112	0.338	0.288	**0.014**	0.276	**0.033**	0.169	0.959	0.138	0.537	**0.021**	0.201	**0.021**	0.702	0.155
C. michauxiana	**0.000**	**0.017**	0.291	0.189	**0.038**	0.377	0.230	0.312	0.619	0.103	0.729	0.586	0.724	**0.005**	0.266	0.332
C. platyphylla	0.475	0.340	0.162	0.151	0.589	0.805	0.237	0.294	0.538	0.677	0.678	0.487	0.801	.	.	.
C. rosea	0.474	**0.000**	*0.069*	0.596	0.372	0.870	0.993	**0.001**	0.742	0.705	0.415	0.986	0.996	**0.006**	0.723	**0.000**
C. tenera	0.675	**0.016**	**0.002**	0.747	0.923	0.768	0.998	0.156	0.276	0.840	0.810	0.769	0.967	0.626	**0.006**	**0.039**
Proportion significant	**2/7**	**5/7**	**1/7**	**0/7**	**3/7**	**1/7**	**1/7**	**1/7**	**0/7**	**0/7**	**1/7**	**2/7**	**0/7**	**3/5**	**2/5**	**3/5**
Total proportion significant	**14/38**	**24/38**	**26/38**	**3/38**	**9/38**	**1/38**	**3/38**	**10/38**	**5/38**	**3/38**	**3/38**	**5/38**	**2/38**	**16/38**	**10/38**	**18/38**

Table 10. Total percent germination in the Main experiment averaged over the soil treatments. Light treatments included continuous darkness (Dark) and a 14 hour photoperiod (Light). Storage treatments included no stratification (0X), 2 months of moist (2M) or submerged (2S) stratification, and four months of moist (4M) or submerged (4S) stratification. Some treatments were not applied when available seed was limited (.). Due to the large number of pots involved, seeds were lost during planting. The number of pots on which average germination is based is in the subscript except when the full complement of six pots was used.

	Dark					Light				
Species	**0X**	**2M**	**2S**	**4M**	**4S**	**0X**	**2M**	**2S**	**4M**	**4S**
C. albursina	0.0	.	.	1.3	.	2.7	.	.	26.7	.
C. appalachica	2.7	3.7	0.0	8.7	0.0	6.7	26.0	4.0	43.3	11.7
C. aquatilis	11.0	27.3	41.3	29.0	28.3	54.7	77.3	59.3	60.3	50.7
C. arctata	3.3	4.3	2.7	20.0	4.7	54.7	47.0	21.3	66.3	53.3
C. aurea	1.7	22.3	4.3	33.7	8.3	7.3	46.7	21.0	55.7	38.3
C. bebbii	1.7	.	.	0.3	.	46.0	.	.	52.7	.
C. bromoides	0.3	0.0	0.0	0.3	0.0	3.3	0.3	0.7	3.3	2.0
C. canescens	0.7	29.7	4.8_5	20.0	12.3	65.0	77.3	38.3	65.3	56.0
C. capitata	0.3	.	.	0.0	.	0.0	.	.	0.3	.
C. cephaoidea	0.3	27.3	2.3	43.7	12.3	45.7	56.3	32.7	59.7	52.0
C. communis	31.0	34.3	22.0	34.7	12.0	68.3	55.0	39.7	54.0	24.3
C. crinita	0.0	0.0	1.3	0.3	2.7	16.7	10.3	7.0	34.3	25.0
C. debilis	0.0	0.0	0.0_5	0.0	0.0	1.3	0.3	0.0	4.0	0.7
C. deweyana	27.3	32.3	23.3	55.7	21.0	48.3	54.3	41.7	65.3	46.0
C. echinata	0.0	0.3	0.0	6.0	1.7	4.3	27.3	3.0	38.7	13.3
C. gracillima	0.0	5.7	0.3	2.7	0.7	20.7	63.7	21.0	87.3	29.0
C. gynandra	25.7	32.3	28.3	21.7	26.3	38.3	38.3	39.3	41.3	25.7
C. hirtifolia	0.3	.	.	0.7	.	0.7	.	.	8.0	.
C. incurva	2.3	31.0	17.0	14.0	3.3	23.0	66.0	59.3	54.3	53.7
C. kelloggii	11.0	40.0	58.3	46.0	43.0	81.3	90.7	86.7	83.7	81.3
C. laxiflora	0.7	1.0	1.3	4.3	0.0	6.3	7.3	8.0	17.0	9.0
C. lupulina	0.3	5.3	19.3	0.3	25.7	3.0	13.3	8.0	16.3	14.7
C. lurida	0.0	11.3	21.3	8.0	35.7	39.0	63.7	62.7	61.0	68.3
C. michauxiana	0.0	15.3	16.7	14.0	24.0	11.3	29.7	16.3	19.3	39.0
C. novae-angliae	0.0	.	.	1.3	.	45.7	.	.	61.7	.
C. pauciflora	0.3	0.7	0.0	3.3	0.0	0.3	0.0	0.3	2.7	0.0

Table 10 cont'd.

	Dark					Light				
Species	**0X**	**2M**	**2S**	**4M**	**4S**	**0X**	**2M**	**2S**	**4M**	**4S**
C. paupercula	2.0	54.3	16.0	43.0	34.3	28.3	52.7	32.3	56.7	33.0
C. pedunculata	27.7	30.3	0.3	20.7	0.0_{5}	23.0	27.7	3.0	33.3	1.0
C. plantaginea	0.3	0.0_{5}	0.0	0.0	0.0	0.7	0.0	0.3	0.8_{5}	0.3
C. platyphylla	1.3	.	.	2.3	.	2.0	.	.	8.7	.
C. prasina	6.3	17.3	9.7	20.7	11.3	49.3	53.0	20.0	56.7	34.3
C. projecta	2.7	1.0	7.0	0.0	0.3	56.7	56.7	52.3	58.0	60.0
C. rosea	0.0	0.7	0.0	2.7	0.0_{5}	2.7	20.3	1.3	15.3	0.7
C. saxatilis	6.7	.	.	13.7	.	11.0	.	.	30.7	.
C. scabrata	0.0	.	.	15.7	.	45.0	.	.	56.7	.
C. scoparia	2.0	1.3	5.0	0.3	3.7	40.3	58.0	44.3	49.7	42.4_{5}
C. sitchensis	1.7	2.3	11.7	1.7	5.7_{7}	21.7	41.3	25.7	39.6_{5}	37.6_{5}
C. sprengellii	2.0	11.0	0.3	12.7	1.3	49.0	63.7	28.3	68.7	46.0
C. stipata	1.7	2.7	10.7	4.7	1.7	36.7	42.3	41.7	30.7	33.0
C. tenera	3.3	2.0	9.0	0.7	2.4_{5}	14.3	17.3	12.7	14.3	14.7
C. tribuloides	6.0	.	.	8.7	.	45.7	.	.	46.7	.
C. trisperma	0.3	.	.	7.0	.	7.0	.	.	66.0	.
C. vulpinoidea	0.0	0.7	23.3	0.0	28.8^{5}	4.7	64.0	62.3	52.7	53.3

Table 11. Percent germination in the Main experiment among dark treatment pots: before and after lids were removed, averaged across soil treatments. "Lids On" refers to total germination after approximately three months in the dark and "Lids Off" refers to additional germination two weeks after lids were removed. Storage treatments (applied before germination) included no stratification (0X), 2 months of moist (2M) or submerged (2S) stratification, and four months of moist (4M) or submerged (4S) stratification. Some treatments were not applied when available seed was limited (.). Species are sorted in decreasing order of germination after lids were removed (no stratification treatment).

	LIDS ON					LIDS OFF				
Species	**0X**	**2M**	**2S**	**4M**	**4S**	**0X**	**2M**	**2S**	**4M**	**4S**
C. cephaloidea	0.3	27.3	2.3	43.7	12.3	47.3	14.7	29.7	4.0	18.3
C. prasina	6.3	17.3	9.7	20.7	11.3	34.7	23.3	13.3	23.0	23.7
C. lurida	0.0	11.3	21.3	8.0	35.7	33.3	24.0	14.7	33.0	5.7
C. bebbii	1.7	0.0	0.0	0.3	0.0	33.0	0.0	0.0	40.3	0.0
C. arctata	3.3	4.3	2.7	20.0	4.7	29.0	40.0	9.3	39.7	38.0
C. kelloggii	11.0	40.0	58.3	46.0	43.0	24.7	19.3	8.3	7.7	3.3
C. scabrata	0.0	0.0	0.0	15.7	0.0	18.0	0.0	0.0	14.7	0.0
C. deweyana	27.3	32.3	23.3	55.7	21.0	17.7	20.0	13.0	5.3	14.7
C. canescens	0.7	29.7	4.8	20.0	12.3	17.3	5.3	12.4	4.0	4.3
C. tribuloides	6.0	0.0	0.0	8.7	0.0	12.0	0.0	0.0	4.0	0.0
C. stipata	1.7	2.7	10.7	4.7	1.7	11.7	22.3	13.3	10.0	2.7
C. aquatilis	11.0	27.3	41.3	29.0	28.3	9.7	1.3	0.0	1.0	0.7
C. appalachica	2.7	3.7	0.0	8.7	0.0	8.7	7.3	6.3	4.0	4.3
C. communis	31.0	34.3	22.0	34.7	12.0	6.3	2.3	0.7	3.0	2.3
C. scoparia	2.0	1.3	5.0	0.3	3.7	5.7	6.3	6.3	7.7	7.1
C. echinata	0.0	0.3	0.0	6.0	1.7	4.0	5.3	5.7	1.0	7.7
C. sprengellii	2.0	11.0	0.3	12.7	1.3	2.7	6.0	1.7	16.7	3.7
C. trisperma	0.3	0.0	0.0	7.0	0.0	2.3	0.0	0.0	3.0	0.0
C. crinita	0.0	0.0	1.3	0.3	2.7	1.7	0.0	0.3	0.0	0.0
C. tenera	3.3	2.0	9.0	0.7	2.4	1.3	6.3	0.0	3.7	0.8
C. gynandra	25.7	32.3	28.3	21.7	26.3	1.0	0.0	0.3	0.3	0.0
C. paupercula	2.0	54.3	16.0	43.0	34.3	0.7	0.0	2.0	0.0	1.3

Table 11 cont'd.

	LIDS ON					LIDS OFF				
Species	**0X**	**2M**	**2S**	**4M**	**4S**	**0X**	**2M**	**2S**	**4M**	**4S**
C. rosea	0.0	0.7	0.0	2.7	0.0	0.7	7.3	0.7	4.7	1.2
C. sitchensis	1.7	2.3	11.7	1.7	5.7	0.7	3.0	0.3	1.7	2.3
C. debilis	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.4	0.7	0.7
C. michauxiana	0.0	15.3	16.7	14.0	24.0	0.3	0.0	0.3	0.7	0.3
C. saxatilis	6.7	0.0	0.0	13.7	0.0	0.3	0.0	0.0	1.3	0.0
C. laxiflora	0.7	1.0	1.3	4.3	0.0	0.3	2.3	2.3	0.7	0.3
C. platyphylla	1.3	0.0	0.0	2.3	0.0	0.3	0.0	0.0	0.0	0.0
C. norvegica	0.0	0.0	0.0	1.3	0.0	0.3	0.0	0.0	0.0	0.0
C. projecta	2.7	1.0	7.0	0.0	0.3	0.3	11.0	3.3	11.7	3.0
C. aurea	1.7	22.3	4.3	33.7	8.3	0.0	0.0	0.0	0.0	0.0
C. pedunculata	27.7	30.3	0.3	20.7	0.0	0.0	0.0	1.0	0.7	0.0
C. incurva	2.3	31.0	17.0	14.0	3.3	0.0	0.0	0.3	0.3	0.0
C. pauciflora	0.3	0.7	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0
C. gracillima	0.0	5.7	0.3	2.7	0.7	0.0	2.0	0.0	0.3	0.0
C. albursina	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0
C. hirtifolia	0.3	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
C. bromoides	0.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.3
C. lupulina	0.3	5.3	19.3	0.3	25.7	0.0	0.0	0.7	0.7	0.0
C. capitata	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C. plantaginea	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C. vulpinoidea	0.0	0.7	23.3	0.0	28.8	0.0	0.3	0.0	0.0	0.0

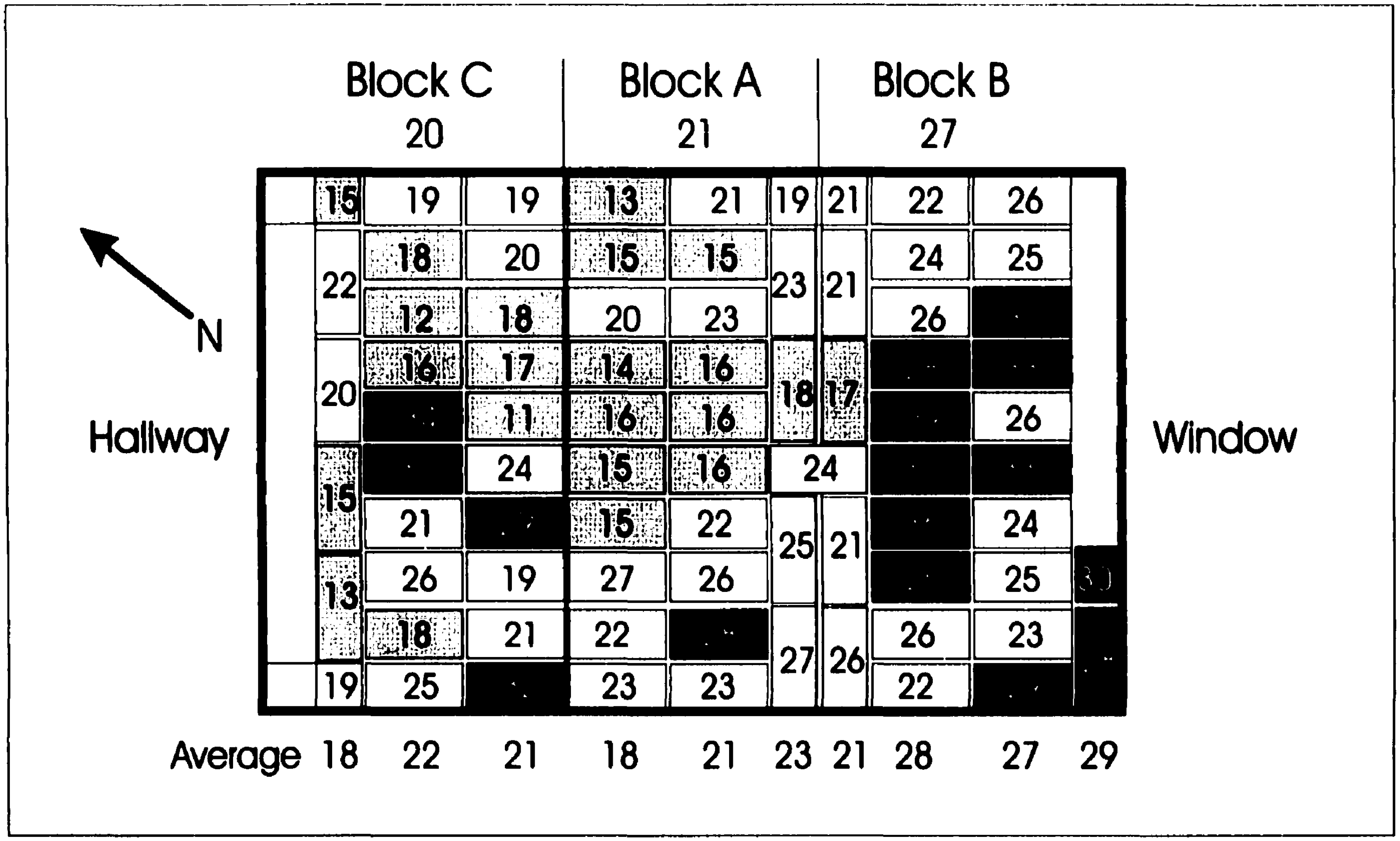


Fig.4. Average percent germination per tray in the Main experiment. Trays with germination greater or equal to 28% are in black and those with germination less than or equal to 18% are in grey. Also shown are average percent germination across tray rows and blocks.

tested) germination in the dark after two but not necessarily four months of submerged stratification, including *C. aquatilis, C. kelloggii, C. lupulina, C. projecta, C. sitchensis,* and *C. stipata*. Only *C. cephaloidea* of the mesic deciduous forest species showed a increase in dark-germination after (four months) submersion (12.3%) compared to dry-storage (0.3%).

Germination was significantly increased by light in 2/3 of species tested and non-significant results predominantly occurred in the group of species with low germination (<25%). *Carex pedunculata*, one of two (other is *C. communis*) documented ant-dispersed species in this experiment (Handel, 1976; 1978a), was also the only example of a species with moderate to high (>20%) germination and a *p*-value for the light effect exceeding 0.10. There was no evidence that perigynial colour was linked to light requirements. There was also considerable seed germination for many species in the dark treatments after lid removal (Table 11), confirming that the dark treatment did not kill seeds but rather prevented or delayed germination. Several species, such as *C. arctata, C. bebbii, C. cephaloidea,* and *C. lurida,* germinated poorly (<5%) after no stratification and three months in the dark, but two weeks after lid removal, germination exceeded 25%.

The effect of soil-moisture regime was only significant in three instances: germination was increased in seeds of *Carex scabrata* and *C. pedunculata* planted on the forest soil-moisture regime while seeds of *C. projecta* germinated better on the wetland soil. Neither *C. pedunculata* nor *C. projecta* had a significant Block effect and when the ANOVAs were run with Block and its associated interactions removed from the model, neither species remained significant for soil-moisture regime.

Lag (Tables 12 and 13). Block effects were significant in 9 of 38 species, most from wet habitats except *Carex cephaloidea* and *C. gracillima*.

Storage was the most frequently significant (30/38) treatment with respect to lag. Storage effects were non-significant only in species, such as *Carex bebbii, C. projecta*, and *C. tenera,* from wet habitats. Three-quarters of all species were

Table 12. ANOVA results (p values) for lag in days: effects, interactions, and contrasts. Inverse lag (days $^{-1}$) was used for the analysis. Contrasts are in the last three columns: stratification of any kind vs. none (Strat), four months vs. two months (4vs2), and submersion vs moist (SvsM) stratification. Positive effects ($p \leq 0.05$) are in **bold** and negative effects are **underlined** for light, soil and the contrasts. Positive effects refer to initiation of germination that was sped up by light (vs. dark), wetland (vs. forest) soil, stratification (vs. no stratification), four (vs. two) months stratification, and submerged (vs. moist) stratification. In other columns, significant results are in bold. Significance at the $0.05 \leq p \leq 0.100$ level is *italicized.* While there are 38 species shown here, only 29 were included in the contrasts because the others did not have enough seed for some treatments (see text). The table is divided into three categories based on total germination in the light after four months of moist stratification: >50%, 25%-50%, <25%, and then sorted alphabetically by species. Block*Stor*Soil interactions are not shown but were significant only for *Carex scabrata* ($p = 0.040$). P values of 0.000 refer to values less than 0.0005.

Germination >50%		Main Effects			Interactions									Orthogonal Contrasts		
Species	**Block**	**Stor**	**Light**	**Soil**	**B*L**	**B*So**	**B*St**	**St*L**	**St*So**	**L*So**	**B*L*So**	**B*St*L**	**St*L*So**	**Strat**	**4vs2**	**SvsM**
C. aquatilis	0.273	**0.017**	**0.009**	0.343	0.707	0.387	0.467	0.605	0.406	0.650	0.301	0.468	0.877	**0.002**	0.956	0.516
C. arctata	0.258	**0.002**	*0.053*	0.749	0.137	0.208	0.208	0.709	**0.021**	*0.073*	0.805	*0.069*	**0.029**	0.141	**0.046**	**0.000**
C. aurea	**0.043**	**0.000**	0.301	0.338	0.399	0.185	0.777	0.240	**0.032**	0.604	*0.056*	0.898	0.666	**0.000**	0.427	**0.000**
C. bebbii	0.864	0.728	**0.025**	0.501	*0.071*	0.685	*0.060*	**0.017**	**0.020**	0.105	0.740	0.686	0.169	.	.	.
C. canescens	0.269	**0.001**	*0.063*	0.597	0.122	0.352	0.743	0.122	0.970	0.494	0.517	0.735	0.741	**0.000**	0.665	**0.024**
C. cephaloidea	**0.013**	**0.000**	*0.070*	0.609	**0.003**	*0.076*	**0.016**	*0.062*	0.733	0.922	0.796	0.113	**0.023**	**0.000**	**0.045**	**0.000**
C. communis	*0.093*	**0.001**	0.586	0.159	*0.061*	0.538	0.327	0.718	0.547	0.298	0.125	**0.014**	0.554	**0.003**	*0.067*	**0.000**
C. deweyana	0.231	**0.000**	0.104	0.362	*0.086*	0.403	0.598	0.362	0.525	0.562	0.617	0.272	0.502	**0.000**	**0.022**	**0.000**
C. gracillima	**0.027**	**0.004**	**0.022**	0.137	*0.062*	0.536	**0.049**	0.209	0.695	0.539	0.608	0.118	0.248	**0.040**	0.454	**0.000**
C. incurva	**0.017**	**0.026**	0.102	0.265	**0.018**	0.684	0.345	0.337	0.870	0.154	0.861	0.240	0.718	**0.006**	0.123	0.126
C. kelloggii	*0.068*	**0.007**	*0.082*	**0.004**	**0.010**	0.973	*0.073*	0.310	0.545	0.798	0.411	0.178	0.578	**0.001**	0.696	*0.072*
C. lurida	**0.012**	**0.003**	0.106	0.583	**0.013**	0.240	0.432	0.261	0.950	**0.024**	0.917	0.204	0.310	**0.000**	0.773	0.690
C. novae-angliae	0.959	**0.043**	**0.015**	0.556	0.747	0.433	0.708	0.547	0.775	0.376	0.644	0.532	0.761	.	.	.
C. paupercula	0.258	**0.000**	0.178	0.474	0.556	0.541	0.933	0.895	0.819	0.375	0.508	0.642	0.480	**0.000**	**0.037**	**0.000**
C. prasina	**0.021**	**0.021**	0.133	0.296	**0.005**	0.290	0.250	*0.078*	**0.019**	0.170	0.797	0.511	0.537	**0.008**	0.796	**0.019**
C. projecta	0.747	0.225	**0.003**	0.624	0.658	0.198	0.285	*0.090*	0.768	0.652	0.102	0.628	0.886	0.180	0.125	0.192
C. scabrata	*0.061*	**0.023**	*0.065*	0.111	0.056	0.601	*0.097*	0.684	0.749	0.460	**0.033**	0.203	0.494	.	.	.
C. sprengelii	0.424	**0.000**	*0.057*	**0.048**	0.237	0.873	0.933	*0.091*	0.455	0.440	0.394	0.959	0.695	**0.001**	0.120	**0.000**
C. trisperma	0.380	*0.052*	*0.062*	0.545	0.508	0.310	0.435	0.786	**0.028**	0.252	0.386	0.227	0.523	.	.	.
C. vulpinoidea	0.410	**0.000**	**0.009**	0.580	0.365	0.660	0.254	**0.002**	0.161	0.121	0.596	0.264	0.636	**0.000**	0.417	**0.000**
Proportion significant	**6/20**	**17/20**	**6/20**	**2/20**	**5/20**	**0/20**	**2/20**	**2/20**	**5/20**	**1/20**	**1/20**	**1/20**	**2/20**	**14/16**	**4/16**	**11/16**

Germination 25-50%		Main Effects			Interactions									Orthogonal Contrasts		
Species	**Block**	**Stor**	**Light**	**Soil**	**B*L**	**B*So**	**B*St**	**St*L**	**St*So**	**L*So**	**B*L*So**	**B*St*L**	**St*L*So**	**Strat**	**4vs2**	**SvsM**
C. albursina	0.406	**0.030**	**0.037**	0.695	0.272	0.500	0.368	**0.001**	0.112	0.112	0.863	0.976	0.695	.	.	.
C. appalachica	0.259	**0.000**	**0.019**	0.360	0.498	0.850	0.446	0.600	**0.022**	0.130	0.141	0.360	0.351	**0.003**	0.134	**0.000**
C. crinita	0.413	**0.027**	**0.001**	**0.003**	0.912	0.973	0.226	**0.000**	**0.039**	0.557	0.290	0.989	0.154	**0.009**	**0.023**	0.773
C. echinata	*0.071*	**0.000**	*0.056*	0.975	*0.091*	0.459	0.440	0.209	0.414	0.267	0.617	*0.074*	0.287	**0.001**	**0.010**	**0.000**
C. gynandra	0.589	**0.007**	**0.035**	0.503	0.631	0.249	0.320	0.144	*0.092*	0.366	0.560	0.854	0.700	**0.005**	0.434	**0.004**
C. pedunculata	0.890	**0.000**	0.768	0.407	0.287	0.648	0.850	0.911	0.133	*0.055*	0.865	0.869	0.546	0.361	0.979	**0.000**
C. saxatilis	0.107	0.193	0.102	0.177	0.361	0.609	0.205	0.997	0.512	0.806	0.290	0.394	*0.076*	.	.	.
C. scoparia	**0.036**	**0.010**	**0.044**	0.113	**0.002**	0.485	0.487	*0.090*	0.729	0.738	0.771	0.422	0.567	**0.005**	0.196	**0.007**
C. sitchensis	0.333	*0.081*	**0.013**	**0.012**	0.555	0.967	0.369	0.528	0.571	0.269	0.980	0.527	0.652	**0.010**	0.928	0.914
C. stipata	0.632	**0.032**	*0.052*	0.815	0.161	0.426	0.785	0.436	0.384	0.632	0.288	0.761	0.999	*0.068*	0.161	**0.015**
C. tribuloides	0.504	0.335	*0.078*	*0.086*	0.382	0.892	0.708	0.965	0.528	0.686	0.773	0.574	0.832	.	.	.
Proportion significant	**1/11**	**8/11**	**6/11**	**2/11**	**1/11**	**0/11**	**0/11**	**2/11**	**2/11**	**0/11**	**0/11**	**0/11**	**0/11**	**6/11**	**2/11**	**6/11**

Germination <25%		Main Effects			Interactions									Orthogonal Contrasts		
Species	**Block**	**Stor**	**Light**	**Soil**	**B*L**	**B*So**	**B*St**	**St*L**	**St*So**	**L*So**	**B*L*So**	**B*St*L**	**St*L*So**	**Strat**	**4vs2**	**SvsM**
C. hirtifolia	*0.088*	**0.003**	0.124	0.732	**0.041**	**0.041**	0.737	0.100	0.134	0.742	**0.050**	*0.070*	0.191	.	.	.
C. laxiflora	0.112	**0.004**	0.200	0.581	0.642	0.400	0.966	0.439	**0.047**	0.963	0.980	0.509	0.983	0.152	**0.021**	**0.002**
C. lupulina	**0.007**	**0.033**	0.118	0.578	0.128	*0.063*	0.267	*0.095*	0.377	0.337	0.382	0.674	0.270	**0.010**	0.246	**0.047**
C. michauxiana	**0.011**	**0.029**	*0.065*	0.300	0.594	0.244	0.138	0.396	0.828	0.178	0.918	0.555	0.779	**0.008**	0.265	0.506
C. platyphylla	0.717	0.409	0.334	**0.011**	0.387	0.979	0.153	**0.008**	0.455	0.568	0.355	0.987	0.757	.	.	.
C. rosea	0.711	**0.000**	**0.043**	0.608	0.813	0.974	0.998	0.089	0.756	0.798	0.401	0.956	0.974	*0.095*	0.105	**0.000**
C. tenera	0.366	0.264	**0.024**	0.542	0.301	0.494	0.690	0.066	0.498	0.307	0.804	0.587	0.278	0.818	0.103	0.196
Proportion significant	**2/7**	**5/7**	**2/7**	**1/7**	**1/7**	**1/7**	**0/7**	**1/7**	**1/7**	**0/7**	**1/7**	**0/7**	**0/7**	**2/5**	**1/5**	**3/5**
Total proportion significant	**9/38**	**30/38**	**14/38**	**5/38**	**7/38**	**1/38**	**2/38**	**5/38**	**8/38**	**1/38**	**2/38**	**1/38**	**2/38**	**22/29**	**7/29**	**20/29**

Table 13. Lags (days) for the Main experiment, averaged over soil. Treatments include continuous darkness (Dark) or a 14-hour photoperiod (Light), no stratification (0X), or two or four months of moist (M) or submerged (S) stratification. When no germination occurred in a pot, the lag was treated as missing. The number of pots on which each lag is based is in the subscript except when the full complement of six pots was used. In some instances, germination occurred in zero pots and no lag could be reported (*). Some treatments were not applied due to limited seed (.).

	Dark					**Light**				
Species	**0X**	**2M**	**2S**	**4M**	**4S**	**0X**	**2M**	**2S**	**4M**	**4S**
C. albursina	*	.	.	28_3	.	37_4	.	.	8	.
C. appalachica	17_1	15_5	*	16_5	*	16_3	11	52_5	10	40
C. aquatilis	17_4	11_5	13_5	11	10_4	14	8	8	8	8
C. arctata	23_3	34	59_4	18	45_3	23	16	35	13	18
C. aurea	17_2	11	15	11	17_5	33_5	11	16	12	14
C. bebbii	19_2	.	.	57_1	.	11	.	.	9	.
C. bromoides	81_1	*	*	25_1	*	39	13_1	17_2	10_2	15_2
C. canescens	21_1	11	16_3	11_4	11_5	12	8	11	9	10
C. capitata	17_1	.	.	*	.	*	.	.	10_1	.
C. cephaloidea	53_1	10	40_3	11	14_5	18	9	15	8	12
C. communis	38	18	28	17	30	26	18	32	14	33
C. crinita	*	*	38_3	29_1	20_3	26	16	26	11	14
C. debilis	*	*	*	*	*	37_2	69_1	*	20_5	63_2
C. deweyana	23	12	26	11	22	18	11	13	8	11
C. echinata	*	13_1	*	10_4	17_2	36_3	9	66_5	9	17_5
C. gracillima	*	12_4	81_1	14_3	25_1	15_5	10	21_5	8	19
C. gynandra	20	13	18	11_5	14	17	10	14	9	14
C. hirtifolia	33_1	.	.	29_1	.	51_2	.	.	12_5	.
C. incurva	36_4	12	15_5	12_4	11_2	14	10	11	10	10

Table 13 cont'd.

C. kelloggii	20_4	12	10	12_5	10	12	9	9	8	8
C. laxiflora	17_2	33_2	21_2	17_5		64_5	34_5	57_5	26	37_5
C. lupulina	25_1	23_2	19_4	17_1	13_3	38_3	22	17_4	33	15
C. lurida	*	13_5	16_5	34_4	15_5	18	11	13	10	11
C. michauxiana	*	45_5	22_4	29_4	21	50_4	15_5	33_4	20_5	16
C. novae-angliae	*	.	.	22_3	.	24	.	.	13	.
C. pauciflora	10_1	47_2	.	21_4	.	10_1	.	89_1	33	.
C. paupercula	41_3	12	25^4	13	22	38	12	34	11	16
C. pedunculata	26	17	17_1	19	.	27	19	41_2	17	29_1
C. plantaginea	13_1	*	8	*	*	45_2	*	29_1	10_1	65_1
C. platyphylla	45_3	.	.	34_4	.	37_3	.	.	30	.
C. prasina	42_3	23	32	16_4	17_5	16	9	20	10	14
C. projecta	17_2	19_2	12_4	*	13_1	13	8	9	9	8
C. rosea	*	23_2	*	16_3	*	28_4	16	53_2	16_5	77_2
C. saxatilis	23_4	.	.	15_5	.	18_5	.	.	13	.
C. scabrata	*	.	.	17_5	.	33	.	.	12	.
C. scoparia	15_2	27_2	13_3	21_1	25	11	8	8	8	8_5
C. sitchensis	17_1	12_3	14_4	20_3	13_4	17	8	11	9_5	8_5
C. sprengellii	38_3	13	65_1	14_5	77_2	20	10	30	12	26
C. stipata	20_3	13_2	16_3	13_5	25_3	14	9	13	9	12
C. tenera	16_4	10_2	12_5	55_2	11_2	11	10	11	9	10
C. tribuloides	17_3	.	.	12_3	.	10	.	.	9	.
C. trisperma	81_1	.	.	15_4	.	30_5	.	.	14	.
C. vulpinoidea	*	13_1	11	*	11_5	16_3	10	10	10	10

significant for stratification of any kind (Strat contrast) and most of the others approached significance. In general, stratification appears to have shortened lags regardless of its effect on total germination. Only 1/4 of species were significantly affected by the duration of stratification (4vs2 contrast), with no pattern with respect to habitat or phylogeny apparent. Submersion only significantly sped up the onset of germination in seeds of wet species, *C. lupulina*, *C. scoparia*, and *C. vulpinoidea*, had no significant effect on 9/38 species (all from wet habitats), and significantly slowed down the rest.

The lag in 14 of 38 species was significantly decreased by light but 10 others approached significance ($0.05 \le p \le 0.10$).

Soil-moisture regime significantly affected the onset of germination in five species, three of which were from the *Phacocystis* section (*Carex crinita, C. kelloggii*, and *C. sitchensis*). In none of these species was block effect significant and when the analysis was re-run without block effect in the model, only *C. crinita* remained significant for soil-moisture regime.

Range (Tables 14 and 15). Effects of dark treatments on range were not tested and few of the other treatment effects were significant. No obvious patterns emerged with respect to habitat or phylogenetic section. However, when range was significantly affected by a treatment, lag was generally also affected. For example, duration of stratification (4vs2 contrast) and application of stratification (SvsM contrast) had significant effects on both the (inverse) lag and (inverse) range of *Carex arctata* germination (Tables 12 and 14). In most instances, when a treatment significantly shortened the range, the onset of germination was also sped up and when the range was increased, the onset of germination was delayed. In contrast, when a treatment significantly affected lag, the range was not necessarily affected.

Overwintered Lath House (Table 16). The data from this experiment are less reliable than from the others because spring flooding and/or rainsplash caused some seeds to move from pot to pot. Any obviously displaced

Table 14. ANOVA results (p values) for range in days: effects, interactions, and contrasts based on Type IV Sums of Squares. Inverse range was used for the analysis and where no germination occurred, range was considered missing. Some effects could not be tested due to missing values. Stratification contrast results are in the last three columns: stratification of any kind vs. none (±Strat), four months vs. two months (4vs2), and submersion vs moist stratification (SvsM) . Positive effects are in **bold** and negative effects are **underlined** for soil and the contrasts. Positive effects refer to ranges that were shortened by wetland (vs. forest) soil, stratification (vs. no stratification), four (vs. two) months stratification, and submerged (vs. moist) stratification. In other columns, significant results are in bold. Significance at the $0.05 \leq p \leq 0.100$ level is *italicized.* Missing results are dues to lack of seed (not subject to certain treatments) or poor germination: missing data (no germination = undefinable range) cause some effects to be incalculable. The table is divided into three categories based on total germination in the light after four months of submerged stratification: >50%, 25%-50%, <25%, then sorted alphabetically by species. P values of 0.000 refer to values less than 0.0005.

Table 14 con'td.

Germination >50%		**Main Effects**		**Interactions**			**Orthogonal Contrasts**		
Species	**Block**	**Stor**	**Soil**	**Bl*So**	**B*St**	**St*So**	**Strat**	**4vs2**	**SvsM**
C. aquatilis	0.587	0.369	0.619	0.542	0.617	0.521	0.273	0.359	0.254
C. arctata	0.826	**0.002**	0.153	0.786	0.416	**0.028**	0.236	**0.001**	<u>**0.022**</u>
C. aurea	**0.045**	0.398	0.370	0.485	0.230	0.813	<u>*0.084*</u>	0.570	0.885
C. bebbii	**0.006**	0.220	0.278	*0.093*	**0.009**	**0.021**	.	.	.
C. canescens	0.913	0.371	0.585	0.500	0.570	0.364	0.239	0.251	0.427
C. cephaloidea	0.163	**0.019**	0.408	0.484	0.294	0.487	*0.070*	0.279	<u>**0.003**</u>
C. communis	*0.055*	0.960	0.433	0.555	*0.088*	0.133	0.784	0.958	0.657
C. deweyana	0.123	**0.001**	0.837	0.141	0.964	0.959	**0.005**	**0.001**	<u>**0.001**</u>
C. gracillima	**0.000**	0.580	0.120	0.905	**0.000**	0.530	0.388	0.416	0.713
C. incurva	0.916	0.215	0.290	0.413	0.478	0.661	0.211	0.659	*0.056*
C. kelloggii	0.235	0.281	0.971	0.787	0.541	0.324	*0.095*	0.663	0.929
C. lurida	0.298	0.224	0.197	0.433	0.572	0.111	<u>**0.042**</u>	0.704	0.754
C. novae-angliae	0.546	**0.049**	0.179	0.537	0.853	0.233	.	.	.
C. paupercula	0.220	0.350	0.735	0.820	**0.029**	0.225	0.565	0.629	*0.093*
C. prasina	0.466	0.261	0.738	0.231	0.458	0.260	0.452	0.936	0.149
C. projecta	0.671	0.457	0.190	0.561	0.570	0.589	0.456	0.188	0.365
C. scabrata	0.302	*0.051*	0.240	0.126	0.588	**0.045**	.	.	.
C. sprengellii	0.695	**0.038**	0.163	0.202	*0.057*	**0.044**	0.264	0.160	<u>**0.016**</u>
C. trisperma	0.376	0.242	0.280	0.603	0.427	0.477	.	.	.
C. vulpinoidea	0.680	0.586	0.514	0.551	0.159	0.193	.	0.359	0.404
Proportion significant	**3/20**	**5/20**	**0/20**	**0/20**	**3/20**	**4/20**	**2/15**	**2/16**	**4/16**

Table 14 cont'd.

Germination 25-50%		**Main Effects**		**Interactions**			**Orthogonal Contrasts**		
Species	**Block**	**Stor**	**Soil**	**Bl*So**	**B*St**	**St*So**	**Strat**	**4vs2**	**SvsM**
C. albursina	.	0.128	0.853	.	.	.	.	.	.
C. appalachica	0.668	0.245	0.415	0.525	0.140	0.481	.	0.211	0.199
C. crinata	**0.007**	*0.094*	0.594	*0.098*	*0.096*	0.241	0.674	**0.031**	0.286
C. echinata	0.681	0.332	0.447	0.642	0.644	0.955	.	0.297	0.483
C. gynandra	0.853	0.135	0.104	0.862	0.771	0.886	**0.023**	0.229	0.972
C. pedunculata	0.672	0.916	0.531	0.569	0.710	0.586	.	.	.
C. saxatilis	0.656	0.482	0.292	0.706	0.677	0.498	.	.	.
C. scoparia	**0.026**	0.530	0.768	*0.075*	0.155	0.149	0.741	0.207	0.692
C. sitchensis	0.946	0.654	0.761	0.510	0.771	0.768	0.447	0.606	0.302
C. stipata	*0.059*	0.298	0.215	0.557	0.114	0.885	0.331	0.102	0.280
C. tribuloides	0.161	0.138	0.536	0.160	0.332	0.343	.	.	.
Proportion significant	**2/10**	**0/11**	**0/11**	**0/10**	**0/10**	**0/10**	**1/5**	**1/7**	**0/7**

Germination <25%		**Main Effects**		**Interactions**			**Orthogonal Contrasts**		
Species	**Block**	**Stor**	**Soil**	**Bl*So**	**B*St**	**St*So**	**Strat**	**4vs2**	**SvsM**
C. hirtifolia	.	.	0.537	.	.	.	.	.	.
C. laxiflora	0.686	0.592	0.139	0.739	0.531	0.732	0.167	0.987	0.800
C. lupulina	**0.027**	0.304	*0.061*	0.266	*0.062*	0.111	.	0.461	0.860
C. michauxiana	0.203	0.247	0.324	0.600	0.729	0.789	0.181	0.838	0.172
C. platyphylla	.	0.690	**0.003**	.	.	.	.	.	.
C. rosea	**0.021**	0.051	**0.000**	0.934	**0.029**	**0.026**	.	.	.
C. tenera	0.218	0.675	0.135	0.912	0.322	0.509	0.602	0.892	0.337
Proportion significant	**2/5**	**0/6**	**2/7**	**0/5**	**1/5**	**1/5**	**0/3**	**0/4**	**0/4**
Total proportion significant	**7**	**5**	**2**	**0**	**4**	**5**	**3**	**3**	**4**

Table 15. Ranges (days) for the Main experiment, averaged over soil. Recall that range is T_{90} - Lag, where T_{90} was the time from planting until 90% of total germination achieved was reached and that scoring of the Main experiment was every fourth day. Treatment labels include no stratification (0X), and two or four months of moist (M) or submerged (S) stratification. When no germination occurred in a pot, the range was treated as missing. The number of pots on which each range is based is in the subscript except when the full complement of six pots was used. In some instances, germination occurred in zero pots and no lag could be reported (*). Some treatments were not applied due to limited seed (.).

	Dark					Light				
Species	**0X**	**2M**	**2S**	**4M**	**4S**	**0X**	**2M**	**2S**	**4M**	**4S**
C. albursina	*	.	.	2_{3}	.	8_{4}	.	.	12	.
C. appalachica	2_{1}	28_{5}	*	9_{5}	*	26_{3}	33	27_{5}	23	39
C. aquatilis	7_{4}	7_{5}	8_{5}	8	8_{4}	35	8	7	10	10
C. arctata	17_{3}	25	8_{4}	37	45_{3}	43	55	53	24	41
C. aurea	2_{2}	14	10	12	11_{5}	20_{5}	20	24	10	15
C. bebbii	2_{2}	.	.	2_{1}	.	34	.	.	7	.
C. bromoides	2_{1}	.	.	2_{1}	.	16	2_{1}	2_{2}	8_{2}	10_{2}
C. canescens	2_{1}	8	10_{3}	7_{4}	14_{5}	32	13	32	15	15
C. capitata	2_{1}	.	.	*	.	*	.	.	2_{1}	.
C. cephaloidea	2_{1}	5	3_{3}	7	11_{5}	47	18	59	13	38
C. communis	3_{1}	23	39	25	48	37	44	38	46	46
C. crinita	*	*	6_{3}	21	18_{3}	33	27	18	22	35
C. debilis	*	*	*	*	*	2_{2}	2_{1}	.	18_{5}	2_{2}
C. deweyana	38	27	17	12	13	36	23	50	14	17
C. echinata	*	2_{1}	*	13_{4}	2_{2}	25_{3}	12	20_{5}	12	38_{5}
C. gracillima	*	9_{4}	2_{1}	5_{3}	14_{1}	40_{5}	15	32_{5}	13	39
C. gynandra	10	16	28	15_{5}	11	42	25	19	12	23
C. hirtifolia	2_{1}	.	.	2_{1}	.	2_{2}	.	.	11_{5}	.

Table 15 cont'd.

C. incurva	4_4	7	11_5	7_4	12_2	42	8	23	11	17
C. kelloggii	17_4	13	12	8_5	8	24	10	8	8	10
C. laxiflora	2_2	10_2	2_2	9_5	*	8_5	36_5	19_5	31	36_5
C. lupulina	2_1	2_2	22_4	2_1	9_3	22_3	24	29_4	43	26
C. lurida	*	7_5	8_5	5_4	7_5	25	28	27	41	16
C. michauxiana	*	20_5	12_4	34_4	12	34_4	16_5	38_4	26_5	31
C. novae-angliae	*	.	.	3_3	.	33	.	.	21	
C. pauciflora	2_1	2_2	*	17_4	*	2_1	*	2_1	4	*
C. paupercula	2_3	9	41_4	7	35	39	19	39	16	50
C. pedunculata	3	29	2_1	19	*	22	22	12_2	17	14_1
C. plantaginea	2_1	*	*	*	*	2_2	*	2_1	2_1	2_1
C. platyphylla	3_3	.	.	3_4	.	34_3	.	.	17	.
C. prasina	14_3	8	35	8_4	26_5	15	12	26	6	29
C. projecta	4_2	6_2	14_4	*	2_1	15	7	11	7	13
C. rosea	*	2_2	*	5_3	*	9_4	60	36_2	39_5	2_2
C. saxatilis	9_4	.	.	24_5	.	31_5	.	.	44	.
C. scabrata	*	.	.	8_5	.	45	.	.	33	.
C. scoparia	6_2	2_2	6_3	2_1	3	8	11	10	6	10_5
C. sitchensis	2_1	6_3	19_4	6_3	8_4	23	15	30	15_5	15_5
C. sprengellii	15_3	23	2_1	13_5	4_2	41	20	48	38	43
C. stipata	3_3	10_2	7_3	7_5	6_3	28	18	28	15	32
C. tenera	8_4	4_2	4_5	2_2	14_2	8	13	4	8	10
C. tribuloides	3_3	.	.	25_3	.	39	.	.	6	.
C. trisperma	2_1	.	.	8_4	.	37_5	.	.	29	.
C. vulpinoidea	*	6_1	10	*	8_5	29_3	10	10	7	15

Table 16. Total germination and onset of germination for the Overwintered Lath House experiment. Average total percent germination in 1997 following one winter ($Germ_{97}$) and additional germination at one census time (May 30, 1998) after a second winter ($Germ_{98}$). Earliest (Min), average (Mean), and latest (Max) dates for onset of germination (lag) are shown. Average lags are also shown, measured as the time from the first day that degree-days began accumulating (March 29, 1997) in days (**$Mean_{days}$**) and degree-days (**$Mean_{dd}$**). Blocks refers to the number of blocks in 1997 in which germination occurred therefore showing the number of blocks on which lags were based. Species that germinated above 10% are shown first, sorted by mean lag then total germination and those with germination less than 10% are next, sorted by total germination.

Germination >10%

		Lag						
Species	**$Germ_{97}$**	**Min**	**Mean**	**Max**	**$Mean_{days}$**	**$Mean_{dd}$**	**Blocks**	**$Germ_{98}$**
C. bebbii	38.7	May 15	May 18	May 23	51	119	6	0.7
C. sitchensis	31.3	May 15	May 18	May 20	51	118	6	0.7
C. canescens	48.7	May 15	May 20	May 27	53	130	6	0.7
C. aquatilis	31.7	May 15	May 20	May 26	53	128	6	0.7
C. projecta	20.0	May 17	May 20	May 26	53	133	6	0.0
C. cephaloidea	48.3	May 16	May 21	May 28	54	135	6	0.3
C. kelloggii	39.3	May 15	May 21	May 30	54	141	6	1.0
C. trisperma	84.0	May 17	May 22	May 29	55	143	5	2.4
C. gracillima	30.7	May 16	May 22	May 26	55	145	6	2.0
C. scoparia	28.7	May 19	May 22	May 28	55	141	6	0.7
C. leptalea	18.0	May 16	May 22	May 28	55	145	5	1.0
C. deweyana	58.0	May 19	May 23	May 26	56	147	6	1.3
C. communis	52.0	May 16	May 23	Jun 06	56	157	6	1.0
C. disperma	51.3	May 20	May 23	May 26	56	151	6	0.3
C. arctata	48.0	May 15	May 23	May 27	56	151	5	0.7
C. prasina	38.7	May 16	May 23	May 30	56	153	6	0.3
C. tribuloides	33.3	May 16	May 23	May 27	56	148	6	1.0
C. appalachica	32.7	May 19	May 23	May 26	56	147	6	2.0
C. albursina	24.4	May 16	May 23	May 29	56	150	5	5.2
C. lurida	23.3	May 15	May 23	May 31	56	156	6	0.0
C. incurva	20.4	May 16	May 23	May 29	56	147	5	1.2
C. saxatilis	20.3	May 16	May 23	Jun 02	56	156	6	0.7
C. echinata	15.3	May 16	May 23	May 26	56	149	6	0.0

Table 16 cont'd

Germination >10%

Species	$Germ_{97}$	Lag Min	Lag Mean	Lag Max	$Mean_{days}$	$Mean_{dd}$	Blocks	$Germ_{98}$
C. tenera	12.7	May 17	May 23	May 26	56	147	6	1.3
C. hirtifolia	11.3	May 19	May 23	May 27	56	148	6	27.0
C. aurea	46.3	May 15	May 24	Jun 02	57	166	6	1.0
C. novae-angliae	35.0	May 20	May 24	May 29	57	159	6	3.0
C. stipata	22.3	May 15	May 24	May 29	57	155	6	0.3
C. scabrata	51.3	May 15	May 25	Jun 01	58	166	6	1.3
C. sprengelii	22.0	May 15	May 25	May 29	58	161	6	0.3
C. lupulina	14.7	May 15	May 25	Jun 04	58	175	6	1.0
C. paupercula	29.3	May 19	May 27	Jun 11	60	195	6	0.3
C. gynandra	24.7	May 20	May 27	Jun 12	60	191	6	0.7
C. vulpinoidea	12.3	May 23	May 27	May 31	60	177	6	0.3
C. rugosperma	54.0	May 24	May 29	Jun 07	62	204	6	0.3
C. laxiflora	20.7	May 20	May 29	Jun 13	62	213	6	1.0
C. normalis	17.7	May 17	May 29	Jul 04	62	239	6	0.7
C. platyphylla	16.0	May 19	May 29	Jun 06	62	205	6	6.0
C. crinita	15.7	May 19	May 29	Jun 21	62	215	6	1.0
C. norvegica	36.5	May 19	May 30	Jun 24	63	243	4[a]	0.0
C. michauxiana	14.0	May 15	Jun 04	Jul 28	68	315	6	0.3
C. pedunculata	27.7	May 24	Jun 06	Jul 04	70	312	6	0.3

Germination <10%

Species	$Germ_{97}$	Lag Min	Lag Mean	Lag Max	$Mean_{days}$	$Mean_{dd}$	Blocks	$Germ_{98}$
C. rosea	9.7	May 23	May 28	Jun 07	61	189	6	1.7
C. bromoides	9.3	May 24	May 31	Jun 21	64	226	6	0.0
C. pauciflora	9.0	May 17	May 30	Jun 11	63	221	6	0.3
C. backii	8.4	May 19	May 31	Jun 27	64	244	4[b]	6.0
C. debilis	8.3	May 17	May 30	Jun 14	63	229	6	3.7
C. flava	6.0	May 22	May 22	May 22	55	139	1[c]	0.0
C. plantaginea	4.3	May 15	May 20	May 29	53	133	5	0.3
C. capitata	3.7	May 23	May 26	May 30	59	170	5	0.0
C. intumescens	2.7	May 24	May 26	May 29	59	172	1[d]	0.7

[a] *C. norvegica*: only four blocks were planted because of lack of seed.
[b] *C. backii*: only four blocks were planted because of lack of seed.
[c] *C. flava*: only one block was planted because of lack of seed.
[d] *C. intumescens:* only two blocks were planted because of lack of seed.

germinants were noted. Additionally, as seedlings were not removed at every census time, seed numbers during inter-harvest periods should have been cumulative but were not always so. Drops may have occurred because the seedlings died or were buried by mud, only to resurface later. I therefore calculated total germination as the sum of the maximum number of seedlings recorded at any one time during each inter-harvest period. I calculated lag as the time when the first germinant was observed in a pot even if the number of seedlings in that pot dropped to zero at later census dates.

The bulk of germination in the Overwintered Lath House experiment occurred from mid May to early July when air temperatures ranged from T_{min}= 6°C and T_{max}= 16°C (mid May) to T_{min}=13°C and T_{max}=23°C (early July). Onset of germination was similar among forest and wetland species (Fig.5). At least a few seeds from most species did not germinate until after a second winter; notable species included *Carex hirtifolia* (27%), *C. backii* (6%), *C. albursina* (5%), and *C. debilis* (4%). *C. pedunculata* was one of the last species to initiate germination in 1997 and this time corresponds to about a week before its seeds are normally shed.

Dormancy Check Greenhouse (Table 17). Total germination across species ranged from 0% to 85%. Germination of seeds of many species was much higher than in the Fresh Seed experiments (though they represent different seed collections). Among the species with moderate to high germination (>10%), lags ranged from 11 to 99 days though slightly less than half these species initiated germination within 15 days. Four species, *Carex disperma, C. flava, C. norvegica,* and *C. scabrata,* achieved moderate germination but onset of germination only occurred after a minimum of 60 days from planting, suggesting non-deep physiological dormancy. Total germination was not achieved particularly quickly in most species except for *C. kelloggii*, *C. prasina*, and *C. projecta,* all of which reached 90% of total germination within two weeks of onset of germination. Several species, such as *C. aurea, C. albursina,* and *C. gracillima,* did not germinate well here but did so in the Main experiment. Lags

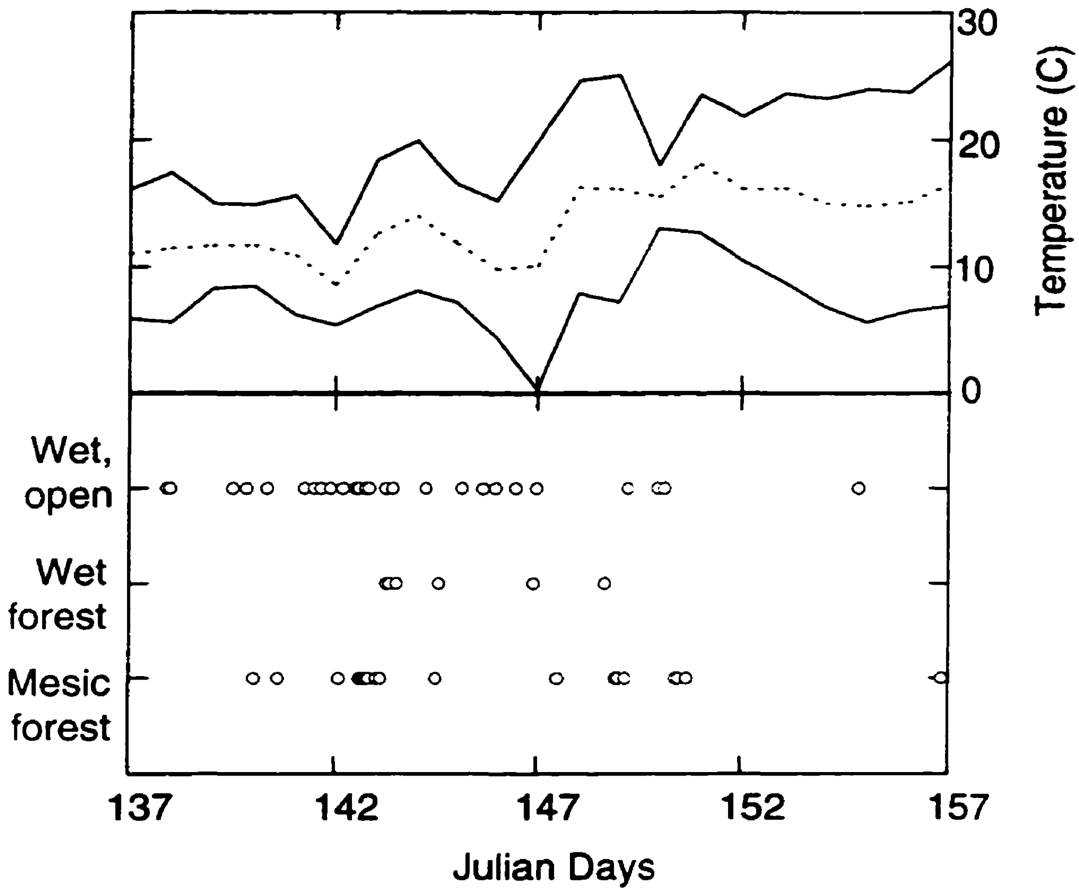


Fig. 5. Daily maximum, average, and minimum air temperatures and onset of germination for 51 *Carex* species in the Overwintered Lath House Experiment. Species are displayed by habitat. Dates range from May 17, 1997 through June 06, 1997.

Table 17. Total germination, lag, and range for the Dormancy Check Greenhouse experiment. Total germination is a percentage and lag and range are measured in days. Blocks refers to the numbers of blocks on which the lag and range are based (number of blocks where germination occurred). Species with germination above 10% are on the left, sorted by lag then range, and those with germination less than 10% are on the right, sorted by germination.

Germination >10%				
Species	**Germ**	**Lag**	**Ran**	**Blocks**
C. aquatilis	59.3	11	33	3
C. tribuloides	64.7	11	26	3
C. kelloggii	84.7	12	9	3
C. projecta	59.3	12	14	3
C. stipata	43.3	12	28	3
C. scoparia	45.3	12	28	3
C. normalis	22.7	12	30	3
C. canescens	65.3	12	35	3
C. bebbii	33.3	12	36	3
C. tenera	14.7	12	63	3
C. prasina	45.3	13	12	3
C. lurida	66.0	15	49	3
C. cephaloidea	53.3	15	66	3
C. incurva	14.0	16	62	3
C. deweyana	68.0	16	35	3
C. gynandra	29.3	18	32	3
C. arctata	81.3	21	42	3
C. pedunculata	58.7	23	28	3
C. saxatilis	22.0	24	83	3
C. communis	70.0	26	38	3
C. rugosperma	66.0	29	36	3
C. paupercula	42.7	30	58	3
C. trisperma	20.7	31	70	3
C. novae-angliae	23.3	35	28	3
C. sprengelii	35.3	46	48	3
C. laxiflora	25.3	53	54	3
C. norvegica	24.0	63	62	3
C. scabrata	22.7	73	44	3
C. flava	42.0	96	29	3
C. disperma	18.0	99	25	3

Germination <10%				
Species	**Germ**	**Lag**	**Ran**	**Blocks**
C. albursina	8.7	42	18	3
C. crinita	8.7	49	75	3
C. sitchensis	8.0	15	74	3
C. gracillima	6.7	15	59	2
C. echinata	5.3	113	12	1
C. rosea	4.7	70	47	3
C. platyphylla	4.0	57	4	2
C. debilis	3.3	51	14	2
C. plantaginea	2.7	62	55	2
C. michauxiana	1.3	71	3	2
C. appalachica	0.7	113	4	1
C. aurea	0.7	15	1	1
C. backii	0.7	84	2	1
C. bromoides	0.7	54	1	1
C. capitata	0.7	113	4	1
C. hirtifolia	0.7	39	2	1
C. intumescens	0.7	121	3	1
C. lupulina	0.7	91	2	1
C. vulpinoidea	0.7	19	1	1
C. leptalea$_{Y}$	0.0	.	.	0
C. pauciflora	0.0	.	.	0

were generally long among most species, especially those with low (<10%) germination; though onset of germination in seeds of three species with low germination, *C. sitchensis*, *C. gracillima*, and *C. aurea,* occurred within 15 days. Species from the section Ovales accounted for five of the eleven species with the shortest lags. Ranges were particularly variable among species with low germination but this is likely due to the confounding effect of few seeds on which to base the range.

Fresh Seed Lath House (Table 18). Total germination across species ranged from 0% to 29%. Only species whose seeds ripened in late June or early July germinated more than 10%. Germination of several species, including *Carex pedunculata,* was dramatically reduced (70.7% to 0.3%) in this experiment compared to the Fresh Seed Greenhouse experiment. *Carex bromoides* was the only exception. Lags were also much longer in the lath house than in the greenhouse among species with moderate to high (>10%) germination. Seeds of some species only germinated after a second winter, but only those of *C. hirtifolia* reached 10% germination by the single census date, May 30, 1998.

Fresh Seed Greenhouse (Table 19). Total germination across species ranged from 0% to 76%. Darkness had a strong inhibitory effect on seeds of all species including *Carex pedunculata*, the only species in the Main experiment whose total germination was unquestionably unaffected by natural light (vs. darkness). Germination was low for most species and there was no pattern with respect to seed ripening date, habitat, or phylogenetic section in evidence among those species that did germinate well (e.g., *C. prasina*, *C. pedunculata*, *C. arctata*, and *C. canescens).* Onset of germination for some species, such as *C. echinata* and *C. stipata*, took more than 60 days while others, such as *C. gynandra* and *C. cephaloidea*, occurred on days 13 and 17, respectively. *Carex pedunculata* germinated better in the light during this experiment than in any other experiment, regardless of treatment.

Table 18. Planting date, total germination and lag for the Fresh Seed Lath House Experiment. Total germination in 1997 ($Germ_{97}$) and at one census time (May 30) the following year ($Germ_{98}$) are percentages. Minimum, mean, and maximum lag in days are shown and mean lag in degree-days is also shown for 1997 germination. Blocks refers to the number of blocks in which germination occurred therefore representing the number of blocks on which lag is based. Species with germination greater than 10% are shown first, sorted by mean lag then total germination, followed by those with less than 10% germination, sorted by total germination.

Germination >10%

			Lag_{days}			Lag_{dd}		
Species	**$Germ_{97}$**	**Date planted**	**Min**	**Mean**	**Max**	**Mean**	**Blocks**	**$Germ_{98}$**
C. bromoides	14.3	Jul 02	Jul 29	Jul 29	Jul 29	389	5	1.7
C. stipata	12.0	Jul 02	Jul 29	Jul 29	Jul 29	389	5	1.3
C. deweyana	29.0	Jul 10	Jul 31	Aug 12	Sep 01	483	6	0.7
C. prasina	19.3	Jul 10	Jul 29	Aug 12	Sep 23	475	6	2.3
C. sprengellii	10.0	Jun 26	Jul 29	Aug 07	Aug 17	639	5	3.7
C. arctata	23.0	Jun 24	Jul 29	Aug 06	Sep 09	643	5	6.3

Table 18 cont'd.

Germination <10%			Lag$_{days}$			Lag$_{dd}$		
Species	Germ$_{97}$	Date planted	Min	Mean	Max	Mean	Blocks	Germ$_{98}$
C. canescens	5.0	Aug 08	Aug 09	Aug 24	Sep 01	212	3	1.0
C. crinita	2.7	Jul 16	Aug 04	Aug 19	Sep 09	467	5	1.0
C. cephaloidea	2.3	Jul 11	Jul 29	Aug 07	Aug 17	403	3	1.7
C. communis	1.0	Jun 20	Sep 09	Sep 09	Sep 09	1143	1	1.0
C. gracillima	1.0	Jun 24	Aug 24	Aug 24	Aug 24	888	1	5.0
C. platyphylla	1.0	Jun 26	Jul 29	Aug 08	Aug 17	657	3	5.7
C. backii	0.3	Jul 10	Sep 01	Sep 01	Sep 01	742	1	0.3
C. disperma	0.3	Aug 8	Aug 11	Aug 11	Aug 11	43	1	0.0
C. hirtifolia	0.3	Jun 26	Aug 17	Aug 17	Aug 17	781	1	10.0
C. laxiflora	0.3	Jun 30	Sep 09	Sep 09	Sep 09	974	1	2.3
C. pedunculata	0.3	Jun 11	Sep 09	Sep 09	Sep 09	1266	1	0.0
C. rugosperma	0.3	Jun 10	Sep 01	Sep 01	Sep 01	1198	1	0.0
C. albursina	0.0	Jul 01	.	.	.	.	0	9.0
C. appalachica	0.0	Jul 16	.	.	.	.	0	1.0
C. debilis	0.0	Aug 14	.	.	.	.	0	2.3
C. echinata	0.0	Aug 08	.	.	.	.	0	0.0
C. gynandra	0.0	Jul 16	.	.	.	.	0	0.7
C. intumescens	0.0	Aug 08	.	.	.	.	0	0.0
C. lurida	0.0	Sep 06	.	.	.	.	0	2.0
C. michauxiana	0.0	Aug 08	.	.	.	.	0	1.3
C. normalis	0.0	Sep 06	.	.	.	.	0	0.0
C. plantaginea	0.0	Jun 17	.	.	.	.	0	3.3
C. projecta	0.0	Sep 06	.	.	.	.	0	0.3
C. rosea	0.0	Jul 16	.	.	.	.	0	1.7
C. scabrata	0.0	Aug 12	.	.	.	.	0	2.3
C. tenera	0.0	Sep 06	.	.	.	.	0	0.0
C. vulpinoidea	0.0	Sep 06	.	.	.	.	0	0.0

Table 19. Total germination, lag, and range for the Fresh Seed Greenhouse experiment averaged over blocks. Planting dates are in 1997. Total germination is a percentage and lag and range are measured in days. Blocks refer to the number of blocks on which the lag and range are based (number of blocks where germination occurred). Species in the first group have germination greater than 10%, sorted by lag (light) then range, and those in the second group have germination less than 10%, sorted by total germination.

Germination>10%		**Light**				**Dark**			
Species	**Planted**	**Germ**	**Lag**	**Range**	**Blocks**	**Germ**	**Lag**	**Range**	**Blocks**
C. gynandra	Aug. 02	13.3	Aug 15	13	2	0.0	.	.	0
C. cephaloidea	Jul. 18	36.0	Aug 04	22	3	0.0	.	.	0
C. arctata	Jun. 27	61.3	Jul 14	54	3	0.0	.	.	0
C. pedunculata	Jun. 27	70.7	Jul 14	17	3	9.3	Aug 07	18	3
C. deweyana	Jul. 18	48.7	Aug 06	24	3	0.7	Sep 14	2	1
C. prasina	Jul. 18	76.0	Aug 09	18	3	0.0	.	.	0
C. sprengellii	Jul. 07	16.0	Aug 19	34	3	0.0	.	.	0
C. communis	Jun. 27	36.0	Aug 15	65	3	0.0	.	.	0
C. canescens	Aug. 06	51.3	Oct 01	26	3	0.0	.	.	0
C. stipata	Jul. 07	12.0	Sep 06	43	2	0.0	.	.	0
C. echinata	Aug. 06	26.0	Oct 11	13	3	0.0	.	.	0

Table 19 cont'd.

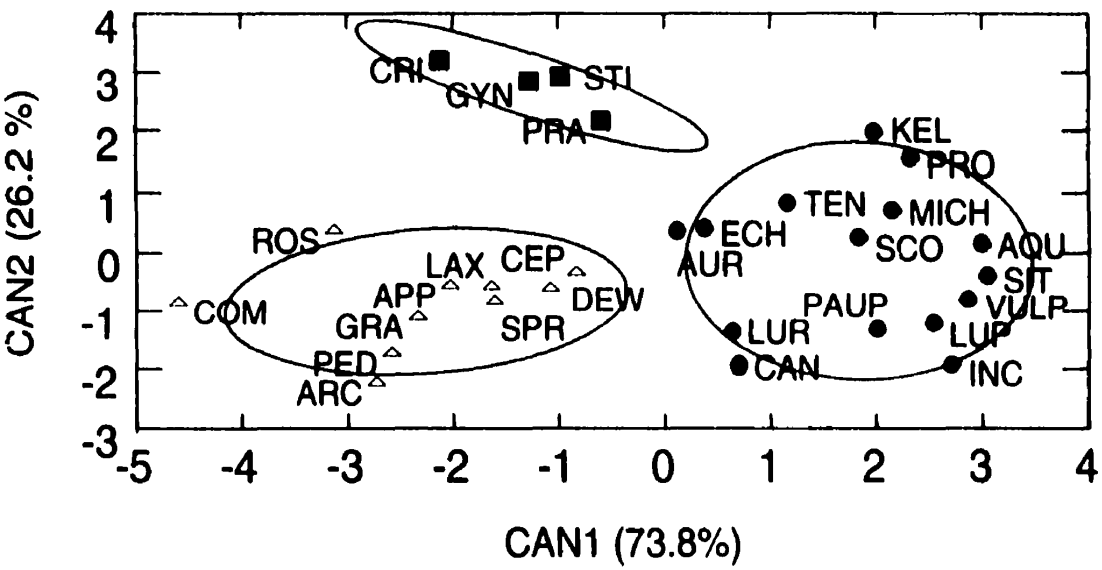
Germination<10%		**Light**				**Dark**			
Species	**Planted**	**Germ**	**Lag**	**Range**	**Blocks**	**Germ**	**Lag**	**Range**	**Blocks**
C. normalis	Sept. 09	3.3	Oct 12	2	2	0.7	Oct 26	2	1
C. tenera	Sept. 09	2.7	Oct 26	5	2	0.0	.	.	0
C. rugosperma	Jun. 27	2.0	Aug 23	29	2	0.7	Sep 10	2	1
C. bromoides	Jul. 07	1.3	Oct 14	4	1	0.0	.	.	0
C. gracillima	Jun. 27	1.3	Jul 20	13	1	0.0	.	.	0
C. disperma	Aug. 06	0.7	Sep 18	2	1	0.0	.	.	0
C. laxiflora	Jul. 07	0.7	Nov 14	4	1	0.0	.	.	0
C. projecta	Sept. 09	0.7	Nov 07	4	1	0.0	.	.	0
C. albursina	Jul. 07	0.0	.	.	0	0.0	.	.	0
C. appalachica	Jul. 18	0.0	.	.	0	0.0	.	.	0
C. backii	Jul. 18	0.0	.	.	0	0.0	.	.	0
C. crinita	Jul. 18	0.0	.	.	0	0.0	.	.	0
C. debilis	Aug. 15	0.0	.	.	0	0.0	.	.	0
C. hirtifolia	Jul. 07	0.0	.	.	0	0.0	.	.	0
C. intumescens	Aug. 06	0.0	.	.	0	0.0	.	.	0
C. lupulina	Sept. 16	0.0	.	.	0	0.0	.	.	0
C. lurida	Sept. 09	0.0	.	.	0	0.0	.	.	0
C. michauxiana	Aug. 06	0.0	.	.	0	0.0	.	.	0
C. plantaginea	Jun. 27	0.0	.	.	0	0.0	.	.	0
C. platyphylla	Jul. 07	0.0	.	.	0	0.0	.	.	0
C. rosea	Jul. 18	0.0	.	.	0	0.0	.	.	0
C. vulpinoidea	Sept. 09	0.0	.	.	0	0.0	.	.	0

Canonical Discriminant Analysis. *Habitat.* The three habitat groups were well separated (Fig. 6). The first canonical axis represented 73.8% of the variance and separated mesic deciduous forest species from those growing in wetland or seasonally flooded habitats. It was mainly determined by three inverse lags: L4SL, L2ML, and L4ML (Table 20). The first two were positively weighted and acted against the last, negatively weighted variable. Fig. 7 shows that while linear relationship between the first canonical axis and L4ML was not particularly strong ($R^2 = 0.0419$), there was a positive linear relationship with the first canonical axis and both L2ML ($R^2 = 0.1953$) and L4SL ($R^2 = 0.5486$). This suggests that onset of germination in the light was similar across all habitats after four months of moist stratification but was generally slower in mesic deciduous forest (vs. wetland or periodically flooded habitat) species after four months of submerged stratification or two months of moist stratification. (Recall that these numbers represent inverse lags and therefore higher numbers mean faster onset of germination.)

The second canonical axis represented 26% of the variance and separated wet forest species from mesic deciduous forest species (Fig. 6). Four variables were heavily weighted on this axis: germination in the Main experiment in the light after no stratification (G0XL) and after moist stratification (GML), the inverse of time to onset of germination in the light after four months of moist stratification (L4ML), and germination in the Dormancy Check Greenhouse experiment (GDCGH) (Table 20). All of these variables had squared correlation of less thatn 0.05 with the second canonical axis (Fig. 8). However, wet forest species had values of L4ML that were at the higher range of mesic deciduous forest species values, so there was a slight difference between the groups. In wet forest species, therefore, onset of germination in the light after four months of moist stratification was as fast as in the fastest mesic deciduous forest species.

Phylogeny. Phylogenetic groups were not as distinct as habitat groups (Fig.9) though three clustered fairly well: IC (*Phacocystis, Bicolores, Anomalae*), KV (*Ovales*), and JC (*Clandestinae, Folliculatae, Limosae, Lupulinae, and*

Fig. 6. Plot of the first and second canonical axes resulting from a canonical discriminant analysis with habitat as the classification variable. Habitats include mesic forest (△), wet forest (■), and wet, open canopy (●). Species names are shortened to the first three or four letters. Ellipses represent a 68.3% confidence interval. Axes are proportional to percent variance.



CAN2 (26.2 %)
CAN1 (73.8%)
CRI
GYN
STI
PRA
KEL
PRO
TEN
MICH
ECH
AUR
SCO
AQU
SIT
VULP
PAUP
LUR
LUP
CAN
INC
ROS
LAX
CEP
APP
DEW
COM
GRA
SPR
PED
ARC
4
3
2
1
0
-1
-2
-3
-5
-4
-3
-2
-1
0
1
2
3
4

Table 20. Total sample standardized canonical coefficients from a canonical discriminant analysis using habitat as the classification variable. Coefficients are proportions of the largest (absolute value) loading on any axis. Numeric variables include total germination (G) and inverse lag (L). Treatment labels in the Main experiment include 0, 2, or 4 months stratification (0X, 2, or 4), moist or submerged stratification (M or S), and light or dark treatments (L or D). Where codes are missing (e.g., ML), values were averaged over the missing character (e.g., 2ML and 4ML). Germination and inverse lag in the Dormancy Check Greenhouse (DCGH) experiment and germination in the Overwintered Lath House (OLH) experiment are also included. Variables that are most heavily weighted are in bold.

		Can1	Can2
Main	G0XD	-0.0846	0.0615
Main	G0XL	-0.3809	**0.9574**
Main	GMD	0.2014	0.1215
Main	GML	0.3554	**-0.9086**
Main	G2SL	-0.0528	-0.2216
Main	G4SL	-0.2769	0.5393
Main	L0XL	-0.0391	-0.4487
Main	L2ML	**0.4209**	-0.3785
Main	L4ML	**-0.6560**	**1.0000**
Main	L2SL	-0.2560	0.2315
Main	L4SL	**1.0000**	-0.5134
	GDCGH	0.2470	**-0.7434**
	LDCGH	0.0232	0.5915
	GOLH	-0.2110	-0.3439

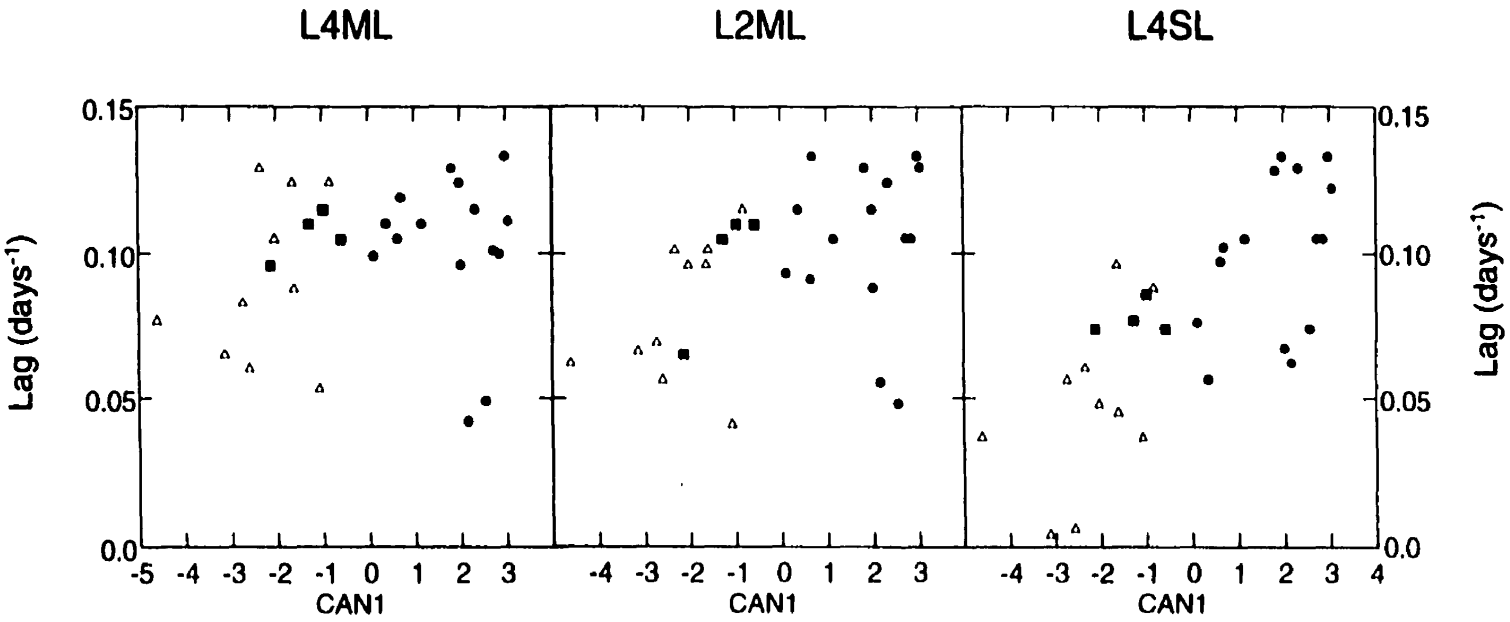


Fig. 7. Plots of inverse lags (days^{-1}) for 4ML, 2ML, and 4SL treatments (cf. Table 4) against position on the first canonical axis. Position on the first canonical axis results from a canonical discriminant analysis with habitat as the classification variable. Habitats include mesic forest (▵), wet forest (▪), and open canopy, wet habitats (•).

Fig. 8. Plots of inverse lag ($days^{-1}$) for the 4ML treatment of the Main experiment (cf. Table 4) and germination (%) for the Dormancy Check Greenhouse experiment, and ML and 0XL treatments of the Main experiment (cf. Table 4) against position on the second canonical axis. Position on the second canonical axis results from a canonical discriminant analysis with habitat as the classification variable. Habitat includes mesic forest (▵), wet forest (▪), and wet, open canopy (•).

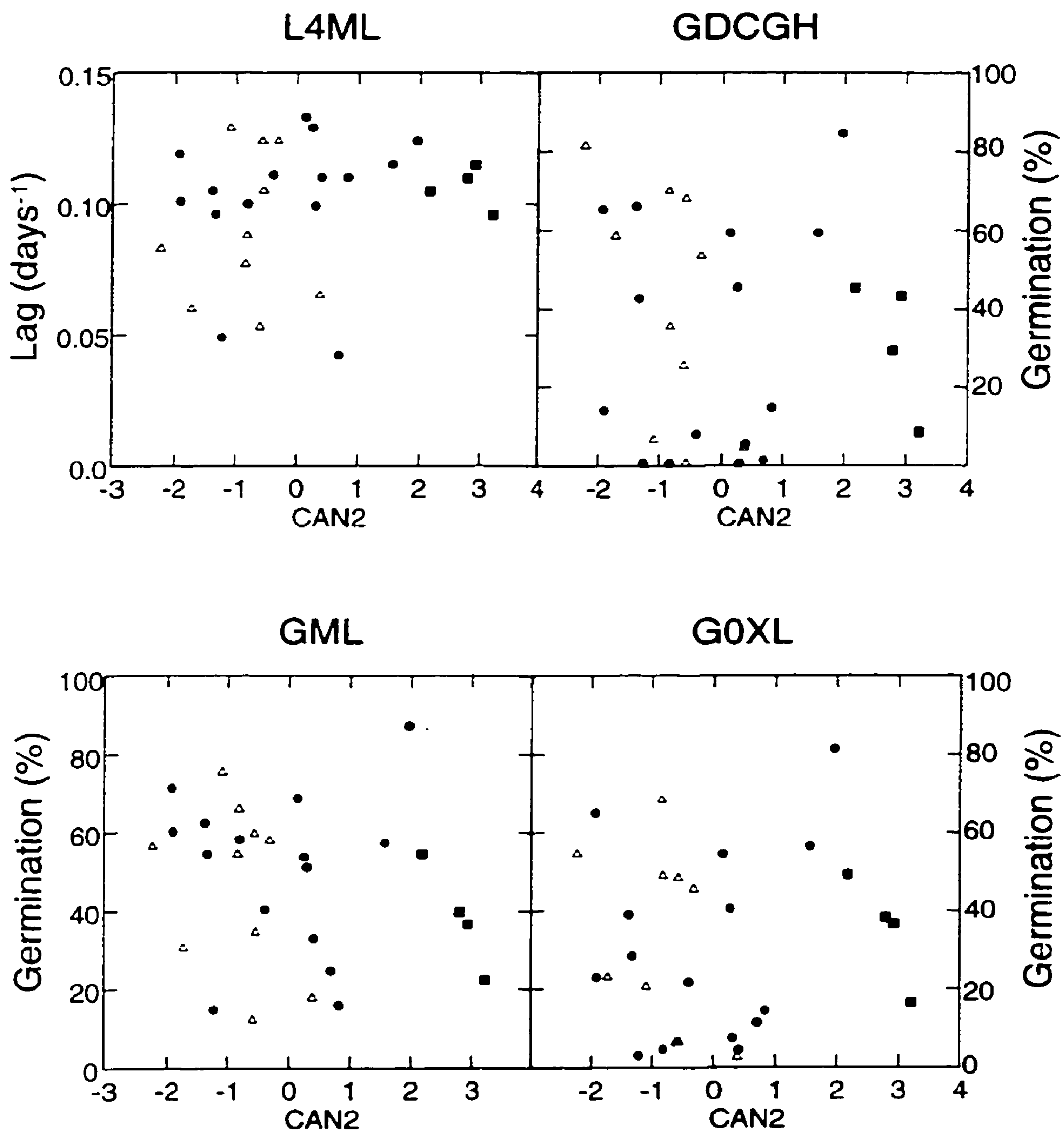
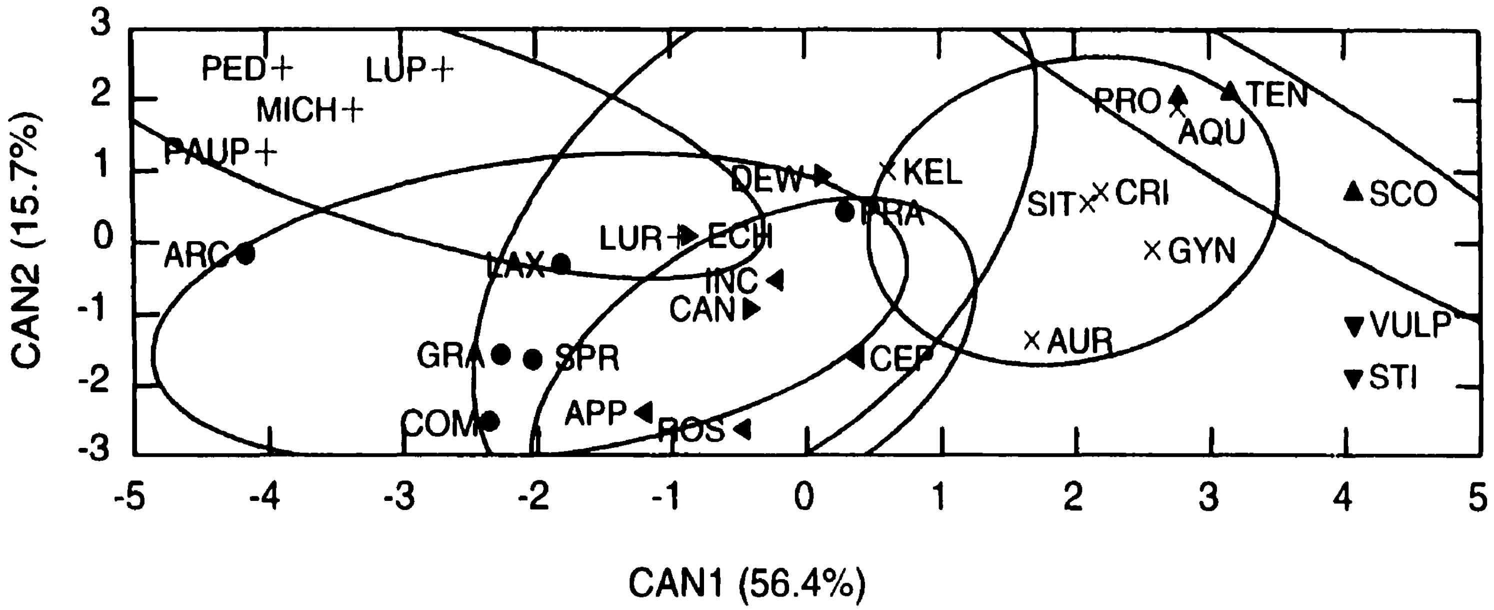

L4ML
GDCGH
GML
G0XL
Lag (days-1)
Germination (%)
CAN2
0.15
0.10
0.05
0.0
100
80
60
40
20
0
-3
-2
-1
0
1
2
3
4

Fig. 9. Plot of the first and second canonical axes resulting from a canonical discriminant analysis with taxonomic groups as the classification variable. Taxonomic groups in the subgenus *Carex* include species in the *Acrocystis, Hymenochlaenae, Laxiflorae, Careyanae,* or *Halleranae* (●), *Phacocystis, Bicolores*, or *Anomalae* (×), *Clandestinae*, *Folliculatae, Limosae, Lupulinae*, or *Vesicariae* (+). Groups in the *Vignea* subgenus include species in the *Ovales* (▲), *Multiflorae* and *Lupulinae* (▼), *Phaestoglochin* or *Foetidae* (◀), *Deweyanae, Glareosae*, or *Stellulatae* (▶). Species names are shortened to the first three or four letters. Axes are proportional to percent variance.



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CRI
GYN
AUR
SCO
VULP
STI
CAN2 (15.7%)
CAN1 (56.4%)

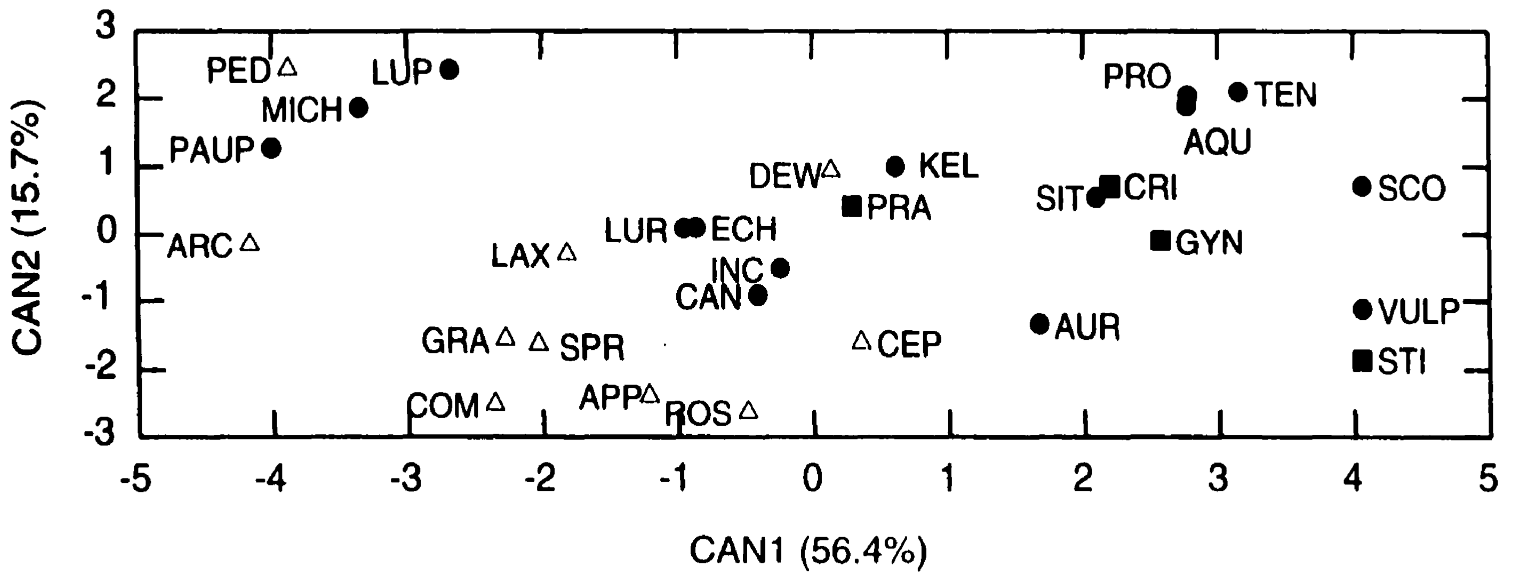
Vesicariae). Because many groups had few members, it is difficult to make generalizations about specific groups. In contrast, when habitat was mapped onto the same graph, an obvious distinction between species from mesic and wet habitats emerged (Fig. 10). Phylogenetic groups from similar habitats tended to cluster together, while phylogenetic groups from the same subgenera did not. There were a few exceptions, such as wet-habitat species *Carex michauxiana, C. paupercula*, and *C. lupulina* and forest species *C. pedunculata*, but these are best described in context of the loadings.

The first canonical axis represented 56.4% of the variance and was a submersion axis. It was predominantly determined by two inverse lags, L4SL and L2SL (Table 21) . The squared correlations for L4SL and L2SL with the first canonical axis were 0.4364 and 0.5485, respectively. The plot of L2SL vs CAN1 had a steeper slope because the values of L2SL for mesic deciduous forest species were much lower than those of L4SL. However, the values of L2SL and L4SL for species of wetlands or seasonally flooded habitats were not different. This means that the onset of germination was about the same after two or four months submersion in most wet-habitat species but was much improved after four months submersion (versus two months) in mesic deciduous forest species (Fig. 11). *Carex michauxiana, C. paupercula*, and *C. lupulina* were apparently more similar to forest species in this respect than to species from wetlands or seasonally flooded areas.

The second canonical axis (CAN2) represented 15.7% of the variance. Although inverse lag after four months of submersion (L4SL) and germination in the light after two months of submersion (G2SL) were heavily weighted on this axis (Table 20), G2SL and CAN2 had a squared correlation of 0.0019 while L4SL and CAN2 have a squared correlation of 0.1238 (Fig. 12). However, this does not explain why *Carex pedunculata* was at the extreme positive end of the axis and I have found no reason for this to be so.

Principal Components Analysis. The first and second principal component axes represented 53.4% and 19.5% of the variance, respectively.

Fig. 10. Plot of the first and second canonical axes resulting from a canonical discriminant analysis with section as the classification variable but labelled by habitat. Habitats include mesic forest (△), wet forest (■), and wet, open canopy forest (●). Species names are shortened to the first three or four letters. Axes are proportional to percent variance.



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GYN
AUR
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VULP
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0
-1
-2
-3
-5
-4
-3
-2
-1
0
1
2
3
4
5
CAN2 (15.7%)
CAN1 (56.4%)

Table 21. Total sample standardized canonical coefficients from a canonical discriminant analysis using taxonomic grouping as the classification variable. Coefficients are proportions of the largest (absolute value) loading on any axis. Numeric variables include total germination (G) and inverse lag (L). Treatment labels in the Main experiment include 0, 2, or 4 months stratification (0X, 2, or 4), moist or submerged stratification (M or S), and light or dark treatments (L or D). Where codes are missing (e.g., ML), values were averaged over the missing character (e.g., 2ML and 4ML). Germination and inverse lag in the Dormancy Check Greenhouse (DCGH) experiment and germination in the Overwintered Lath House (OLH) experiment are also included. Variables that are contributing to the separation are in bold.

		CAN1	**CAN2**	**CAN3**
Main	G0XD	-0.0034	0.2677	0.0739
Main	G0XL	0.2700	-0.3587	**1.0000**
Main	GMD	-0.1127	0.1968	-0.4270
Main	GML	**-0.5602**	0.4526	**0.6279**
Main	G2SL	0.0777	**-0.8063**	**-0.6988**
Main	G4SL	0.2038	0.0186	-0.3477
Main	L0XL	-0.2854	-0.0033	-0.4343
Main	L2ML	-0.0950	-0.0997	**-0.6297**
Main	L4ML	0.4864	-0.2462	0.2373
Main	L2SL	**1.0000**	-0.2067	**0.6183**
Main	L4SL	**-0.7677**	**1.0000**	0.0896
	GDCGH	-0.2771	0.4807	-0.3339
	LDCGH	0.1347	0.1094	0.1986
	GOLH	0.0566	-0.4982	-0.0572

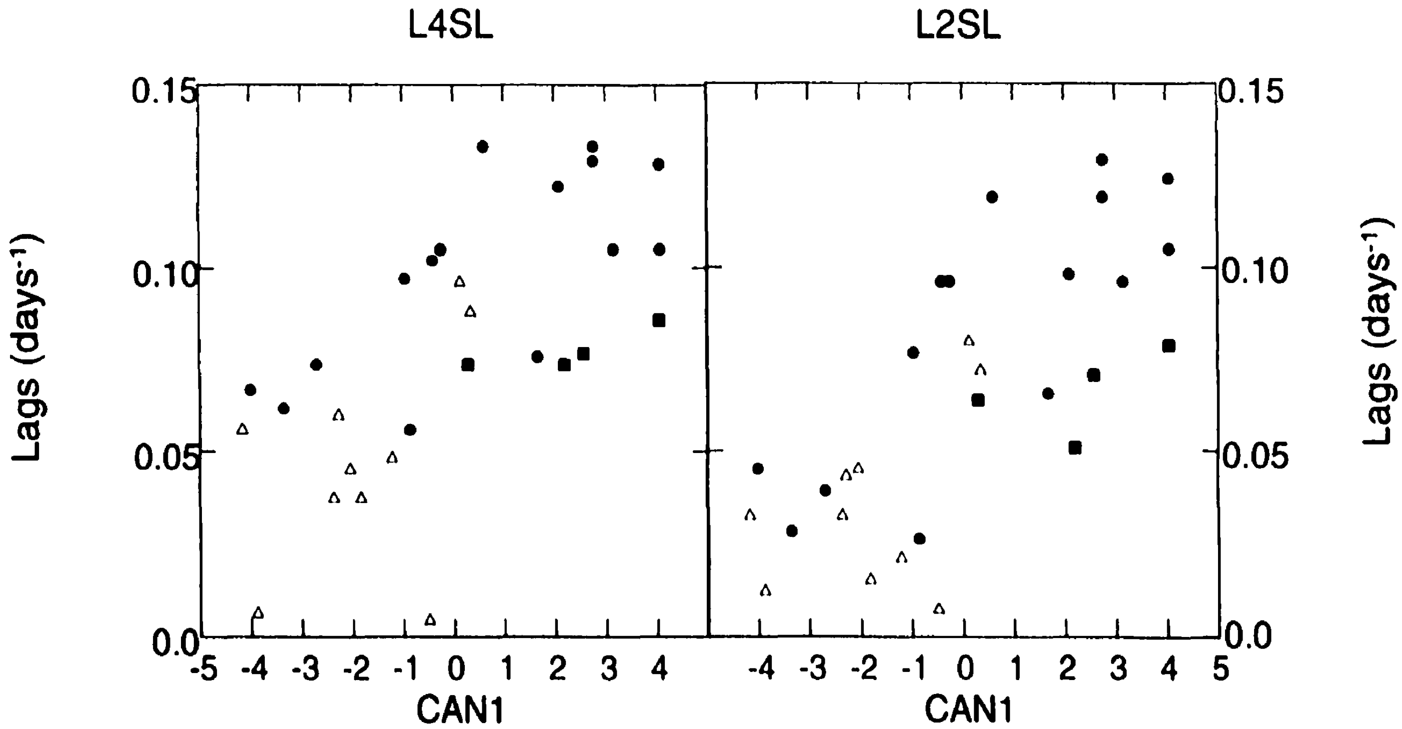

Fig. 11. Plots of inverse lags (days^{-1}) for 4SL and 2SL treatments (cf. Table4) in the Main experiment against position on the first canonical axis. Position on the first canonical axis results from a canonical discriminant analysis with taxonomic group as the classification variable. Plots are labelled by habitat: mesic forest (^), wet forest (■), wet, open canopy (•).

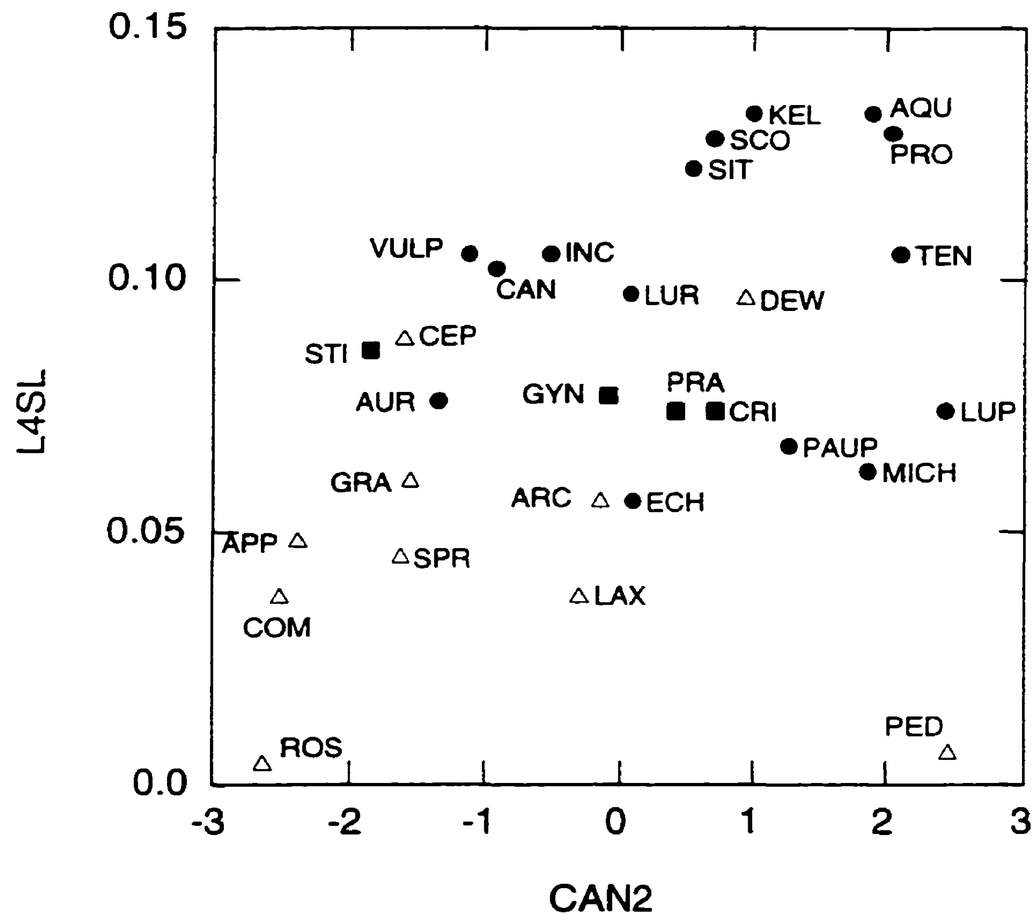

Fig.12. Inverse lag ($days^{-1}$) for L4SL treatment (cf. Table 4) in the Main experiment against position on the second canonical axis. Position on the second canonical axis results from a canonical discriminant analysis with taxonomic group as the classification variable and represents 15.7% of the variance. Plots are labelled by habitat: mesic forest (△), wet forest (■), and wet, open canopy (●). Species names are shortened to the first three or four letters.

Fig. 13 illustrates that much of the variation in germination behaviour observed in these experiments was habitat-based. The greatest distinction lay between species of mesic deciduous forests and those of wetland or seasonally flooded habitats. The seed germination behaviour of species growing in wet areas in the forest were more similar to other species of wet habitats. These findings reflect the results of the CDA: differences observed in germination behaviour are clearly linked to habitat.

Contingency Table. The χ^2 test suggests that phylogenetic group is not independent of habitat (p=0.038) and that species within a given group are more likely to be in similar habitats. Wet forest species were comparatively low in number in the contingency table (Table 22) and I therefore tried grouping them with open, wet species, resulting in a χ^2 with a probability of 0.017. Alternatively, grouping wet forest species with mesic deciduous forest species resulted in a probability of 0.047. Therefore, it seems clear that habitat and phylogenetic grouping are not independent. The plot (Fig. 9) resulting from the CDA analysis using phylogenetic groups (section) showed no separation among subgenera. When the same plot was relabelled by habitat (Fig. 10), habitat groups remained fairly separate. In contrast, when I mapped phylogenetic groups on the corresponding habitat plot (not shown), distinctions were not apparent. Habitat is therefore more likely to be driving any pattern observed in germination behaviour.

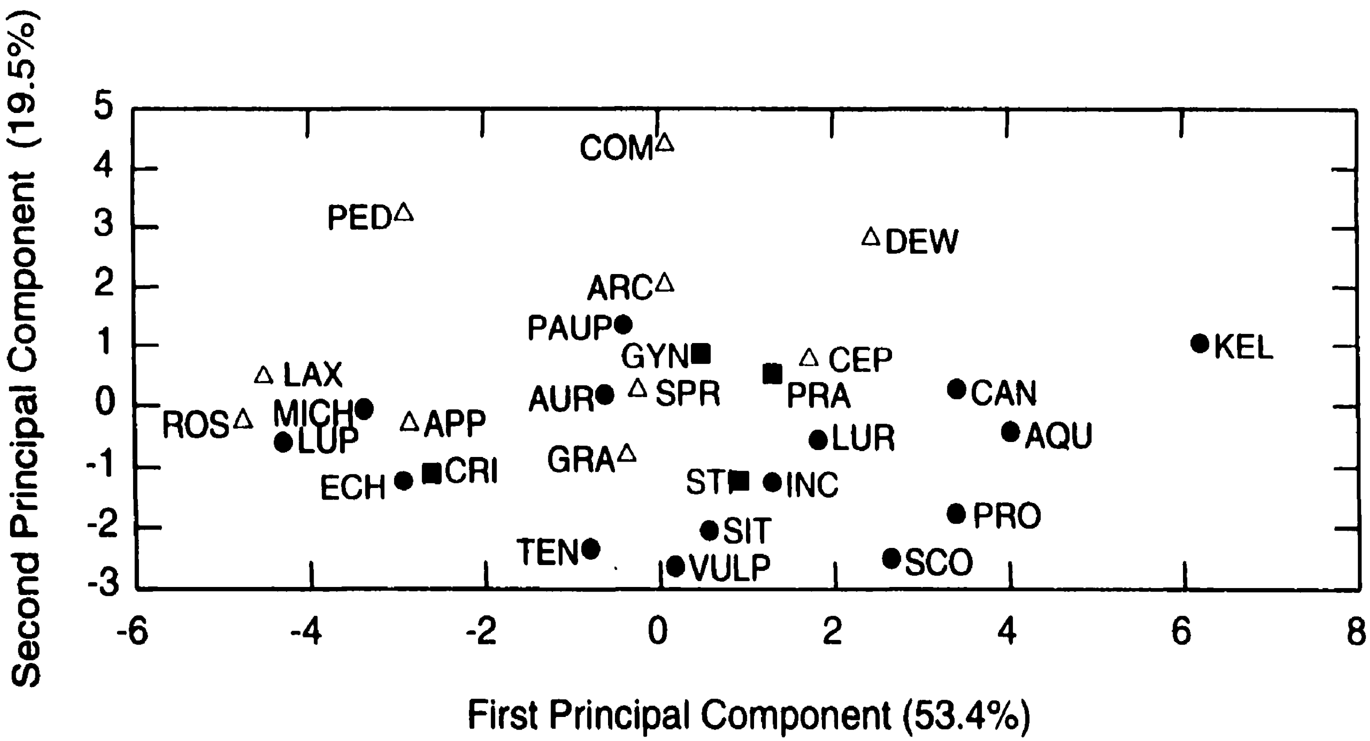

Fig. 13. Principal Components Analysis of the variables used in the Canonical Discriminant Analysis. Mesic forest (▵), wet forest (■) and open, wet habitats (●). Species names are shortened to the first three or four letters. Axes are proportional to percent variance.

Table 22. Frequency of taxonomic groups (cf. Table 8) in three habitats: mesic forest, wet forest, and wet, open canopy habitats.

Group	Mesic Forest	Wet Forest	Wet, Open	Total
HC	5	1	0	**6**
IC	0	2	4	**6**
JC	1	0	4	**5**
KV	0	0	3	**3**
LV	0	1	1	**2**
MV	3	0	1	**4**
NV	1	0	2	**3**
Total	**10**	**4**	**15**	**29**

Discussion

It is generally believed that germination responses to environmental stimuli result from adaptations to local environmental conditions (Thompson, 1981; Fenner, 1985; Baskin and Baskin, 1998). The results from these analyses clearly demonstrate that for those *Carex* species tested, germination behaviour was strongly linked to habitat. Germination of fresh seeds in almost all species was very low or zero but increased with dry storage and/or stratification, suggesting physiological dormancy; Steshenko (1966), Grime et al. (1981), and Schütz (1997b) reported similar after-ripening effects in *Carex* seeds. Much of the variation among seeds from different habitats was reflected in the seeds' responses to storage, especially submerged stratification. Germination of seeds from mesic deciduous forest species was lower and slower after submerged stratification than after moist stratification, suggesting that submersion was less effective in breaking dormancy and/or may have killed many of these seeds. This agrees with previous observations that dormancy release is usually an aerobic process (Bewley and Black, 1994; Baskin and Baskin, 1998) and that, in some seeds, such as *Digitaria ischaeum* (Comes et al., 1978) and *Rumex acetosa* (Voesenek and Blom, 1992), embryos are killed by flooding. In contrast, seeds of many - though not all - species from wet areas in deciduous forests, wetlands, and seasonally flooded habitats germinated equally well after moist or submerged stratification and in four species (*C. lupulina, C. lurida, C. tenera,* and *C. vulpinoidea*), all from seasonally flooded habitats, germination was faster and/or greater after submersion. As seedling colonization in wetland or seasonally flooded habitats usually occurs immediately after spring flood waters recede (Harris and Marshall, 1963; Meeks, 1969; Schneider, 1994), seeds from mesic forest species would be at a disadvantage in a wet habitat. Therefore, the ability to survive and come out of dormancy under submerged, anaerobic conditions may be important in creating a species distribution barrier.

The weakness of this interpretation is that seeds of four species (*Carex aurea, C. canescens, C. echinata,* and *C. paupercula*) from wetland or seasonally flooded habitats germinated less and/or more slowly after submerged than after moist stratification. There are few examples in the literature of submersion causing this effect in wetland seeds, though this may reflect infrequent testing of submersion as a stratification treatment. One such example is *Leucospora multifida* (Scophulariaceae), a mudflat species whose seeds were prevented from breaking dormancy under submerged conditions (Baskin and Baskin, 1994). However in this instance, if dormancy loss in seeds of *Leucospora multifida* began the preceding fall (i.e., in aerobic conditions), then it continued through winter even under submerged conditions, though not to the same extent (Baskin and Baskin, 1994). This may have occurred in these four *Carex* species because seeds in this study were subject to dry storage before stratification and most germinated to some degree in the Dormancy Check Greenhouse experiment, both suggesting that dormancy loss could have begun in these seeds prior to stratification. However, the adaptive advantage of such behaviour is not readily apparent.

Alternatively, seeds of these *Carex* species may not normally be subjected to submersion either because they germinate in the year of dispersal or seeds are dispersed to areas that are not flooded during the winter. While fresh seeds of *Carex canescens* and *C. echinata* germinated in the greenhouse, onset of germination only occurred after 56 and 66 days, respectively. Seeds of both species ripened in August and frost normally occurs in October, therefore making germination of fresh seeds unlikely to lead to successful establishment. Germination in the Fresh Seed Lath House experiment was also very low in both species. *Carex aurea* and *C. paupercula* were not included in the Fresh Seed experiments. *Carex aurea* was found growing on a gravelly substrate near the edge of a small stream while the other three species were found growing in sphagnum moss. In neither habitat were seeds likely to fall into open water so perhaps the ability to survive or lose dormancy during submersion is not required in seeds of these species for successful establishment.

In addition to differences in the effects of submersion on germination behaviour, habitats also differed on the basis of seed responses to moist stratification. Seed germination in all mesic deciduous forest species was greater and faster after moist stratification than after dry storage, with two exceptions: *Carex pedunculata* and *C. communis*. Seeds of these species are both ant-dispersed (Handel, 1976, 1978), ripen early in the growing season, and will potentially germinate the same summer (Handel, 1976; this study, Table 18). Ant-dispersal may provide the seeds with an unoccupied microsite (Handel, 1976) that is comparatively rich in nutrients (Beattie, 1985) and therefore suitable for plant growth. Germination in a particularly good site during the year of dispersal may therefore give both species an advantage over congeners. While this may be the case, dark-germination as a proportion of light-germination increased with dry storage (however, recall different seed collections for Fresh Seed and Main experiments), suggesting that fresh seeds may have been conditionally dormant. As stated in the literature review, a conditionally dormant seed will germinate under a narrower range of environmental conditions (e.g., light) than a fully non-dormant seed (Baskin and Baskin, 1998). Beatty (1991) failed to find seeds of *C. pedunculata* in the seedbank despite its presence in the vegetation. Perhaps *C. pedunculata* does not form persistent seedbanks and relies on physical dispersal rather than temporal dispersal to safe-sites. An alternative solution is that Beatty (1991) did not sample ant debris piles, where many of the seeds would be found.

In about half the species of wet habitats (wet deciduous forests, wetlands, and seasonally flooded areas) germination was about the same after moist stratification or dry storage in contrast to most (i.e., not *Carex pedunculata* and *C. communis*) mesic deciduous forests species. Requirements for dry storage and/or stratification may therefore have been satisfied more quickly in these species. Alternatively, moist stratification may have failed to completely remove conditional dormancy such as was the case in *C. comosa* (Baskin et al., 1996). Seeds of six (of nine) of these species germinated more in the dark after submerged stratification than after either moist stratification or dry storage and therefore this latter option is more likely for these species at least.

Though species of wetlands or seasonally flooded habitats and wet areas in deciduous forests were clearly separated in the CDA, I observed no single or simple difference in response to treatments among these species. Schütz (1997a) observed that for caespitose *Carex:* 1) threshold temperatures for germination were very high (>10°C), 2) seeds of wet forest species were able to germinate at slightly lower (not defined) temperatures than those of open, wet habitats, and 3) closed canopies were inhibitory to germination of seeds from both habitats. He concluded that only those *Carex* species capable of germinating at mean spring temperatures of about 7-10°C (i.e., forest species), when the canopy was not fully developed, could successfully establish in a forest (excluding clearings or large gaps). However, the results of my Overwintered Lath House experiment show that the mean date for onset of germination in caespitose wet forest species and caespitose wetland or seasonally flooded species were May 26 and May 25, respectively, and average daily temperatures for the previous five days were T_{min}= 7°C and T_{max}= 16°C. Therefore, at least for the species I tested, though high threshold temperatures were observed, the distinction that Schütz described between species from these two different habitats does not appear to apply.

There may have been a difference in seed germination responses among habitats with respect to temperature or light. Though I did not directly test effects of light intensity or temperature, one of the blocks in the Main experiment received considerably more sunlight than the other two, resulting in higher daytime soil temperatures in that block. This appears to have led to block by light interactions, which were significant almost exclusively for species from wetland or seasonally inundated habitats. Sensitivity to photon flux density (light intensity) has been shown to be species-specific (Ellis et al., 1989) and perhaps these species of open habitats were more responsive to a greater light intensity than those of forested habitats. Germination may also have been stimulated by larger day to night fluctuations in temperature as previously observed in seeds of other wetland species (Thompson et al., 1977; Thompson and Grime, 1983).

While the germination responses of *Carex* species in this study to stratification varied with habitat, effects of soil moisture and light were consistent across all habitats. Significant differences were not observed in the effect of forest soil and wetland soil treatments, possibly because the frequent overhead misting did not allow sufficient differences between soil types to develop. Alternatively, *Carex* species may be very tolerant of a range of soil moisture levels and this may not be a determining factor governing distribution. In contrast, seed germination in almost all species was significantly increased by light, which seems to be a response characteristic of *Carex* seeds (e.g., Amen and Bonde, 1964; Georges and Lazarre, 1983; Haggas et al., 1987). There has been no report to my knowledge of negatively photoblastic *Carex* seeds and only one, *Carex flacca* (Taylor, 1956), of non-dormant seeds that germinate equally well in light and darkness. In this study, the seeds of one species, *Carex pedunculata,* were light-requiring at maturity but gained the ability to germinate in darkness with dry storage. *Carex pedunculata* is ant-dispersed and its fresh seeds will germinate from ant-debris piles outside the perimeter of ant-colonies, close to the soil surface (Handel, 1976). Ant-dispersal is particularly important for *C. pedunculata* because it is a poor competitor (Handel, 1978b) and ant-debris piles provide both an unoccupied and nutrient-rich site (Beattie, 1985). Perhaps it is light-requiring on dispersal to prevent germination in the ant nest, but if it remains in the dark and ungerminated until the following spring, it will attempt to colonize the site whether buried or not. In contrast, though fresh seeds of the other known ant-dispersed species in this study, *C. communis* (Handel, 1978a), germinated, they never fully gained the ability to germinate in the dark. Fresh *C. pilulifera* seeds, also ant-dispersed, only germinated exterior to the ant nests (Kjellson, 1985), suggesting a similar light requirement.

Conclusion

Among those *Carex* species tested, seed germination behaviour was closely linked to habitat. This was particularly evident in the results of the canonical discriminant analysis. Distinctions among habitats were primarily linked to differences in the effects of submerged, and secondarily, moist stratification on seed germination. Submerged stratification was much less effective for seeds of mesic deciduous forest species in breaking dormancy then moist stratification: germination was diminished and among those seeds that did germinate, onset of germination was delayed. In contrast, dormancy in seeds from wet areas in deciduous forests, wetlands, and seasonally flooded areas was broken by one or all of dry storage, moist stratification, or submerged stratification. Though distinct in the canonical discriminant analysis, the responses of seeds from wet areas in deciduous forests could not be simply or easily distinguished from those of wetland and seasonally flooded habitats. Germination of fresh seeds from all habitats was generally low but increased with dry storage and/or stratification suggesting physiological dormancy. Spring germination in seeds of all species generally began in late May or early June, at fairly high temperatures, which is unusual for forest species but consistent among *Carex* species. Large fluctuations in temperature may be especially effective in promoting germination of seeds from wet habitats but further study is necessary. Finally, light increased germination in all species, except *Carex pedunculata*, an ant-dispersed species, on which it had no effect.

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Appendix

An electronic appendix is available and includes data files (Excel97) and SAS program files (txt).

Excel files:

For each experiment there are at least three kinds of files. The 'raw' data file represents the data as entered, the screened ('scr') data file shows corrections or changes, and the 'calc' file shows the calculations used for lag and range. The 'calc' file has cumulative germination on the left, the calculations on the right (to calculate lag and range) and finally, the data in a summarized form. The Main experiment is split into blocks (one per worksheet) and is therefore also summarized (all blocks together) in "Main DATA dec 98". Temperature data is included in these files.

1. Main experiment

a) **MAIN calc dec98.xls**

b) **MAIN raw dec 98.xls**

c) **MAIN scr dec98.xls**

d) **MAIN DATA dec98.xls**: summarized data from the Main experiment. Data taken from here for the ANOVAs (germination, lag, range, population effects). Also includes data describing germination in dark pots after lids were removed.

The following files prefixed with "P-VALUES" include Sums of Squares, degrees of freedom, Mean Squares, F-ratios, and P-values for various ANOVAs using Main experiment data. The files usually include three types of spreadsheets: Data (raw output for all species), Pivot (pivot table reporting p-values), and p-values (same as pivot but formatted and sorted for the thesis).

e) P-VALUES TOT GERM dec98.xls: total germination.

f) **P-VALUES ILAGDAYS dec 98.xls**: inverse lag in days.

g) **P-VALUES ILAGDD dec98.xls**: inverse lag in degree-days

h) **P-VALUES IRANDD dec98.xls**: inverse range in degree-days.

i) **P-VALUES IRANDAYS dec98.xls**: inverse range in days

j) **P-VALUES NO BLOCK dec98.xls**: total germination and inverse lag in days and degree-days. BLOCK WAS REMOVED FROM THE MODEL STATEMENT.

2. Dormancy Check Greenhouse

a) **DCGH calc dec98.xls**

b) **DCGH raw dec98.xls**

c) **DCGH scr dec98.xls**

3. Overwintered Lath House

a) **OLH calc dec 98.xls**

b) **OLH raw dec 98.xls**

c) **OLH scrI dec98.xls**

d) **OLH scrII dec98.xls**

4. Fresh Seed Greenhouse

a) **FSGH calc dec98.xls**

b) **FSGH raw&scr dec98.xls**

5. Fresh Seed Lath House

a) **FSLH calc dec98.xls**

b) **FSLH raw dec98.xls**

c) **FSLH scr dec98.xls**

6. Canonical Discriminant Analysis (CDA)

a) **CANDISC dec98.xls**: input data (for SAS) used in all CDA and the PCA

b) **CDA hab dec98.xls**: scores on Canonical Axes used for plots (CDA based on 3 habitat groups)

c) **CDA sec dec98.xls**: scores on Canonical Axes used for plots (CDA based on taxonomic groups)

7. Principal Components Analysis (PCA)

PCA dec98.xls: scores on the Principal Component axes used for plots

8. Seed weights

SEED WEIGHTS.xls: includes seed weights with and without perigynia.

SAS files:

The filename is followed by a description.

ANOVA germ&lag.txt: ANOVAs using germination and lag data

ANOVA no blocks.txt: ANOVAs using germination and lag data with Block missing from the model.

ANOVA pop.txt: ANOVAs using germination to test for population effects

ANOVA range.txt: ANOVAs using range (only light treatments)

Candisc.txt: Canonical Discriminant Analysis

Contingency Table.txt: Chi-square of habitat and sectional grouping (to test for independence).

PCA.txt: Principal Components Analysis