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Growth and Macronutrient Accumulation of *Chasmanthium latifolium* (Michx.) Yates and *Hakonechloa macra* Makino 'Aureola' in Response to Temperature

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Abstract. **Optimum growing temperatures were determined for *Hakonechloa macra* Makino 'Aureola' and *Chasmanthium latifolium* (Michx.) Yates, two shade-tolerant ornamental grasses found naturally in regions differing in temperature conditions. Plants were grown in four growth chambers at average daily temperatures of 13, 19, 25, and 31 °C for 12 weeks. After the treatment period, plants were destructively harvested to quantify growth and shoot tissue concentrations of N, P, K, Ca, and Mg. Optimal growth occurred at an average daily temperature of 25 °C for both grasses, but *Hakonechloa* was better able to tolerate lower temperatures. *Hakonechloa* died at 31 °C, while *Chasmanthium* growth was only slightly reduced at this temperature. Nutrient concentrations in shoot tissue for both species increased with increasing temperatures up to the temperature supporting optimal growth. At 13 and 19 °C, the concentrations of most nutrients were higher for *Hakonechloa* than for *Chasmanthium*, possibly reflecting the greater growth (higher nutrient demand) of *Hakonechloa* at lower temperatures. When compared on a per plant basis at each grasses' optimum temperature for growth, *Chasmanthium* has a much greater demand for nutrients than *Hakonechloa*, reflecting the greater growth potential of *Chasmanthium*.**

The development and use of new or underutilized plants is a major focus for nurserymen, landscape designers, and gardeners alike. Currently, there is great interest in the use of ornamental grasses because of the myriad of forms that exist, each differing in foliage color, height, shape, and texture (Darke, 1994a). *Hakonechloa macra* 'Aureola' is a variegated, perennial grass that performs well in low light and provides gardeners with an alternative plant form for use in shaded locations. Unlike many perennial grasses, *Hakonechloa* is particularly slow growing, contributing to an insufficient supply of stock plants, and high prices for this cultivar in the nursery trade.

Temperature has particular relevance to *Hakonechloa macra* 'Aureola' because it grows naturally in the forested, mesic mountains of central, Pacific Japan where temperatures are moderated considerably by elevation and maritime proximity (Watson and Dallwitz, 1992). Optimizing *Hakonechloa* growth in a nursery setting may entail growing it at lower temperatures than most ornamental grass species.

Chasmanthium latifolium, commonly known as northern sea oats, is another ornamental grass native to moist, shaded, woodland environments of the southeastern United States (Darke, 1994b). *Chasmanthium* naturally experiences warm, humid summers unlike those experienced by *Hakonechloa*.

Information on optimal growing temperatures for ornamental grasses is very limited, but Lavis-Ham (1993) found that among three ornamental grass species and one sedge, temperature optima for growth varied by as much as 10 °C. Warm-season forage grasses originating from tropical climates grow best between 27 and 35 °C, while cool-season grasses perform best between 16 and 24 °C (Burger, 1984; Treharne and Cooper, 1969). The following study was undertaken to establish the optimum growing temperatures and to determine tissue nutrient concentrations of two shade-tolerant woodland grass species adapted to regions with different growing season temperatures.

Materials and Methods

Plant material. *Chasmanthium latifolium* plants were grown from seed for 12 weeks, while *Hakonechloa macra* 'Aureola' plants were grown from divisions of container-grown plants for 4 weeks prior to use in experiments. During this period, plants were maintained in a greenhouse with set points of 21 °C day/17 °C night and natural lighting (photoperiod ranged from 9 to 12.5 h). Both grasses were potted in 325-mL containers with a 3 pine bark : 2 sphagnum peat moss : 1 sand (by volume) mixture amended with dolomitic limestone at 5.75 kg·m^{-3}. Plants were irrigated as needed, and a soluble 20N–8.74P–16.6K fertilizer (Peters 20–20–20 General Purpose Fertilizer; Scotts Co., Marysville, Ohio) was provided at 150 ppm N every 7 to 10 d. At the start of the temperature studies, *Hakonechloa* plants weighed 7.1 g, were 10.1 cm tall, and had 13.6 tillers per plant. *Chasmanthium* plants weighed 3.0 g, were 17.0 cm tall, and had 2.1 tillers per plant. The initial values for each species are 2-year averages (n = 30), since plants were statistically similar both years.

Growing conditions. *Hakonechloa* and *Chasmanthium* plants were grown under four day/night temperature combinations for 12 weeks in four growth chambers (Environmental Growth Chambers, Chagrin Falls, Ohio). Fourteen-hour day and 10-h night treatments were 15/10, 21/16, 27/22, and 33/28 °C and resulted in average daily temperatures (ADT) of 13, 19, 25, and 31 °C. During the day, light was generated by 9 Sylvania VHO 115W fluorescent bulbs and four 40W incandescent bulbs per chamber. Photosynthetically active radiance (*PAR*) was maintained at 450 µmol·m^{-2}·s^{-1} by replacing VHO bulbs every 1000 h and adjusting chamber shelves to control the distance between light source and plant canopy. Light intensity was monitored twice weekly using a LI-COR model LI-190 PAR sensor and LI-189 light meter (LI-COR, Lincoln, Nebr.) placed at plant canopy. Plants were spaced 10 cm apart and were shifted to new positions every 3 days, according to a mapped plan, to compensate for the unavoidable *PAR* gradient (380–540 µmol·m^{-2}·s^{-1}) that existed within each chamber. Plants were fertilized at every irrigation with a soluble 20N–4.37P–16.6K fertilizer (Peters 20–10–20 Peatlite Special, Scotts Co.) at 200 ppm N. Plants were fertigated as needed through a modified flood and drain system according to Elliott (1992).

Data collection. After 12 weeks of culture in the growth chambers, all plants were destructively harvested, and the number of tiller buds, shoots, and inflorescences were counted. Shoot and root fresh and dry weights, plant height and width, leaf area, and shoot length were recorded. Root weights reflect the combined weight of roots, rhizomes, and crowns. Plant height was measured from the potting medium surface to the apex of the foliage, without extending overarching leaf blades. Plant width was measured twice, at right angles to each measurement. Plant size was then calculated by multiplying height × width1 × width2. Leaf area was quantified using a LI-COR model LI-3100 leaf area meter (LI-COR). Average shoot length per plant was determined by measuring the entire length of every shoot, including the stem and leaf blade. Culms and blades were dried at 70 °C for ≈72 h and

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weighed to determine dry weight. Shoot tissue samples were ground to pass through a 40-mesh (0.4-mm holes) screen. Tissue concentrations of Ca, K, Mg, and P were determined using 0.3-g subsamples analyzed at the Univ. of Massachusetts Plant and Soil Testing Laboratory (Amherst) by inductively coupled argon plasma spectrophotometry. Prior to analysis, plant tissue digests were prepared by a modification of procedures reviewed by Jones and Case (1990). Tissue subsamples were dry-ashed for 6 h in a muffle furnace (Fisher Scientific, Pittsburgh), cooled, then dissolved and brought up to a 15-mL total volume using a 10% HCl acid solution. Shoot tissue subsamples (0.12 g) were analyzed for total N through dry combustion analysis, using a Leco CNS-2000 analyzer (Leco Corp., St. Joseph, Mich.).

Experimental design and analysis. The experiment was conducted from April through June of 1998, and was repeated at the same time in 1999. There were 20 replicates per species placed in each chamber according to a completely randomized design. The data from 1998 and 1999 were combined for analysis, as there were no interactions or treatment differences between years. Analysis of variance and trend analyses were performed using SAS/STAT (SAS Institute, Cary, N.C.).

Results and Discussion

Growth response to temperature. Both species responded markedly to changes in temperature. Shoot and root growth of *Chasmanthium* and *Hakonechloa*, quantified by plant size, leaf area, shoot length, shoot weight, and root weight, were optimal at 25 °C (Table 1). Lavis-Ham (1993) established temperature optima for the ornamental grasses *Pennisetum alopecuroides* (L.) Spreng., *Schizachyrium scoparium* (Michx.) Nash, and *Imperata cylindrica* (L.) Beauv. at 20–25, 30, and 30 °C, respectively. *Hakonechloa* ceased to grow and died after 4 weeks at 31 °C, while shoot and root growth of *Chasmanthium* was only reduced. In fact, *Chasmanthium* shoot and root growth at 31 °C was considerably better than at 13 or 19 °C. At 13 °C, little new root and shoot growth was evident for either grass species. Anthocyanin pigmentation caused pronounced reddening of stems and leaf blades of both *Hakonechloa* and *Chasmanthium* at 13 °C. Reddening also occurred at 19 °C, but to a lesser extent. In addition to reddening, *Chasmanthium* shoots at the two lowest temperatures developed a yellow-green color. Shoot and root growth of *Hakonechloa* and *Chasmanthium* increased as the temperature increased from 13 to 25 °C (Table 1). Relative to the maximum growth attained under optimum temperatures, *Hakonechloa* growth was enhanced significantly more than *Chasmanthium* growth when temperature was raised from 13 to 19 °C (Table 1).

Treharne and Cooper (1969) demonstrated that many temperate *Poaceae* show maximal net photosynthesis around 20 to 25 °C, which is parallel to the temperature range of activity they observed for ribulose-1,5-biphosphate carboxylase and 1,6-bisphosphatase in temperate graminoids. The activity and temperature sensitivity of these enzymes may be a significant limiting factor in leaf photosynthesis and therefore growth and temperature sensitivity in grasses. Temperature sensitivity among plants is in large part due to genetics and species origin (Pollock and Eagles, 1988; Treharne and Cooper, 1969). *Chasmanthium* originates from the southeastern United States, which is typically warmer and more humid compared to the mild, forested, central Pacific region of Japan, the provenance of *Hakonechloa*. This difference in provenance apparently portends a genetic intolerance of *Hakonechloa* to warm temperatures, and increased heat tolerance of *Chasmanthium*. The tolerance of *Hakonechloa* and *Chasmanthium* to temperatures below and above 25 °C may be a result of photosynthetic acclimation to temperature. Photosynthetic acclimation results from genetically controlled increases, at different temperatures, in the activity of the enzymes involved in photosynthesis (Berry and Bjorkman, 1980; Holaday et al., 1992).

Hakonechloa produced the greatest number of total shoot growing points (shoots plus tiller buds) at 19 and 25 °C (Table 2). As temperature increased, the proportion of *Hakonechloa* shoot growing points that were in the form of tiller buds decreased and the number of shoots increased. Higher temperatures promoted outgrowth of *Hakonechloa* tiller buds into new shoots, but not production of new tiller buds (Table 2). *Chasmanthium* produced the most shoot growing points at 25 °C, which is higher than the 19 °C observed for *Hakonechloa*. Increasing temperature, up to the optimal growth temperature of 25 °C, produced modest increases in the number of *Chasmanthium* shoots and large increases in tiller buds. In contrast to *Hakonechloa*, temperature increases appeared to promote both production of new tillers and development of tillers into shoots in *Chasmanthium*. *Hakonechloa* produced the most inflorescences at 19 °C and some at 25 °C as well (Table 1). All *Chasmanthium* plants bloomed heavily at 25 °C, some bloomed sparingly at 31 °C, and none bloomed at 19 °C or 13 °C (Table 1). The narrow temperature requirement that *Chasmanthium* has for flowering is an important consideration, since this species is cultivated for its attractive seed heads.

Nutrient concentrations in response to temperature. Concentrations of nutrients in shoot tissue of *Chasmanthium* exhibited a quadratic relationship to temperature, with the exception of P, where the relationship was linear (Table 3). All *Hakonechloa* tissue nutrient concentrations exhibited a significant linear response to temperature. Since *Hakonechloa* plants died after 4 weeks at 31 °C, the data could not be used to test for a quadratic relationship between temperature and nutrient concentration in this species. With the exception of Ca in *Chasmanthium*, shoot tissues of both grasses contained maximum nutrient concentrations at 25 °C, the temperature that supported optimum growth. Shoot tissue nutrient concentrations were similar for both grasses, when compared at the optimal growing temperature of each grass. Two exceptions were Mg and N, where *Hakonechloa* tissue concentrations were higher than those of *Chasmanthium*. The nutrient concentrations observed for *Chasmanthium* and *Hakonechloa* shoot tissue are comparable to those reported for container-grown *Pennisetum alopecuroides* 'Hameln' and *Phalaris arundinaceae* L. var. *picta*, two grasses commonly utilized as ornamentals (Mills and Jones, 1991).

At 13 and 19 °C, *Hakonechloa* had higher nutrient concentrations than *Chasmanthium*,

Table 1. Plant size, leaf area, inflorescence production, shoot length, shoot fresh weight, shoot dry weight, root fresh weight and root dry weight for *Chasmanthium latifolium* and *Hakonechloa macra* 'Aureola' grown at different average daily temperatures.

					Shoot		Root	
Avg daily temp (°C)	Plant size (dm^3)	Leaf area (cm^2)	Inflorescences (no./plant)	Shoot length (cm)	Fresh wt (g)	Dry wt (g)	Fresh wt (g)	Dry wt (g)
				Chasmanthium				
13	5.1	84	0	13.4	2.3	0.5	2.6	0.3
19	17.9	300	0	16.3	8.7	2.7	12.0	2.2
25	152.5	1431	7.5	44.8	40.8	11.5	52.2	11.0
31	47.5	766	0.4	27.4	23.1	8.5	30.3	6.2
Linear	*	*	*	*	*	*	*	*
Quadratic	*	*	*	*	*	*	*	*
				Hakonechloa				
13	5.5	92	0	13.1	1.8	0.2	7.1	1.3
19	12.4	218	2.6	17.5	4.7	1.1	8.9	1.9
25	27.8	484	1.0	21.6	10.0	2.6	10.5	2.0
Linear	*	*	*	*	*	*	*	*

*Significant at $P \leq 0.05$.

Table 2. Tiller bud and shoot counts for *Chasmanthium latifolium* and *Hakonechloa macra* 'Aureola' grown at different average daily temperatures.

Avg daily temp (°C)	Tiller buds (no./plant)	Shoots (no./plant)	Total shoot growing points (no./plant)	Tiller buds/total shoot growing points (%)
		Chasmanthium		
13	3.7	5.4	9.1	41
19	13.3	10.5	23.8	56
25	30.6	15.9	46.5	66
31	22.4	15.1	37.5	60
Linear	*	*	*	
Quadratic	*	*	*	
		Hakonechloa		
13	17.3	10.0	27.3	63
19	23.0	16.3	39.3	59
25	17.7	20.8	38.5	46
Linear	NS	*	*	

NS, *Nonsignificant or significant at $P \leq 0.05$, respectively.

Table 3. Shoot tissue concentration and accumulation of Ca, K, Mg, N, and P for *Chasmanthium latifolium* and *Hakonechloa macra* 'Aureola' grown at different average daily temperatures.

Avg daily temp (°C)	Ca ($mg \cdot g^{-1}$)	Ca (mg/plant)	K ($mg \cdot g^{-1}$)	K (mg/plant)	Mg ($mg \cdot g^{-1}$)	Mg (mg/plant)	N ($mg \cdot g^{-1}$)	N (mg/plant)	P ($mg \cdot g^{-1}$)	P (mg/plant)
					Chasmanthium					
13	2.5	1.2	15.6	7.7	2.5	1.2	22.5	11.1	2.4	1.2
19	2.4	6.6	18.9	51.2	2.5	6.9	22.6	61.3	2.6	7.0
25	2.6	30.2	21.8	250.0	2.6	29.9	23.6	270.8	3.6	41.2
31	3.5	29.9	21.6	184.4	2.4	20.8	27.6	235.9	3.8	32.6
Linear	*	*	*	*	*	*	*	*	*	*
Quadratic	*	*	*	*	*	*	*	*	NS	*
					Hakonechloa					
13	2.0	0.4	21.2	4.3	2.8	0.6	24.6	5.0	3.0	0.6
19	2.3	2.7	21.7	24.9	3.0	3.4	26.6	30.5	3.5	4.0
25	3.3	8.6	26.1	67.4	3.4	8.9	33.9	87.5	3.7	9.5
Linear	*	*	*	*	*	*	*	*	*	*

NS, *Nonsignificant or significant at $P \leq 0.05$, respectively.

with the exception of Ca. This may be attributed to the stronger growth of *Hakonechloa* at cooler temperature in comparison to *Chasmanthium*. Low temperatures can reduce ion uptake for warm-season grasses, like *Hakonechloa* and *Chasmanthium*, by hampering membrane fluidity and limiting the function of the membrane-bound proton pumps of root cells (Marschner, 1995), and the ability of ion carrier proteins to catalyze transport (Bravo and Uribe, 1981). *Hakonechloa* may be better adapted than *Chasmanthium* at maintaining ion uptake in cool roots. Some researchers believe it is a demand for nutrients by the shoots, and not a direct effect of temperature on the root system, that is the driving force in modulating ion uptake rates and tissue nutrient concentrations (Engels et al., 1992; White et al., 1991). Watts (1974) demonstrated that shoot growth and nutrient uptake rates increased (demand increased) when shoot meristems of *Zea mays* L. were grown at a warmer temperature outside a cold root zone, compared to meristems grown within this cold zone. Furthermore, White et al. (1991) observed that relative accumulation for K, Ca, and Mg were nearly identical to relative shoot and root growth rates of rye (*Secale cereale* L.) and wheat (*Triticum aestivum* L.) grown at warm shoot zone/cold root zone temperatures.

This study has determined that the optimum ADT for growth and nutrient uptake of *Hakonechloa macra* 'Aureola' and *Chasmanthium latifolium* is close to 25 °C. Although both species are shade tolerant, *Hakonechloa* performed better at ADTs of 13 and 19 °C, but died at 31 °C, while *Chasmanthium* growth was only slightly reduced at 31 °C. Shading during nursery production has been shown to improve container production of *Hakonechloa* (Harvey and Brand, 2001).

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