

PHENOLOGY OF *POTAMOGETON CRISPUS* (CURLYLEAF
PONDWEED) IN BLUE LAKE, OREGON: FORMATION AND SPROUTING
OF TURIONS IN THE PACIFIC NORTHWEST OF NORTH AMERICA.

by

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ABSTRACT

An abstract of the thesis of Steven W. Wells for the Master of Science in Environmental Sciences and Resources presented July 12, 2006.

Title: Phenology of *Potamogeton crispus* (Curlyleaf pondweed) in Blue Lake, Oregon: Formation and sprouting of turions in the Pacific Northwest of North America.

The timing of turion formation and sprouting in Blue Lake, Oregon was investigated to assist with plant management in the northwest of the United States, specifically for controlling the formation of new turions. *Potamogeton crispus* (Curlyleaf pondweed) is a widespread, introduced plant in the western USA. It creates nuisance conditions in Blue Lake, which lies within the metropolitan area of Portland, Oregon. *P. crispus* propagates primarily vegetatively via turions, which are condensed stem apices with four to eight dormant buds in the leaf axils. It also propagates vegetatively from stem and

rhizome fragments as well as sexually via seed. Management focuses on preventing new turion formation, exhausting the existing turion bank and controlling the plant biomass.

The formation and sprouting of *P. crispus* turions in Blue Lake was investigated by sampling bimonthly using a rake and dredge over a one year period (11/6/03 to 1/11/05). Data on stem and turion mass, length, and number of leaves and buds were collected.

In Blue Lake, new turion formation initiated in early April and continued through January, peaking on 21 May 2004. Sprouting initiated in October and continued throughout the fall, winter and into the spring. Sprouting peaked on 24 February 2004. In Blue Lake, denticulate turions were more important for propagation than the spiculate turions. Additionally, the lateral-stem position of formation was more important for propagation than the apical-stem position of formation.

These data in conjunction with other North American studies suggest there are specific times to manage *P. crispus*, which optimizes control efforts while minimizing effects upon desirable monocots and other organisms. Management of *P. crispus* is focused on the formation of new

turions. Management should first be done when water temperatures are near 10°C but are not greater than 15°C, which is generally between mid-March to early April. Subsequent management is also recommended when water temperatures are between 15°C and 17°C, which is generally between late spring to early summer.

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Introduction

Aquatic plants

Function

Aquatic plants have important economic and ecological functions in freshwater resources. Economic functions of aquatic plants directly and indirectly involve agriculture, water utilization, wildlife, sports, aesthetics/ornamentals and weed control (Catling and Dobson 1985; Sculthorpe 1967). Ecological functions of aquatic plants include temperature control (i.e. shading, altering water movement), bank and streambed stabilization (roots and flow reduction), silting, habitat (e.g. spawning beds, predator refuge, resting sites, physical structure) and food (waterfowl, fish, macroinvertebrates, etc.) (Champion and Tanner 2000; Kalff 2002; Sculthorpe 1967). Ecological functions also include the uptake of light, nutrients and chemicals. These uptakes alter the pH, light and concentrations of dissolved gases and nutrients (Champion and Tanner 2000; Hafez et al. 1998; Kalff 2002; Scheffer et al. 1993; Sculthorpe 1967).

Weeds and their management

Management of nuisance aquatic plants is important for the protection of freshwater resources. Nuisance aquatic plants (i.e. invasive, exotic) are not native to a given area and cause economic and/ or

ecological impacts. Nuisance aquatic plants exacerbate the limited supply and availability of freshwater by choking waterways, affecting drinking water quality, impacting hydropower generation and land values, altering other plant and animal species, and reducing recreational uses (Lovell and Stone 2005; Pimentel et al. 2000; Pimentel et al. 2005; Rockwell 2003). In the United States as a whole, a total of \$110 million is invested annually in the control of nonindigenous aquatic plants (Pimentel et al. 2005).

There are many things to consider when managing for nuisance aquatic plants. Considerations include the objectives of management, biology of the target and non-target species, spatial and temporal scales, funding, legal constraints, and the possible impacts of management activities (Madsen 2000). Management objectives distinguish between eradication and control. The goal of eradication is to remove the entire population of a species from a specific area, whereas, control is done to keep the population below a defined threshold through containment or suppression. Biological considerations include mobility, aggressiveness, dispersal mechanisms, establishment requirements, seed viability, modes of reproduction and life history. Management can have direct and indirect ecological impacts that vary across different spatial and temporal scales (e.g. food web interactions, nutrient cycling, alternative stable states, and community composition and structure) (Madsen 2000). Some management

options are non-selective, such as mechanically harvesting aboveground plant biomass, regardless of species. Other management options are more specific to the targeted species, such as using diver-operated suction harvesters. Management can also have indirect deleterious effects. For example, the successful removal of a large patch of nuisance plants is a disturbance event that may ultimately favor another species becoming a nuisance (Madsen 2000). Methods are broadly characterized as physical, mechanical, chemical and biological.

Physical control manipulates the environment, and the changes in the environment affect the plant. Bottom barriers cover sediment with fabric or other material that prevents new growth. Bottom barriers are direct and effective and may last several seasons, although they can require maintenance, are non-selective and are generally limited to small-scale applications such as around docks, boat launches and swimming beaches (Madsen 2000). Water level control involves either raising or lowering water levels. Lowering water levels exposes plants to desiccation and freezing temperatures, while raising water levels limits light, wind and insect pollinated reproduction and decreases the area available for colonization by rooted aquatic plants. Drawdown can be inexpensive, effective and selective. The degree of selectivity for drawdown is influenced by the plant biology (e.g. maximum depth of colonization, phenology), timing of

application and the morphometry of the waterbody. Limitations of drawdown are that it requires the ability to control water level and it can cause economic (e.g. collapse of retaining wall), ecological and recreational impacts (Madsen 2000). Sediment removal creates deeper water. This is effective and has long-term results, but is very expensive and requires disposal of dredge spoils (Madsen 2000). Incoming light can be absorbed using dyes, shade cloth and riparian trees (Madsen 2000). These methods are generally inexpensive and effective but are non-selective and may be aesthetically unappealing.

Mechanical control removes plant biomass or prevents plants from establishing. Manual removal involves pulling plants by hand or rake and is technologically easy and inexpensive. Hand removal, however, is labor intensive and effective on small spatial scales (Madsen 2000). Cutting plants with a mechanical blade is quick and can be used on large spatial scales but it is non-selective, short-term, does not remove plant biomass and spreads plant fragments (Madsen 2000). Harvesting is the mechanical cutting and removal of plants and has direct and immediate, although short-term, results. Harvesting is expensive, non-selective, requires disposal of plant material and can increase turbidity (Madsen 2000). Sediment agitation and rotoation physically disturb sediments and prevent seedling and clone establishment. Sediment agitation and rotoation are non-selective and can

spread plant fragments and increase turbidity (Madsen 2000). Grinders cut, grind and dispose of plant material in the waterbody. Grinders remove plants without disposal costs but are non-selective and their effects are short-term (Madsen 2000).

Chemical control is done with registered aquatic herbicides that have different modes of action (i.e. systemic versus contact) as well as modes of application (e.g. liquid, pellet). There are less than ten different aquatic herbicides that are registered for use in the United States. It is required that registered aquatic herbicides cannot pose more than a one in a million chance of causing significant damage to human health, the environment, and wildlife resources (Madsen 2000). Herbicides can be applied and take effect within a short period of time, but their use in aquatic environments is limited and there are adverse environmental impacts, such as secondary pest outbreaks, toxic effects on nontarget organisms, including humans, and the development of resistance in the target species (OTA 1993).

Aquatic herbicides registered in the United States that are used for controlling submersed plants include Diquat, complexed copper, Endothall, Fluridone and 2,4-D. Diquat is a non-selective herbicide that affects the shoot portion of the plant but is not effective against roots, rhizomes and tubers. Diquat will bind to particulate and dissolved organic matter (Madsen 2000). Complexed copper is used primarily to control phytoplankton and

can be mixed with diquat (Madsen 2000). Endothall is a non-selective herbicide that does not interact with particulate and dissolved organic matter but it cannot be mixed with chelated copper compounds (Madsen 2000). Fluridone is a non-selective systemic herbicide that requires long exposure times but can be used in low concentrations (Madsen 2000). 2,4-D is a systemic herbicide that works with dicots in a short time period but it is not effective against monocots such as *Potamogetons* as well as some dicots like *Hydrilla* (Madsen 2000).

Biological control uses specific organisms to manage the target species. Extensive research is required to assess the risks posed by introducing a biocontrol agent (Madsen 2000). There are some insect biocontrol agents for aquatic plants, such as *Prokelisia marginata*, which is used for *Spartina* spp. and *Galerucella pusilla* used to control *Lythrum salicaria*. *Neochetina* spp. are waterhyacinth weevils that can reduce growth but are often not effective in reducing surface mats (Madsen 2000). Grass carp (*Ctenopharyngodon idella* Val.) are long-lived, non-selective herbivorous fish that have been used to control aquatic plants. Grass carp are relatively inexpensive but they are persistent, difficult to contain within a waterbody and tend to either remove all vegetation or have little effect (Madsen 2000).

Potamogeton crispus

Plant morphology

Potamogeton crispus is a rhizomatous, rooted, submersed freshwater vascular aquatic plant that flowers above water (Wehrmeister 1978). Stems of *P. crispus* are laterally compressed, simple or slightly branched, pale green to reddish in color with a 0.5 to 2 mm diameter (Figure 1b and 1g) (Catling and Dobson 1985; Fernald 1989; Wehrmeister 1978). Stem roots (Figure 1c) develop at nodes (Figure 1h) and are usually in pairs. Rhizomes (Figure 1e) are round in cross-section, branching and pale red to brown in color (Wehrmeister 1978). Emergent inflorescences are radially symmetric with an inferior ovary, sessile or on pedicels and are arranged in 3 to 5 whorls on compact spikes developing in multiple shoot meristems (Catling and Dobson 1985; Fernald 1989; Wehrmeister 1978).

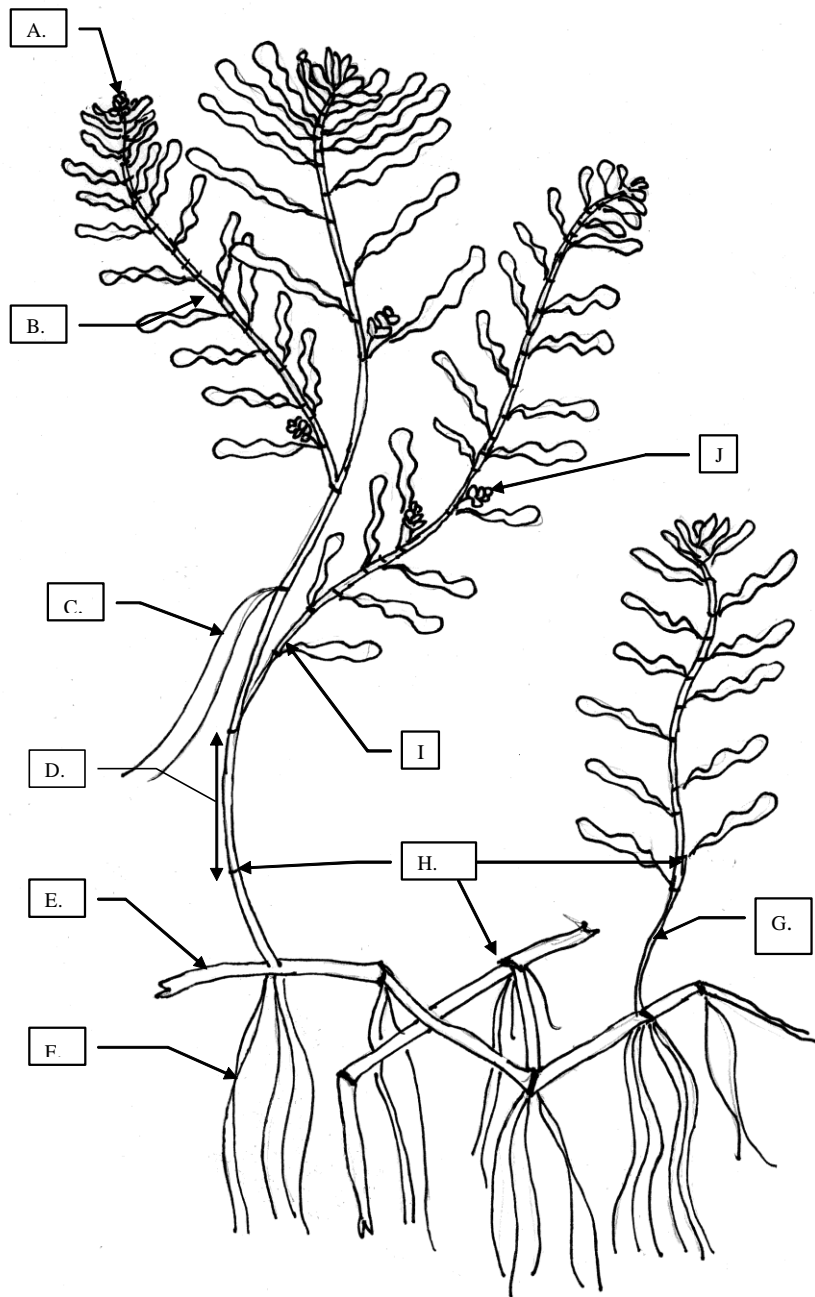


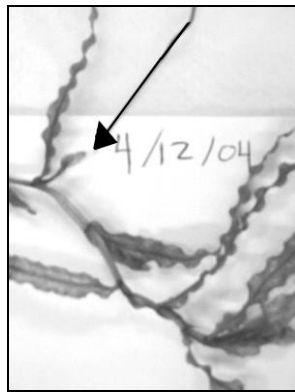
Figure 1: A schematic drawing of *P. crispus* plant. *P. crispus* plant bearing spring foliage and showing a) new turion forming on apical-stem position; b) an axillary stem; c) stem roots; d) an internode; e) rhizomes; f) roots attached to rhizomes; g) a main stem; h) nodes; i) leaf axil; j) a new turion forming on lateral-stem position, which is located in the leaf axil.

Two morphological types of foliage (spring and winter) are exhibited on *P. crispus*, depending on the developmental stage. Winter foliage develops on stems of recently sprouted turions (Figure 2a). Winter foliage is alternate, 5 to 7.5 mm in width, exhibits flat to serrulate margins, an acute leaf tip, inconspicuous veins and is both flexible and blue-dark green in color (Figure 2a) (Wehrmeister 1978). Spring foliage develops in leaf axils of decaying winter foliage (Catling and Dobson 1985; Wehrmeister 1978). Spring foliage is brittle, alternate, 7.5 to 15 mm in width, 30 to 80 mm in length, possesses undulate to serrulate margins, a rounded leaf tip, prominent veins and is red to light green in color (Figure 2c) (Wehrmeister 1978).

a)



b)



c)

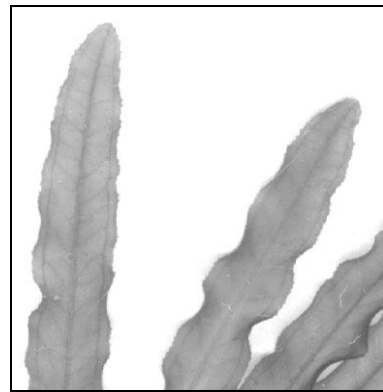


Figure 2: Photographs of *P. crispus* foliage. The plant parts shown include a) the winter foliage still attached to the sprouting turion; b) the spring foliage; the arrow shows an axillary bud breaking dormancy in the leaf axil, and c) the leaf margin, tip and veins of the spring foliage.

Distribution

P. crispus is a cosmopolitan plant that is introduced and naturalized in the United States (Bolduan et al. 1994; Champion and Tanner 2000; Correll and Correll 1972; Fedorov 2001; Fernald 1989; Good 1974; Hafez et al. 1998; Healy and Edgar 1980; Jian et al. 2003; PLANTS USDA-NRCS 2005). *P. crispus* is native to Central and Atlantic Europe, Mediterranean and Asia Minor (i.e. Eurasia) (Bolduan et al. 1994; Catling and Dobson 1985; Fernald 1989; Stuckey 1979; Woolf and Madsen 2003). Globally, *P. crispus* is found on all continents except Antarctica. In the United States, *P. crispus* is present in all continental states (Correll and Correll 1972; Falter et al. 1974; PLANTS USDA-NRCS 2005; Stuckey 1979). Although, *P. crispus* is commonly represented in community composition, it does not always dominate the community structure (Good 1974; Pip 1986).

The *Potamogetonaceae* family is globally widespread (Good 1974; Pip 1986) and adapted for a wide range of aquatic habitats (Pip 1986). Many species within the *Potamogetonaceae* family are also cosmopolitan and they are similar to *P. crispus* in that they are commonly represented in community composition although they do not always dominate the community structure (Good 1974). Some species in this family exhibit terrestrial forms under certain conditions (Spencer and Ksander 1992). The

Potamogetonaceae family relies heavily upon vegetative reproductive structures (e.g. turions and winter buds) (Hofstra et al. 1995; Spencer and Ksander 1992).

The *Potamogeton* genus exhibits variety in form, adaptability to environment and diversity in range. This genus is one of the most common and widespread of vascular aquatic plant groups (Moore 1913; Pip 1986). There are about 100 species within the *Potamogeton* genus and many hybrids (Good 1974; Pip 1986; Ridley 1930). Different *Potamogeton* species often co-occur within the same geographical area (Pip 1986). *Potamogeton* species are common in eutrophic systems (Polunin 1960) and propagate predominantly vegetatively (Appendix A) (Moore 1913).

P. crispus is found in a wide variety of habitats. It is found in lakes, ponds, paddy fields, canals, rivers and springs throughout most of the world. It grows in clear to turbid waters (Correll and Correll 1972; Stuckey 1979; Wehrmeister 1978) in both temperate and tropical environments (Catling and Dobson 1985; Fedorov 2001; Good 1974; Healy and Edgar 1980), that exhibit a pH range between 6.4 to 9.8 (Catling and Dobson 1985; Hellquist 1980; PLANTS USDA-NRCS 2005). Rhizomes anchor the plants enabling *P. crispus* to grow in flowing waters (e.g. rivers and canals) (Harman 1974). Stem diameter and internode length are variable depending upon water depth and flow (Tobiessen and Snow 1984). *P.*

crispus is tolerant of anaerobic conditions and brackish water with conductivity exceeding 150 μS (Bolduan et al. 1994; Jian et al. 2003; Nichols and Shaw 1986; McCombie and Wile 1971). It obtains carbon primarily as carbon dioxide but is capable of bicarbonate uptake, especially in alkaline conditions (Bolduan et al. 1994; Kadono 1980).

P. crispus populations are more abundant under certain environmental conditions. It grows best in hard ($\text{Ca}^{2+} + \text{Mg}^{2+} : \text{N}^{+} + \text{K}^{+} > 5:1$), eutrophic ([nitrate]: 2.0 to 24.0 mg/L and [phosphate]: 0.2 to 1.12 mg/L) and alkaline waters (14.6 to 207.5 mg HCO_3^- /L (Bolduan et al. 1994; Catling and Dobson 1985; Correll and Correll 1972; Hellquist 1980; Jian et al. 2003). *P. crispus* grows best in fine substrates with organic matter content between 10-25% (Nichols and Shaw 1986). Optimal growth occurs at 30°C (Nichols and Shaw 1986) at depths between one to three meters (Bolduan et al. 1994; Jian et al. 2003).

P. crispus has local and long-distance dispersal mechanisms. Dispersal mechanisms include seed, turions, and stem fragments (Catling and Dobson 1985; Guppy 1894; Hunt and Lutz 1959; Kunii 1982). Turions and vegetative growth are the primary means of local spread (Catling and Dobson 1985; Hofstra et al. 1995; Kunii 1982; Moore 1913; Wehrmeister 1978). Seeds are considered the predominant long-distance colonizing propagule (Hofstra et al. 1995). Seeds are hardy and remain viable a long

time. *P. crispus* seeds eaten by dabblers such as *Fulica atra* (coots), *Cygnus olor* (mute swans) and mallards are often undigested (Polunin 1960; Ridley 1930). Guppy (1894) found that *P. crispus* seeds passing through waterfowl germinated earlier and that seed germinated readily after drying for 18 months, and after six years storage in both light and dark conditions. Germination was not impaired by enclosure in ice and mud for one to two weeks or immersion in salt water (Guppy 1894).

There are anthropocentric and natural vectors associated with the spread of these dispersal mechanisms. Populations often start with a single colonizing propagule or several propagules of identical genotype (Hofstra et al. 1995). Anthropocentric vectors include both deliberate human activities such as planting/ stocking and aquarium releases, and the accidental spread of propagules as contaminants (e.g. seed and mud on waders). Natural vectors include water currents, migrating waterfowl and flotsam (Catling and Dobson 1985; Guppy 1894; Hunt and Lutz 1959; Kunii 1982). Water currents can disperse turions and detached stem fragments (Catling and Dobson 1985; Polunin 1960; Ridley 1930). Polunin (1960) found that migrating waterfowl, while in flight, had *Potamogeton* plant fragments draped around their necks. Turions often have spines along the edges of leaf bases that can stick in feathers and fur. Seeds and turions embedded in mud can also stick to feet and fur (Hofstra et al. 1995).

There is no agreement regarding the means of introduction into North America, but once introduced, its spread within North America was facilitated by intentional and accidental human activities. Catling and Dobson (1985) stated that the means of introduction to North America are unknown. Stuckey (1979), however, reported that *P. crispus* was introduced into North America in the mid-1880's as an ornamental plant. Spread within North America has been associated with contaminated fish introductions and hatchery personnel (Bolduan et al. 1994; Stuckey 1979). Wildlife managers in eastern U.S. intentionally planted *P. crispus* in marshes for waterfowl food (Stuckey 1979). It was also introduced within North America by aquarium plant releases (Healy and Edgar 1980).

Phenology

Growth

P. crispus is a perennial plant that exhibits a phenology similar to a winter annual. Reproductive structures of most aquatic plants sprout and germinate in response to warming water temperatures, but *P. crispus* turions sprout in fall, winter and early spring (Sastroutomo 1980; Wehrmeister 1978; Woolf and Madsen 2003). Although the season of seed germination is unknown (Wehrmeister 1978), seeds are thought to germinate in late autumn to early spring (Catling and Dobson 1985; Muenscher 1936).

The rate of plant growth is primarily determined by water temperature. During winter, *P. crispus* develops and maintains leafy biomass under low light intensities (Stuckey et al. 1978; Tobiessen and Snow 1984; Wehrmeister 1978) and even under winter ice (Bolduan et al. 1994; Jian et al. 2003; Moore 1913; Nichols and Shaw 1986; Waisel 1971; Wehrmeister 1978). Little plant growth, however, occurs when water temperatures are below 5°C (Tobiessen and Snow 1984). Vigorous growth in main stems, foliage, rhizomes and roots begins late winter to early spring at bottom water temperatures between 10° and 15°C (Kunii 1982; Tobiessen and Snow 1984; Waisel 1971).

The transition from winter to spring foliage is rapid and occurs in late winter to early spring. Both winter and spring foliage are generally present in February. The main stems elongate and the spring foliage develops in leaf axils of winter foliage (Kunii 1982). Usually by the end of April, the spring foliage predominates (Wehrmeister 1978).

P. crispus quickly reaches the water surface and forms a canopy. Growth in stems occurs through both internode elongation and node increment (Kunii 1982). When the main stems are near the water surface and spring foliage has replaced the winter foliage, flower bud initiation begins and axillary buds break dormancy, beginning the development of axillary stems (Figure 2b) (Catling and Dobson 1985; Kunii 1982;

Wehrmeister 1978). The branching axillary stems in the upper portions of main stems form the canopy (Kunii 1982; Tobiessen and Snow 1984; Waisel 1971).

Peak plant biomass is reached in spring to early summer between April and July (Catling and Dobson 1985; Champion and Tanner 2000; Harman 1974; Kunii 1982; Sastroutomo 1981; Sastroutomo et al. 1979; Tobiessen and Snow 1984; Wehrmeister 1978; Woolf and Madsen 2003). Flowering is initiated between April and June (Catling and Dobson 1985; Hunt and Lutz 1959; Kunii 1982; Teltscherova and Hejny 1973; Wehrmeister 1978) and flowering peaks between May and June (Catling and Dobson 1985; Hunt and Lutz 1959; Teltscherova and Hejny 1973).

Senescence generally occurs in early summer but the timing and extent of plant dieback varies. Plant dieback begins between mid to late summer following peak turion formation (Catling and Dobson 1985; Harman 1974; Moore 1913; Wehrmeister 1978; Woolf and Madsen 2003). Dieback occurs either ubiquitously among the population or among scattered individuals. Catling and Dobson (1985), Chambers (1982), Champion and Tanner (2000), Harman (1974), Kunii (1982), Moore (1913), Sastroutomo (1980), Sastroutomo (1981), Stuckey et al. (1978) and Wehrmeister (1978) found that plant dieback ranged from individuals to entire populations, with individual plants sometimes remaining. Conversely, Chambers et al. (1985),

Rogers and Breen (1980), Sastroutomo et al. (1979), Tobiessen and Snow (1984), and Woolf and Madsen (2003) found that plant dieback was ubiquitous among the populations with no remaining individual plants. Kunii (1982) found that senescence occurred earlier in lakes and reservoirs versus rivers and streams.

Dieback is associated with summer conditions. Dieback is associated with increasing daylength (Wehrmeister 1978) and water temperature (25°-35°C) (Chambers 1982; Chambers et al. 1985; Tobiessen and Snow 1984; Wehrmeister 1978). Catling and Dobson (1985), Moore (1913) and Wehrmeister (1978) found that dieback could be delayed with cooler water temperatures. Kunii (1989) observed year round vegetative growth in a Japanese river that exhibited water temperatures between 8.7° and 24.7°C. Champion and Tanner (2000) observed plant dieback in New Zealand streams when water temperatures exceeded 19°C.

Plant dieback generally marks the onset of a rest period. The length of this rest period varies according to habitat conditions such as temperature and light intensity (Catling and Dobson 1985; Kunii 1982; Sastroutomo 1981). During this period, *P. crispus* persists as dormant turions, sprouting turions, rhizomes, seeds and/ or stem fragments (Sastroutomo 1981; Wehrmeister 1978).

Reproduction and propagation

P. crispus exhibits both sexual and asexual reproduction. Sexually, *P. crispus* reproduces via wind pollinated seed (Muenscher 1936; Sculthorpe 1967). Asexually, *P. crispus* propagates vegetatively via turions, stem fragments and rhizomes (Harman 1974; Irmisch 1851; Kunii 1982; Moore 1913; Poovey et al. 2002; Wehrmeister 1978).

P. crispus is extremely fecund. Many turions are formed and they represent a large percentage of peak standing biomass (Table 1). Yeo (1966) obtained 23,000 turions in one growing season from a 6 m² plot of *P. crispus* by continually removing the turions once formed. *P. crispus* seed production is also considerable (Table 1). Hunt and Lutz (1959) reported that an average of 140 kg/ hectare of seed was produced.

Table 1: Density of *P. crispus* reproductive propagules. Density is shown as number/ m² and the percentage of total standing biomass represented by reproductive propagules estimated from sediment dredges during peak turion formation.

Author	Turions		Seed #/ m ²
	#/ m ²	% biomass	
Kunii 1982	200 - 1,700	42	
Rogers and Breen 1980	1,000 - 1,500	23	1,445
Sastroutomo et al. 1979	2,088	23	
Wehrmeister 1978	1,500*		
Woolf and Madsen 2003	726 - 2,713	22 - 58	

* converted from #/ inch²

Turions are the chief reproductive structure for this plant (Catling and Dobson 1985; Irmisch 1851; Kunii 1982; Moore 1913; Sastroutomo 1981; Wehrmeister 1978). They function in dispersal and perennation (Moore 1913; Wehrmeister 1978). In most cases, *P. crispus* turions sprout one bud at a time despite having several viable, dormant buds (Jian et al. 2003; Moore 1913; Wehrmeister 1978; Woolf and Madsen 2003). Removing a sprouting bud induces the sprouting of a remaining dormant bud (Jian et al. 2003; Moore 1913). If a turion is broken so that each resultant piece possesses a dormant bud, the buds on both pieces can sprout (Moore 1913). Vegetative growth can occur from stem fragments, rhizomes and turions. Propagation via turions, however, is more common (Harman 1974; Moore 1913; Poovey et al. 2002; Wehrmeister 1978). Seedlings are rarely encountered in North America (Catling and Dobson 1985; Correll and Correll 1972; Hunt and Lutz 1959; Moore 1913; Muenscher 1936; Wehrmeister 1978).

Turions are compressed stem apices that usually separate from the parent plant upon maturation. *P. crispus* turions were first described by Irmisch (1851) and are engorged with starch (Moore 1913; Wehrmeister 1978). *P. crispus* turions have a central axis (i.e. stem apex), along which, dormant buds develop in leaf axils (Figure 3a) and are protected by hardened leaf bases (Figure 3b) (Wehrmeister 1978). Turions form from the

basal portions of stem apices, and the leaf bases are the basal portions of leaves, in which, the cells swell and distend with starch (Moore 1913; Wehrmeister 1978). As dormant buds develop in leaf axils, the distal portions of leaves disintegrate and decay, eventually leaving hardened, brittle leaf bases (Figure 3b). Turions are delineated from stem apices once the leaves of the shoot apex become triangular in shape, thick and horny in texture (Sastroutomo 1980). Some turions bear small firm spines along the margin of the leaf base. The color of turions changes as they mature from green to red-brown, dark brown and sometimes black (Catling and Dobson 1985; Sastroutomo 1981; Wehrmeister 1978). When turions are mature, the tissue in the stem below the turion weakens and the turions abscise from the plants (Moore 1913; Wehrmeister 1978).

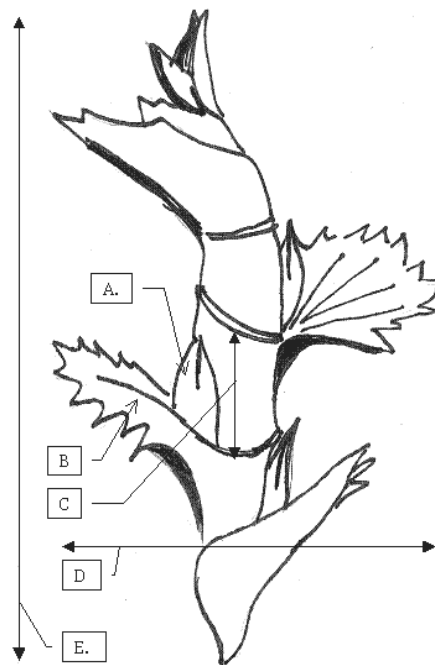


Figure 3: Schematic drawing of a *P. crispus* turion. The turion shows a) a dormant bud in leaf axil; b) a leaf base; c) an internode; d) the width measurement; e) the length measurement.

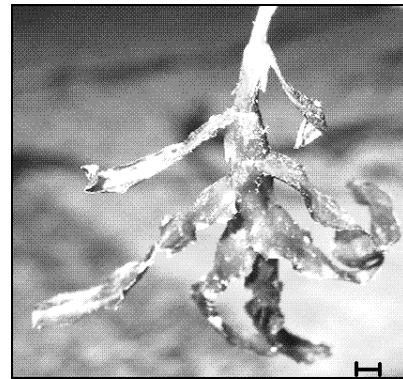
P. crispus turions form in several locations on the plant. Turions form in the leaf axils of axillary and main stems (lateral-stem formation) (Figure 1j, 4a and 4b), terminal stem apices (apical-stem formation) (Figure 1a and 4c) and occasionally directly off rhizomes (Moore 1913; Wehrmeister 1978). Turion formation can occur on green, non-dormant, newly sprouted turions under long days (14 hr) and high temperatures (28° – 30°C) (Sastroutomo 1980). Turion formation in these newly sprouted turions, however, is inhibited under short daylengths (8 hr) and low temperatures during autumn and winter (Sastroutomo 1980). Turion formation proceeds from the lower

to the upper nodes of the plant (Kunii 1982). Turions in lower nodes are greater in size and mass than those in upper portions of plants (Kunii 1982).

a)



b)



c)

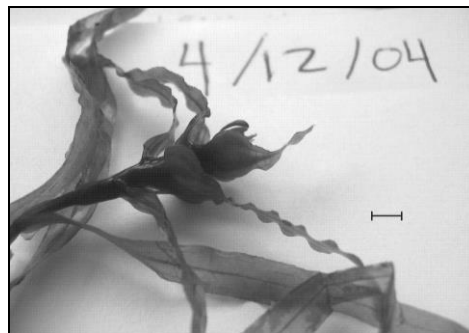
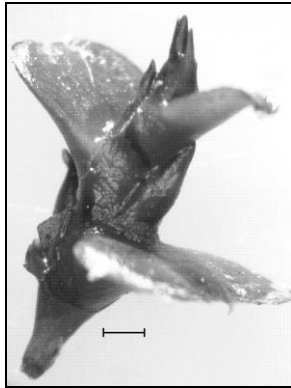


Figure 4: Photographs of turion formation in lateral- and apical-stem positions. Photographs of turion formation showing a) the lateral-stem position in a leaf axil, b) a new turion in the lateral-stem position showing the decay of distal portion of leaves and c) the apical-stem position. Scale bars represent approximately 5 mm.

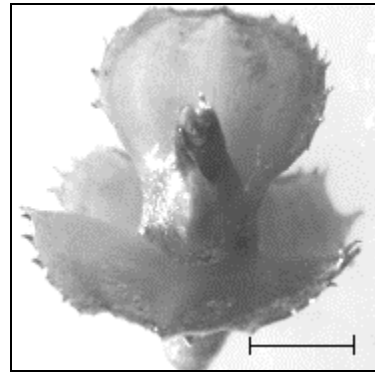
P. crispus forms denticulate and spiculate turions (Catling and Dobson 1985; Moore 1913; Waisel 1971; Wehrmeister 1978). Although no studies have compared the viability of denticulate and spiculate turions,

both types of turions are similar in function and internal structure (Moore 1913). Denticulate turions are more numerous and they have greater mass than spiculate turions (Moore 1913). Denticulate turions are characterized by large, denticulate (i.e. tooth shaped) leaf bases that often have small spines along the margin. Denticulate turions tend to have shorter internodes and more dormant buds compared to spiculate turions (Figure 5a and 5b) (Moore 1913; Waisel 1971; Wehrmeister 1978). Spiculate turions have small, spinous leaf bases with smooth margins (Figure 5c and 5d) (Moore 1913; Waisel 1971; Wehrmeister 1978).

a)



b)



c)



d)

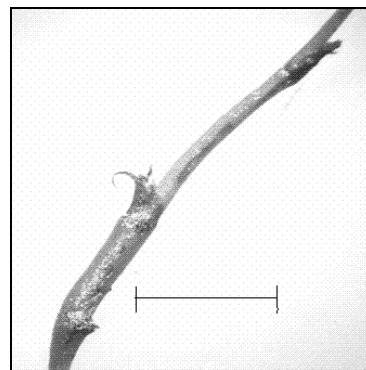


Figure 5: Photographs of denticulate and spiculate turions. Photographs of turions showing the a) side view of a denticulate turion with dormant buds between leaf bases, b) ventral view of denticulate turion with small spines along leaf base, c) spiculate turion with spinous leaf bases and dormant buds, and d) long internodes of spiculate turions. Scale bars represent approximately 5 mm.

It appears that there are differences in the manner of formation between denticulate and spiculate turions. Although, both types are formed in apical and lateral stem apices and there is no difference in the onset and time period of formation (Wehrmeister 1978). Moore (1913), Waisel (1971)

and Wehrmeister (1978) found that spiculate turion formation is more common in lower portions of plant, often directly attached to stems or rhizomes. Denticulate turions are formed in leaf axils throughout the plant (Waisel 1971). Moore (1913) found that denticulate turions were formed predominantly on healthier plants and spiculate turions were formed on plants that appeared “nutritionally starved” or “young”.

Turion formation in lateral-stem positions is different than in apical-stem positions. Kunii (1982), Moore (1913) and Wehrmeister (1978) found that turion formation, irrespective of turion-type, was more common in lateral-stem positions than in apical-stem positions. Sastroutomo et al. (1979), however, found that turion formation was more abundant and occurred over a longer period in apical-stem positions. There is a positive relationship between formation in the apical-stem position and water temperature (Wehrmeister 1978). Kunii (1982) found that turion formation in apical-stem positions was more common in small plants whereas formation in lateral-stem positions was more common in large plants.

New turion formation begins in late spring to early summer between April and June (Table 2). The initiation of turion formation is associated with increasing daylength (greater than 12 hr) and water temperature (greater than 12°C) (Chambers 1982; Chambers et al. 1985; Kunii 1989;

Sastroutomo 1980; Waisel 1971, Wehrmeister 1978; Woolf and Madsen 2003).

Table 2: Timing and associated parameters for onset of turion formation as reported in other studies.

	Onset of formation		
	Water temp (°C)	Daylength (hr)	Timing (mo.)
Bolduan et al. 1994		14	May
Catling and Dobson 1985	>12	>12	
Chambers 1982	>12	>12	June
Chambers et al. 1985	>12	>12	June
Jian et al. 2003			April
Kunii 1982			April
Moore 1913			May
Nichols and Shaw 1986			June
Rogers and Breen 1980	<20	<12	June
Sastroutomo 1980	>12	>12	June
Sastroutomo 1981			May
Waisel 1971	20	16	
Wehrmeister 1978		14	April
Woolf and Madsen 2003	11		May-June

The time period and extent of turion formation vary with habitat.

Although an individual turion forms in about 14 days (Sastroutomo 1981), plants form turions over a two to six month period (Bolduan et al. 1994; Catling and Dobson 1985; Chambers 1982; Chambers et al. 1985; Jian et al. 2003; Kunii 1982; Moore 1913; Nichols and Shaw 1986; Rogers and Breen 1980; Sastroutomo 1980; Sastroutomo 1981; Waisel 1971;

Wehrmeister 1978; Woolf and Madsen 2003). Cooler water temperatures delay turion formation, thereby allowing continued growth in vegetative meristems (Catling and Dobson 1985; Moore 1913; Wehrmeister 1978). Conversely, warmer water temperature increases turion formation in apical-stem positions and turion formation in the apical-stem position terminates growth in that axis (Moore 1913; Wehrmeister 1978). Once initiated with one inductive photoperiod and several thermoperiods, the timing and extent of turion formation are dependent on the PAR photon fluence rate and R:FR value (Chambers et al. 1985). Sastroutomo (1980) reported that increases in temperature, daylength and irradiance all increase the extent of turion formation.

Turion formation peaks in mid to late spring between May and June (Table 3). Peak turion formation is associated with daylengths greater than 14 hr and water temperatures generally greater than 15°C (Table 3). The timing of peak turion formation is similar to the timing of peak plant biomass (Kunii 1982; Wehrmeister 1978; Woolf and Madsen 2003), and flowering (Catling and Dobson 1985; Moore 1913; Woolf and Madsen 2003). Sastroutomo (1981), however, found that plant biomass peaked prior to the period of peak turion formation.

Table 3: Timing and associated parameters for peak turion formation as reported in other studies.

	Peak formation		
	Water temp (°C)	Daylength (hr)	Timing (mo.)
Bolduan et al. 1994	5-20		
Catling and Dobson 1985			
Chambers 1982	16		
Chambers et al. 1985	30	>16	
Jian et al. 2003			
Kunii 1982	16-22	>16	May
Moore 1913			
Nichols and Shaw 1986			
Rogers and Breen 1980			
Sastroutomo 1980			
Sastroutomo 1981	>15	>14	
Waisel 1971			
Wehrmeister 1978		>14	May
Woolf and Madsen 2003		>14	June

Turion formation often ends prior to or upon reaching seasonal maxima for temperature and daylength (Jian et al. 2003; Kunii 1982; Rogers and Breen 1980; Waisel 1971; Wehrmeister 1978; Woolf and Madsen 2003). Kunii (1989) found that the period of turion formation in a Japanese river, continued through summer maxima and lasted until October.

Cooler water temperatures are associated with the initiation of turion sprouting. Turions begin sprouting between September and October

(Catling and Dobson 1985; Jian et al. 2003; Kunii 1982; Moore 1913; Nichols and Shaw 1986; Rogers and Breen 1980; Sastroutomo 1980; Sastroutomo 1981; Wehrmeister 1978; Woolf and Madsen 2003) in water temperatures less than 20°C (Kunii 1982; Rogers and Breen 1980). The green-colored, non-dormant turions that were recently formed are more likely to sprout than the old, brown-colored, dormant turions that were formed the previous season (Rogers and Breen 1980; Sastroutomo 1981). These green, non-dormant turions initiate sprouting in response to cooler water temperatures in both light and dark conditions (Sastroutomo 1981).

Water temperature and light intensity affect the time period and extent of turion sprouting. The time period turions sprout ranges from two to nine months (Catling and Dobson 1985; Jian et al. 2003; Moore 1913; Nichols and Shaw 1986; Rogers and Breen 1980; Sastroutomo 1981; Wehrmeister 1978; Woolf and Madsen 2003). The period of turion sprouting occurs when water temperatures are less than 25° to 30°C (Jian et al. 2003; Moore 1913; Rogers and Breen 1980). Jian et al. (2003) found that the time course of sprouting was affected by water depth despite there being no effect upon the final sprouting percentage. Sprouting peaks between September and November (Catling and Dobson 1985; Jian et al. 2003; Kunii 1982; Moore 1913; Sastroutomo 1981; Wehrmeister 1978; Woolf and Madsen 2003) with water temperatures ranging between 10° and 18°C

(Kunii 1982; Sastroutomo 1981; Waisel 1971)) and is positively associated with light intensity (Kunii 1982). Waisel (1971) found that *P. crispus* turions sprouted the best at 10°C while none sprouted at 30°C. Sastroutomo (1981) and Wehrmeister (1978) found that cold treatment (5°C) increased sprouting, although sprouting was inhibited at water temperatures less than 4°C (Sastroutomo 1981). Light intensity has a quantitative effect on sprouting (Kunii 1982). Sprouting was found to be better in light (Jian et al. 2003), decreased in crowded plant beds (Wehrmeister 1978), inhibited at depths greater than 10.3 m (Jian et al. 2003), and inhibited by both increased crowding from other plants and no light (Catling and Dobson 1985).

Many turions sprout. During the period of peak sprouting, greater than half of the turions were sprouting (Jian et al. 2003; Rogers and Breen 1980; Waisel 1971; Woolf and Madsen 2003). Sastroutomo et al. (1979) found that 47% of all the turions collected during the study period were sprouting.

P. crispus seeds rarely germinate outside the native range. *P. crispus* in North America rarely germinates in the field (Catling and Dobson 1985; Correll and Correll 1972; Hunt and Lutz 1959; Moore 1913; Muenscher 1936; Wehrmeister 1978). Although Moore (1913) and Catling and Dobson (1985) found a few germinated seeds in the field, Wehrmeister

(1978) found that 0% of the collected seeds were germinated. Martin (1951) reported that *P. crispus* seeds were usually sterile. Muenscher (1936) and Wehrmeister (1978) reported that 0% of the seeds germinated after one year in dry storage. Germination percentages from seeds collected in a South African river were 0.001% (Rogers and Breen 1980).

P. crispus seed germination is more common in the native range. Guppy (1894) found that 68% of *P. crispus* seeds germinated in first year and 10% in second year when in water storage. Similarly, when *P. crispus* seeds were in wet mud storage, 6% germinated in first year and 26% germinated in second year (Guppy 1894). Teltscherova and Hejny (1973) found that 60 to 70% of *P. crispus* seeds germinated.

Management

Methods and importance of phenology

There are several management options available for *P. crispus*. The best strategy for managing *P. crispus* integrates outreach to prevent the introduction and establishment of new propagules, different control techniques to manage the existing population and monitoring to assess efficacy and guide future management. *P. crispus* can be managed using hand pulling/ raking, bottom barriers, mechanical harvesting, sediment

agitators, grass carp, contact herbicides such as Diquat or Endothall and the systemic herbicide, Fluridone.

The phenology of *P. crispus* affects the efficacy of management. It is most important to prevent turion formation. Managing for plant biomass provides short term control but allows turions to form and produce plants the following year. The sprouting turions that have already formed are difficult to control because turions are numerous, small, and contain several dormant buds that sprout one at a time throughout the fall, winter and spring.

The timing of application varies with the different management methods. Hand pulling/ raking has the greatest efficacy against *P. crispus* when water temperatures are between 10° and 15°C but before the end of April in North America. Plants will be nearing water surface and beginning to form new turions. Hand pulling/ raking and harvesting should be done before peak turion formation and plant biomass because the collection of plants separate and disperse the turions. Bottom barriers and sediment agitators work best when operational in late winter before the plants have become established. Chemical efficacy is related to plant metabolism and as such, efficacy is greatest at higher water temperatures, such as 25°C (Netherland et al. 2000; Poovey et al. 2002). Netherland et al. (2000) and Poovey et al. (2002), however, demonstrated that the contact herbicides,

Endothall and Diquat, were effective at reducing plant biomass and turion formation at 10°C to 15°C.

Research Purpose

The efficacy of management for *P. crispus* can be increased by targeting reproduction at certain times of the year. The plant primarily propagates through turions and preventing new turion formation is easier and more effective than preventing sprouting of existing turions and controlling plant biomass. Management should occur in late winter to early spring to prevent reproduction. *P. crispus*, however, exhibits variation in its phenology, especially in the timing for the onset of formation and the time period of sprouting. Considerable work has been done throughout the world on *P. crispus* and yet to date, no study has specifically addressed the phenology of this plant in the Pacific Northwest of the United States, which has a moderate climate that is different than many areas already addressed in the literature. This descriptive study was undertaken in Blue Lake, Oregon to determine the timing of both turion formation and turion sprouting to improve management in the Pacific Northwest.

Materials and Methods

Study area: Blue Lake, Oregon

Climate

Blue Lake has a moderate climate. It is located 161 km (100 miles) east of the ocean and 305 m (1,000 ft) south of the Columbia River, in the Pacific Northwest of the United States. Blue Lake experiences cool, wet winters and warm, dry summers. Extreme temperatures are rare (Taylor 2005). There are, however, occasional ice storms and high wind events occur several times a year (Taylor 2005).

Blue Lake is in the Willamette Valley, which has a relatively mild climate. Days with air temperatures above 32°C (90°F) occur only five to 15 times per year on average, and days with air temperatures below 18°C (0°F) occur about once every 25 years (Taylor 2005). The growing season is long. The mean growing season is 150 – 180 days (Taylor 2005). Moisture is abundant most of the year and is negatively associated with increasing temperature (i.e. coolest months are the wettest) (Taylor 2005).

Basin morphology

Blue Lake is a 24.7-hectare (61-acre) natural floodplain lake that lies parallel to the Columbia River in the eastern portion of Multnomah County, Oregon (N 45° 33'14" and W 122°26'19") (Figure 6) (Johnson et al.

1985). Blue Lake's elevation is 4.3 m (14 ft) above sea level. It is located three miles northwest of Troutdale and 11 miles east of the Portland city center (Pfauth and Sytsma 2004). Blue Lake Regional Park is on the northern shoreline and residential development occupies the eastern and southern shorelines (Figure 6). Maximum depth is 7.3 m (24 ft) but nearly half of the lake is 3 m (10ft) or less (Beak 1983).



Figure 6: Aerial photograph of Blue Lake. Photo obtained from Google Earth 2005. Scale bar represents approximately 150 m.

Hydrology

Blue Lake has a relatively small watershed. Lake surface represents most (59.4%) of the watershed (Johnson et al. 1985). The total watershed area is 51.8 hectares (128 acres). The area of Blue Lake Regional Park is

41 hectares (101 acres), and this includes the surface area of Blue Lake (Johnson et al. 1985). The remaining watershed area is private residence (Figure 6). The watershed is restricted by dikes to the north and a sandstone ridge to the south that divides Blue Lake and Fairview Lake (Figure 6) (Johnson et al. 1985). Interlachen Lane forms the watershed boundary to the east and west (Johnson et al. 1985).

Groundwater seeps and springs are the primary source of water for Blue Lake. Although dikes to the north prevent surface flow exchange with the Columbia River, subsurface seepage occurs through the permeable sand base (Johnson et al. 1985). Surface flow and runoff also provide water during periods of high precipitation. There are three small ponds located northwest of Blue Lake and all are interconnected with each other through culverts. Water flows back and forth through the culvert depending on water levels (Johnson et al. 1985).

The water levels of Blue Lake can be controlled. A weir drains into Salmon Creek on the east end of Blue Lake and this creek eventually drains into the Columbia River (Johnson et al. 1985). Groundwater from the Blue Lake Aquifer can be pumped into Blue Lake from the Portland Well Field (Beak 1983).

Trophic status

Blue Lake is an eutrophic lake that supports a variety of plant and animal life. The trophic state index (TSI) was determined to be between 50 and 70 in 2003 (Pfauth and Sytsma 2004). Eutrophic lakes exhibit TSI's between 50 and 65, whereas hypereutrophic lakes have TSI's between 65 and 100 (Carlson 1977). Phosphorus concentrations in Blue Lake range from 0.04 to 0.6 mg/L and sources include rainwater, groundwater, surface runoff, and anoxic sediments (Johnson et al. 1985). Blue Lake thermally stratifies in the summer, creating anoxic sediments that release phosphorus. Total phosphorus in the groundwater pumped from the Blue Lake Aquifer was 0.12 mg/ L (Beak 1983). Approximately half of the lake sediment area is within the depth of colonization for rooted aquatic plants (Johnson et al. 1985).

Weed problems and management

Blue Lake has a history of nuisance aquatic plants due to its shallow depth and high nutrient concentrations. *Myriophyllum spicatum* (Eurasian watermilfoil) was a major problem from the 1970's throughout the 1990's (Johnson et al. 1985). More recently, the dominant plants are *P. crispus* and *Elodea canadensis* (American waterweed) (Pfauth and Sytsma 2004). Other plant species inhabiting Blue Lake include *P. foliosus*, *P. pectinatus*, *Chara* spp., and *Nymphaea odorata* (Pfauth and Sytsma 2004).

Aquatic plant populations in Blue Lake have been managed in the past. A mechanical harvester was used in Blue Lake during the summer of 1971. The mechanical harvester was effective at removing plant biomass but it also created plant fragments that were not collected by the conveyor belt and hence reestablished elsewhere in the lake (Pfauth and Sytsma 2004). Water levels were drawn down in 1981 in an effort to control for *M. spicatum* (Johnson et al. 1985). The drawdown in Blue Lake failed to significantly control the *M. spicatum*, and it damaged retaining walls and docks (Pfauth and Sytsma 2004). Multnomah County applied bottom barriers in the swimming area of Blue Lake in 1982 (Beak 1983). Ten meter by 20 meter panels of fiberglass fabric were installed and monitored for *M. spicatum* regrowth. Bottom barriers were effective at preventing new growth under the barriers but plants did drift, settle and establish on top of the barrier (Pfauth and Sytsma 2004). Since the mid-1990's, Metro has purchased well water from the City of Portland to raise the water level in an effort to control nuisance aquatic plants. This practice does not suppress plant growth but it does improve aesthetics (Pfauth and Sytsma 2004). The water used to raise lake levels, however, contains high levels of phosphorus, which may contribute to algal productivity (Johnson et al. 1985). Metro applied the herbicide, 2, 4-D, to control *M. spicatum* (Johnson et al. 1985).

Sampling

Dates

Twenty sampling dates, approximately twice a month, were chosen depending on weather and boat availability (Table 4). One sampling date was excluded because samples were degraded.

Table 4: Sampling dates. N is number of sampling sites/ sampling date.

Date	N	Date	N
2/10/04	35	5/21/04	21
2/17/04	16	6/14/04	20
2/24/04	20	7/16/04	22
3/2/04	20	9/9/04*	20
3/24/04	20	10/11/04	20
3/31/04	20	11/15/04	20
4/5/04	21	11/29/04	16
4/12/04	20	12/6/04	20
4/19/04	20	12/20/04	20
4/26/04	22	1/10/05	20

* excluded because samples degraded

Locations

The eastern 1.2 hectares (3.0 acres) were chosen as the study area because *P. crispus* populations were abundant and depth and substrate were uniform. These data were collected from preliminary sampling (11 November 2003 and 1 January 2004), vegetation maps (Pfauth and Sytsma 2004) and personal communication with Blue Lake Metro Regional Park staff (Dwight Vermass, Metro staff, personal comm., 2004).

The entire study area was suitable habitat for *P. crispus*. Analysis of bathymetric maps indicated 1.2 m (3.9 ft) was the average depth of the study area and the maximum depth was 2.4 m (7.8 ft) (Figure 7). Sediment within the study area was soft, organic-rich mud, and included imported sand and gravel surrounding residential docks.

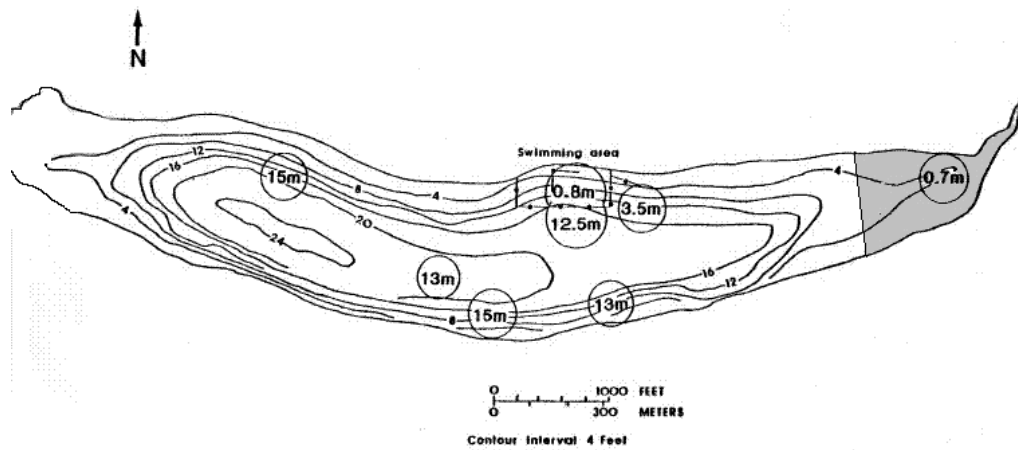


Figure 7: Bathymetric map of Blue Lake showing study area. The approximate location of the study area is shaded in grey. Map from Beak (1983).

There was a mean of 21 sample sites per sampling date. The number of sample sites per sampling date varied because plastic bags containing samples sometimes broke during transport and storage.

Sample sites within the study area were randomly determined. The spatial vectors for each sample site were sequentially determined with random numbers. A number between one and 360, corresponding to a 360° coordinate system, was used for direction while a random number between

two and 12 was used for magnitude, corresponding to the time (seconds) the boat was driven at full throttle. After the time expired, the engine was turned off via the emergency engine-shut off switch and a 4.5 kg (10 lb) bell anchor was thrown from the stern. The oars were used in water depths prohibitive of engine use and the travel time was then tripled.

Sampling Methods

Plants were sampled with a plant rake. The plant rake produced a rectangle-shaped quadrat that was 0.408 m² in size. The plant rake was thrown twice at each sample site approximately perpendicular to the port side. All raked material was collected in marked plastic bags.

Turions in the sediment were sampled with a Petite Ponar dredge. The sediment dredge produced a square-shaped quadrat that was 0.026 m² in size. It was deployed once from the port side at each sample site. Dredge spoils were collected in marked plastic bags.

Each sample site was described using a DataSonde 4A Multiprobe Hydrolab. Water temperature, depth, dissolved oxygen (DO), and pH were measured within five cm of the sediment at each sample site. After the anchor was thrown from the stern, the Hydrolab was deployed from the port side. Measurements were recorded when temperature values had stabilized ± 0.01 , depth values ± 0.1 , DO values ± 0.01 and pH values \pm

0.01. The unit was calibrated according to the Hydrolab manual for pH and DO before sampling. The depth accuracy was checked by measuring at water surface. The unit was not calibrated for temperature.

Plant and turion measurement

The *P. crispus* population in Blue Lake was described using data regarding the growth of the plants, new turion formation and the sprouting of turions. Plant measurements were done on intact plants and potential plant propagules. Intact plants had stems and leaves and either rhizomes or attached turions. Potential plant propagules had at least seven cm of stem and spring foliage. Potential plant propagules were measured because vegetative growth can occur from stem fragments devoid of rhizomes and roots.

The formation of turions was measured using the new turions that were attached to either the terminal stem apex or leaf axil of rooted, erect plants. Turion formation was measured with the onset, time period and extent of formation for all turions, turion types (denticulate and spiculate) and the stem position of formation (lateral and apical). Onset, within this text, represents the date of first observation. The time period or duration is the length of time measured in Julian calendar days the process was

observed. Extent is a quantitative assessment represented by density (number/ unit area and weight/ unit area).

The sprouting of turions was measured using the turions collected from the sediment. Sprouting was measured with the onset, time period and extent of sprouting for all turions and turion types. Stem position of formation was not measured for sprouting turions because most mature turions separated from plants.

Dredge and rake spoils were cleaned using a sieve. The sieve consisted of metal screens with pore diameters of 1.27 mm and 5.76 mm. Samples were stored for up to two days in the greenhouse in tap water until all samples had been sieved. The number of turions, plants and apparent sprouting turions found at each sample site were recorded after sieving.

Sieved *P. crispus* samples were refrigerated in tap water in marked plastic bags for up to ten days prior to measurement. Samples that had not been measured after ten days were discarded. Sprouting turions were measured first because low water temperature affects sprouting.

Physical measurements

The turions were described with several measurements. The fresh and dry weight (mg) were obtained using an OHAUS® Explorer digital scale. Dry weight was measured following oven drying at 70°C (158°F) for

48 hours in aluminum trays. The length and width dimensions were measured for the turions as the greatest linear dimensions along both longitudinal (Figure 3e) and latitudinal axes (Figure 3d) before oven drying.

Newly formed turions that were separated from the parent plant during collection were identified using the origin and status of attached vegetation, the presence/ absence of both sprouting buds and attached vegetation, the leaf bases, and both bud and bud sheath development (Table 5) as well as the year of formation (Appendix B).

Table 5: Traits used to differentiate new and old turions.

Trait	New turion	Old turion
Leaf Base	* not distinct	* distinct, often with spines on edge
	* attached intact leaves on distal portion	* no attached leaves
	* attached decaying leaves on distal portion	
	* pliable, soft, fleshy to touch	* brittle, hard, thorny to touch
Buds	* not distinct	* distinct
	* inconspicuous or small if present	* well-developed
	* sprouting buds rare	* sprouting buds present
		* missing bud with remaining bud sheath
Apparent color	* green (light to dark)	* brown (light to dark)
		* red (yellow to red)
		* green (dark)
		* black
Collection location	* attached to healthy ^T plants	* sediment
		* attached to non-healthy ^{TT} plants
Winter foliage	* never attached	* attached to sprouting bud
Spring foliage	* healthy ^T plants attached to basal tip of turion	* healthy ^T plants attached to sprouted bud of turion
		* non-healthy ^{TT} plants attached to basal tip of turion

^T healthy plants were rooted, erect and possessed intact, green leaves

^{TT} non-healthy plants were not rooted nor erect and lacked leaves and/ or displayed signs of senescence such as yellowing or decaying vegetation

The number of leaf bases, dormant buds and sprouting buds was counted for the turions. The presence of buds was determined by a visual inspection of leaf axils using a hand lens (10X magnification) and a dissecting microscope (100X magnification). A bud was sprouting when a rudimentary shoot was visible (Figure 8).

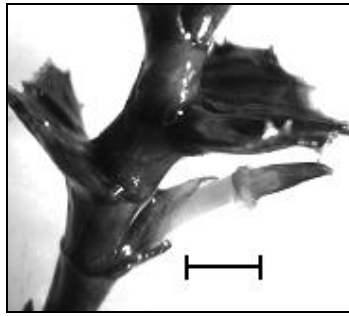


Figure 8: Photograph of sprouting bud on turion. Scale bar represents approximately 5 mm

Turions were separated into denticulate and spiculate turions according to Table 6. This was not done for all turions. Immature development precluded the determination of turion type for some of the new turions. Additionally, the turion type was not determined for both old and new turions when the length/ width ratios ranged from 2.3 to 2.6 mm.

Table 6: Traits distinguishing denticulate and spiculate turions.

Traits	Denticulate	Spiculate
Length	10 - 50 mm	3 - 11.5 mm
Width	5 - 13 mm	1.5 - 3 mm
L/ W ratio	< 2.3* mm	> 2.6* mm
# buds	more (0 - 7)	less (0 - 7)
Bud status	small, protected	large, exposed
Internode length	3 - 7 nodes	6 - 13 nodes
Leaf bases	large, square margin	spinous, acute margin

* Turions were not typed when ratios ranged from 2.3 to 2.6 mm

Plants were separated by the dominant type of foliage (i.e. spring, winter) and measured. Several traits were used to separate the spring and

winter foliage (Table 7). The leaves were removed with a scalpel and the defoliate main stems, axillary stems and rhizomes were separated, counted and measured. The stem position of attached new turions was recorded (e.g. apical). The fresh and dry weight (mg) was measured. The main stem, axillary stem, and rhizome lengths (mm) were measured. The number of main stems, axillary stems, rhizomes, stem roots, rhizome roots, apparent nodes, and new turions were counted. Appendix C provides traits used to separate main stems, axillary stems and rhizomes. Nodes were counted when visually distinct with a hand lens (10X magnification).

Table 7: Traits used to differentiate the spring and winter foliage.

Traits	Winter	Spring
Leaf width (mm)	5 - 7.5	7.5 - 15
Leaf length (mm)	-	30 - 80
Margin	flat	undulate
Apparent color	dark green	light green-red
Feel to touch	flexible	crisped
Leaf tip	acute	rounded
Midveins	inconspicuous	prominent

Measurements for individual plants were recorded separately but *P. crispus* has multiple main stems, axillary stems and rhizomes per plant. Measurements for each plant, therefore, represented the sum of a parameter (e.g. # nodes) for a particular plant part (e.g. main stem).

Climate

Mean monthly air temperature and total monthly precipitation were used to determine if the weather in 2003, 2004 and 2005 was different than that in the 1965-2005 time period. National Oceanic and Atmospheric Administration (NOAA) data collected from the Troutdale (45°33' N and 122°23' W) and Portland International Airport (45°35' N and 122°36' W) weather stations were used for these analyses. The monthly weather data for these stations were aggregated over a 40 year time period to estimate the climate. The weather data for the three individual years during data collection were then compared to the 40 year climate data.

Statistical analysis

Variables and methods

Transformations were made to the data when it was appropriate. Tests for random distributions were performed using goodness of fit tests for the Poisson and Chi-Square distributions. Normality was determined with the ratio of skewness to its standard error, rejecting normality with a ratio less than negative two or greater than two (Zar 1996). The logarithmic transformation ($X+1$) was applied to data for plant dry weight, plant stem length, turion data for both new and old turions regarding the number of turions, turion dry weight, and the number of denticulate and spiculate

turions. The logarithmic transformation ($X+1$) was also applied to data for the number of new turions in apical- and lateral-stem positions as well as the number and dry weight of old denticulate and spiculate turions that were both sprouting and non-sprouting. Measures of central tendency were directly back-transformed, however, the measures of variance could not be directly back-transformed (Zar 1996). The 0.95 confidence interval of the transformed data was calculated using the transformed standard error and the $t_{0.05(2),N}$ value and this was used to calculate the confidence limits for the transformed data. These confidence limits were then back-transformed, and used to calculate the 0.95 confidence interval in the original units. The 0.95 confidence interval was used to estimate the standard deviation by assuming that with a normal distribution, the 0.95 confidence interval equals two standard deviations.

Tests of difference were done using the t-test and ANOVA. Significance for all tests was alpha of 0.05. The t-test was used to investigate the differences between the new denticulate and spiculate turions as well as those turions formed in lateral- versus apical-stem positions. These tests compared the means for turion weight, length, width, the number of buds and the number of leaf bases. The t-test was also used to investigate the differences between sprouting and non-sprouting turions as well as old denticulate and spiculate turions. Single-factor ANOVA was

used to investigate differences between old turions with either one, two or three sprouting buds. Subsequent multiple comparison tests were done with the Tukey Test.

Figures and tables describing the climate, plant growth, turion formation and sprouting were made with DeltaGraph (5.0) and Microsoft Excel (2000). Figures describing the dry weight, number of buds, number of leaf bases, and length and width dimensions for both the new and old turions were made and analyzed with SPSS (10.1).

The 0.95 confidence intervals for the climate data of the 1965 to 2005 period were used to compare the mean monthly weather data for 2003, 2004 and 2005 to the aggregate monthly data for the 1965 to 2005 period. A significant difference was a difference at alpha of 0.05 for both mean monthly air temperature and total monthly precipitation for two consecutive months in relation to the 1965-2005 time period.

Results

Physical characteristics of Blue Lake

The physical characteristics encountered in Blue Lake during the study period exhibited average seasonal changes. Water temperature ranged from approximately 3° to 26°C (Figure 9). Abiotic parameters measured at each sample site, which ranged in depth from 0.4 to 1.4 m, had a moderately high pH and were always aerobic (Table 8). Beak (1983) reported pH from 6.81 to 8.97 in 1982. Although, Beak (1983) reported that oxygen decreased to 0.5 mg/ L, this occurred in the deeper areas outside the study area.

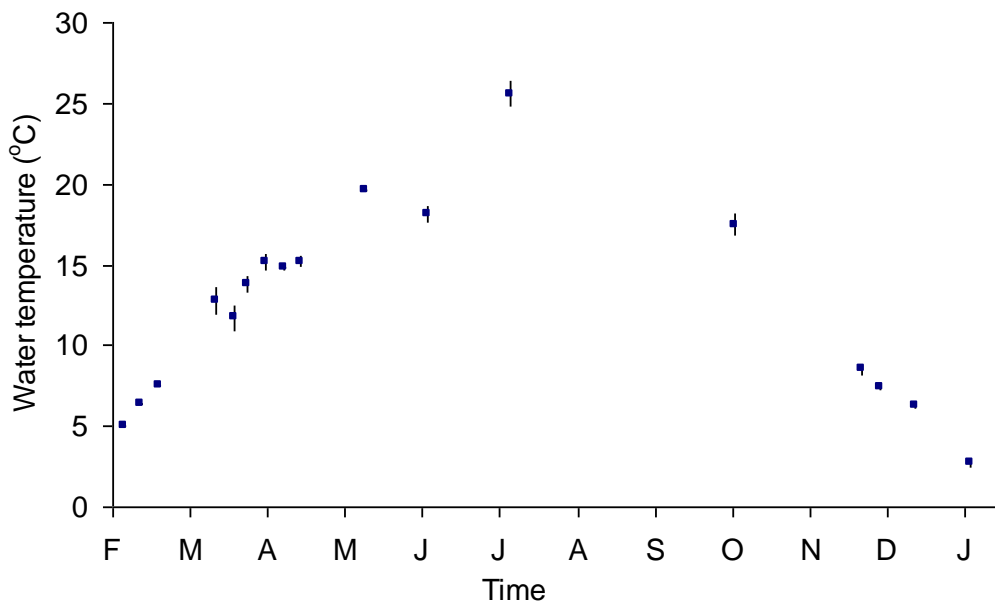


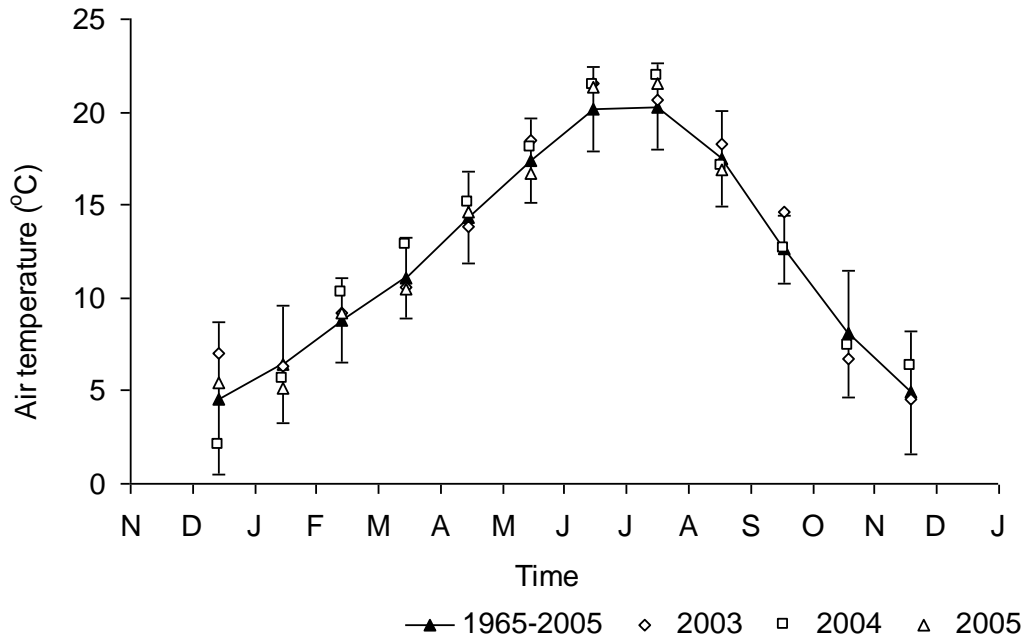
Figure 9: Bottom water temperature in study area. Temperature (°C) calculated within five cm of sediment surface in study area (mean \pm 2 SD).

Table 8: Abiotic parameters of the study area. Values represent mean and 1 standard deviation or standard error. N represents the number of sites per sampling date.

Sampling Date	N	Water temp (°C)		Dissolved O ₂ (mg/ L)		pH		Depth (m)		Daylength (hr)
		mean	SD	mean	SE	mean	SE	mean	SE	
2/10/04	35	5.63	0.25	12.78	0.5	7.84	0.0	1.4	0.1	10.1
2/17/04	16	4.97	0.04	11.25	0.3	7.42	0.0	1.2	0.1	10.5
2/24/04	20	6.41	0.07	10.55	0.2	7.36	0.0	1.2	0.1	10.8
3/2/04	20	7.57	0.09	10.42	0.5	7.56	0.0	1.2	0.1	11.2
3/24/04	20	12.8	0.46	9.991	0.5	7.47	0.1	1.4	0.1	12.4
3/31/04	20	11.7	0.41	9.988	0.5	7.68	0.1	1.1	0.1	12.8
4/5/04	21	13.8	0.28	9.319	0.5	7.59	0.1	1.3	0.1	13.0
4/12/04	20	15.2	0.28	10.53	0.6	8.29	0.1	0.8	0.1	13.4
4/19/04	20	14.8	0.10	9.098	1.5	8.05	0.1	1.3	0.2	13.7
4/26/04	22	15.2	0.19	8.786	0.7	7.77	0.1	0.9	0.1	14.1
5/21/04	21	19.6	0.07	8.735	0.3	8.73	0.1	1.2	0.1	15.1
6/14/04	20	18.1	0.29	9.374	0.4	8.65	0.0	0.9	0.1	15.7
7/16/04	22	25.6	0.42	6.870	0.7	7.46	0.0	0.6	0.1	15.3
10/11/04	20	17.5	0.37	8.855	0.7	7.83	0.0	1.1	0.2	11.2
11/15/04	20	-	-	-	-	-	-	1.1	0.1	9.5
11/29/04	16	8.51	0.19	-	-	8.16	0.1	0.8	0.1	9.0
12/6/04	20	7.44	0.12	12.23	0.3	7.67	0.0	0.4	0.1	8.8
12/20/04	20	6.32	0.16	13.66	0.5	7.88	0.0	0.7	0.1	8.7
1/10/05	20	2.77	0.17	14.42	0.3	7.39	0.0	0.9	0.1	10.6

The weather data for the study period were not different than data representing the 1965 to 2005 period. Air temperature and precipitation in the study years were within the approximate 0.95 confidence interval for the monthly means in the period, 1965 to 2005 (Figure 10). Precipitation had greater variance than air temperature. January and February 2005 were drier months while April and May 2005 were wetter months.

a)



b)

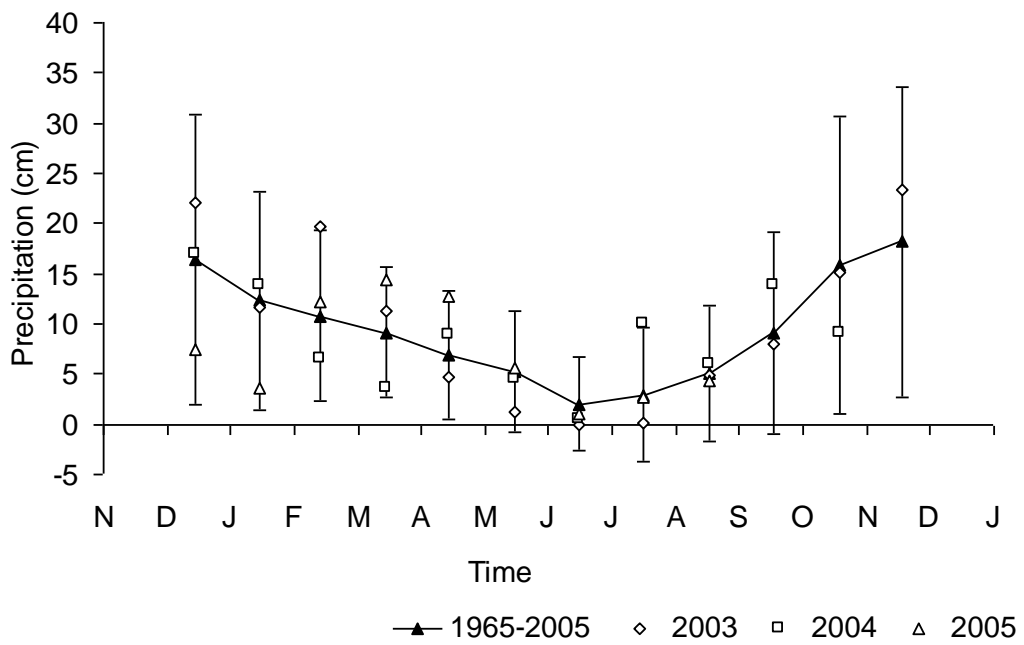


Figure 10: Weather for Blue Lake, OR for the study period and the period, 1965-2005. Weather is represented by a) the mean monthly air temperature ($^{\circ}\text{C}$) and b) the total monthly precipitation (cm). Mean \pm 2 standard deviations ($n = 38$) for period, 1965-2005.

Growth

In February, the spring foliage began to develop in the leaf axils of the winter foliage. Plant growth, however, was minimal. Plants possessed only main stems (Figure 12a) and size was at the seasonal minima measured by dry weight (Figure 11), stem length and the number of nodes (Figure 12a and 12b). Spring foliage continued to replace winter foliage through March and into April.

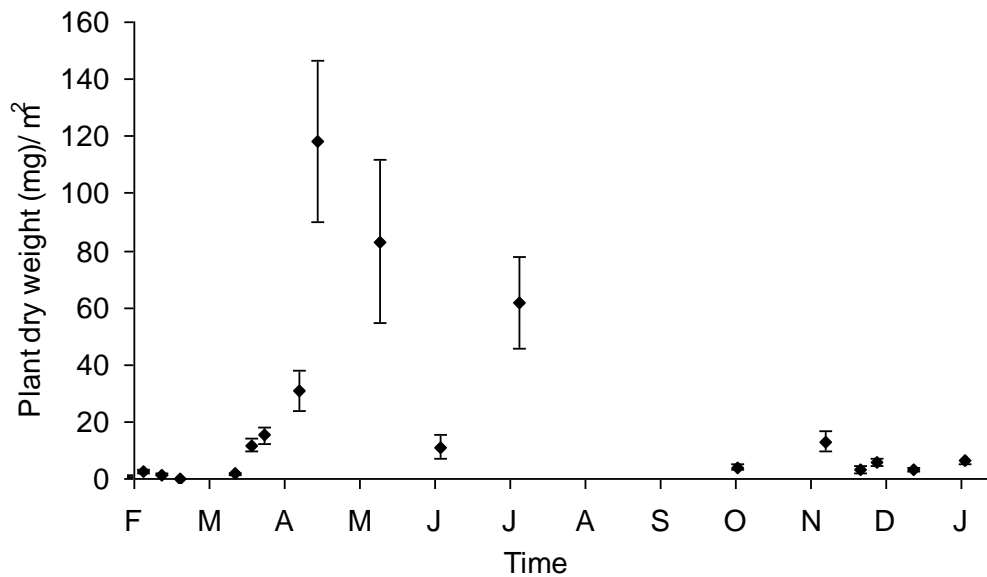


Figure 11: Plant density in relation to time. Density presented as plant dry weight (mg/m^2) (geometric mean \pm 1 SE).

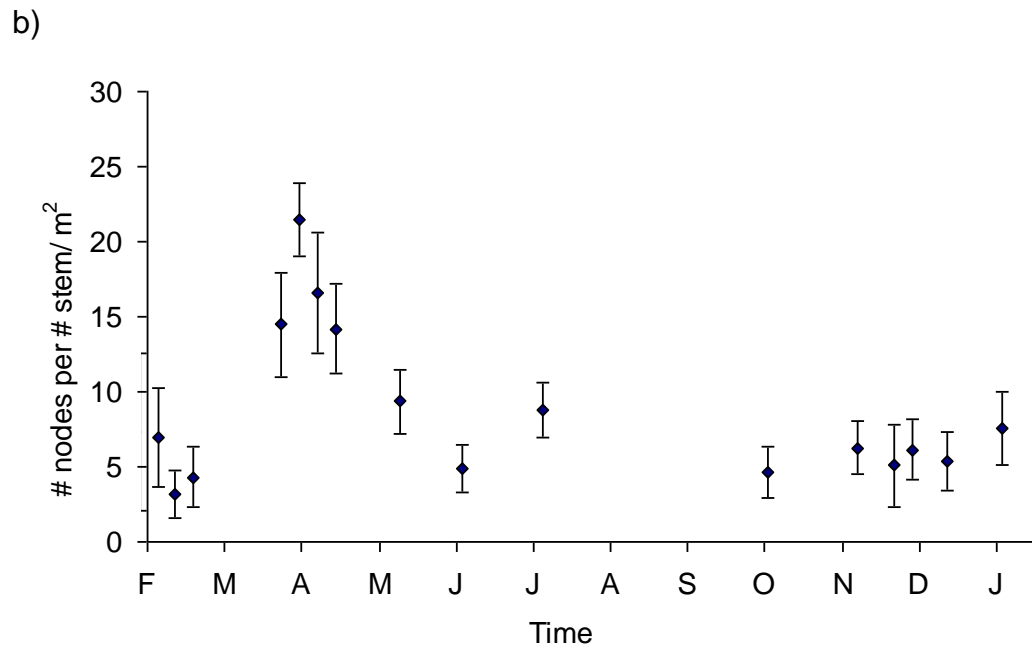
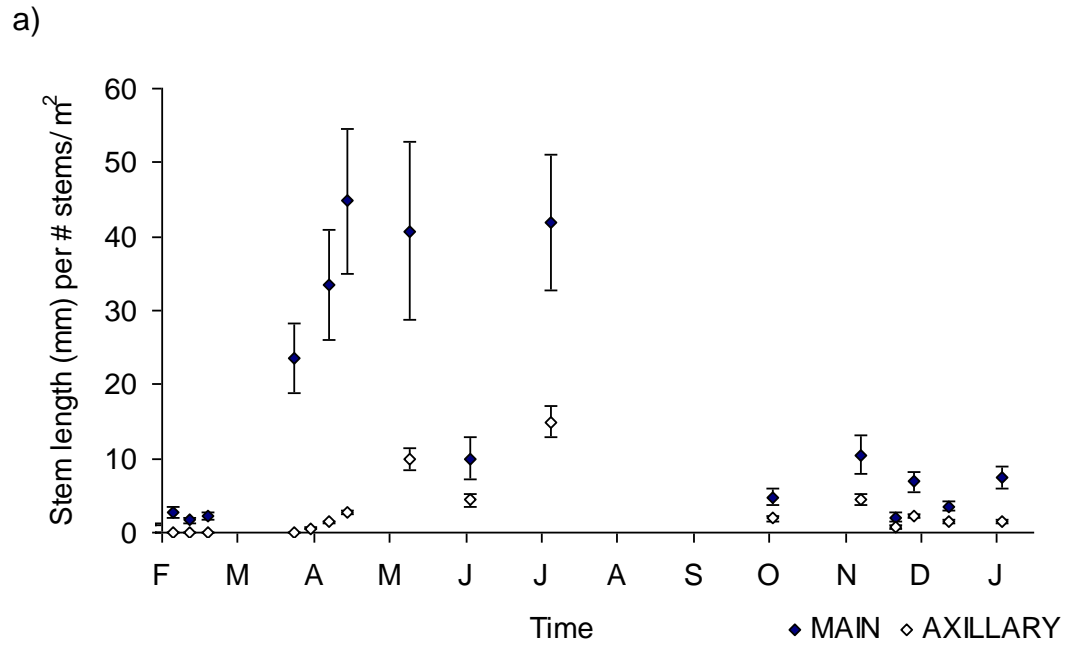


Figure 12: Plant size in relation to time. Plant size represented by a) stem length

(mm) per # stems/ m² for main and axillary stems (geometric mean \pm 1 SE) and b) # of nodes per # stem/ m² (mean \pm 1 SE).

By April, the spring foliage predominated and growth was vigorous. Growth occurred through internode length and node increment. This is demonstrated with the increased main stem length and number nodes (Figure 12a and 12b). The greatest change in main stem length occurred in early April (Figure 12a). Axillary stems first contributed to the total stem length in the beginning of April (Figure 12a). The axillary stems were nine percent ($n = 191$) of the total number of stems and 0.01% ($n = 116$ mm) of the total stem length by mid-April.

P. crispus peaked in biomass and was capable of reproduction early in the growing season. Individual plants were observed near the water surface at the end of March and plants were at the surface by early April. The canopy was forming by late April shown by the sudden increase in the stem length and number of nodes for axillary stems (Figure 12a and 12b). The rate of change for axillary stem length peaked between late April and early May. The main stem lengths peaked by late April and remained fairly constant throughout the remaining period of growth while the axillary stem lengths continued to increase through mid-July as the canopy continued to develop (Figure 12a). First emergent inflorescences were observed on 19 April 2004. By April, plants had greater than 15 nodes per stem (Figure

12b). Peak turion formation coincided with 15 to 20 nodes per stem (Figure 13).

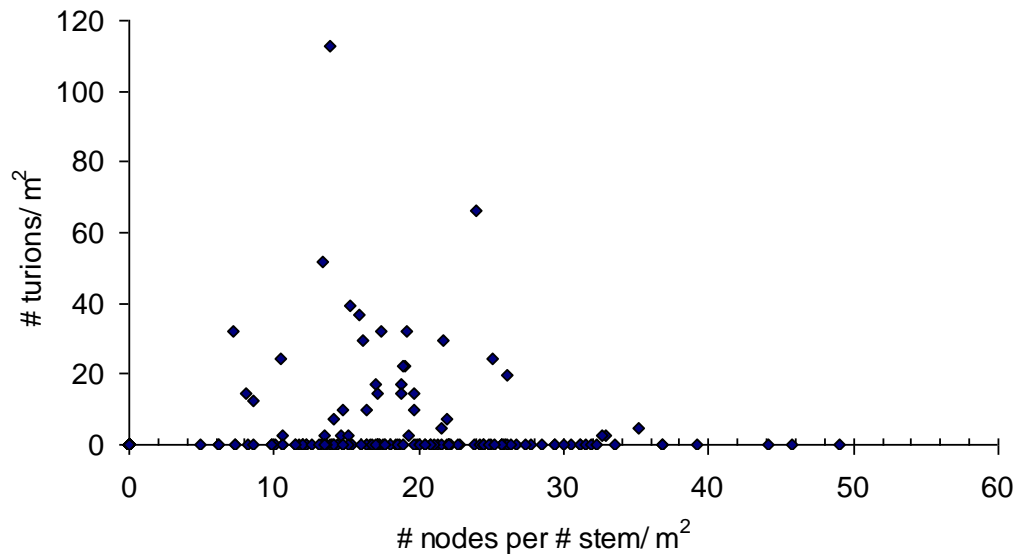


Figure 13: New turion density in relation to plant size. Turion density presented as # turions/ m² and plant size is represented by # of nodes per stem/ m². N = 353; node data absent for 24 and 31 March 2004.

Plant biomass decreased following reproduction. Plants continued to grow in June but no further increases in the 2004 growing season were observed in both the main and axillary stem length (Figure 12a) and plant dry weight (Figure 11). Plant dieback occurred from August to October. Healthy plants were found as late as December and January but it was not ubiquitous to the entire population. Plant senescence was determined by foliage and stems yellowing, falling to sediment and the plant weight approaching the seasonal minimum (Figure 11).

Formation of turions

Turions are compact vegetative propagules. Sixty-seven percent ($n = 166$) of the new turions had a dry weight less than or equal to twenty mg (Figure 14a). Eighty-one percent ($n = 84$) of new turions had two to five buds/ turion, while 91% ($n = 96$) had three to six leaf bases (Figure 14b and 14e). The length and width dimensions represented both types of turions; 95% ($n = 105$) of the width dimensions ranged from 4 to 14 mm and 69% ($n = 77$) of the length dimensions ranged from 10 to 15 mm (Figure 14c and 14d).

Figure 14: New turion size. Turion data presented as frequencies of a) turion dry weight (mg), b) number of dormant buds/ turion, c) greatest latitudinal dimension (mm), d) greatest longitudinal dimension (mm) and e) the number of leaf bases/ turion.

a)

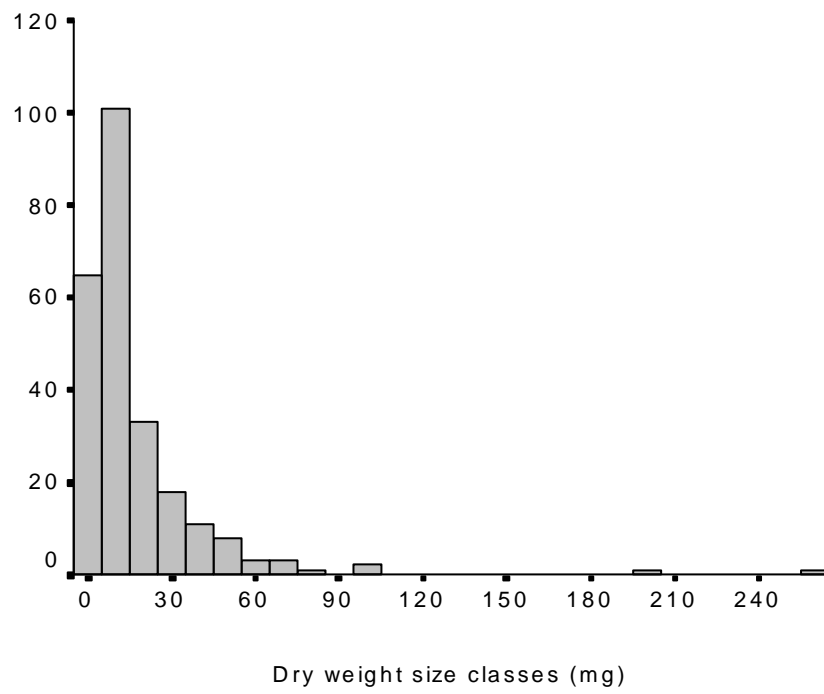


Figure 14: New turion size (continued)

b)



c)

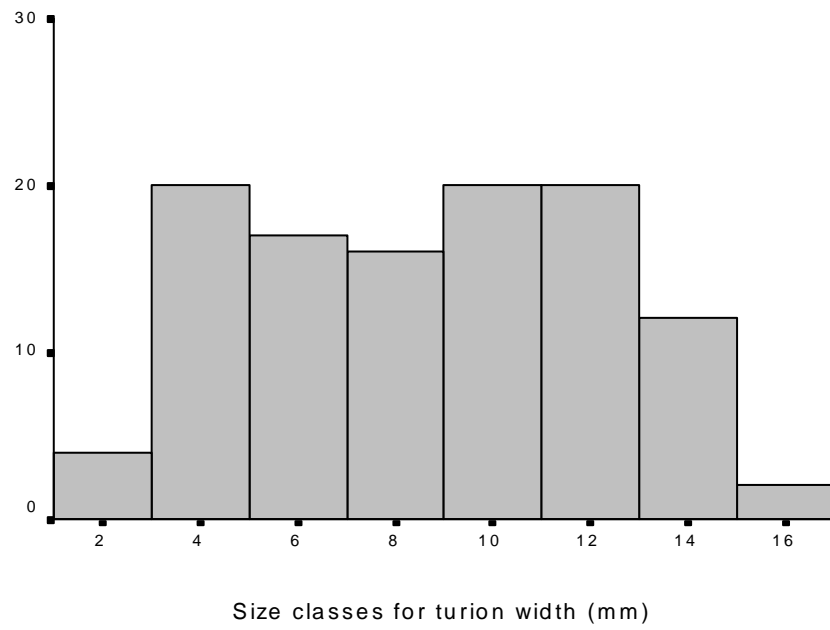
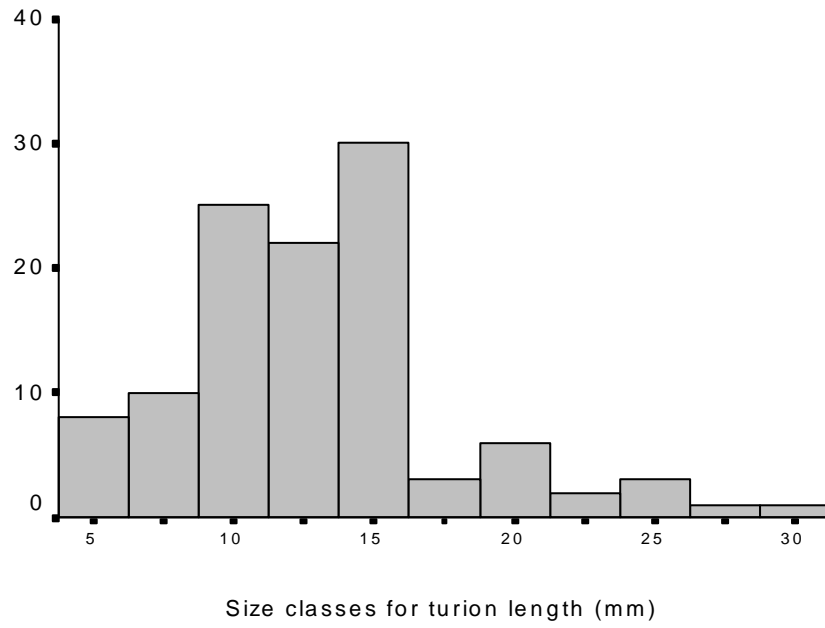
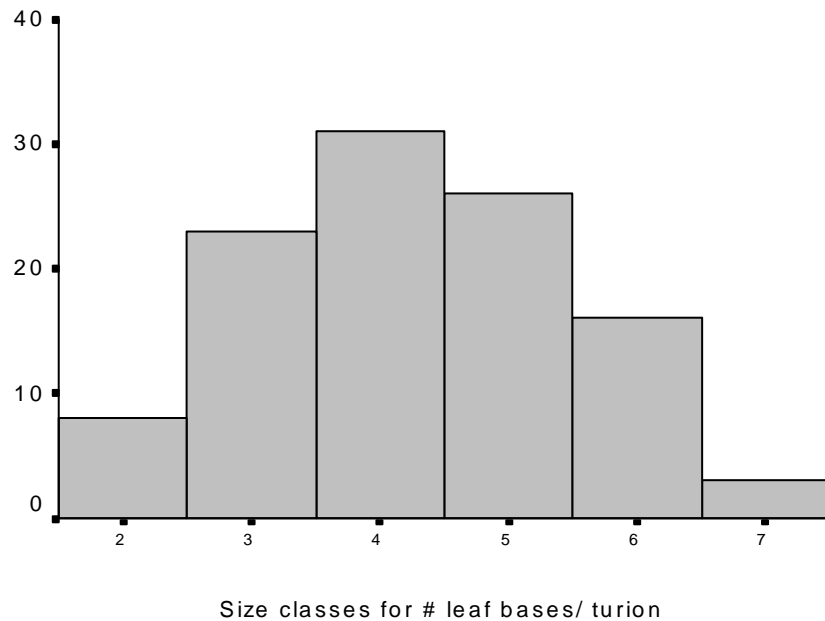


Figure 14: New turion size (continued)

d)



e)



Newly formed denticulate turions were morphologically different than spiculate turions. Denticulate turions had a greater weight/ unit area of turion (dry weight (mg)/ length*width (mm²)) than spiculate turions [t-test assuming unequal variances: $t_{\text{stat}} = 4.405$, d.f. = 95, $P_{2 \text{ tail}} = 2.780 \text{ E-}5$]. Denticulate turions had a greater turion dry weight [t-test assuming equal variances: $t_{\text{stat}} = 4.466$, d.f. = 96, $P_{2 \text{ tail}} = 2.180 \text{ E-}5$]. Spiculate turions were longer [t-test assuming equal variances: $t_{\text{stat}} = -3.111$, d.f. = 106, $P_{2 \text{ tail}} = 2.395 \text{ E-}3$], while denticulate turions were wider [t-test assuming equal variances: $t_{\text{stat}} = 6.721$, d.f. = 106, $P_{2 \text{ tail}} = 9.340 \text{ E-}10$]. There was no difference between the newly formed denticulate and spiculate turions regarding the number of buds [t-test assuming equal variances: $t_{\text{stat}} = 2.572$,

d.f. = 100, $P_{2 \text{ tail}} = 0.012$] nor leaf bases [t-test assuming equal variances: $t_{\text{stat}} = 0.934$, d.f. = 103, $P_{2 \text{ tail}} = 0.353$].

There were no morphological differences between newly formed turions in lateral-stem and apical-stem positions. There was no difference between turions in the apical- and lateral-stem position regarding the turion dry weight [t-test assuming equal variances: $t_{\text{stat}} = 1.207$, d.f. = 235, $P_{2 \text{ tail}} = 0.229$]. There was no difference regarding the turion length and width [t-test assuming equal variances for length: $t_{\text{stat}} = 0.591$, d.f. = 106, $P_{2 \text{ tail}} = 0.556$; t-test assuming equal variances for width: $t_{\text{stat}} = -0.705$, d.f. = 106, $P_{2 \text{ tail}} = 0.482$]. There was no difference between turions formed in apical- and lateral-stem positions regarding the number of leaf bases [t-test assuming equal variances: $t_{\text{stat}} = 1.432$, d.f. = 103, $P_{2 \text{ tail}} = 0.155$].

Denticulate and spiculate turions formed in both apical- and lateral-stem positions. There were significant differences between denticulate and spiculate turions regarding dry weight, and the length and width dimensions. There were no differences, however, in turion dry weight nor length and width dimensions relative to the stem position of formation.

In Blue Lake, Oregon, turion formation was initiated between late-March and early April. Onset of formation (5 April 2004) was associated with a daylength of 13.0 hr and a bottom water temperature of $13.8 \pm 0.1^{\circ}\text{C}$ (mean \pm SE). The first new turion found was a single spiculate turion and

was followed by a single denticulate turion a week later. Turions formed two weeks earlier in apical-stem positions than they did in lateral-stem positions (Table 9).

Turion formation occurred over a period of 281 days, extending from 5 April 2004 to 10 January 2005 (Figure 15). There was no difference in the time period of formation between spiculate and denticulate turions (Figure 16). There was a difference in the time period turions formed in the apical-versus the lateral-stem position. Turions were formed in the lateral-stem positions over a longer time period than they were formed in apical-stem positions (Figure 17a and 17b). Formation in the apical-stem positions occurred for 103 days, commencing on 5 April 2004 and ending after 16 July 2004. Formation in lateral-stem positions occurred for 267 days, beginning on 19 April 2004 and ending on 10 January 2005. On 10 January 2005, five new turions were found in lateral-stem positions while there were zero turions in apical-stem positions (Table 9).

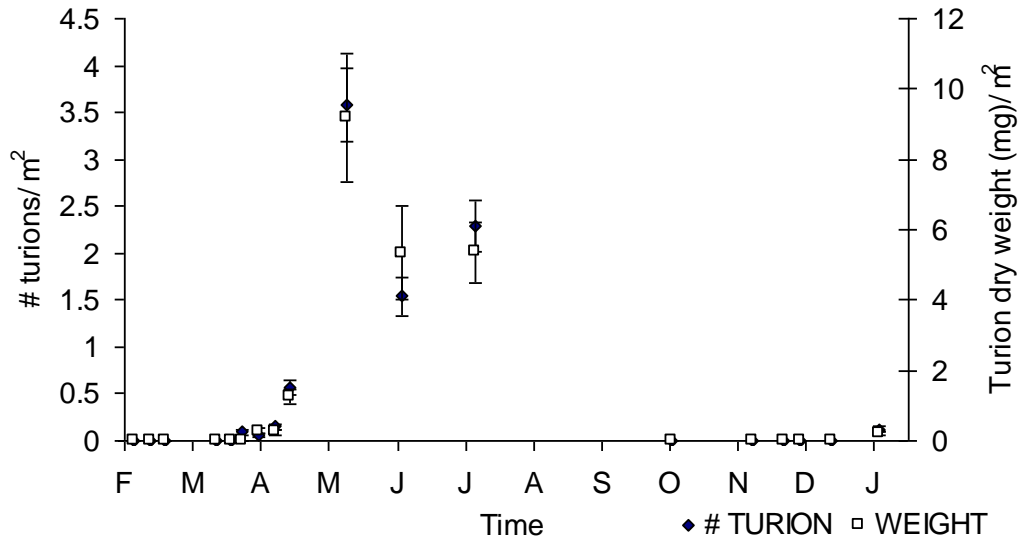


Figure 15: New turion density in relation to time. Density represented by # turions/ m² (geometric mean ± 1 SE) and turion dry weight (mg)/ m² (geometric mean ± 1 SE).

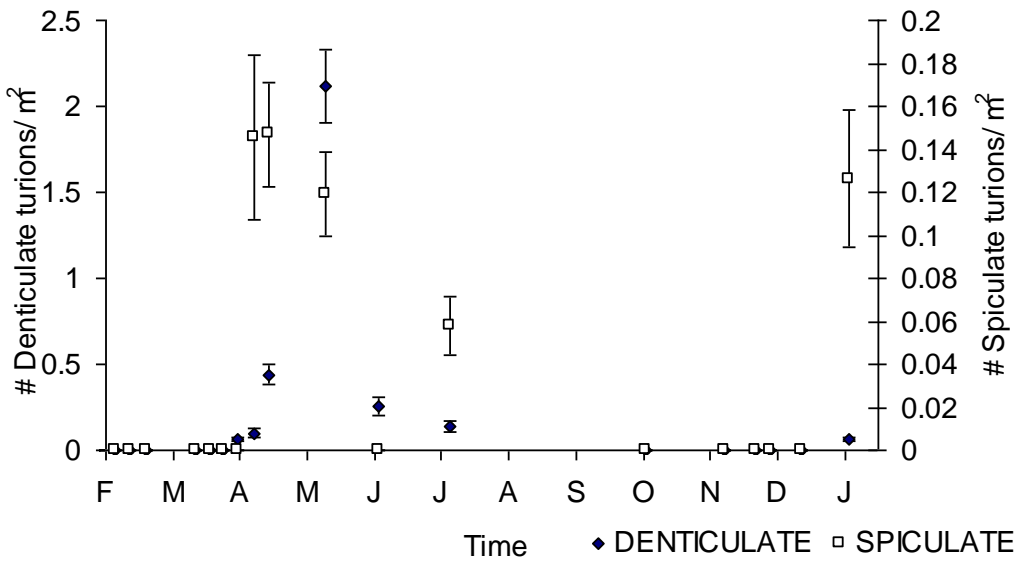


Figure 16: Density of new denticulate and spiculate turions in relation to time. Density represented by # turions/ m² (geometric mean ± 1 SE).

Table 9: Plant rake data summarizing new turion formation. N is the number of sample sites per sampling date, n_T is # new turions per sampling date, n_D is # new denticulate turions per sampling date, n_S is # new spiculate turions per sampling date, n_A is # apical-stem position turions per sampling date, n_L is # lateral-stem position turions per sampling date, n_{PT} is # plants per sampling date and n_{P1} is # plants with attached new turions per sampling date.

Sampling Date	N	Total new turions			Turion types						Stem positions for formation						Plants with turions			
		mean	SE	n _T	Denticulate		Spicular		n _D	n _S	Apical		Lateral		n _A	n _L	mean	SE	n _{PT}	n _{P1}
2/10/04	35	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	8	0
2/17/04	16	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	7	0
2/24/04	20	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	6	0
3/2/04	20	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0	0
3/24/04	20	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	8	0
3/31/04	20	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	48	0
4/5/04	21	0.1	0.0	2	0.0	0.0	0.0	0.0	0	1	0.1	<0.1	0.0	0.0	1	0	0.1	0.1	44	2
4/12/04	20	0.1	0.0	1	0.1	<0.1	0.0	0.0	1	0	0.0	0.0	0.0	0.0	0	0	0.1	0.1	102	1
4/19/04	20	0.1	0.0	7	0.1	<0.1	0.1	<0.1	2	5	0.1	<0.1	0.1	<0.1	2	4	0.1	0.1	61	3
4/26/04	22	0.6	0.1	18	0.4	0.1	0.1	<0.1	15	3	0.2	<0.1	0.4	0.1	3	15	0.5	0.2	121	9
5/21/04	21	3.6	0.4	107	2.1	0.2	0.1	<0.1	55	2	0.1	<0.1	3.5	0.4	3	101	2.4	0.3	75	45
6/14/04	20	1.5	0.2	66	0.3	0.1	0.0	0.0	12	0	0.1	<0.1	1.5	0.2	1	62	1.0	0.3	129	24
7/16/04	22	2.3	0.3	109	0.1	<0.1	0.1	<0.1	7	1	0.1	<0.1	1.9	0.2	2	100	1.5	0.3	53	28
10/11/04	20	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	25	0
11/15/04	20	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	46	0
11/29/04	16	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	15	0
12/6/04	20	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	38	0
12/20/04	20	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	19	0
1/10/05	20	0.1	0.0	5	0.1	<0.1	0.1	<0.1	1	4	0.0	0.0	0.1	<0.1	0	5	0.1	0.1	45	3

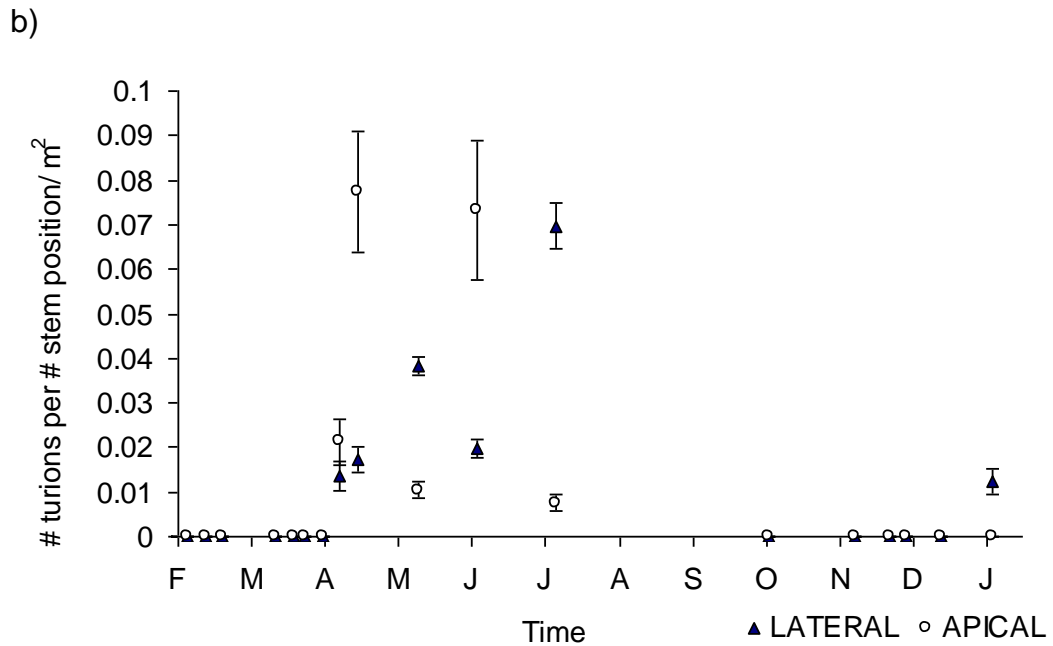
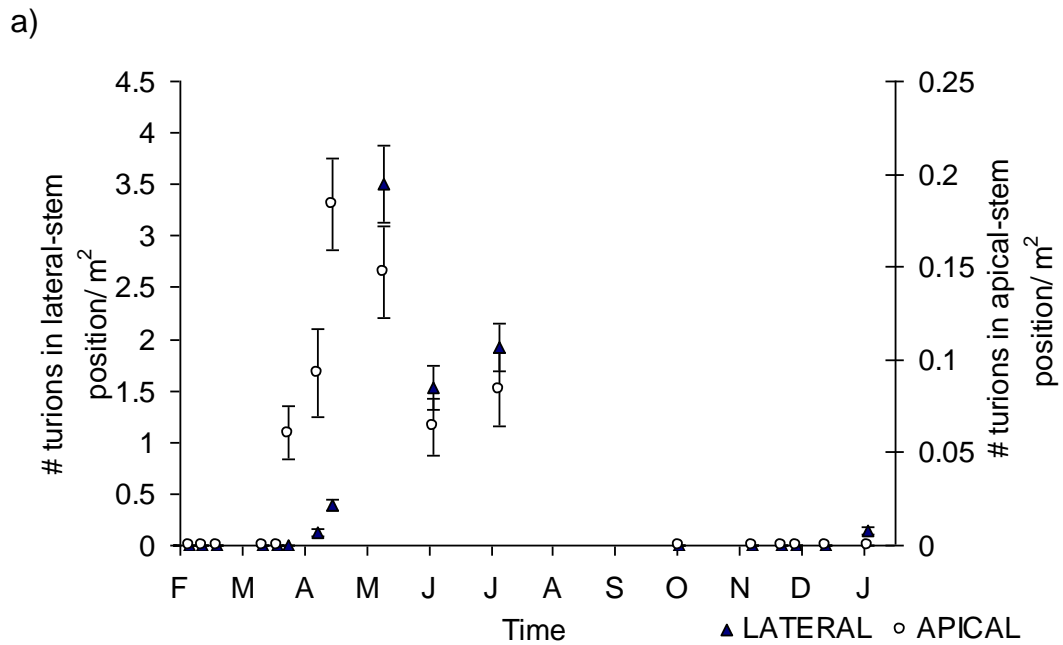


Figure 17: Density of turion formation in apical- and lateral-stem positions in relation to time. Density represented by a) # turions/ m² for each stem position (geometric mean \pm 1 SE) and b) # turions per # stem position/ m² (geometric mean \pm 1 SE).

Total formation peaked on 21 May 2004, measured with density of new turions (Figure 15) as well as the frequency of plants with attached turions (Table 9). Denticulate and spiculate turions differed in the extent as well as the timing of peak formation. The density of denticulate turions was greater than spiculate turions and definitively peaked on 21 May 2004 (Figure 16). The density of spiculate turions peaked between late April and late May (Figure 16).

Turion formation was greater in lateral-stem positions (Figure 17a). Although there was no significant difference between the peak number of denticulate and spiculate turions relative to the number of stem positions available (Figure 17b), there were many times more lateral-stem positions available compared to the apical-stem positions. For example, the number of lateral-stem positions available was estimated from the number of nodes whereas the number of apical-stem positions available was estimated from the number of main and axillary stems. The density of new turions formed in the lateral-stem position definitively peaked on 21 May 2004 (Figure 17a). Formation in apical-stem positions peaked on 19 April 2004 (Figure 17a).

Sprouting of turions

Turions are small and have several buds. Eighty-two percent (n = 239) of the old turions, irrespective of time or type, had a dry weight equal to or less than ten mg (Figure 18a); 6.62 ± 0.1 mg was the geometric mean \pm SE and there was a range of 213.1 mg. Turions had zero to seven dormant buds but 76% (n = 305) had two to four dormant buds/ turion (Figure 18b). Most length/ width ratios ranged from 1.5 mm to 6.0 mm for turions (Figure 18c and 18d).

Figure 18: Old turion size. Size presented as frequencies of a) turion dry weight (mg), b) number of buds/ turion, c) greatest latitudinal dimension (mm) and d) greatest longitudinal dimension (mm).

a)

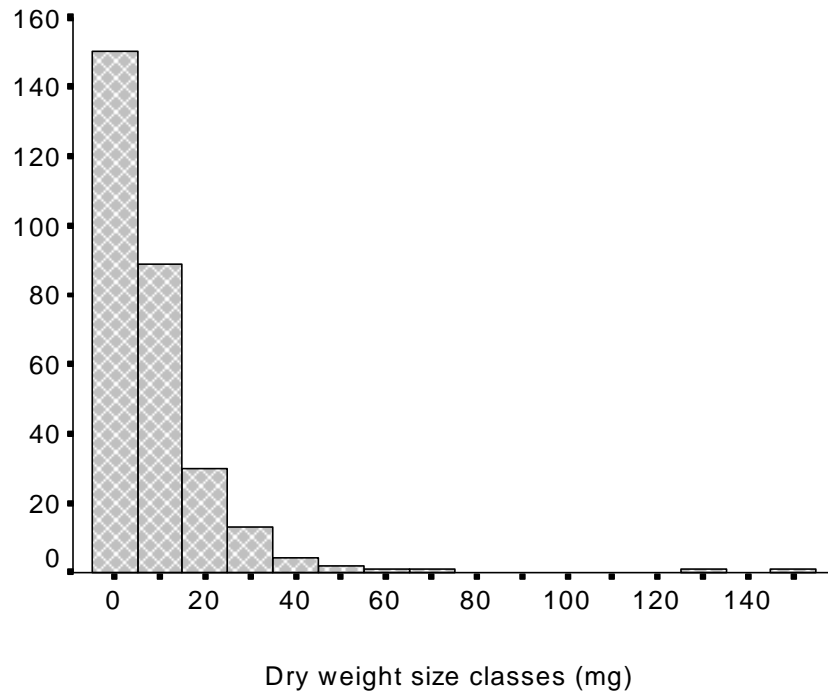
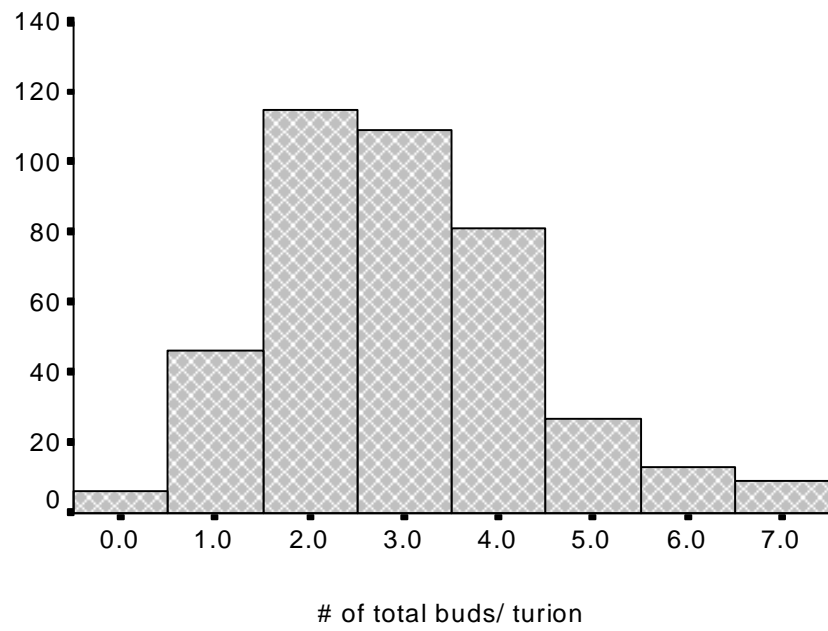


Figure 18: Old turion size. (continued)

b)



c)

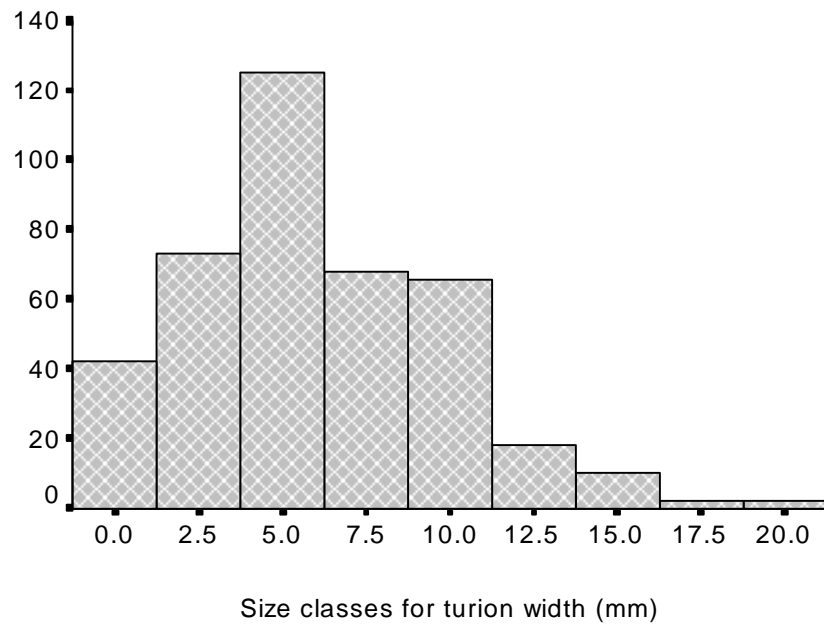
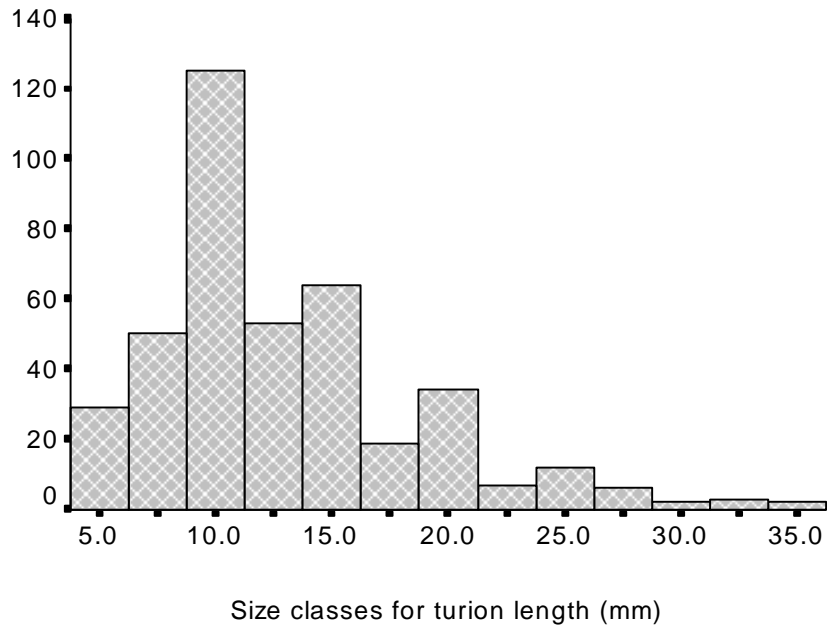


Figure 18: Old turion size. (continued)

d)



There were morphological differences between the old denticulate and spiculate turions. Denticulate turions, both sprouted and non-sprouted, had a significantly greater weight/ unit area turion (mg/mm^2) in comparison to spiculate turions [t-test assuming equal variances: $t_{\text{stat}} = 3.897$, d.f. = 361, $P_{2 \text{ tail}} = 1.16 \text{ E-}4$]. Denticulate turions had a significantly greater dry weight [t-test assuming equal variances: $t_{\text{stat}} = 11.10$, d.f. = 359, $P_{2 \text{ tail}} = 8.4 \text{ E-}25$]. Denticulate, in relation to spiculate turions, had a significantly greater number of leaf bases [t-test assuming equal variances: $t_{\text{stat}} = 5.543$, d.f. = 364, $P_{2 \text{ tail}} = 5.72 \text{ E-}8$] and dormant buds [t-test assuming equal variances: $t_{\text{stat}} = 6.402$, d.f. = 364, $P_{2 \text{ tail}} = 4.75 \text{ E-}10$]. Spiculate turions were

significantly longer [t-test assuming equal variances: $t_{\text{stat}} = -9.592$, d.f. = 364, $P_{2 \text{ tail}} = 1.42 \text{ E-}19$] while denticulate turions were significantly wider [t-test assuming equal variances: $t_{\text{stat}} = 18.60$, d.f. = 364, $P_{2 \text{ tail}} = 9.66 \text{ E-}55$].

Many turions sprout and one bud sprouting at a time is common. Twenty-two percent ($n = 78$) [$P(0.18 \leq p \leq 0.27) = 0.95$] of the total turions sprouted (Table 10). Eighty two percent ($n = 64$) of the turions that were sprouting had one sprouted bud. There was no difference found between the sprouting turions with one, two or three sprouting buds. Turions with either one, two or three sprouting buds, showed no significant difference between means for total turion dry weight [Single-Factor ANOVA: $F_{\text{stat}} = 0.742$, d.f. = 90, $P_{2 \text{ tail}} = 0.479$], width dimension [Single-Factor ANOVA: $F_{\text{stat}} = 1.171$, d.f. = 92, $P_{2 \text{ tail}} = 0.315$], number of leaf bases [Single-Factor ANOVA: $F_{\text{stat}} = 0.649$, d.f. = 92, $P_{2 \text{ tail}} = 0.525$] and number of dormant buds [Single-Factor ANOVA: $F_{\text{stat}} = 0.937$, d.f. = 92, $P_{2 \text{ tail}} = 0.395$].

Turions that were sprouting had more dormant buds than turions that were non-sprouting [t-test assuming equal variances: $t_{\text{stat}} = 2.550$, d.f. = 350, $P_{2 \text{ tail}} = 0.011$]. There was no difference found between sprouting and non-sprouting turions in weight/ unit area of turion (mg/mm^2) [t-test assuming equal variances: $t_{\text{stat}} = -0.031$, d.f. = 373, $P_{2 \text{ tail}} = 0.975$]. There was no difference in dry weight between sprouted and non-sprouted turions [t-test assuming equal variances: $t_{\text{stat}} = 0.668$, d.f. = 345, $P_{2 \text{ tail}} = 0.505$].

Additionally, there was no difference between sprouted and non-sprouted turion length [t-test assuming equal variances: $t_{\text{stat}} = -0.707$, d.f. = 350, $P_{2\text{ tail}} = 0.480$], width [t-test assuming equal variances: $t_{\text{stat}} = 1.642$, d.f. = 350, $P_{2\text{ tail}} = 0.102$] and the number of leaf bases [t-test assuming equal variances: $t_{\text{stat}} = 1.779$, d.f. = 350, $P_{2\text{ tail}} = 0.076$].

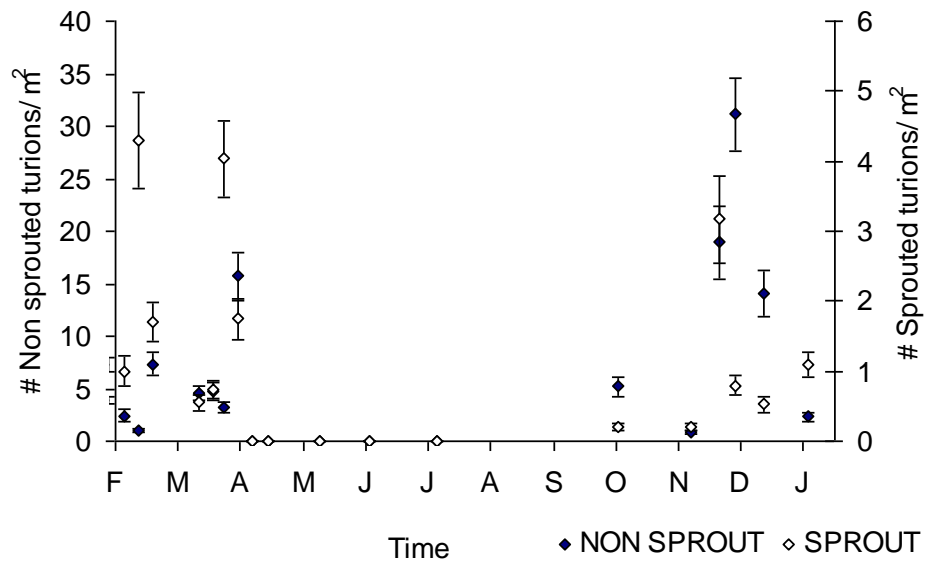
Table 10: Sediment dredge data summarizing old turion sprouting. N is # sample sites per sampling date, n_T is # old turions per sampling date, n_D is # old denticulate turions, n_S is # old spiculate turions, n_{SP} is # old sprouting turions and n_N is # old non-sprouting turions.

Sampling Date	N	Total old turions			Turion types						Sprouting status					
		(# / m ²)		n _T	Denticulate		Spicular		n _D	n _S	Sprout		Non-sprout		n _S	n _N
		mean	SE		mean	SE	mean	SE			mean	SE	mean	SE		
2/10/04	35	7.6	0.6	35	8.1	0.6	0.0	0.0	35	0	1.1	0.1	3.9	0.3	7	28
2/17/04	16	3.6	0.8	11	2.8	0.5	0.6	0.2	7	4	1.0	0.2	2.5	0.5	3	8
2/24/04	20	5.3	0.9	24	6.0	1.0	0.4	0.1	20	2	4.3	0.7	1.0	0.2	15	9
3/2/04	20	11.1	1.6	23	14	1.6	1.2	0.2	18	5	1.7	0.3	7.4	1.1	7	16
3/24/04	20	6.3	0.9	16	3.9	0.6	0.7	0.1	13	3	0.5	0.1	4.6	0.7	5	11
3/31/04	20	7.4	1.2	22	2.5	0.4	3.7	0.5	12	10	0.7	0.1	4.8	0.8	3	19
4/5/04	21	10	1.5	26	5.5	0.8	2.2	0.3	14	10	4.0	0.5	3.2	0.5	10	16
4/12/04	20	26	3.3	41	9.7	1.3	3.9	0.7	17	23	1.8	0.3	16	2.3	8	33
4/19/04	20	0.0	0	31	0.0	0.0	0.0	0.0	18	12	0.0	0.0	0.0	0.0	-	-
4/26/04	22	0.0	0	22	0.0	0.0	0.0	0.0	15	7	0.0	0.0	0.0	0.0	-	-
5/21/04	21	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0
6/14/04	20	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0
7/16/04	22	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0
10/11/04	20	5.3	0.9	25	4.1	0.6	1.6	0.3	13	12	0.2	0.1	5.2	0.9	1	24
11/15/04	20	1.3	0.2	7	0.2	0.1	1.2	0.2	1	6	0.2	0.1	0.9	0.2	1	6
11/29/04	16	35	4.5	33	9.0	1.7	12	2.1	15	16	3.2	0.6	19	3.5	7	26
12/6/04	20	35	4	37	17	2.2	7.2	1.0	24	13	0.8	0.1	31	3.5	4	33
12/20/04	20	15	2.4	31	5.5	0.9	6.2	1.0	13	18	0.5	0.1	14	2.2	3	28
1/10/05	20	3.9	0.7	20	2.0	0.4	1.8	0.3	12	8	1.1	0.2	2.3	0.4	4	16

Sprouting initiated on 11 October 2004 and continued through early May (Figure 19). The onset of sprouting in Blue Lake, Oregon was associated with a daylength of 11.17 hr and a bottom water temperature of $17.5 \pm 0.1^{\circ}\text{C}$ (mean \pm SE). Spiculate turions sprouted before the denticulate turions in Blue Lake (Figure 20a and 20b). Spiculate turions began sprouting in October. Denticulate turions began sprouting in late November.

A greater percentage of turions were sprouting in late winter and early spring relative to fall and early winter. The extent of sprouting, regardless of turion type, peaked on 24 February 2004 but the density also peaked on 5 April 2004 and 29 November 2004 (Figure 19a and 19b). The greatest density of non-sprouted, old turions was found in the fall (Figure 19a and 19b).

a)



b)

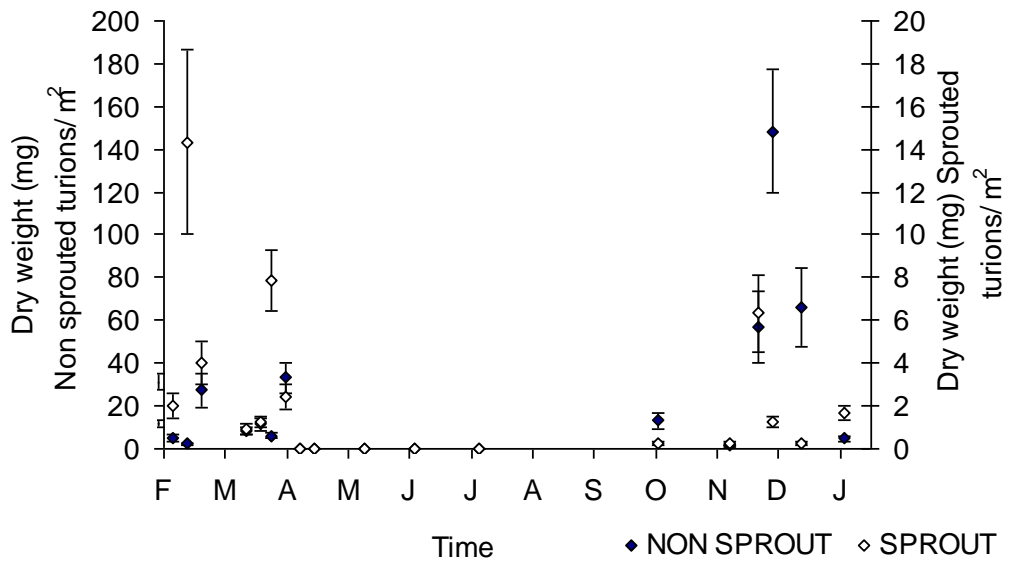
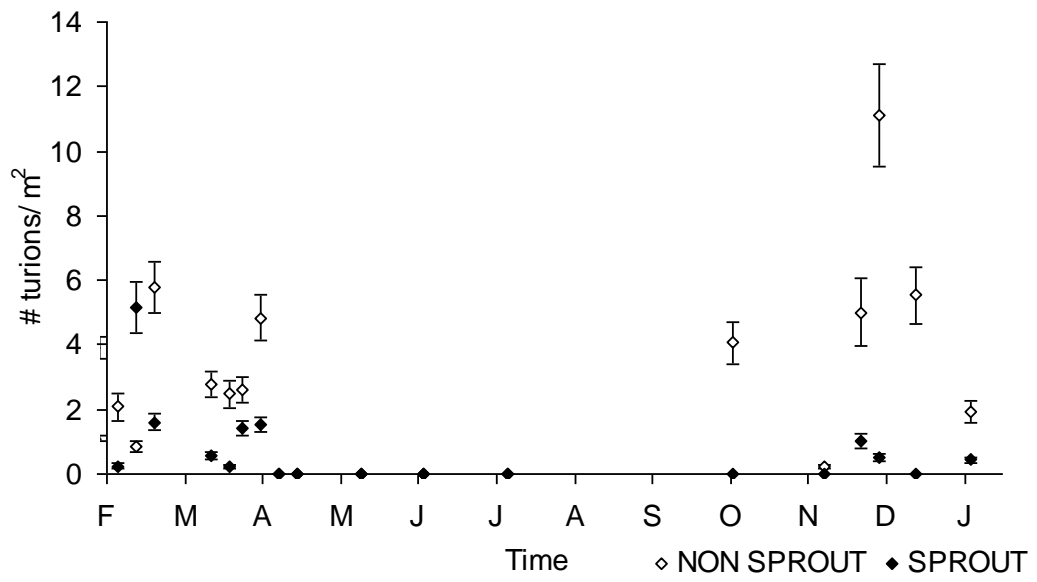


Figure 19: Density of old turions that are non-sprouting and sprouting. Density represented by a) # turions/ m² (geometric mean ± 1 SE) and b) turion dry weight (mg)/ m² (geometric mean ± 1 SE).

Figure 20: Density of old denticulate and spiculate turions in relation to time. Density represented by both # turions/ m² (geometric mean ± 1 SE) for both sprouting and non-sprouting a) denticulate turions and b) spiculate turions, and by dry weight (mg)/ m² (geometric mean ± 1SE) for both sprouting and non-sprouting c) denticulate turions and d) spiculate turions.

a)



b)

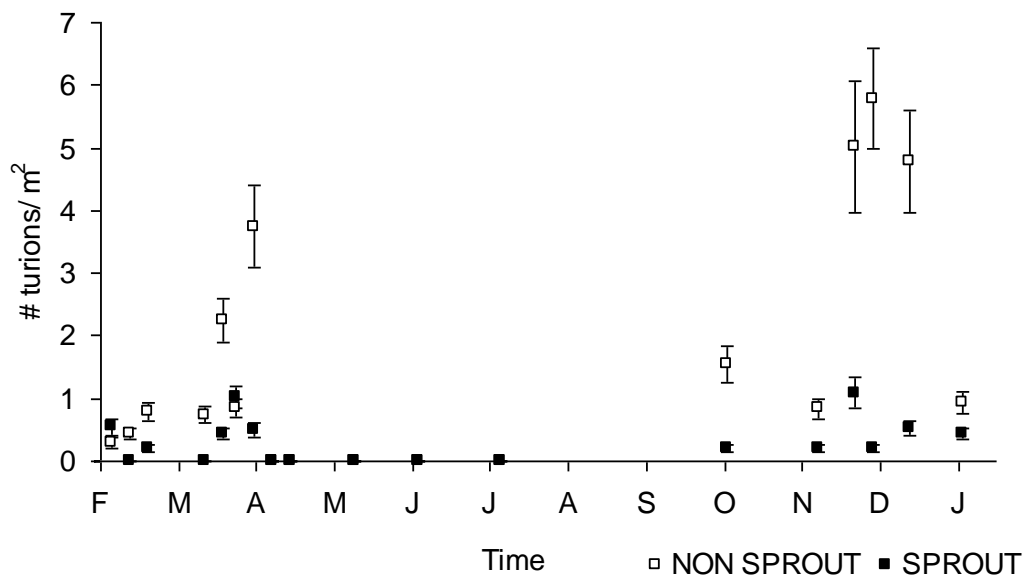
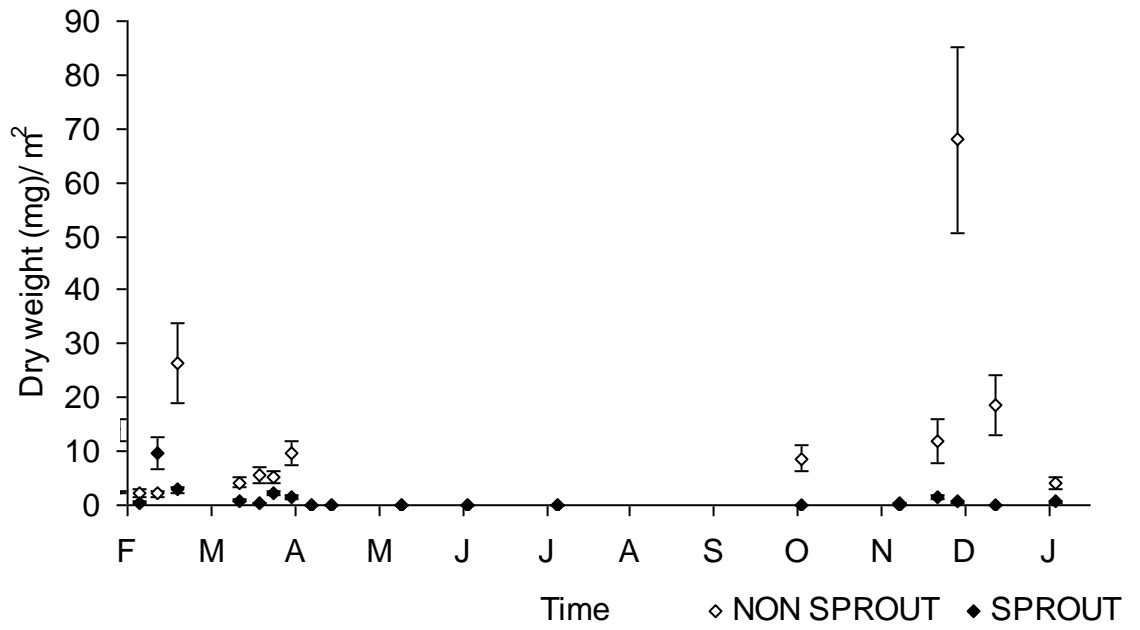
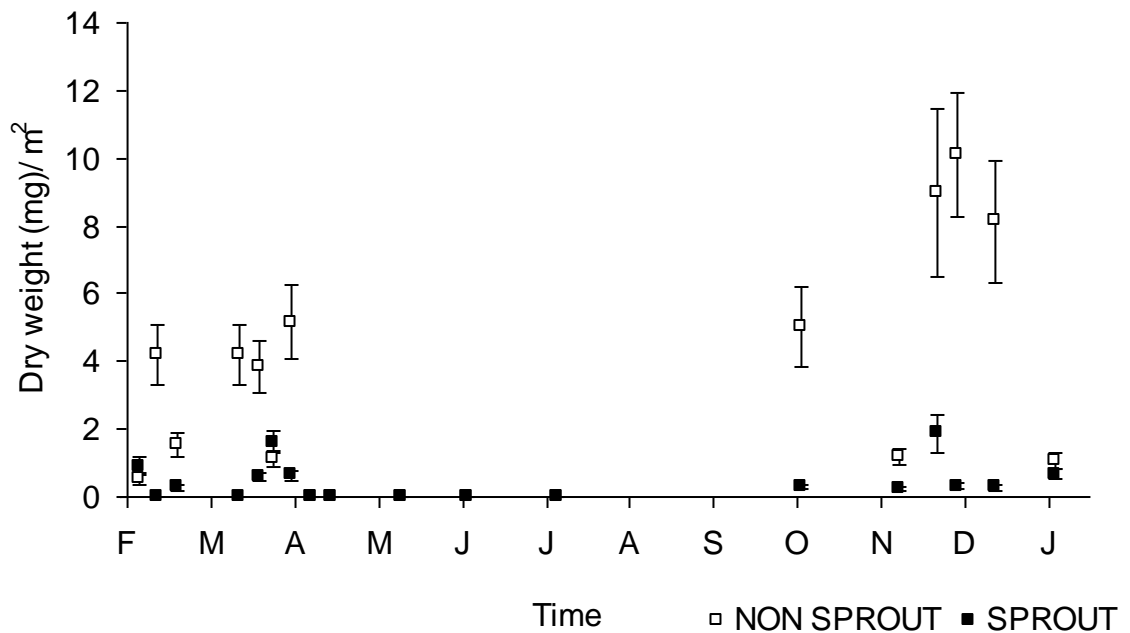


Figure 20: Density of old denticulate and spiculate turions in relation to time. (continued)

c)



d)



The timing and extent of peak sprouting differed between turion types. A greater number of denticulate turions sprouted (Figure 20a and 20b) but there were many more denticulate turions relative to spiculate turions (Table 10) and the final percentage sprouted was similar for denticulate and spiculate turions (25%, n=53 and 18%, n=24, respectively). The density of sprouting denticulate turions peaked on 24 February 2004 (Figure 20a). The density of sprouting spiculate turions peaked on 29 November 2004 and 5 April 2004. Although the density of sprouting spiculate turions was similar on

5 April and 29 November 2004, there were significantly more non-sprouted turions found on 29 November (Table 14 and Figure 20b).

The extent of non-sprouting turions differed between the turion types. There were more non-sprouting denticulate turions compared to non-sprouting spiculate turions (Figure 20a and 20b), however, there were more denticulate turions relative to spiculate turions. The peak in density for non-sprouting denticulate turions occurred on 6 December 2004 (Figure 20a). There was an additional peak in dry weight on 2 March 2004 for non-sprouting denticulate turions. The peak in density for non-sprouting spiculate turions occurred in late fall on 29 November through 20 December 2004 (Figure 20b).

Conclusions

Physical characteristics of Blue Lake

Blue Lake experiences a moderate climate. Blue Lake experienced a cool, wet winter and a warm, dry summer. During the study period, bottom water temperatures did not fall below freezing or exceed 30°C (Figure 21). The air temperature and precipitation encountered at Blue Lake during the study period was not different than the weather encountered over the last 40 years.

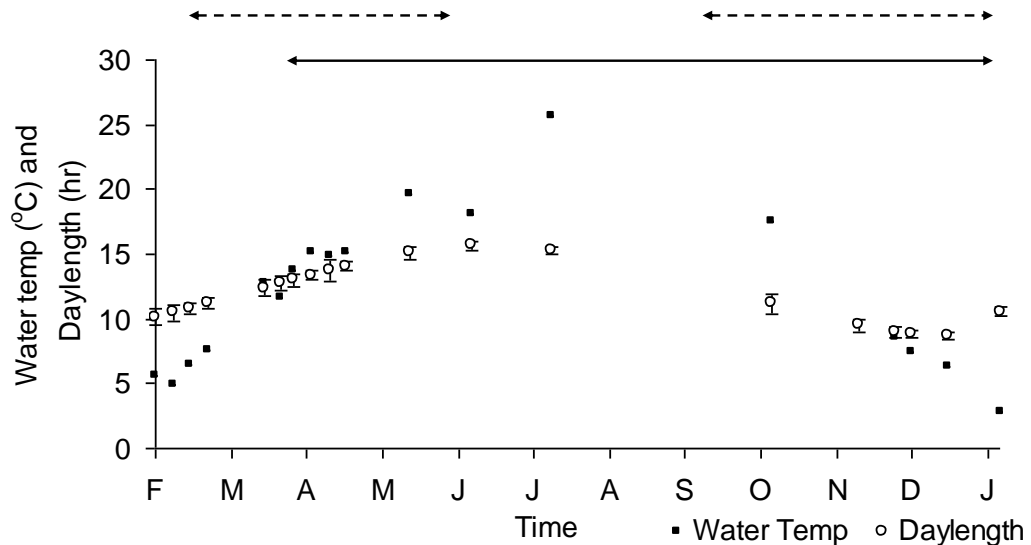


Figure 21: Summary of turion formation, sprouting, water temperature and daylength for Blue Lake, OR. Temperature (°C) (mean \pm 1SD) and daylength (hr) for Blue Lake represent the time period, 2004-2005. The solid arrow indicates period of turion formation and dashed arrow indicates period of turion sprouting.

Growth

P. crispus achieved peak plant biomass early in the growing season. The transition between the winter and spring foliage began in February and was completed by the end of April. Vigorous growth occurred initially in the main stems through increases in internode length and node increment, beginning in mid-March. The growth rate of the main stems peaked in early April as the water temperature approached 10°C (Figure 21). Axillary stems form the canopy and developed in April and May once the main stems were near the water surface. Axillary stem length peaked in late May.

The moderate climate of Blue Lake extended the period of growth for *P. crispus*. *P. crispus* plant biomass decreased following reproduction but plant growth continued through summer thermal maxima in Blue Lake (Figure 21, 11 and 12). Plant dieback in Blue Lake was not ubiquitous to the entire population and healthy plants were found as late as January.

Formation of turions

The formation of turions was initiated by early spring in Blue Lake and this is common throughout the Northern Hemisphere. In Blue Lake, plants were flowering by mid-April. New turions were present on plants by 5 April 2004 in Blue Lake, which means turion formation began in March. Turion formation began when water temperatures were greater than 12°C and daylengths were greater than 12 hr (Figure 21), which is similar to other Northern Hemisphere studies. In Blue Lake, there was no difference in the onset of formation between denticulate and spiculate turions or between the apical- and lateral-stem positions of formation.

The period of turion formation was longer in Blue Lake than in other Northern Hemisphere studies. In the Northern Hemisphere, the time period of turion formation ranges from two to six months but lasted over nine months in Blue Lake. Although turion formation as late as December and January was uncommon, three individual, healthy, rooted plants bearing new turions were collected on 10 January 2005. On 29 November 2004, plants were retrieved from the anchor with attached new turions. Additionally, on 15 November 2004, turion formation was observed on plants collected from the nearby Columbia River.

The time period for turion formation in the lateral-stem positions was longer than formation in the apical-stem positions in Blue Lake, and this appears to be related to water temperature. Turion formation in the apical- and lateral-stem positions began approximately the same time but turion formation between November and January only occurred in lateral-stem positions in Blue Lake. The rate and extent of formation in apical-stem positions is positively associated with water temperature and turion formation in apical-stem positions terminates growth along that stem apex. Formation in lateral-stem positions, however, does not terminate growth along the stem apex. It therefore seems that cooler water temperatures would prolong growth of the axillary stem apices and this would allow for continued formation in lateral-stem positions.

P. crispus responds to environmental conditions to maximize reproduction. The period of plant growth, the rate of senescence and the rate of turion formation vary depending upon environmental conditions. The onset of formation is triggered before summer water temperatures induce plant dieback. Once formation has been initiated in healthy, rooted plants, the extent and timing of peak formation are dependent upon available photosynthate concentrations. Two peaks in biomass have been observed in

P. crispus populations that grow year round. Non-rooted plants form turions under short daylengths (8 hr) and high water temperatures, and these conditions could apply to plant fragments that drift into shallow areas during the fall. Additionally, turions can form on plants still attached to the recently sprouted turion under long days (greater than 12 hr daylength) and high water temperatures (28 – 30°C). This implies turion formation occurs as long as possible depending on the environmental conditions.

It is likely that the time period of turion formation in Blue Lake was longer than other Northern Hemisphere studies because of the moderate climate. Timing for the onset and peak of turion formation in Blue Lake was similar to other Northern Hemisphere studies but formation continued into winter with water temperatures less than 10°C and daylengths less than 10 hr (Figure 21). In most studies, turion formation ended prior to or upon reaching seasonal maxima for water temperature and daylength. In Blue Lake, however, turion formation proceeded through the summer maxima. Water temperatures in Blue Lake, however, did not exceed 30°C, and these findings suggest that, once initiated, turion formation occurs as long as possible. The precise timing of formation of individual turions in Blue Lake, however, is unknown. It is possible that the attached new turions collected in

the late fall and early winter were formed earlier in the season and persisted on plants that continued growth due to cooler summer water temperatures.

The timing of peak formation in Blue Lake was similar to other Northern Hemisphere studies and occurred in the spring with water temperatures between 15° and 20°C and daylengths around 14 to 17 hr (Figure 21). The density of new turions peaked on 21 May 2004 in concert with peak plant biomass. Peak turion formation also coincided with 15-20 nodes per stem. In the Northern Hemisphere, turion formation peaks between May and June and is associated with seasonal peaks in stem length and number, peak standing plant biomass and peak flowering.

The number of turions formed during peak formation in Blue Lake was less than other Northern Hemisphere studies but the magnitude of formation varies. The magnitude of formation can also vary within a waterbody from year to year. At peak formation in Blue Lake, turions represented between eight and 17% of the total plant biomass. During peak turion formation in other studies, turions represented between 20 to 58% of the total plant biomass. Turion formation in Blue Lake, however, was underestimated compared to other studies due to methodology. Turion formation in Blue Lake was measured using the turions attached to plants after collection,

bagging and sieving. Other studies estimated turion density by counting turions in the sediment, both with and without attached plants. It is likely turions were separated from the plants during collection, bagging and sieving in Blue Lake.

Turion formation in Blue Lake occurred predominantly in lateral-stem positions and was of the denticulate type. This is common throughout the Northern Hemisphere. Denticulate and spiculate turions formed in both stem positions in Blue Lake. Additionally, both denticulate and spiculate turions were formed on the same plant. This finding contrasted Moore (1913), Waisel (1971) and Wehrmeister (1978) that found spiculate turions were generally formed in leaf axils located on lower portions of the plant, directly attached to rhizomes and/ or on smaller plants. Additionally, spiculate turions were formed on healthy, rooted plants in Blue Lake, whereas Irmisch (1858) and Moore (1913) reported that spiculate turions formed on decaying, floating stems and/ or sickly-looking plants. These incongruent findings, however, are based on observations of morphologic features.

Sprouting of turions

P. crispus turions began sprouting in the fall when water temperatures were less than 20°C. In Blue Lake, spiculate turions initiated sprouting before denticulate turions. No other study has compared the onset of sprouting for spiculate and denticulate turions but in Blue Lake spiculate turions began sprouting in October whereas denticulate turions began sprouting in late November. Denticulate turions were found to have a greater weight per unit area of turion, implying greater carbohydrate storage. This might explain why spiculate turions sprout first and represent a larger fraction of the sprouting turions earlier in the year. Interestingly, there was no difference in onset of formation between spiculate and denticulate turions in Blue Lake as would be expected if the onset of sprouting was related to when the turions were formed.

Sprouting in Blue Lake peaked in a different time of year compared to other Northern Hemisphere studies. Turion sprouting in Blue Lake peaked in late February, whereas in other Northern Hemisphere studies it peaked in the fall, between October and November. The water temperatures associated with peak sprouting in Blue Lake were between 5° and 10°C (Figure 21), whereas water temperatures elsewhere were between 10° and 17°C. The

sprouting of denticulate turions peaked earlier in the year compared to spiculate turions in Blue Lake. Sprouting of denticulate turions clearly peaked in late winter, demonstrated with the density and the relative sprouting percentage for that type of turion (75%, n= 15). The peak in sprouting of spiculate turions happened in the spring according to the density and the relative sprouting percentage for that type of turion (40%, n= four). It should be noted that the peak in sprouting for spiculate turions was less discernable compared to the peak in sprouting for denticulate turions. It is unclear, however, why denticulate turions peaked in sprouting before spiculate turions.

The delayed peak in sprouting relative to the onset of sprouting observed in Blue Lake compared to other Northern Hemisphere studies might be due to differences in light intensity. Sprouting is associated with increased light intensity and cooler water temperatures except with newly formed turions that sprout in response to water temperature only. Additionally, the time course of sprouting is positively associated with light intensity. The light intensity was not measured in Blue Lake but the water temperature in Blue Lake during the fall and winter was similar to other North American studies. The underwater light environment is influenced by a suite

of complex factors such as the community composition and structure of macrophytes and algae, as well as the water depth, clarity and color. The long growing season and moderate plant dieback experienced in Blue Lake might reduce the underwater light reaching the sediment during the fall. Therefore, it is possible the majority of turions sprouted later in winter when there was greater light penetration.

The time period turions sprout in the Northern Hemisphere varies between two and nine months. Turions sprouted for approximately seven months in Blue Lake. Although Sastroutomo (1981) found that sprouting was inhibited in water temperatures less than 4°C, sprouting was observed in Blue Lake when water temperatures were less than 3°C (Figure 21).

Many turions sprout, regardless of type. Generally, one bud sprouts at a time event though there are several dormant buds. Twenty-two percent of all turions found in Blue Lake sprouted and this might be an underestimation of the final sprouting percentages. It is likely that sprouted buds were separated from turions during the collection and cleaning of samples. During the period of peak sprouting in Blue Lake, 63% of the turions were sprouting. This is similar to other Northern Hemisphere studies. Despite there being many more denticulate versus spiculate turions, the final percentage

sprouted for each type was similar: 25% (n= 53) of denticulate turions and 18% (n= 24) of spiculate turions. Additionally, there was no difference between sprouting and non-sprouting turions regarding the turion weight and weight per unit area of turion in Blue Lake and there were significant differences between denticulate and spiculate turions in these parameters. Greater than 80% of the sprouting turions in Blue Lake had one sprouting bud. Sprouting one bud at a time might reduce competition among buds for both light and carbohydrate reserves as well as reducing light competition between different turions in the same area. The consecutive sprouting of buds might offset costs associated with herbivory and other types of damage as well. This is supported by Jian et al. (2003) who found that removing sprouting buds promoted further sprouting and, when no sprouting buds were removed, few additional dormant buds sprouted.

Management implications

It is most important to prevent turion formation. *P. crispus* populations emerge and reproduce early in the growing season. Managing for plant biomass between April and July provides short term control but allows turions to form and produce plants the following year. Turion formation proceeds from the lower portions of the plant towards the upper portions, which means the extent of formation observed near the water surface is not indicative of that below. Controlling the sprouting of turions that have already formed is much less effective than preventing or reducing turion formation. There are many turions and they are small, which makes their physical removal difficult and time consuming. Further, turions have several dormant buds and removing a sprouted bud induces the sprouting of another bud. Turions sprout in the fall, winter and spring and management that increases light penetration would actually favor increased sprouting.

Management that targets *P. crispus* turion formation is most effective when applied in late winter to early spring with an additional application in late spring to early summer. The first application targets the growing vegetation to prevent and reduce turion formation and should be done when bottom water temperatures are near 10°C but are not greater than 15°C to

allow for maximum plant growth before turion formation has peaked. It is unlikely management will be completely effective. *P. crispus* is fecund and has large variation in its phenology. The second application, applied with water temperatures between 15°C and 17°C, targets those plants that survived the first management effort and formed turions in the late spring and early summer.

Plants are growing by mid-March and early April, which implies an increasing plant metabolism despite low water temperatures. At this time, plants are developing from the sprouted turions that formed earlier and these plants have yet to form turions themselves. Many turions at this time are still sprouting, and the carbohydrate reserves in the turions will be at a seasonal minimum (Woolf and Madsen 2003). *P. crispus* is one of the only plants growing in the mid March to early April time period and water clarity should be relatively high. Management therefore, will be less likely to be hindered by as well as negatively impact adjacent vegetation.

Future questions

The effect water temperature has on turion formation in lateral- and apical-stem positions needs to be confirmed. Does warmer water temperature increase turion formation in apical-stem positions and likewise does cooler water temperatures increase formation in lateral-stem positions? Can thermal thresholds be identified? What happens if the turions formed on apical-stem positions are continually removed? Are more turions formed, are they formed in the same stem position and what effect does this have on the termination of growth along the stem apex? Are the turions formed in either the apical- or lateral-stem positions more likely to establish into plants?

What happens if fruit are removed? Yeo (1966) showed that *P. crispus* will continue to make new turions if the turions are continually removed as they form. Does the formation of fruit terminate growth on that stem apex?

Under what environmental conditions can *P. crispus* plants maintain vegetative growth? Kunii (1982) found that plant dieback in rivers occurred later in the year than in lakes. Is the onset of the growing season different in rivers and streams versus lakes and reservoirs? Is dieback simply a function of water temperature? If so, can thermal thresholds for plant dieback be

identified? Can vegetative growth continue if the initiation of turion formation is prevented?

Once turion formation has been initiated by temperature and daylength, the magnitude of formation is affected by the PAR photon fluence rate and the R:FR value, but what environmental conditions affect the time period of turion formation once it has been initiated? Were the new turions collected on rooted plants in December and January formed in the late fall and winter or were they formed earlier on plants that persisted from the summer? Water temperature affects the rate of plant growth. Does water temperature affect the time required to form turions?

The differences observed between denticulate and spiculate turions need to be confirmed. Turion formation needs to be induced on plants grown under different light and nutrient conditions to address differences between denticulate and spiculate turions and the stem position of formation. Do spiculate turions really initiate sprouting earlier in the year compared to denticulate turions? Are there differences in the timing of peak sprouting between denticulate and spiculate turions? What factors can explain these differences? Similar percentages of denticulate and spiculate turions sprout but are there differences in the likelihood of establishing into plants? Are

there differences in the carbohydrate reserves of denticulate versus spiculate turions?

Why was the period of peak sprouting in Blue Lake different than other studies? Sprouting needs to be explored under various light intensities as well as water temperatures. Can sprouting be induced at water temperatures less than 4°C?

The fate of abscised turions is unknown. How far do turions disperse from the location of formation and are there differences in dispersal between turion types and the stem positions of formation? How long do non-sprouted turions remain viable in sediment and is this different between the types of turions? It was rare that plants were attached to sprouting turions and stem positions of turion formation were not considered in the sprouting analysis. What effect does the stem position of formation have on the onset and extent of sprouting?

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Appendices

Appendix A

Appendix A: Reproductive strategies of common freshwater aquatic plants in North America.

Plant	Asexual							Sexual
	Turions OR Axillary buds	Stem fragments	Rhizomes	Stolons	Tubers	Spores OR Budding	Seed	Seed
<i>Potamogeton crispus</i>	X	X	X					X
<i>P. pusillus</i>	X	X	X					X
<i>P. nodosus</i>		X	X					X
<i>P. natans</i>		X	X					X
<i>P. illinoensis</i>		X	X					X
<i>P. foliosus</i>		X	X					X
<i>Stuckenia pectinatus</i>					X			X
<i>Zannichellia palustris</i>		X	X				X	
<i>Ruppia maritima</i>		X	X				X	
<i>Elodea canadensis</i>	X	X		X				X
<i>Hydrilla verticillata</i>	X	X		X	X			X
<i>Egeria densa</i>		X		X				X
<i>Najas spp.</i>		X						X
<i>Eichhornia crassipes</i>				X				X
<i>Pistia stratiotes</i>				X			X	
<i>Lemna spp.</i>						X		X
<i>Spirodela spp.</i>	X							
<i>Wolffia spp.</i>	X							
<i>Ceratophyllum demersum</i>	X	X						X
<i>Myriophyllum aquaticum</i>	X	X	X					X
<i>Myriophyllum spicatum</i>	X	X	X					X
<i>Cabomba caroliniana</i>		X	X					X
<i>Nymphaea odorata</i>			X					X
<i>Nuphar polysepala</i>			X					X
<i>Azolla pinnata</i>		X				X		
<i>Salvinia molesta</i>		X				X		

Appendix B

Appendix B: Traits used to determine year of formation for turions relative to time of collection. Year (2003, 2004) indicates the estimated growing season for turion formation.

Trait	Date of Collection				
	Winter 03	Spring 04	Summer 04	Fall 04	Winter 04
1. Location of attached plant					
a) Basal tip of turion	2003	2004*	2004	2004	2004
b) Turion bud	2003	2003	2003*	2004	2004
2. Status of attached plant					
a) Spring foliage decaying	2003	2003*	2004	2004	2004
b) Spring foliage healthy	2003	2004	2004	2004	2004
c) Winter foliage plant	2003	2003	2004*	2004*	2004
3. Turion and leaf bases					
a) hard, brittle	2003	2003	2004*	2004*	2004
b) soft, pliable	2003	2004	2004	2004	2004
c) decaying leaves on distal portion	2003	2004	2004	2004	2004
4. Bud development					
a) well-developed	2003	2003*	2004	2004	2004
b) inconspicuous	2003*	2004	2004	2004	2004

* indicates uncertainty associated with year of formation; most probable year is provided

Appendix C

Appendix C: Traits used to separate main stems, axillary stems and rhizomes.

Trait	Vegetative structure		
	Main stem	Axillary stem	Rhizome
1. Growth form			
a) relative # nodes	intermediate	greatest	least
b) relative internode length	greatest	least	intermediate
c) cross-sectional shape	flattened	flattened	round
d) origin of attachment	rhizome, turion	main stem	turion, rhizome
2. Roots			
a) # roots* cluster ⁻¹	~2	0	2-10+
b) relative # roots*structure ⁻¹	intermediate	least	greatest
3. Leaves			
a) present	yes	yes	no
4. Color			
a) Apparent color	green-red	green-red	white-light brown

Appendix D

Appendix D: Locations of various studies.

Authors	Continent	Country	Region	Waterbody (s)
Ali et al. 2000	Asia	India	N.A.	Lake Nainital
Bolduan et al. 1994	North America	Canada and USA	N.A.	N.A.
Boylen and Sheldon 1976	North America	USA	New York	Lake George
Catling and Dobson 1985	North America	Canada and USA	N.A.	N.A.
Chambers 1982	Europe	Scotland	N.A.	lakes and lochs
Chambers et al. 1985	Europe	Scotland	Perthshire	Loch Drumore
Chambers et al. 1989	North America	Canada	Alberta	Saskatchewan River
Clos 1856	Europe	France	Toulouse	N.A.
Guppy 1894	Europe	England	near London	N.A.
Hafez et al. 1998	Africa	Egypt	N.A.	Ismailia canals
Harman 1974	North America	USA	New York	Otsego Lake
Hellquist 1980	North America	USA	New England	N.A.
Hofstra et al. 1995	Australia	New Zealand	throughout	lakes and rivers
Hunt and Lutz 1959	North America	USA	Michigan	Erie Club marsh
Irmisch 1851	Europe	Germany	Regensburg	N.A.
Jian et al. 2003	Asia	China	Hubei province	Liangzi Lake
Kunni 1982	Asia	Japan	near Chiba	Lake Ojagaike
Kunii 1989	Asia	Japan	N.A.	Narutoh River
Martin 1951	North America	USA	Maryland	N.A.
McCombie and Wile 1971	North America	Canada	Toronto	impoundments
Moore 1913	North America	USA	New York	lakes and ponds
Muenscher 1936	North America	USA	New York	lakes and ponds
Netherland et al. 2000	North America	USA	Texas	tanks
Nichols and Shaw 1986	North America	USA	N.A.	N.A.
Pfauth and Sytsma 2004	North America	USA	Oregon	Blue Lake
Poovey et al. 2002	North America	USA	Texas	outdoor tanks
Riemer and Toth 1969	North America	USA	New Jersey	N.A.
Rogers and Breen 1980	Africa	South Africa	north-eastern	Pongolo River
Sastroutomo 1980	Asia	Japan	near Chiba	concrete ponds
Sastroutomo 1981	Asia	Japan	near Chiba	Lake Ojagaike
Stuckey 1979	North America	USA	N.A.	N.A.
Stuckey et al. 1978	North America	USA	Ohio	Delaware Wildlife Area
Teltscherova and Hejny 1973	Europe	Bohemia	southern	ponds
Tobiessen and Snow 1984	North America	USA	New York	Collins Lake
Wehrmeister 1978	North America	USA	Ohio	Delaware Wildlife Area
Woolf and Madsen 2003	North America	USA	Minnesota	lakes

Appendix E

Appendix E: Summary of new turions and turion formation as well as old turions and turion sprouting for denticulate and spiculate turions.

	Denticulate	Spiculate
<u>Formation of new turions</u>		
Onset (month)	April	April
Peak (month)	May	April
Duration (# months)	~9	~9
<u>New turions</u>		
Weight/ Area* (mg/ mm ²)	0.21	0.08
Dry weight (mg)	21.4	6.70
Length/ Width* (mm/ mm)	1.49	5.10
Stem position	apical & lateral	apical & lateral
<u>Sprouting of old turions</u>		
Onset (month)	Nov	Oct
Peak (month)	Feb	April
Duration (# months)	~6	~7
<u>Old turions</u>		
Weight/ Area* (mg/ mm ²)	0.19	0.11
Dry weight (mg)	19.9	4.32
Length/ Width* (mm/ mm)	1.50	7.94
Buds ⁺ (#)	3	2
Leaf bases ⁺ (#)	4	3

* indicates a mean value while ⁺ are mean values rounded to whole number