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YIELD AND MORPHOLOGICAL RESPONSES OF WILD BLUEBERRY (*VACCINIUM* SPP.) TO FOREST HARVESTING AND CONIFER RELEASE TREATMENTS

by

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Masters Thesis submitted in partial fulfilment of the requirements for the degree
Masters of Science in Biology

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May, 1997

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Late August, given heavy rain and sun
For a full week, the berries would ripen.
At first, just one, a glossy purple clot
Among others, red, green, hard as a knot.
You ate that first one and its flesh was sweet
Like thickened wine: summer's blood was in it
Leaving stains upon the tongue and lust for
Picking. Then red ones inked up and that hunger
Sent us out with milk-cans, pea-tins, jam-pots
Where briars scratched and wet grass bleached our
boots.

Round hayfields, cornfields and potato-drills
We trekked and picked until the cans were full,
Until the tinkling bottom had been covered
With green ones, and on top big dark blobs burned
Like a plate of eyes. Our hands were peppered
With thorn pricks, our palms sticky as Bluebeard's.

We hoarded the fresh berries in the byre.
But when the bath was filled we found a fur,
A rat-grey fungus, glutting on our cache.
The juice was stinking too. Once off the bush
The fruit fermented, the sweet flesh would turn sour.
I always felt like crying. It wasn't fair
That all the lovely canfuls smelt of rot.
Each year I hoped they'd keep, knew they would not.

- Seamus Heaney

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Abstract

Moola, F.M. 1997. Yield and morphological responses of wild blueberry (*Vaccinium* spp.) to forest harvesting and conifer release treatment, northwestern Ontario. Master of Science thesis, Lakehead University, Thunder Bay, Ontario.

This thesis synthesizes three papers on the effects of forestry practices on the growth and fruit production of lowbush (*V. angustifolium*) and velvet leaf (*V. myrtilloides)* blueberry in i) young jackpine, ii) boreal mixedwood and iii) lowland black spruce plantations in northwestern Ontario. The main objectives of the three papers were to investigate: **i)** the impacts of forest herbicide and alternative conifer release treatments on the growth and fruit production of *Vaccinium* spp.; **ii)** the phenology of *Vaccinium* spp. in order to determine an optimal spray time that might reduce susceptibility of blueberry to herbicide injury and **iii)** the morphological plasticity of velvet leaf blueberry bushes growing in clearcut, partial cut and uncut second-growth boreal mixedwood forests.

i) It was shown that application of Vision® herbicide significantly affects the abundance, growth and reproductive performance of *Vaccinium* spp. in treated clearcuts. Compared with untreated areas, fruit productivity of *Vaccinium* spp. in Vision® treated plantations was reduced by as much as 58 % three years after disturbance. Reductions in berry production were attributed to toxic effects of the herbicide to stems and below-ground reproductive tissue. Conversely, percent cover and the number, dry weight and fresh weight of berries increased significantly after brushsaw cutting.

ii) Patterns of leaf development in *V. angustifolium* and *V. myrtilloides* indicated that selective control of competing vegetation in plantations with reduced damage to *Vaccinium* spp. may be

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possible with herbicide application before active growth of new blueberry shoots (i.e. early May) or during leaf senescence and abscission (i.e. September to October). Foliage of blueberry turned colour in late August with about 30 % abscission by the last week of September. With most of the foliage lost by early autumn, application of foliar herbicides at this time may have limited effects upon blueberry growth and fruit production, since without leaves, little herbicide can be absorbed or translocated to below-ground vegetative organs.

iii) *V. myrtilloides* was able to persist in both open and closed habitats in boreal mixedwood forests managed for commercial timber exploitation. Persistence under heavy shade conditions was attributed to plasticity in morphological and biomass allocation. Specific leaf area, individual leaf weight, number of berries, number of reproductive shoots and the proportion of total biomass in stems and foliage changed along a gradient in understory light (% PPFD) from 0 % to 67 % PPFD in forests harvested by clearcutting and shelterwood logging. Reproductive performance of *V. myrtilloides* was best under the partial shade conditions associated with shelterwood cutting.

The results of this thesis indicate that clearcut logging and silvicultural strategies of weed suppression such as herbicide application can adversely affect both the berry production and vegetative growth of *Vaccinium* spp. in northwestern Ontario. Conversely, partial cutting and conifer release with brushsaw cutting offer a silvicultural alternative that is less destructive to blueberry.

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Acknowledgements

I would like to extend my appreciation to Dr. Azim Mallik, who with his great enthusiasm and encouraging support has been a wonderful supervisor and a dear friend over the last two years. In addition, I am grateful to Drs. Mark Johnston, Alastair Macdonald and Richard Reader who reviewed the thesis. I am particularly thankful to Mark, who introduced me to the wonders of multivariate analysis of ecological data, statistical computing and ballroom dancing (almost). I owe much to my family - especially to my parents - committed social activists, they read to me Rachel Carson's 'Silent Spring" when I was 7 years old and encouraged me to walk gently upon this earth. My friends provided me with much moral support, and nourishment during the long evenings at my computer - they include the members of the Ontario Public Interest Group, my fellow graduate peers at the Biology Department, the Aardvark Ecology Co-operative in Thunder Bay, Gan Ainm, Evan, Jason, Shawn, Jim, Katherine, Deirdre and Irene, and especially Sara Wilson, who shared with me many horrid mosquito-infested mornings, clutching a battered F.E.C guide as we attempted to distinguish lowbush from velvet leaf blueberry. We had tonnes of fun nonetheless.

Finally, I am indebted to the wonderful staff at the Centre for Northern Forest Ecosystem Research, the Canadian Forest Service and Lakehead University, who despite vicious government cut-backs to staff and resources were always available to assist me in my research. This thesis would never have been completed if weren't for their help. Thank you.

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List of papers

This thesis synthesizes the following three papers.

I) Moola, F.M., Mallik, A.U., and Lautenschlager, R.A. 1997. Effects of conifer release treatments on the growth and fruit production of *Vaccinium* spp. in northwestern Ontario. Accepted with revision, Canadian Journal of Forest Research (re-submitted).

II) Moola, F.M., and Mallik, A.U. 1997. The phenology of *Vaccinium* spp. in northwestern Ontario: implications for the timing of forest herbicide treatments. Canadian Journal of Botany, submitted.

III) Moola, F.M. and Mallik, A.U. 1997. Morphological plasticity and regeneration strategies of velvet leaf blueberry (*Vaccinium myrtilloides*) following canopy disturbance in the management of boreal mixedwood forests. Forest Ecology and Management, submitted.

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Introduction

Blueberry plants (*Vaccinium* spp.) are deciduous ericaceous shrubs endemic to the boreal forest region of Canada (Hall et al. 1979; Vander Kloet and Hall 1981). The range of the velvet leaf blueberry (*V. myrtilloides*) extends from central Labrador to Vancouver Island (Vander Kloet and Hall 1981). The ecological range of the lowbush blueberry (*V. angustifolium*) is more restricted. In Canada it is found from the east coast of Newfoundland to Lake Winnipeg in Manitoba (Hall *et al.* 1979). Both species provide a major food source for black bear (*Ursus americanus* Pallas) in late summer (Rogers 1976, 1987; Arimond 1979). Major weight gains of bears coincide with the maturation and ripening of fruits in July-August and the reproductive success of individual female bears is highly associated with fruit yield (Rogers 1976). Black bears typically exploit areas with dense concentrations of blueberries and there is evidence that bear-human conflicts are most likely to occur during years of poor berry production (Zager 1980). In addition to bears, many woodland and moorland animals and many species of birds depend upon the berries (Martin *et al.* 1951) which are high in carbohydrates and total energy content (Usui et al. 1994).

Although berry productivity is often variable from year to year (Vander Kloet and Hill 1994), several authors have reported that yields increase significantly following forest disturbances such as fire and clear-cutting (Peters 1958; Vander Kloet and Hall 1981; Minore 1984; Usui 1994). Usui *et al.* (1994) reported that *V. angustifolium* production in young clearcuts in northern Ontario was approximately 2300 kg per hectare. Commercial cultivation of both species of blueberry is important to the economies of Quebec and the Atlantic provinces of Canada and in the northwestern and lake states of the United States

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(Hoefs and Shay 1980). Open field cultivation of blueberries in Nova Scotia generated over 30 million dollars for the province in 1993 (Lynch 1995). Similar large-scale cultivation has not proven as successful in northwestern Ontario or Manitoba (Hoefs and Shay 1980), although wild berry picking from forest openings is an important pass-time for many rural people in the provinces. The demand for wild berries in jams, jellies, juices, fruit leathers, liquors and wines has received increasing commercial attention as a non-timber "special" forest product (Kardell 1980; Minore 1984; Freed 1995). The sale of wild blueberries in jams, jellies, pies and cakes is practiced by at least one native-Canadian run business near Kenora, northwestern Ontario (M. Kenney, personal communication).

Because forest fire is actively prevented today, clearcut logging is the main disturbance affecting *Vaccinium* spp. in boreal forests (Atlegrim and Sjöberg 1996). Certain *Vaccinium* species (e.g. *V. angustifolium* Ait.; *V. myrtilloides* Michx..; *V. myrtillus* L.; *V. alaskanense* How.; *V. ovalifolium* Smith; *V. parvifolium* Sm.; *V. vitis-idaea* L.) have been reported to be particularly sensitive to some forestry practices such as clearcutting and herbicide treatment (Lund-Høie and Gronvøld 1987; Balfour 1989; Hamilton et al. 1991; Freedman et al. 1993; Atlegrim and Sjöberg 1996; Hannerz and Hånell 1997). The use of clearcutting in association with silvicultural treatments such as conifer release with herbicides and artifical reforestation has led to declines in *Vaccinium* spp. abundance and fruit production in conifer plantations in boreal forest areas of Canada, Fennoscandia and Eastern Europe (Stoyanov 1986; Lund-Høie and Gronvøld 1987; Balfour 1989; Hamilton et al. 1991; Freedman et al. 1993; Atlegrim and Sjöberg 1996; Hannerz and Hånell 1997). Kardell (1979) reported an 80 % decrease in bilberry (*V. myrtillus*) and 10 % drop in lingonberry (*V. vitis-idaea*) fruit yields during the first decade

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after clearcutting of coniferous forests in Sweden. Conversely, Arimond (1979), Lautenschlager (1993) and Newton et al. (1989) have argued that commercial forestry practices can be used to increase the abundance and fruit yields of understory shrubs, including *Vaccinium* spp., in the management of food resources for wildlife. Arimond (1979) has suggested that thinned boreal forest stands with low tree density create better black bear (*U. americanus*) habitat, in part due to the greater availability of blueberries. Similarly, Newton et al. (1989) have argued that herbicide treatment for conifer release on young plantations may benefit understory shrubs such as *Vaccinium* spp., by releasing them from competition from taller hardwood species; for the benefit of snow-shoe hare (*Lepus americanus* Allen), white-tailed deer (*Odocoileus virginianus* Boddaert) and moose (*Alces alces* Clinton). To date, minimal data has been gathered on the impacts of logging and silvicultural treatments such as herbicide spraying on the lowbush and velvet leaf blueberry to support the hypothesis that *Vaccinium* spp. will benefit from forest management.

The objective of this thesis was to investigate whether boreal forests managed for commercial timber production may also conserve *Vaccinium* spp. that are important for wildlife and berry pickers. As noted by Reader and Bricker (1992), the impacts of logging on understory vegetation that are economically less important than timber, have not been examined in detail. This is especially so for *Vaccinium* spp. which are a dominant understory component of many boreal forests that are exploited for commercial logging (Hall et al. 1979; Vander Kloet and Hall 1981; Atlegrim and Sjöberg 1996; Hannerz and Hånell 1997). The effects of forestry practices on billberry (*V. myrtillus*) have been recently investigated in Sweden (Atlegrim and Sjöberg 1996; Hannerz and Hånell 1997)

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and there is strong evidence that logging can significantly reduce abudance and berry production as a result of mechanical damage to above-ground stems, intense competition from early-successional species, susceptibility to frost in clearings, and greater sensitivity to microclimatic change resulting from canopy removal (e.g. increased solar radiation, decreased humidity, higher ground temperature) . Much less is known about the effects of commercial forestry practices on the lowbush and velvet leaf blueberry in Canada.

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This thesis is presented in the form of three separate papers detailing the impacts of conventional and alternative harvesting and conifer release practices on *V. angustifolium* and *V. myrtilloides* in northwestern Ontario. The investigations were performed at three experimental sites: i) representing young regenerating jack pine (*Pinus banksiana* Lamb.) plantation, ii) boreal mixedwood forest dominated by white spruce (*Picea glauca* [Moench] Voss); black spruce (*P. mariana* [Mill.] BSP.) and trembling aspen (*Populus tremuloides* Michx.) and iii) lowland black spruce (*P. mariana*) plantation near Atikokan, Nipigon, and Thunder Bay, respectively. The main objectives of the three papers in this thesis are:

i) ***Paper One***: to determine the growth and fruit production of *V. angustifolium* and *V. myrtilloides* following operational herbicide (Vision®) and alternative conifer release treatments in a young jack pine plantation near Atikokan, northwestern Ontario.

ii) ***Paper Two:*** to document the phenological events of *V. angustifolium* and *V. myrtilloides* in a young lowland black spruce plantation near Thunder Bay, northwestern Ontario. The vegetative and generative phenology of *Vaccinium* spp. were discussed in relation to the optimal timing of herbicide (Vision ®) application to reduce damage to blueberry plants.

iii) ***Paper Three:*** to determine whether changes in light intensity following clearcutting and shelterwood logging affect abundance, growth, morphological plasticity, biomass allocation and fruit production of *V. myrtilloides* in a 55 year old boreal mixedwood forest near Nipigon, northwestern Ontario.

The field investigations that comprise this thesis were conducted during the growing seasons of 1994, 1995 and 1996.

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Effects of conifer release treatments on the growth and fruit production of *Vaccinium* spp. in northwestern Ontario

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Abstract: Berry production and vegetative recovery of lowbush blueberry (*Vaccinium angustifolium* Ait.) and velvet leaf blueberry (*Vaccinium myrtilloides* Michx.) were documented for three growing seasons (1994, 1995, 1996) after manual brushsaw cutting, single operational and multiple non-operational Vision® herbicide (a.i., glyphosate), and control treatments in a young jack pine (*Pinus banksiana* Lamb.) plantation near Atikokan, northwestern Ontario. Number of berries per hectare (both species combined) was significantly reduced (by 34% and 58%, 1995 and 1996 respectively) following operational single Vision® treatment. The single Vision® treatment also reduced fresh weight and dry weight of berries by 39 % and 19 %, respectively in 1995 and 69 % and 80 %, respectively in 1996. However, *V. angustifolium* was more sensitive to the herbicide treatments than *V. myrtilloides*. Fruit production of *V. angustifolium* was consistantly lower in both the single and multiple Vision® treatments in all three years of the study. Berry number of *V. myrtilloides* in 1994, 1995, and 1996 was significantly reduced by 87, 100 and 100% percent respectively only by the multiple Vision® treatment. The pubescent foliage of *V. myrtilloides* might have hindered absorption of glyphosate and thus decreased its sensitivity to single Vision® treatment.

At the end of the 1996 growing season the cover of *V. angustifolium* and *V. myrtilloides*, respectively, were highest on the brushsaw (16.6 % and 16.7 %) and control (14.0 % and 18.1 %)

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plots, intermediate in the operational Vision® treated plots (0.6 %, 5.6 %), and lowest on the multiple herbicide treated plots (0.2 %, 0.4 %). Compared with controls, the reductions in cover of both blueberry species were only significant following herbicide application. Four growing seasons post-treatment, neither *V. angustifolium* nor *V. myrtilloides* benefited from the more open conditions (increased available light, and reduced overtopping cover) created by the conifer release treatments.

Discriminant Analysis of 11 vegetative parameters (height, number of unaffected, partially defoliated, severely defoliated and dead stems, dry weight of live and dead stems, dry weight of rhizomes and leaves, leaf area and leaf weight) of the two *Vaccinium* spp. suggests that the recovery of both species of blueberry was significantly lower in Vision® treated plots compared to the brushsaw and control plots. Both species exhibited greater stem defoliation and mortality, lower percent cover and lower leaf area in the single and multiple Vision® treatments.

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Introduction

Production of wild blueberries (*Vaccinium* spp.) in northern ecosystems is important to commercial growers and harvesters, a variety of wildlife, First Nations, and other berry pickers. Conifer release with herbicides can damage blueberry plants and reduce cover (Balfour 1989; Freedmat et al. 1993) and fruit quality (Roy et al. 1989) in treated areas. During the last three decades conifer release with herbicides has become increasingly common in northern ecosystems (Kuhnke and Brace 1986; Maass 1989; Campbell 1990). This practice, coupled with increasing public concern about chemicals in the environment (Johnson et al. 1995), stimulated controversy (Freedman 1991) and in Ontario led to the development of the Vegetation Management Alternatives Program (Wagner et al. 1995). Public concern arose over both presumed toxic effects and the potential of changing wildlife habitat (Lautenschlager 1993). At recommended rates and under normal use scenarios, herbicides used for conifer release in northern ecosystems pose minimal toxicological hazard for terrestrial vertebrates and pose no risk of bioaccumulation in the environment (Morrison and Meslow 1983; Newton et al. 1984). They do, however affect populations indirectly by changing their habitat (Lautenschlager 1993) and wildlife species that are sensitive to microhabitat changes may be vulnerable (Runciman and Sullivan 1996).

We initiated this study because of concerns expressed that conifer release with the broad spectrum herbicide glyphosate[1] might significantly reduce short-term blueberry production in treated areas which may have adverse effects on the physical condition and reproductive potential of black bear

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[1] Vision® commercial formulation containing glyphosate, 356 g/L present as isopropylamine salt.

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(*Ursus americanus* Pallas). Major weight gains in bears coincide with periods of fruit maturation and ripening (July-August). Rogers (1976, 1987) reported that blueberry production in northern Minnesota was critical for black bear growth and reproductive success. Others (Arimond 1979; Kolenosky and Strathearn 1987) have drawn similar conclusions. Although late summer blueberry crops seem to be an important food source for black bears, Martin et al. (1951) listed 32 other species of wildlife including, grouse (Tetraonidae), willow ptarmigan (*Lagopus lagopus alleni* L.), red fox (*Vulpes vulpes* Desmarest), black-tailed deer *(Odocoileus hemionus* Boddaert), American Robin (*Turdus migratorius* L.), thrushes (Turdinae, Muscicapidae), chipmunk (*Eutamias* spp.), eastern cottontail (*Sylvilagus floridanus* Allen) and porcupine (*Erethizon dorsatum* L.) that commonly eat fruits of this genus.

Several *Vaccinium* spp. are susceptible to glyphosate, although no study has documented elimination of the species from sprayed plots. Moderate to severe damage to foliage and aerial shoots as well as reduced cover has been reported in *V. angustifolium* and *V. myrtilloides* in Nova Scotia (Freedman et. al. 1993), *V. myrtillus* L. in Sweden (Lund-Høie and Grønvold 1987), and *V. alaskanense* How., *V. ovalifolium* Smith, and *V. parvifolium* Sm. in British Columbia (Balfour 1989) following silvicultural use of the herbicide in forest plantations. Conversely, the lignonberry (*V. vitis-idea* L.) is extremely tolerant to glyphosate (Lund-Høie and Grønvold 1987), perhaps owing to the leathery nature of its leaves which may hinder absorption of the herbicide. In *Vaccinium* spp. that are susceptible to glyphosate, maximum effects are observed in the first or second post-spray growing season (Freedman et al. 1993) and vegetative recovery can be slow (Lund-Høie and Grønvold 1987).

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Freedman et al. (1993) reported a progressive increase in cover of *Vaccinium* spp. during succession six years after a spray solution containing glyphosate was aerially applied on regenerating clearcuts in Nova Scotia; however, blueberry cover did not reach the pre-treatment level within the experimental period.

Although reductions in *Vaccinium* spp. cover and shoot damage associated with herbicide spray solutions containing glyphosate have been found, data documenting direct effects of this herbicide on berry production are not available. The objective of this study was to document, 2, 3, and 4 growing seasons post-treatment, growth and fruit production of lowbush (*V. angustifolium*) and velvet leaf (*V. myrtilloides*) blueberry following operational Vision®, multiple Vision®, brushsaw cutting, and no treatment (control) in a young jack pine (*Pinus banksiana*) plantation. In order to determine if cover and fruit production of *V. angustifolium* and *V. myrtilloides* benefited from the more open conditions associated with these conifer release alternatives, available light (% PPFD[2]) and cover of vegetation overtopping *Vaccinium* spp. following these treatments were also assessed 4 growing seasons after treatment.

As it is unlikely that black bears or other wildlife can distinguish between *V. angustifolium* and *V. myrtilloides* in their foraging efforts (Arimond 1979), the influence of conifer release treatments on the combined fruit production of both species is discussed with reference to the potential impacts on wildlife.

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[2] Photosynthetic photon flux density (PPFD: 400-700 nm).

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Study Area

The study area was located in the Boreal Forest Zone (Rowe 1972), approximately 53 km north of Atikokan, northwestern Ontario, near the southwest shore of Clearwater Lake (49°00°N, 91°57°W). Prior to harvesting the stand was dominated by jack pine, which was harvested using chain saws and skidders in 1986/87. The area was mechanically site prepared in the fall of 1987 with heavy drags of barrels and chains, and planted with jack pine (3000 seedlings/ha) in the spring of 1988. When the study was initiated (August 1992), the young jack pine were overtopped by a combination of trembling aspen (*Populus tremuloides* Michx.), green alder (*Alnus crispa* [Ait.] Pursh), pin cherry (*Prunus pennsylvanica* L.f.), beaked hazel (*Corylus cornuta* Marsh.), and willow (*Salix* spp.). Ground vegetation consisted mostly of bunchberry (*Cornus canadensis* L.), creeping snowberry (*Gaultheria hispidula* [L.] Muhl), large-leaved aster (*Aster macrophyllus* L.), red raspberry (*Rubus ideaus* L.), bluebead lilly (*Clintonia borealis* [Ait] Raf.), violets (*Viola* spp.), and lowbush blueberry (*Vaccinium angustifolium*), and velvet leaf blueberry (*Vaccinium myrtilloides*). The soil had a thin organic layer (mean thickness = 4.16 cm) over fresh, deep sand and cobbles. Prior to conifer release treatment in 1992, the average cover and height of *Vaccinium* spp. (both species combined) in the study area was 16.9 % and 23.64 cm, respectively (Brian Polhill[3], unpublished data). Daily temperature and rainfall data measured at 18:00 hr from April 23 to September 29, 1994, 1995, and 1996, was obtained from a weather station approximately 65 km southeast of the treatment plots. With the exception of brushsaw cut plots, where *Vaccinium* spp. cover was significantly lower than in the single and multiple Vision®

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[3] Brian Polhill, Renewal Specialist, Ontario Ministry of Natural Resources, Northwest Science and Technology, Thunder Bay, Ontario.

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plots, treament plots did not differ significantly in blueberry abundance.

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Materials and Methods

Experimental design

The experiment used a completely randomized design with 4 replicates of the following treatments: (1) manual cutting of non-pine woody vegetation that overtopped *Vaccinium* spp. with brushsaws after maximum leaf flush (between late June and early July 1993), (2) operational (single) aerial treatment in late August 1992 with a spray solution containing Vision® (glyphosate - 1.5 kg a.i./ha) herbicide, (3) non-operational multiple Vision® treatments -- the operational aerial Vision® treatment (August 1992), followed by annual backpack (1993, 1994, 1995) Vision® treatments and (4) untreated control.

Berry Production

In August 1994 (2 growing seasons post-treatment) berries of both *V. angustifolium* and *V. myrtilloides* were collected from 6 randomly placed 2 x 2 m quadrats which were placed within each treatment plot replicate. This produced 24 quadrats per treatment (6 x 4); a total of 96 (24 x 4) quadrats were examined. In 1995 and 1996 (3 and 4 growing seasons post-treatment) berries were collected from 9, rather than 6, randomly placed 2 x 2 m quadrats within each treatment replicate for a total of 144 quadrats examined. The harvested berries were frozen after picking and brought to the laboratory. All berries were thawed, counted and weighed fresh and again after drying at 70° C for 36 hours.

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Leaf area and specific leaf area

Ten mature leaves of *V. angustifolium* and *V. myrtilloides* were harvested at random in August 1996 from nine 2 x 2 m quadrats of each treatment plot. Harvested leaves were flattened and then immediately placed in plant presses in the field. The leaves were brought to the laboratory and their area determined using a Delta T, MK2 leaf area meter (Delta-T Devices Ltd. Burwell, Cambridge, England). Dry biomass of the harvested leaves was determined after oven drying at 70°C for 24 hours. Specific leaf area was calculated by dividing the measured leaf area by the oven dry weight (Mallik 1994).

Vegetative characteristics

Pre-treatment blueberry (*Vaccinium* spp.) height and cover data at the genus level were obtained from the Northwest Science and Technology unit of the Ontario Ministry of Natural Resources (Brian Polhill, personal communication). Measurements were taken in the summer of 1992 from 20 crop-tree centered 1.13 m radius circular plots located within each treatment plot.

The vegetative recovery of *Vaccinium* bushes was examined in 1996 in all the treatment plots. Percentage cover, density and average height of *V. angustifolium* and *V. myrtilloides* bushes were recorded in nine 2 x 2 m quadrats randomly located in each treatment plot. Vegetative characteristics of both blueberry species were determined by excavating one bush from each 2 x 2 m quadrat. Bush size was standardized by including all connecting rhizomes and above ground stems from a 40 x 40 cm frame randomly located within the quadrat. Dry weights of live and dead stems, leaves and rhizomes of each excavated bush were determined after oven drying at 70° C for 48 hours. The amount of

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injury suffered by *V. angustifolium* and *V. myrtilloides* plants was estimated by counting the number of live, partially defoliated, severely defoliated and dead bushes within each 2 x 2 m quadrat.

Percent photosynthetic photon flux density (% PPFD) and cover of vegetation overtopping *Vaccinium* spp.

An estimate of the percentage of full sunlight (% PPFD) available to *Vaccinium* spp. in each treatment plot was measured above 10 randomly chosen blueberry bushes using a Sunfleck PAR ceptometer (Decagon Devices, Inc. Pullman, Washington, USA) following the methodology of Messier and Puttonen (1995a). On a completely overcast day, the mean of five instantaneous light measurements was recorded above each blueberry bush (*Iu*). Ambient overstory PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$) (*Io*) conditions were measured with a quantum sensor linked to a LI-1000 datalogger (LI-COR, Lincoln, NE, USA) placed in an open gravel pit adjacent to the treatment plots. The data logger was programmed to compute the mean PPFD every 5 sec. over a 1 min period. Dividing instantaneously taken readings of *Iu* by *Io* provided a measurement of the percent of above canopy PPFD (% PPFD) transmitted above each blueberry bush at a given time.

The cover of non-crop tree vegetation that overtopped *Vaccinium* spp. was measured in the treatment plots in 1996. The abundance of vegetation taller than *Vaccinium* spp., such as trembling aspen (*P. tremuloides*), green alder (*A. crispa*), pin cherry (*P. pensylvanica*), beaked hazel (*C. cornuta*), and willow (*Salix* spp.) was estimated as the proportion of blueberry canopy obscured by a perpendicular projection of the foliage of overtopping vegetation. The abundance of vegetation

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above *Vaccinium* spp. was assessed from within nine 2 x 2 m quadrats, randomly located in each of the treatment plots.

Data Analysis

The data did not meet the assumptions required for the use of a one-way analysis of variance, since the samples were not taken from normally distributed populations of blueberry. Therefore, nonparametric analysis was employed to determine whether reproductive and vegetative parameters of *Vaccinium* spp. differed among treatments. Moreover, the sample size for each treatment was small and some samples had outliers. Since the Mann-Whitney and Kruskal-Wallis tests involve rank comparisons, outliers were less influential on the test results (Norusis 1995). Following the detection of significant differences among means with the Kruskal-Wallis test, a series of Mann-Whitney tests was employed for the pair-wise comparison of the different treatment means. This was done in order to identify which treatments were significantly different from each other. The observed significance level for the Mann-Whitney test was adjusted with the Bonferroni procedure: for 6 comparisons, the observed significance level for each comparison had to be less than 0.05/6, or 0.008, for the difference to be significant at the 0.05 level. Discriminant Analysis was initially performed on 13 vegetative characteristics of *Vaccinium* spp.: height, cover, number of unaffected, partially defoliated, severely defoliated and dead stems, dry weight of live and dead stems, dry weight of rhizomes and leaves, leaf area, inividual leaf weight and specific leaf area. The data were log transformed prior to analysis since the vegetative parameters did not meet the criterion of homogeneity of variance. The percent cover and specific leaf area variables were removed from the analysis after they were found to be highly

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correlated with the number of unaffected bushes and leaf area variables respectively; the data were then re-analyzed with the remaining 11 variables.

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Results

Fruit production of *Vaccinium* spp.

When compared with control means, the number of berries per hectare (both species combined) 3- (1995) and 4- (1996) growing seasons post-treatment (Tables 2, 3) was reduced by 34 % and 58 %, respectively following the operational Vision® treatment. The operational Vision® treatment also reduced fresh weight and dry weight of berries by 39 % and 19 %, respectively 3 growing seasons post-treatment (Table 2) and 69 % and 80 %, respectively 4 growing seasons post-treatment (Table 3). However, *V. angustifolium* was more sensitive to the herbicide treatments than *V. myrtilloides*. Its berry production (berry number, fresh weight and dry weight) were consistantly lower in both the single and multiple Vision® treatments in all three years of the study (Tables 1, 2, 3). Berry number, of *V. myrtilloides* in 1994, 1995, and 1996 was significantly reduced by 87, 100 and 100 percent respectively only by the multiple Vision® treatment (Tables 1, 2, 3). Similarly, only the multiple Vision® treatment adversely affected the fresh weight and dry weight of *V.myrtilloides* fruit in 1994, 1995 and 1996. The brushsaw treatment had no significant effect on the fruit production (number, fresh weight and dry weight of berries) of either blueberry species individually, or their combined fruit yield in all years (Tables 1, 2, 3).

Cover of *Vaccinium* spp.

Blueberry cover consisted entirely of discrete ramets connected underground by creeping rhizomes. No evidence of regeneration by seed was observed in any of the treatment plots.

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At the end of the 1996 growing season the cover of *V. angustifolium* (Table 5) and *V. myrtilloides* (Table 6), respectively, were highest on the brushsaw (16.6 % and 16.7 %) and control (14.0 % and 18.1 %) plots and lowest on the multiple herbicide treated plots (0.2 %, 0.4 %). Compared with the controls, reduction in cover for both blueberry species was only significant following herbicide application. Single herbicide Vision® treatment reduced *V. angustifolium* cover by 95.9 % and *V. myrtilloides* cover by 67.3 %. The multiple herbicide treatment reduced the cover of *V.angustifolium* and *V.myrtilloides* by 98.7 % and 98.0 %, respectively.

Further evidence of the adverse effect of herbicide application on *Vaccinium* spp. cover is seen when pre-treatment cover in 1992 (Brian Polhill, unpublished data) and post-treatment cover in 1996 are compared. That comparison shows that treatments reduced *Vaccinium* spp. cover by an average of 67.2 % on the single Vision® plots and 97.2 % on the multiple Vision® treated plots. Conversely, mean *Vaccinium* spp. cover increased from 12.1 % prior to brushsawing, to 33.3 % 3 growing seasons post-treatment, a change of approximately 63.6 %, on the brushsaw treated plots. This was similar to the mean increase in blueberry cover on the control plots (above 50.0 %) during the same period.

Leaf area, dry leaf weight, and specific leaf area

Both *V. angustifolium* and *V. myrtilloides* responded to herbicide treatment with significant changes in leaf morphology (Table 4). Leaves of both blueberry species in the control plots were significantly larger than those from the single Vision® and multiple Vision® treated plots but not the brushsaw treated plots. There was no statistical difference in the dry weight of individual leaves produced by *V. angustifolium* among treatments. Conversely, mean dry leaf weight of *V. myrtilloides*

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was highest in the control, and significantly less in the brushsaw and all herbicide treated plots. Specific leaf area (SLA = leaf area/dry leaf weight) among the treatments was less variable in *V. angustifolium* than *V. myrtilloides*. In *V. angustifolium*, specific leaf area was only reduced by the multiple Vision® treatment. Values for *V. myrtilloides* in the control were significantly less in the single Vision® and multiple Vision® treated sites, but not the brushshaw sites.

Injury to foliage and stems

Many of the blueberry plants receiving herbicide treatments were top-killed and malformed. The single and multiple herbicide treatments resulted in significant injury to the foliage and stems of both blueberry species; a large proportion of *V. angustifolium* bushes in the single herbicide treated plots had defoliated, deformed or dead stems (Table 5). The adverse effects were more pronounced in the multiple herbicide treatment plots. Many of the affected plants in the multiple sprayed plots produced small roseate leaves or were almost totally defoliated; 98 % of plants were either severely defoliated or dead by the end of the 1996 growing season. In comparison, 92 % and 97 % of *V. angustifolium* bushes in the control and brushsaw treatments were uninjured, respectively. Comparable morphological abnormalities were exhibited by *V. myrtilloides* following herbicide treatment (Table 6). Similar to *V. angustifolium*, the highest number of severely defoliated and dead bushes were obtained in the multiple herbicide treated plots. Significantly fewer bushes were adversely affected by the single herbicide treatment and far fewer in the brushsaw and control plots; 23 %, 2 % and 4 %, respectively. Leaves of both blueberry species were normal in appearance in the brushsaw and control plots.

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Discriminant Analysis of vegetative parameters of *Vaccinium* spp.

The results of significance tests for univariate equality of group means indicated that of the 11 vegetative parameters investigated in the Discriminant Analysis, 10 were significantly different amongst the treatment groups for *V. angustifolium* and all 11 for *V. myrtilloides.* The treatment means for height, and number of unaffected, severely defoliated and dead stems, dry weight of live and dead stems, dry weight of rhizomes and leaves, leaf area and individual leaf weight were significantly different among the 4 treatments (Tables 5, 6). The number of partially defoliated *V. angustifolium* bushes was not affected by the conifer release treatments. Discriminant Analysis confirmed the separation of the 144 *V. angustifolium* and *V. myrtilloides* samples into 4 groups (Figs. 1 and 2) with 93.06 % and 92.31 % accuracy respectively. Two of the three discriminant functions obtained from the analysis explained 97.38 % of the variance with the first discriminant function accounting for slightly over 94.3% of the variance in *V. angustifolium* (Table 7). In *V. myrtilloides*, the first two discriminant functions accounted for 96.9 % of the variance; 92.08 % of this was explained by discriminant function 1 (Table 7). For both *Vaccinium* spp., function 1 was highly correlated with leaf area, dry weight of leaves, and dry weight of dead stems; this indicates that these vegetative parameters are likely the best predictor variables for the separation of the 4 treatment groups on the basis of vegetative recovery following the conifer release treatments. As displayed in the ordination diagram (Figs. 1 and 2), *Vaccinium spp.* recovery was significantly different in clearcuts that were sprayed with the multiple Vision® herbicide as compared to the brushsaw and control treatments. Quadrats from the brushsaw and control clearcuts formed one group in the ordination diagram and were separate from

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the multiple herbicide treated plots. Conversely, the recovery of single herbicide bushes of both blueberry species did not appear to be as adversely affected (Figs. 1 and 2).

Percent PPFD and cover of vegetation overtopping *Vaccinium* spp.

The percent of full sunlight transmitted above *Vaccinium* spp. (% PPFD) was significantly greater in the study plots that had received conifer release treatment than in the control plots, in which an average of only 11.4 % of full sunlight reached the level of blueberry foliage (Table 9). Highest light availability was measured in the multiple Vision® (71.9 % PPFD) and single Vision® (56.3 % PPFD) treated plots. However, there was no significant difference in % PPFD between the two herbicide treatments. Similarly, the brushsaw treatment (45.4 % PPFD) provided as significant an increase in the availability of sunlight above the *Vaccinium* spp. bushes, as the single Vision® treatment.

The cover of vegetation overtopping *Vaccinium* spp. was greatest in the control (71 %) , intermediate in the brushsaw cut (42 %) and operational Vision® (53 %) treated plots, and lowest on the multiple Vision® (20 %) treated plots. Percent cover was significantly different between all the release treatments and the control, but did not differ between the brushsaw and single Vision® treatment plots (Table 9).

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Discussion

Blueberry fruit production was highly variable in time and space and consequently these results are difficult to interpret, primarily because of the high degree of variability associated with some of the measurements. This is a common observation in studies of *Vaccinium* species (Vander Kloet and Hill 1994). High variability in fruit production among quadrats was particularly evident in the single Vision® sprayed plots, in which some quadrats had low yields while others had relatively high yields. The high berry production of some blueberry bushes in the single Vision® treated plots might have resulted from reduced exposure to the herbicide due to physical shielding from taller, overtopping vegetation (Freedman et al. 1993). This is a common phenomenon observed following glyphosate spraying (Lund-Høie 1985; Freedman et al. 1993). Despite the difficulties in estimating berry yield, the results of this three year study suggest that conifer release treatment with Vision® herbicide in forest ecosystems can adversely affect the morphology, growth and fruit production of wild blueberry. However, the response to single Vision® treatment appears to be species specific. Unlike the lowbush blueberry, wild patches of velvet leaf blueberry did not appear to be as adversely affected by the single Vision® treatment. Indeed, in all three seasons (1994, 1995, 1996) we failed to find any statistically significant differences in the dry weight, fresh weight or number of fruits produced in the single Vision® sprayed plots, compared to the control. The variable sensitivity of the two blueberry species to single Vision® treatment may be due to differences in the degree to which glyphosate was absorbed by the foliage of exposed bushes (Grossbard and Atkinson 1985). Extensive injury or the death of vegetation treated with foliar-applied herbicides, such as Vision® depends upon the rapid absorption of

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the active ingredient in sufficient quantity before the herbicide is washed off by rain (Neal et al. 1985). The presence of pubescence or a waxy cuticle on the foliage of exposed plants, however, may decrease cuticular permeability to the herbicide, resulting in a lower absorption (Neal et al. 1985). The velvet leaf blueberry is metabolically susceptible to the toxic effects of glyphosate, given the extensive injury and death of aerial shoots that were observed following single Vision® treatment in this study and by Freedman et al. (1993). However, the chemical must be absorbed in order to cause such effects. It appears that under operational spay conditions, the pubescent foliage of *V. myrtilloides* may restrict the amount of glyphosate that is absorbed to levels that are insufficient to kill the entire plant. Although many aerial sprouts were extensively defoliated or killed by spraying, some survived and continued to produce fruit. These sprouts are expected to progressively develop a larger foliar area (Freedman et al. 1993). Therefore, fruit production by *V. myrtilloides* in single Vision® clearcuts will likely remain high.

Nevertheless, although *V. myrtilloides* was less susceptible to glyphosate than *V. angustifolium*, the significant reduction in berry production by *V. angustifolium* contributed to an overall drop in the availability of blueberries on sprayed clearcuts in all three years of the study. In clearcuts where *V. angustifolium* forms a major component of the *Vaccinium* spp. cover, the short-term reduction in fruit availability in sprayed areas may be important.

Fruit production of *V. angustifolium* and *V. myrtilloides* were not assessed in this study prior to application of the treatments. Since the magnitude and direction of changes in berry production reflect the amount of foliage that was available prior to treatment (Hamilton et al. 1991), the dissimilar

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responses of the two blueberry species to single Vision® application may not be as great as they appear, if the two species differed in their fruit production before the treatments were applied.

Although the reduction in lowbush blueberry yield associated with the multiple Vision® treatment was dramatic, this was an experimental treatment and is unlikely to be used operationally for conifer release. The reduction in fruit yield caused by the multiple Vision® treatment was likely due to the excessive injury and mortality of reproductive shoots. Compared with the control, blueberry cover of both species was significantly reduced in the multiple Vision® treated plots, and almost all plants producing abnormal foliage were defoliated completely or killed. In addition, lower fruit production might have been due to the fact that the regeneration of blueberry sprouts from surviving rhizomes and stem bases likely reduced allocation of biomass to sexual organs. Vila and Terradas (1995) have attributed similar reductions in the biomass of reproductive structures in burned patches of *Erica multiflora* L. to the cost of vegetative recovery.

Discriminant Analysis of 11 vegetative parameters (height, number of unaffected, partially defoliated, severely defoliated and dead stems, dry weight of live and dead stems, dry weight of rhizomes and leaves, leaf area and leaf weight) of the two *Vaccinium* spp. suggests that the growth of both blueberry species was significantly reduced in Vision® treated plots compared to the brushsaw and control plots. Both species exhibited greater stem defoliation and mortality, lower percent cover and reduced leaf area in the single and multiple Vision® treatments. The minimal vegetative recovery of blueberry species, especially by *V. angustifolium*, following Vision® treatments, observed in this study and elsewhere (Freedman et al. 1993; Lund-Høie and Grønvold 1987) was likely due to reduced

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potential for clonal revegetation. Like most ericaceous shrubs, *Vaccinium* spp. are able to recover quickly after disturbances such as fire and manual cutting (Yarborough et al. 1986) that destroy above-ground stems and foliage, by re-sprouting from buds at the base of surviving stumps or from underground rhizomes (Mallik 1991, 1993). Similar rapid revegetation of Vision® treated areas was not observed in this study especially by *V. angustifolium*; this was perhaps due to the toxicity of the herbicide to perennating tissues (Freedman et al. 1993). With sufficient absorption and subsequent translocation to below-ground components, glyphosate can cause significant injury to meristematic tissues or kill the entire rhizome of exposed plants (Sprankle et al. 1975). As recovery of *Vaccinium* spp. from seed is unlikely due to the paucity of seedling regeneration (Vander Kloet and Hill 1994), extensive injury or mortality of rhizomes may delay revegetation of sprayed areas for several years compared to the brushsaw cut plots (Lund-Høie and Grønvold 1987).

Of the vegetative parameters examined in the Discriminant Analysis, leaf area was the most important variable explaining the separation of sprayed and unsprayed plots. The herbicide effects on leaf morphology should be investigated further to determine if reduced yield is due to leaf abnormalities. Inefficient photosynthesis in abnormal leaves might explain the poor berry production in severely affected bushes found in the multiple herbicide treated plots.

Results of this study suggest that fruit production by *Vaccinium* spp. is not consistent with Lautenschlager's (1993) conceptual model of the effect of no treatment and conifer release treatment with herbicides on browse biomass. Neither *V. angustifolium* nor *V. myrtilloides* benefited from the open conditions created by conifer release treatments with Vision® in the first four years after the

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treatment. Compared with the controls, even brushsaw cutting failed to increase fruit yields by either blueberry species despite the increased availability of light. Although there is evidence that fruit production by *Vaccinium* spp. can benefit from silvicultural treatments that reduce or eliminate overstory cover in more mature, closed forests (Minore 1984), our results suggest that increased availability of light following brushsaw cutting and Vision® treatments did not increase blueberry production above that in controls in young jack pine plantations in northwestern Ontario. This may reflect the ability of *Vaccinium* spp. to exploit small gaps within the canopy of forest plantations, where the transmission of light to the understory is higher. In addition, both blueberry species are relatively shade tolerant (Vander Kloet 1988) and there is evidence that fruit production in *V. angustifolium* and *V. myrtilloides* may benefit from intermediate levels of shade (Hoefs and Shay 1981). Similar to other shade-tolerant ericaceous plants such as *Kalmia. angustifolia* var. *angustifolia* (Mallik 1994), *V. ovalifolium* (Alaback and Tappeiner 1991) and *Gaultheria shallon* Pursh. (Bunnell 1989; Messier 1992; Huffman et al. 1994), *V. angustifolium* and *V. myrtilloides* can persist under shade by producing taller aerial shoots and developing larger leaves. The possession of these traits may facilitate the capture of light under conditions of above-ground competition from invading hardwoods, with little cost to fruit production in young forest plantations.

Our results show that year to year variation in berry production by *V. angustifolium* and *V. myrtilloides* in northwestern Ontario clearcuts is high regardless of treatment. Fruit production in all treatment plots was significantly lower in 1995 than that in 1994 and 1996. The poor berry yields in 1995 may have been a result of the unfavourable weather conditions which characterized much of the

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summer growing season; in particular, abnormally high daytime temperatures and a severe deficit in precipitation. The influence of meteorological conditions on annual fruit production in wild *Vaccinium* spp. is well known (Minore 1984; Hoefs and Shay 1981). Reductions in fruit production at moderate levels of moisture stress have been attributed to the high stomatal resistance of *Vaccinium* spp. at reduced water potentials (Davies and Johnson 1982), as well the absence of adaptive traits for drought tolerance such as a high leaf diffusive resistance (Erb et al. 1988). The drop in berry production in 1995 was less drastic in the control plots than that in the Vision® treated plots, perhaps due to the presence of more favourable near-ground microclimatic conditions (e.g., cooler daytime temperatures, higher relative humidity and lower duff temperatures; Reynolds et al. 1997) for blueberry growth (Hoefs and Shay 1981).

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Conclusions and Management Implications

Silvicultural treatment of clearcuts with spray solutions containing Vision® herbicide affected both berry production and vegetative growth of *Vaccinium* spp. in northwestern Ontario clearcuts. Although the velvet-leaf blueberry (*V. myrtilloides*) was less susceptible to Vision® than the lowbush blueberry (*V. angustifolium*), the significant reduction in berry production by *V. angustifolium* contributed to an overall drop in the availability of blueberries on sprayed clearcuts in 1994, 1995 and 1996. Berry production by *Vaccinium* spp. is extremely variable from year to year and complete fruiting failure is not uncommon (Vander Kloet and Hill 1994). Consequently, the adverse effects of Vision® treatment on blueberry fruit production may be minimal for those wildlife species that have a diverse diet, and presumably are well adapted to extreme seasonal fluctuations in the availability of berries. Usui et al. (1994) suggested that other fruit yielding species such as bunchberry (*C. canadensis*), red elderberry (*Sambucus pubens* Michx.), wild rose (*Rosa* spp.), and pin cherry (*P. pensylvanica*) may be eaten by wildlife during natural periods of reduced blueberry availability. With the exception of *Prunus* spp., little data is available on the effects of Vision® treatment on fruit production of these other species. The manufacturer of Vision® (Monsanto Canada, INC.) reports significant control of cherry (*Prunus* spp.) in clearcuts sprayed with solutions containing Vision®. Hence the importance of *Prunus* spp. and other fruit yielding vegetation as substitutes for blueberry in Vision® treated areas should not be over-emphasized.

Species with large foraging ranges, such as bears, may abandon glyphosate treated clearcuts, presumably to forage in nearby untreated forest cutovers or gaps within uncut forests (Hamilton et al.

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1991). Reduced use of glyphosate treated clearcuts due to berry failure by shrubs such as *Vaccinium* spp. has been observed in radio-collared grizzly bears (*Ursus arctos* L.) (Hamilton et al. 1991). Although bears are likely to forage in nearby untreated areas, their emmigration from sprayed clearcuts may have adverse impacts on bear populations that are close to human settlements. Evidence of increased incidence of conflict with humans has been reported during periods of natural blueberry failure (Zager 1980). Forest managers therefore may want to consider the consequences of Vision® herbicide treatments on bears and other wildlife using regenerating clearcuts close to human communities. Brushsaw cutting could be used as an alternative in these areas since it has no detrimental effect on growth and fruit production of *Vaccinium* spp. and is more acceptable to the public than the silvicultural use of herbicides such as Vision® (Johnson et al. 1995).

Although the brushsaw treatment did not have a stimulating effect on blueberry production, increased vegetative regeneration (Lund-Høie and Grønvold 1987) and higher fruit yields may be possible if blueberry stems were physically cut along with competing vegetation, rather than simply released from competition. Commercial blueberry growers have long known that the cultural practice of pruning blueberry fields by fire or mowing increases fruit yields (Yarborough et al. 1986). These practices effectively remove older, less productive stems while stimulating the development of taller, branched shoots with more reproductive buds (Trevett 1962). Brushsaw cutting for silvicultural purposes may have indirect benefits for wildlife and berry pickers by stimulating vegetative regeneration and promoting greater fruit production in wild patches of *Vaccinium* spp.

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Table 1. Means (and standard errors) of fruit production in 1994 by *V. angustifolium*, *V. myrtilloides* and both species combined following conifer release treatments

	Vaccinium angustifolium berries			*Vaccinium myrtilloides* berries			Total berry yield (both species combined)		
Treatment	Number (/ha)	Fresh weight (g/ha)	Dry weight (g/ha)	Number (/ha)	Fresh weight (g/ha)	Dry weight (g/ha)	Number (/ha)	Fresh weight (g/ha)	Dry weight (g/ha)
Control	32600a (21793)	4595a (3509)	544a (395)	64687a (34035)	7502a (4413)	1126a (363)	97287a (55828)	12097a (7922)	1670a (758)
Brushsaw	10325ab (5434)	1311ab (698)	188ab (100)	61563a (26063)	13853a (8385)	1444a (555)	71888a (31497)	15164a (9083)	1632a (655)
Single herbicide	7567bc (6895)	391bc (308)	77bc (29)	75909a (41839)	8048a (4451)	1230a (688)	83476a (48734)	8439a (4759)	1307a (717)
Multiple herbicide	1425c (1424)	180c (180)	23c (23)	10937b (9820)	593b (498)	108b (27)	12362b (11244)	773b (678)	131b (50)

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Mann-Whitney nonparametric test. Observed significance level was adjusted with the Bonferroni procedure; ($P \leq 0.008$).

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Table 2. Means (and standard errors) of fruit production in 1995 by *V. angustifolium*, *V. myrtilloides* and both species combined following conifer release treatments

	Vaccinium angustifolium			*Vaccinium myrtilloides*			Total berry yield (both species combined)		
Treatment	Number of berries (/ha)	Fresh weight (g/ha)	Dry weight (g/ha)	Number of berries (/ha)	Fresh weight (g/ha)	Dry weight (g/ha)	Number of berries (/ha)	Fresh weight (g/ha)	Dry weight (g/ha)
Control	4722a	239a	64a	25347a	1329a	307a	30069a	1568a	371a
	(2193)	(94)	(26)	(9648)	(534)	(118)	(11841)	(628)	(144)
Brushsaw	12292a	777a	172a	42500a	2658a	484a	54792a	3435a	656a
	(6173)	(394)	(66)	(15336)	(934)	(154)	(21509)	(1328)	(220)
Single herbicide	1250b	26b	110b	18611a	933a	192a	19861b	959b	302b
	(1250)	(25)	(11)	(8290)	(423)	(82)	(9540)	(448)	(93)
Multiple herbicide	0c	0c	0c	0b	0b	0b	0c	0c	0c
	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Mann-Whitney nonparametric test. Observed significance level was adjusted with the Bonferroni procedure (P≤0.008).

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Table 3. Means (and standard errors) of fruit production in 1996 by *V. angustifolium*, *V. myrtilloides* and both species combined following conifer release treatments

	Vaccinium angustifolium			*Vaccinium myrtilloides*			Total berry yield (both species combined)		
Treatment	Number of berries (/ha)	Fresh weight (g/ha)	Dry weight (g/ha)	Number of berries (/ha)	Fresh weight (g/ha)	Dry weight (g/ha)	Number of berries (/ha)	Fresh weight (g/ha)	Dry weight (g/ha)
Control	219931a (56719)	48771a (12985)	6361a (1812)	315030a (80325)	51579a (14014)	6786ab (1899)	534961a (137044)	100350a (26999)	13148a (3711)
Brushsaw	373056a (84860)	56025a (12907)	7875a (1736)	433125a (144434)	55106a (17046)	12106a (3886)	806181a (229294)	111132a (29953)	19980a (5622)
Single herbicide	2778b (1584)	261b (141)	22b (15)	221181a (76961)	30347a (10584)	2582b (1089)	223959b (78545)	30608b (10725)	2604b (1104)
Multiple herbicide	0c (0)	0c (0)	0c (0)	0b (0)	0b (0)	0c (0)	0c (0)	0c (0)	0c (0)

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Mann-Whitney nonparametric test. Observed significance level was adjusted with the Bonferroni procedure; ($P \leq 0.008$).

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Table 4. Means (and standard errors) of leaf characteristics measured from *V. angustifolium and V. myrtilloides* plants following conifer release treatments

	Vaccinium angustifolium			*Vaccinium myrtilloides*		
Treatment	leaf area (cm^2)	dry weight (g/leaf)	specific leaf area (cm^2/g)	leaf area (cm^2)	dry weight (g/leaf)	specific leaf area (cm^2/g)
Control	2.06a (0.13)	0.039a (0.003)	57.28a (3.75)	2.53a (0.15)	0.039a (0.003)	71.68a (5.72)
Brushsaw	1.59a (0.08)	0.027a (0.002)	59.95a (1.78)	1.85b (0.08)	0.028b (0.002)	67.76ab (2.14)
Single herbicide	0.69b (0.06)	0.014a (0.002)	57.27a (2.96)	1.19c (0.09)	0.020c (0.002)	65.96b (2.77)
Multiple herbicide	0.21c (0.03)	0.009a (0.002)	30.21b (4.06)	0.45d (0.06)	0.016d (0.005)	48.18c (4.24)

Note: Unlike letters in a column indicate values significantly different at the 0.05 level determined by the Mann-Whitney nonparametric test. Observed significance level was adjusted with the Bonferroni procedure ($P \leq 0.008$).

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Table 5. Means (and standard errors) of percent cover, aerial shoot and rhizome characteristics of *V. angustifolium* bushes in 1996 following conifer release treatments

Treatment	Cover (%)	Height (cm)	Number of bushes/m^2				Dry weight (g)			
			Unaffected	Partially defoliated	Severely defoliated	Dead	Live stem	Dead stem	Rhizome	Leaf
Control	13.97a (3.38)	21.27a (0.66)	2.31a (0.76)	0.13a (0.05)	0.007a (0.007)	0.06a (0.04)	11.27a (0.98)	0.23a (0.09)	9.33a (0.98)	4.35a (0.50)
Brushsaw	16.61a (3.41)	16.82b (0.56)	2.34a (0.50)	0.03a (0.02)	0a (0)	0.04a (0.02)	15.08a (1.33)	0a (0)	12.58a (1.05)	5.41a (0.37)
Single herbicide	0.57b (0.19)	17.35c (0.36)	0.15b (0.05)	0.06b (0.04)	0.09b (0.07)	0.33b (0.13)	5.43b (0.38)	1.49b (0.24)	8.65a (0.49)	1.47b (0.14)
Multiple herbicide	0.18b (0.06)	16.26d (0.59)	0c (0)	0.04c (0.02)	0.67c (0.15)	1.31c (0.29)	2.77c (0.09)	3.45c (0.15)	8.93a (0.29)	0.43c (0.02)

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Mann-Whitney nonparametric test. Observed significance level was adjusted with the Bonferroni procedure; ($P \leq 0.008$).

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Table 6. Means (and standard errors) of percent cover, aerial shoot and rhizome chracteristics of *V. myrtilloides* bushes in 1996 following conifer release treatments

Treatment	Cover (%)	Height (cm)	Number of bushes/m^2				Dry weight (g)			
			Unaffected	Partially defoliated	Severely defoliated	Dead	Live stem	Dead stem	Rhizome	Leaf
Control	18.14a (3.35)	23.97a (1.02)	1.99a (0.40)	0.04a (0.03a)	0.02a (0.02)	0.07a (0.03)	12.85a (0.58)	0.12a (0.03)	12.88a (1.11)	3.25a (0.27)
Brushsaw	16.71a (3.69)	22.78a (1.03)	1.81a (0.41)	0a (0)	0a (0)	0.05a (0.03)	10.57a (0.65)	0b (0)	13.68a (1.04)	4.30b (0.25)
Single herbicide	5.94b (2.14)	20.10a (0.89)	0.69b (0.15)	0.63b (0.27)	0.17b (0.06)	0.24a (0.08)	5.34b (0. 40)	1.76c (0.28)	10.69a (0.58)	1.73c (0.18)
Multiple herbicide	0.36b (0.08)	17.80b (0.95)	0.04b (0.01)	0.07b (0.03)	0.17b (0.06)	1.33b (0.28)	5.42b (0.54)	4.08d (0.35)	10.32a (0.54)	0.98d (0.09)

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Mann-Whitney nonparametric test. Observed significance level was adjusted with the Bonferroni procedure; ($P \leq 0.008$).

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Table 7. Summary of discriminant analysis of eleven vegetative characteristics of *V. angustifolium and V. myrtilloides*

	Function	Eigenvalue	% Variance	Canonical correlation	df	Significance
V.angustifolium	1	18.2095	94.3	0.9736	33	0.0000
	2	0.5944	3.1	0.6106	20	0.0000
	3	0.506	2.6	0.5796	9	0.0000
V.myrtilloides	1	12.9374	92.1	0.9635	33	0.0000
	2	0.6776	4.8	0.6355	20	0.0000
	3	0.4350	3.1	0.5506	9	0.0000

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Table 8. Pooled within-group correlations among discriminating variables and canonical discriminant functions of eleven vegetative characteristics of *V. angustifolium* and *V. myrtilloides*

	V.angustifolium			*V.myrtilloides*		
Vegetative parameters	Function 1	Function 2	Function 3	Function 1	Function 2	Function 3
Height	0.06533	0.39301	0.47202	0.09749	0.05382	0.14541
Number of unaffected bushes	0.20924	0.24709*	0.12147	0.11607	0.15804	0.24461
Number of partially defoliated bushes	0.00556	0.09934	0.29740	0.11546	0.48312*	0.06273
Number of severely defoliated bushes	0.20148	0.40290*	0.31462	0.14755	0.01605	0.04385
Number of dead bushes	0.18698	0.30032*	0.20717	0.16133	0.31751*	0.02357
Dry weight of live stems/bush	0.28261*	0.17576	0.10386	0.23963	0.27626	0.42795
Dry weight of dead stems/bush	0.44242	0.38056	0.05644	0.57331*	0.23561	0.13419
Dry weight of leaves/bush	0.39448*	0.13077	0.13438	0.32370*	0.10321	0.17946
Dry weight of rhizomes/bush	0.02039	0.31550*	0.20157	0.05290	0.03194	0.08508
Leaf area	0.38702*	0.31925	0.13393	0.34567*	0.41039	0.51748
Individual leaf weight	0.23290	0.08622	0.58634	0.16180	0.00070	0.44107

* denotes largest absolute correlation between each variable and any discriminant function.

Table 9. Means (and standard errors) of percent cover of vegetation overtopping *Vaccinium* spp. and percent PPFD in treatment plots

Treatment	Cover (%) of vegetation overtopping *Vaccinium* spp.	Percent PPFD
Control	70.9a (4.51)	11.43a (2.21)
Brushsaw	42.0b (3.86)	45.45b (4.7)
Single herbicide	53.19b (4.62)	56.34bc (4.98)
Multiple herbicide	20.06c (2.44)	71.86c (5.48)

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Mann-Whitney nonparametric test. Observed significance level was adjusted with the Bonferroni procedure; ($P \leq 0.008$). PPFD refers to the percent photon flux density transmitted above *Vaccinium* spp. in the treatment plots.

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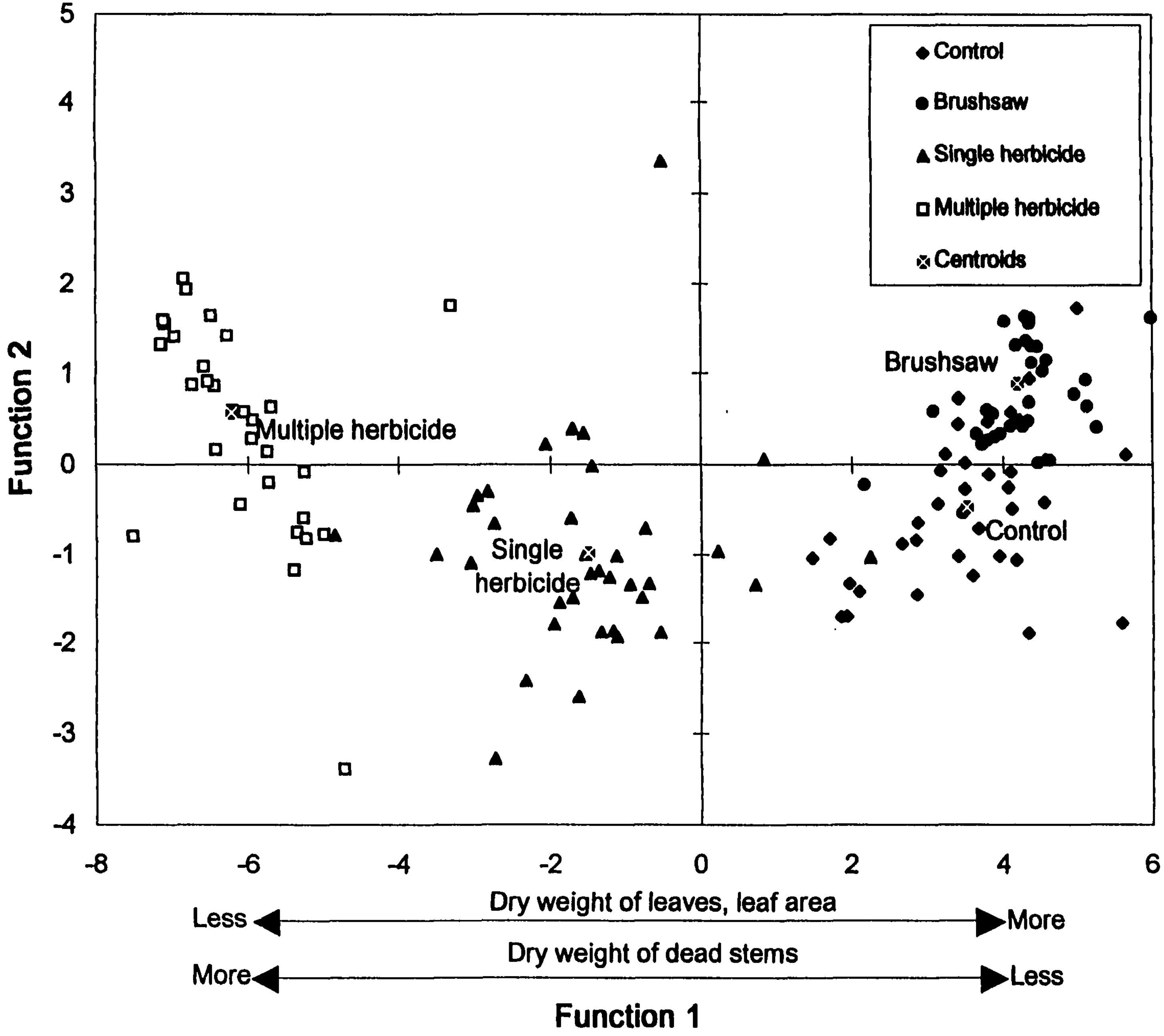

Fig. 1. Ordination diagram of Discriminant Analysis using 11 vegetative characteristics of *V. angustifolium*

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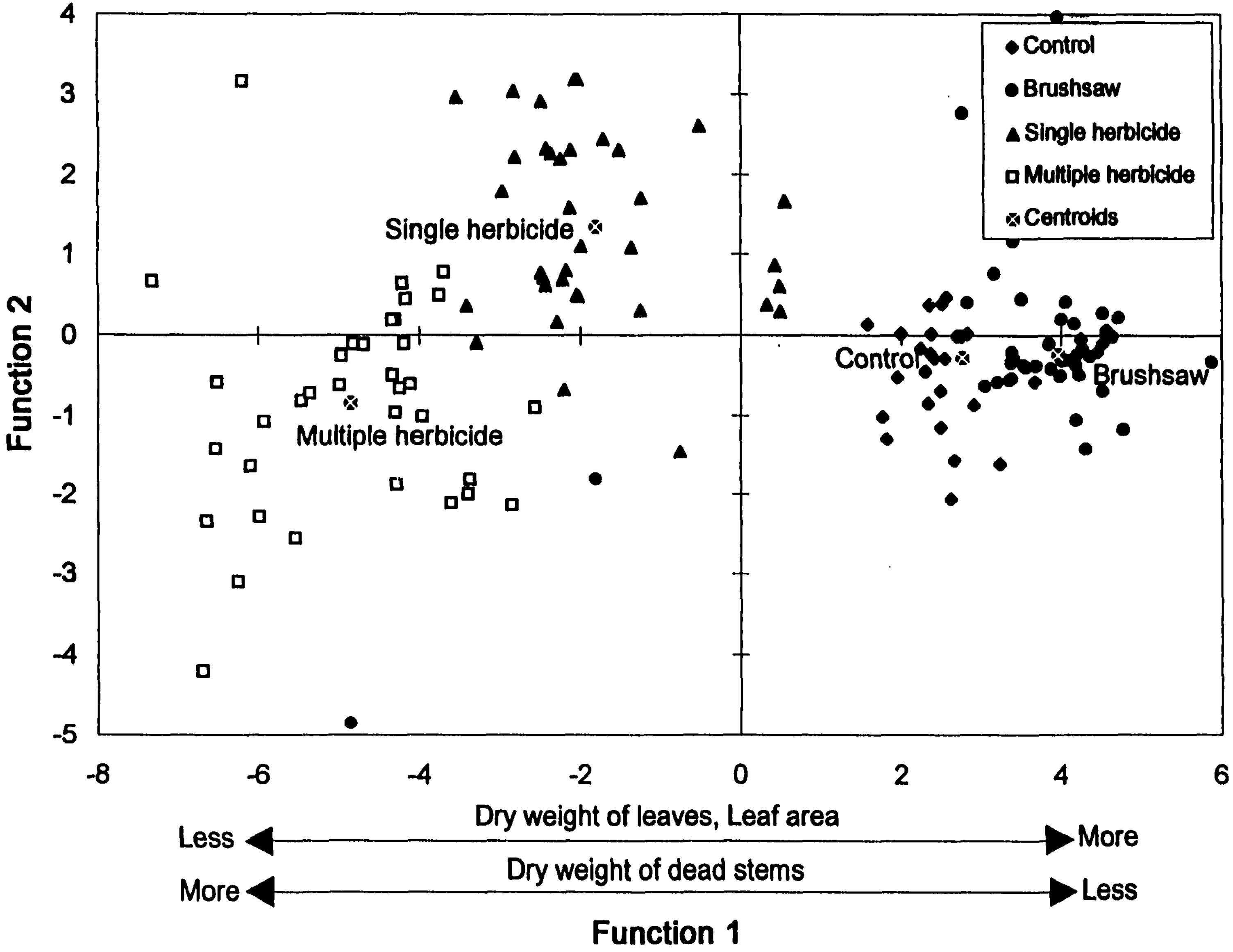

Fig. 2. Ordination diagram of Discriminant Analysis using 11 vegetative characteristics of *V. myrtilloides*

The phenology of *Vaccinium* spp. in northwestern Ontario: implications for the timing of forest herbicide treatments

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Abstract: Concerns about adverse ecological impact of herbicides on the environment and human health have encouraged silviculturalists to develop integrated vegetation management (IVM) practices that minimize damage to noncrop species that are of wildlife and/or economic importance. Consistent with the goal of IVM is the need for a better understanding of the phenology of these species, since susceptibility of plants to foliar herbicides has been shown to be related to the timing of lifecycle events. Reduced damage to *Vaccinium* spp. may be possible if treatments were timed to take advantage of phenological periods when blueberry plants are less susceptible to uptake and translocation of the herbicide.

This study reports on the phenology of 180 vegetative and 180 reproductive shoots of lowbush blueberry (*Vaccinium angustifolium*) and velvet leaf blueberry (*V. myrtilloides*) in a young black spruce (*Picea mariana* [Mill.] BSP.) plantation near Thunder Bay, northwestern Ontario. Leaves of both species emerged in mid-May and remained uniformly green until mid-August. By late August, the majority of tagged shoots had turned red and were beginning to deteriorate. Approximately 30 % of tagged shoots lost their leaves by September 25 in both *V. angustifolium* and *V. myrtilloides*. Flowering in *V. angustifolium* began in late May and flowers remained on reproductive shoots for approximately three weeks. Green fruits were first observed on 13 % of tagged *V.*

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angustifolium shoots on June 26. The number of fruiting stems declined progressively after June 26 with the complete disappearance of fruit from tagged shoots by September 11. Fruit set occurred in 30 % of tagged *V. myrtilloides* shoots with complete disappearance of berries by September 11 as well.

Patterns of leaf development in *V. angustifolium* and *V. myrtilloides* suggest that *Vaccinium* spp. species may be less susceptible to foliar applied herbicides if applications are made during or following the period of leaf senescence (i.e., between late August and late September).

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Introduction

During the past 30 years many young forest plantations in Canada have been treated with foliar herbicides to control competing vegetation and release conifers (Kuhnke and Brace 1986; Maass 1989; Wagner 1993). The most popular herbicide prescribed for the silvicultural suppression of competing vegetation in Canadian forests is glyphosate (Vision® commercial formulation containing glyphosate, 356 g/L present as isopropylamine salt) (Cambell 1990). In 1996, approximately 72,000 ha of new plantations in Ontario were treated with Vision® herbicide for vegetation management purposes (Roy Maki, Forestry Specialist, Monsanto Canada Inc., personal communication). As a broad-spectrum herbicide, this chemical is effective in supressing many common competing species in young conifer plantations, such as trembling aspen (*Populus tremuloides* Michx.), green alder (*Alnus crispa* [Ait.] Pursh), pin cherry (*Prunus pensylvanica* L.f.), beaked hazel (*Corylus cornuta* Marsh.), willow (*Salix* spp), Canada blue-joint grass (*Calamagrostis canadensis* Michx. Beauv.) and red raspberry (*Rubus idaeus* L. var. *strigosus* Michx. Maxim.) (Sutton 1984; Lund-Høie and Grønvold 1987; Freedman et al. 1993; Bell et al. 1996, submitted).

Although often not the intended target of vegetation management practices, several fruit producing shrub species, such as blueberry (*Vaccinium angustifolium* Ait., *V. myrtilloides* Michx.) that are important to wildife and humans are adversely affected by Vision® (Balfour 1989; Freedman et al. 1993; Moola et al. 1997, submitted). Significant foliar damage, reduced cover and lower fruit yields of the wild lowbush blueberry (*V. angustifolium*) have been observed for up to four years following operational Vision® treatment to regenerating clearcuts (Freedman et al. 1994; Moola et al. 1997, submitted).

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Fruit production by the velvet leaf blueberry (*V. myrtilloides*) is less sensitive to Vision®, although reduced cover and significant damage to aerial stems have also been observed (Freedman et al. 1993; Moola et al. 1997, submitted). Since foliar applications of the herbicide are typically made in mid- to late-summer when blueberries are ripe, wildlife and berry pickers may be accidentally exposed to residues of the herbicide through consumption of contaminated fruit. Residues of Vision® remain above permissible levels (0.01 ppm) established by the Health and Welfare Canada, Food and Drug Regulation (1980) for up to 60 days after application (Roy *et al.* 1989). At the recommended rates and under normal use, vegetation management with herbicides such as Vision® pose minimal toxicological hazards for terrestrial vertebrates and pose no risk of bioaccumulation in the environment (Morrison and Meslow 1983; Newton et al. 1984). Nevertheless, public concerns about the adverse impact of forest herbicides on the environment and human health continues to generate controversy (Johnson et al. 1995). Due to social pressure, the silvicultural use of forest herbicides has been restricted in five Canadian provinces and in several regions of the USDA Forest Service, and they are currently banned in Sweden (Wagner 1993).

Extensive injury or the death of vegetation treated with foliar-applied herbicides, such as Vision®, depends upon the rapid foliar absorption and subsequent translocation of the herbicide to perennating tissues (Neal et al. 1985). For this reason, selective control of competing vegetation with minimal damage to *Vaccinium* spp. may be possible if spraying occurs at a time when leaves are not present on blueberry bushes. The effect that time of herbicide application has on the severity of injury to blueberry bushes in regenerating forests is

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unknown. However, research in commercial blueberry (*V. angustifolium*) fields has shown that later applications of the foliar herbicides, 2,4-D and 2,4,5-T during leaf senescence results in significantly reduced damage to aerial shoots (Trevett 1961). The reduced damage associated with delayed spraying has been attributed to the limited absorption of foliar herbicides by blueberry stems during this period (Trevett 1961).

The objective of the present study was to document the phenological events of the lowbush (*V. angustifolium*) and velvet leaf blueberry (*V. myrtilloides*) in a young black spruce (*P. mariana* [Mill.] BSP.) plantation in northwestern Ontario. Phenological diagrams detailing leaf emergence, senesence and abcission were used to determine the period when blueberry plants may be less susceptible to foliar applied herbicides such as Vision®. Knowledge of the duration of fruiting may also assist forest managers to spray within the "window" of time when berries are not present on blueberry bushes.

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Study area

Phenology of *V. angustifolium* and *V. myrtilloides* was examined in three adjacent strip cuts, 50 x 100 m in size, located beside highway 527, approximately 60 km northeast of Thunder Bay, Ontario. Prior to harvesting, the forest was a black spruce - feather moss type, approximately 80 years of age. Soils were shallow and moist over scattered rocks and frequent stones. Topography was flat to gently rolling.

Mature black spruce was full-tree harvested in February 1984 and the area mechanically site prepared with a Bracke-skidder in the fall of 1987. The strip cuts were planted with black spruce paper pot seedlings (2470 seedlings/ha), spaced 0.8 x 1.8 m apart in June 1988. At the time the study was initiated (May 1995) the sites were open (91.0 % PPFD, 30 cm above the ground) with little overstory development; black spruce > 2 m tall were present at < 10 % cover. The dominant vegetation was low ericaceous shrubs (< 2m) such as *Ledum groenlandicum* Oeder (9.9 % cover), *V. angustifolium* (27.2 % cover), and *V. myrtilloides* (8.8 % cover). Ground vegetation consisted mostly of *Sphagnum magellanicum* Brid., *S. fuscum* (Schimp.) Klinggr., *G. hispidula* (L.) Muhl., *Arctostaphylos uva-ursi* (L.) Spreng. and *Carex* spp. Patches of bare ground and exposed bedrock were common and the microptopography consisted of low to intermediate hummocks with hollows.

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Materials and methods

Vegetative and reproductive phenology

Before the onset of leaf development in May 1995, three reproductive and three vegetative shoots were tagged with coloured plastic bands on twenty randomly chosen *V. angustifolium* and *V. myrtilloides* bushes in three adjacent strip cuts. The three areas were treated as replicates. A total of 180 vegetative and 180 reproductive shoots were tagged in each blueberry species (20 plants x 3 shoots x 3 replicates). The stage of development for both vegetative and reproductive shoots was recorded weekly from May 15th, 1995 to October 2nd, 1995.

Daily rainfall (mm/24 hours) and air temperature (°C taken at 13:00 hr.) was obtained from the Ontario Ministry of Natural Resources. Weather data was measured at the Hick's Lake Weather station located approximately 8 km from the study sites.

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Results

Figures 1, 2, 3 and 4 show the vegetative, flowering and fruiting phenologies of *V. angustifolium* and *V. myrtilloides*, respectively. The lines indicate periods during which leaves, flowers or fruits were found on the bushes in the study site. Both species of blueberry displayed similar fruiting phenologies and retained their foliage until approximately the same date. Vegetative buds which were formed in 1994 were swollen by mid May of 1995; emerging leaves were first observed in both blueberry species on May 15. Leaves had fully unfolded by late May and they remained uniformly green until mid August. By late August, the leaves on 82 % of tagged vegetative shoots in *V. angustifolium* had turned red and were beginning to deteriorate. A lower percentage of tagged vegetative shoots of *V. myrtilloides* had changed colour by the end of August (69 %). Approximately 40 % of *V. angustifolium* and 32 % of *V. myrtilloides* shoots had lost their leaves by October 2 (Figs. 1 and 2).

In *V. angustifolium* reproductive buds were strongly swollen by May 22 and flowering began soon thereafter. Flower set was relatively high as 82 % of the tagged reproductive shoots had produced flowers by June 5. Flowering continued until the middle of June.

Green fruit was first observed on 13 % of tagged *V. angustifolium* reproductive shoots on June 26. Peak fruiting occurred on July 3 at which time 14 % of reproductive shoots had developed berries. The number of fruiting stems declined progressively after July 3, with the complete disappearance of fruit from tagged shoots by the first week of September (Fig. 3).

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Reproductive bud burst and flowering occurred approximately a week later in *V. myrtilloides* than in *V. angustifolium*. Flowers of V. myrtilloides were first observed on June 5, and by June 19 were present on 49 % of reproductive shoots. Flowers had completely faded by the end of June.

Fruit first appeared on June 19 and remained on tagged shoots until September 11 (Fig. 4). At peak fruiting, 30 % of tagged *V. myrtilloides* shoots had developed berries.

The death of tagged shoots was relatively high in both blueberry species. By October 2, 24 % of *V. angustifolium* and 31 % of *V. myrtilloides* vegetative shoots had died. Extensive mortality of tagged vegetative shoots ($\geq$ 11 %) was first observed on August 22 and July 24 in *V. angustifolium* and *V. myrtilloides*, respectively (Figs. 1 and 2). The mortality rate of reproductive shoots was not recorded.

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Discussion

Although *Vaccinium* spp. are common in the understory of young conifer plantations (Hamilton et al. 1991; Freedman et al. 1993; Usui et al. 1994; Moola et al. 1997, submitted), their limited root system and short stature make them poor competitors with planted or naturally occurring conifer seedlings for moisture, nutrients, or light. A possible exception may be in conifer plantations on northern Vancouver Island that are dominated by *V. ovalifolium* Smith (C. Prescott, personal communication). Furthermore, unlike other ericaceous understory plants of temperate forests such as *Kalmia angustifolia* var. *angustifolia* L. (Mallik 1993, 1994), *Calluna vulgaris*, *Erica cinerea* (Gimingham, 1972; Mallik and Gimingham 1983, 1985), *Gaultheria shallon* Pursh. (Bunnell 1990), or *Ledum groenlandicum* (Inderjit and Mallik 1996), evidence of allelopathic growth inhibition of conifer seedlings has not been established in *Vaccinium* spp. (A.U. Mallik, personal communication). In conifer plantations V*accinium* spp. are not considered undesirable species that require suppression (Haeussler et al. 1990). Conversely, their presence following clearcutting may be desirable. No beneficial effects of *Vaccinium* spp. on planted or naturally occurring conifer seedlings have been reported in the literature. However, *Vaccinium* spp. may contribute to soil stability due to their dense network of roots and rhizomes (Vander Kloet and Hall 1981; Haeussler et al. 1990), provide wildlife browse (Martin et al. 1951; Peters 1958; Rogers 1976; Arimond 1979) and have potential commercial value as a non-timber forest product (Minore et al. 1979; Freed 1995).

Given the importance of *V. angustifolium* and *V. myrtilloides* to wildlife and berry pickers, it is important that foliar herbicide treatment be timed to take advantage of phenological periods when blueberry plants are less susceptible to uptake and

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translocation of the herbicide. The results of this study suggest that herbicide application before active growth of new shoots (i.e. early May) or during the period of leaf senescence and abscission (i.e. September to October) may reduce the susceptibility of *Vaccinium* spp. to foliar herbicides such as Vision®. Foliage of both *V. angustifolium* and *V. myrtilloides* significantly changed colour late in August with about 30 % abscission by the last week of September (Figs. 1 and 2). With most of the foliage lost by early autumn, application of foliar herbicides at this time may have negligible effects upon blueberry growth and fruit production, since without leaves, little herbicide can be absorbed and translocated to perennating tissues (Trevett 1961). Reduced herbicide damage in commercial blueberry fields has been reported with autumn applications of the foliar herbicides 2,4-D and 2,4,5-T (Trevett 1961).

The interaction between seasonal timing of herbicide treatments and the effective control of competing vegetation in conifer plantations is poorly documented and incomplete phenological data is available for some competing species in northwestern Ontario (Bell 1992). Nevertheless, there is evidence that while delayed spraying may protect *Vaccinium* spp., it will likely reduce the effective control of undesirable species whose foliage, like blueberry, deteriorates in late summer. The Vision® label suggests that maximum control of mixed hardwoods, raspberry (*Rubus* spp.), alder (*Alnus* spp.) and perennial grasses is achieved with treatment to green or slightly coloured foliage, prior to the onset of leaf abscission. In northwestern Ontario, this is usually during the period from August to early-September under normal weather conditions. Similar results have been found by Bell et al. (1992) for the optimal suppression of red raspberry (*R. idaeus*) in

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northwestern Ontario and by LePage and Pollack (1988) for the control of thimbleberry (*R. parviflorus*) in British Columbia. These findings suggest that the optimal suppression of competing vegetation and the preservation of *Vaccinium* spp., may be conflicting objectives if pursued on the same site, since blueberry is susceptible to injury during spray periods that maximize herbicide efficacy. A possible exception may be on sites dominated by *C. canadensis*, since this species remains susceptible to Vision® until significantly later in the season (Bell at al. 1996, submitted).

Roy et al. (1989) reported that although residues of Vision® progressively declined with time in treated plantations, traces of the chemical on ripe blueberries remained above permissible levels for up to 60 days following spraying. Our results indicate that fruit remains on lowbush and velvet leaf blueberry bushes from mid-June until the end of August (Figs. 3 and 4). Delaying herbicide treatment until after berries have dropped by early September may minimize the ingestion of contaminated fruits by humans and wildlife. Considering the significant public concern over the perceived toxicological effects of forest herbicides (Johnson et al. 1995), timing the treatments to avoid the period when fruits are available for consumption may be more socially acceptable.

The high percentage of dead shoots in *V. angustifolium* and *V. myrtilloides* by mid-August may have been a result of the unfavourable weather conditions which characterized much of the summer growing season in 1995 (Fig. 5). In particular, abnormally high afternoon temperatures and a severe deficit in precipitation may have induced drought stress in developing blueberry shoots. The influence of meteorological

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conditions on the growth and fruit production of wild *Vaccinium* spp. is well known (Minore 1984; Hoefs and Shay 1981). Poor water efficiency has been reported for unshaded *V. angustifolium* bushes colonizing clearcuts in eastern Manitoba (Hoefs and Shay 1981). The susceptibility of *Vaccinium* spp. to drought stress has been attributed to the absence of adaptive traits for drought tolerance such as a high leaf diffusive resistance (Erb et al. 1988). Northwestern Ontario has a sunny, dry, continental climate and moisture shortage may be a limiting factor for the growth of *Vaccinium* spp. on some logged sites characterized by a sparse canopy of overtopping vegetation (Moola and Mallik, unpublished data).

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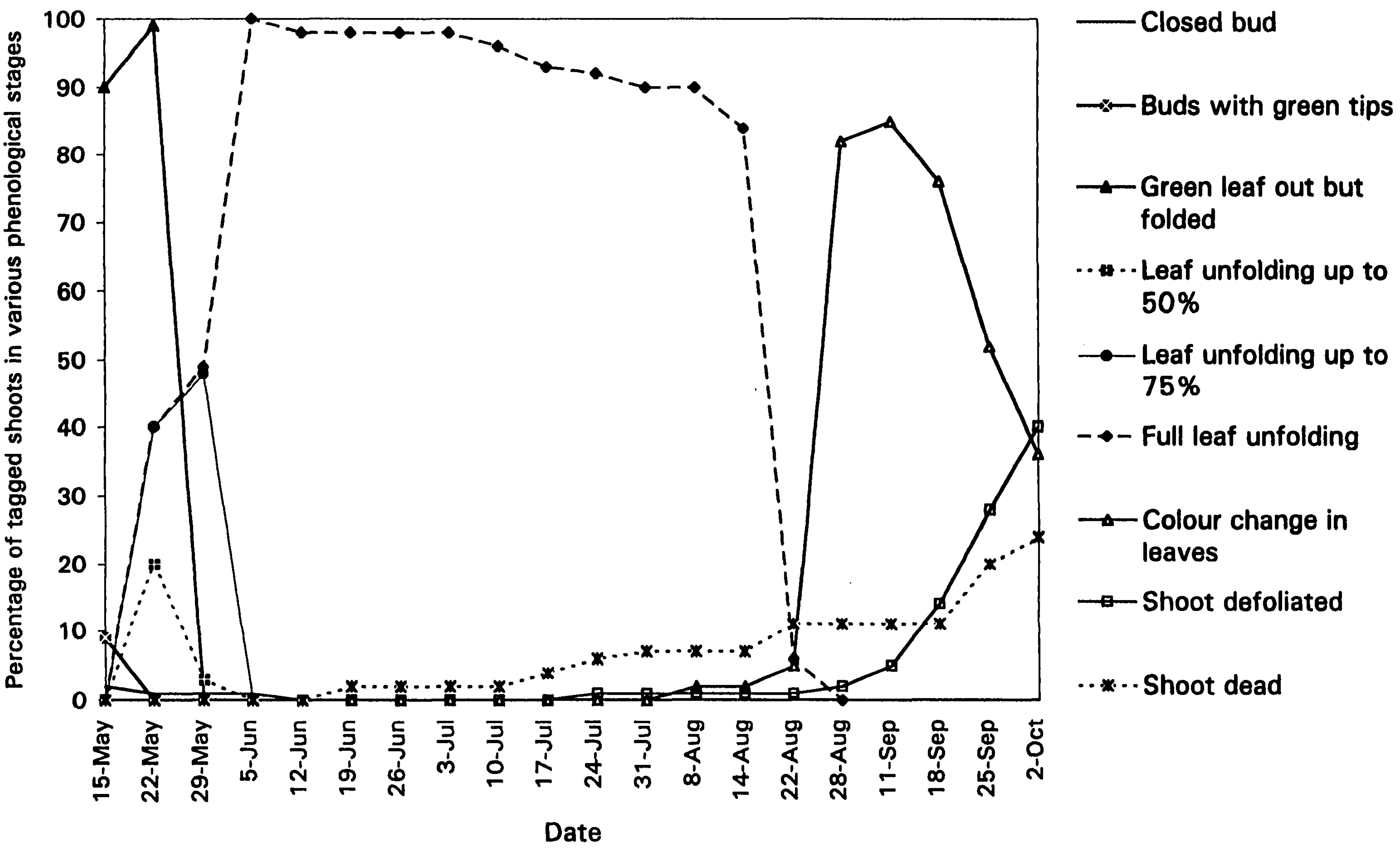

Fig. 1. Phenological development of vegetative shoots of *V. angustifolium* during the 1995 growing season

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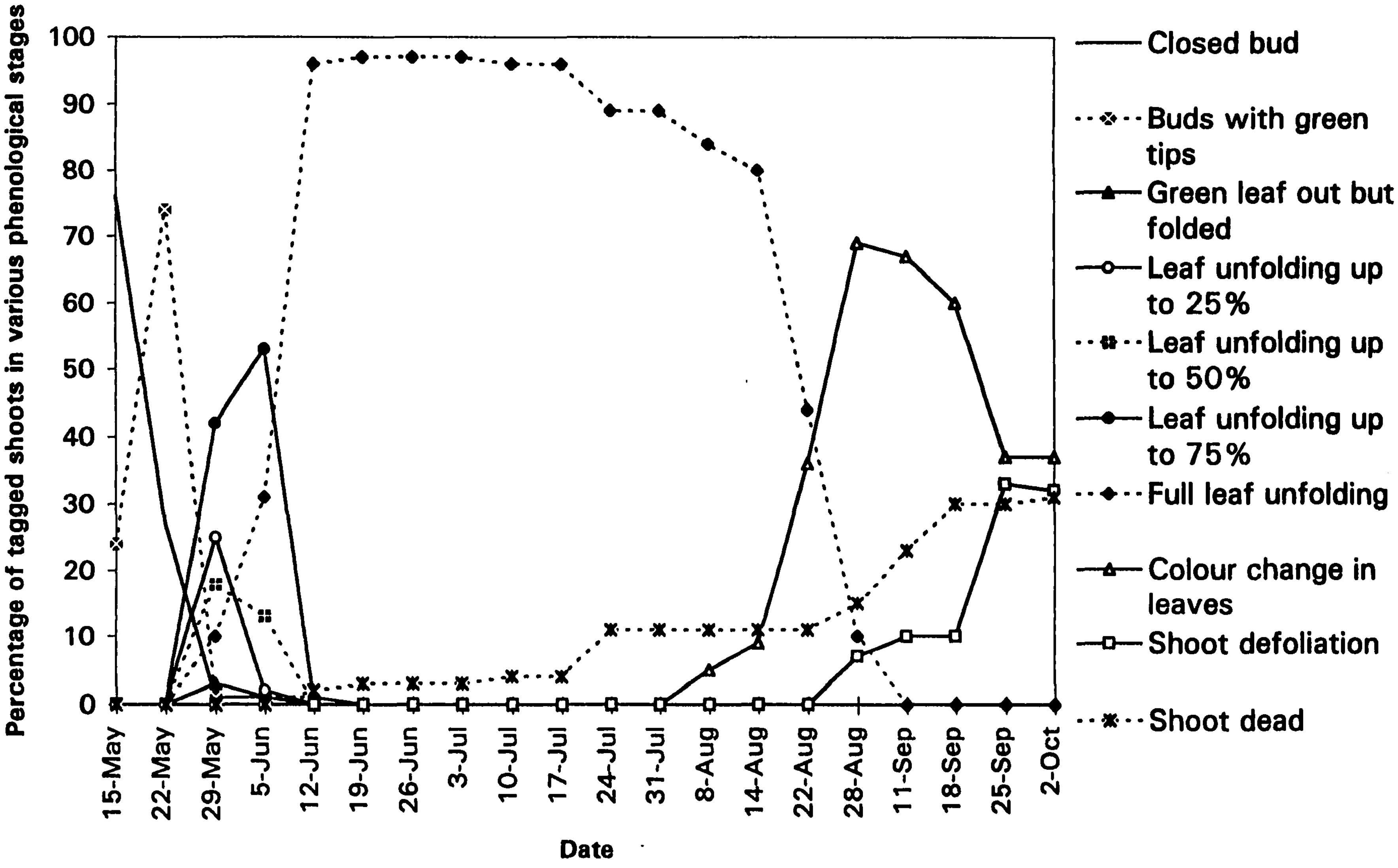

Fig. 2. Phenological development of vegetative shoots of *V. myrtilloides* during the 1995 growing season

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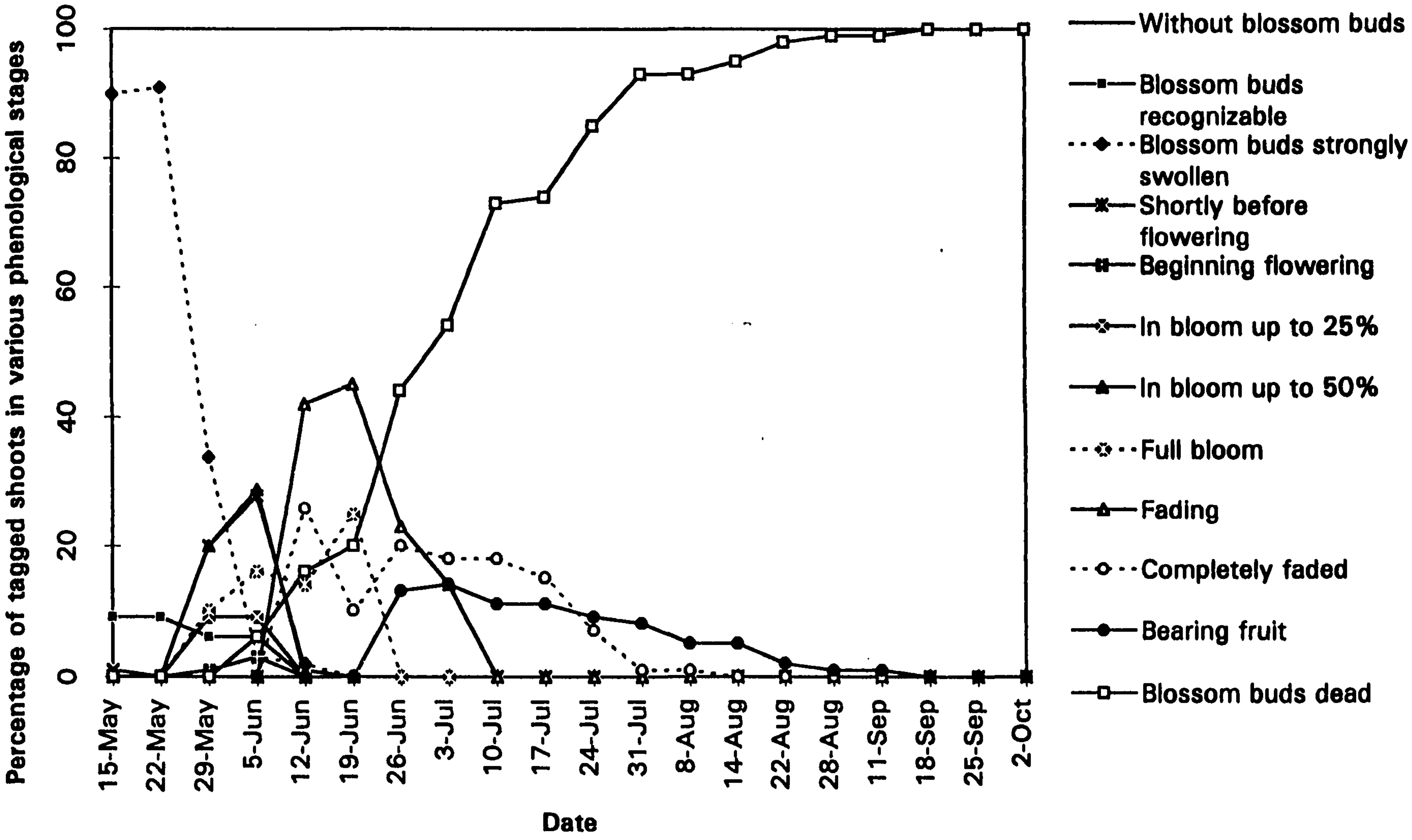

Fig. 3. Phenological development of generative shoots of *V. angustifolium* during the 1995 growing season

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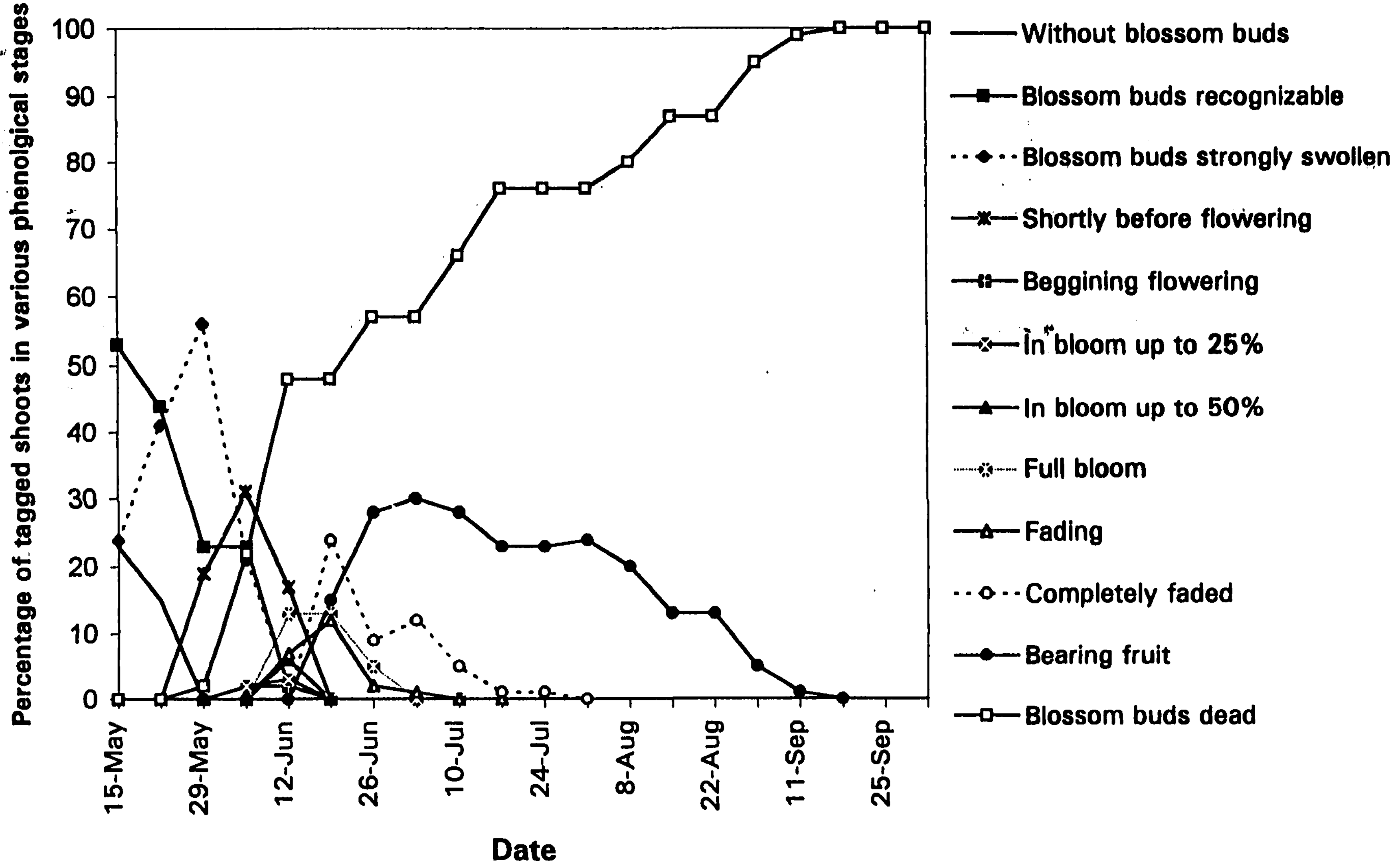

Fig. 4. Phenological development of generative shoots of *V. myrtilloides* during the 1995 growing season

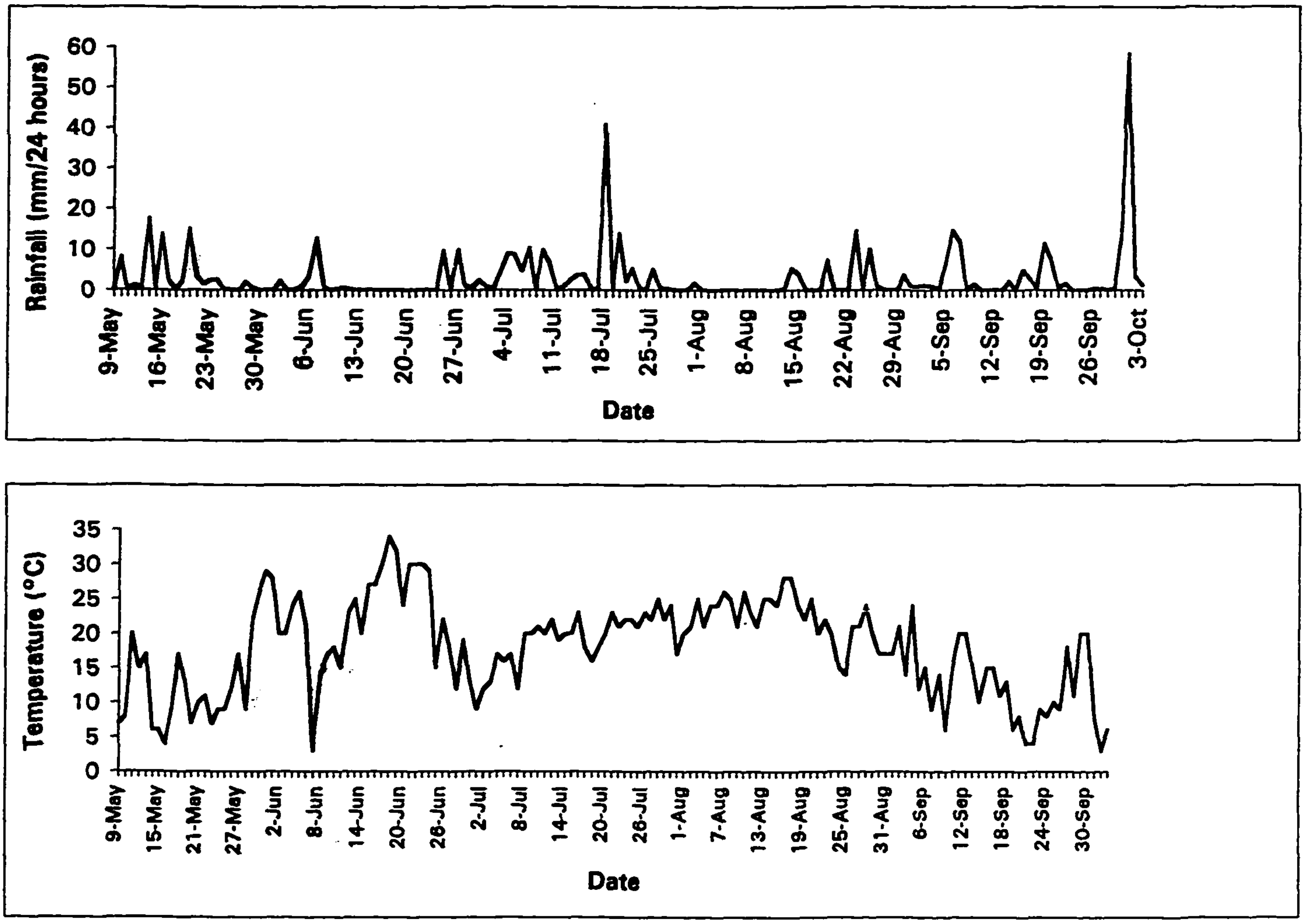

Fig. 5. Daily precipitation and temperature during 1995 growing season

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Morphological plasticity and regeneration strategies of velvet leaf blueberry (*Vaccinium myrtilloides*) following canopy disturbance in the management of boreal mixedwood forests

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ABSTRACT: The effects of canopy disturbance on the abundance, growth, morphological plasticity, biomass allocation and fruit production of velvet leaf blueberry (*Vaccinium myrtilloides*) were examined in 1996 in a second-growth boreal mixedwood forest near Nipigon, northwestern Ontario that had been logged by either shelterwood cutting or clearcutting in 1993.

We found that *V. myrtilloides* was able to persist in both open and closed canopy boreal mixedwood forests managed for commercial timber extraction. Persistence under heavy shade conditions was accompanied by significant morphological and biomass allocation plasticity. Specific leaf area, leaf area, individual leaf weight, and the proportion of total biomass in stems and foliage changed along an understory light gradient from 0 % to 67 % PPFD (percent photon flux density). The degree of above-ground morphological plasticity may explain blueberry's ability to survive under low light conditions.

Reproductive performance of *V. myrtilloides* was greatest under the partial shade conditions associated with shelterwood cutting. Blueberry bushes growing in clearcuts overgrown with three-year old aspen (*Populous tremuloides* Michx.) saplings remained mostly vegetative whereas the number, fresh weight and dry weight of berries in shelterwood cuts was 94 % greater than that produced after clearcutting. We attributed

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the lower fruit yields in the clearcuts to heavy shading from regenerating hardwoods, and mechanical damage to above-ground biomass.

The paucity of seedling regeneration as well as extensive mechanical damage to above-ground stems by logging equipment delayed vegetative regeneration of *V. myrtilloides* in large canopy openings of the clearcut blocks. Unlike other more aggressive ericaceous species (e.g. *Kalmia angustifolia*, *Gaultheria shallon*), *V. myrtilloides* was unable to resist invasion from faster growing hardwood species (e.g. *P. tremuloides*) and was rapidly overtopped. *V. myrtilloides* plants in the uncut control blocks received 3.9 % of full sunlight, whereas those growing in the partial cut and clearcut blocks received an average of 25.3 % and 32.5 % PPFD, respectively. Cover of vegetation over-topping blueberry plants was highest in the uncut forest (90.3 %), but was not significantly different between the partial cut (45.5 %) and clearcut (50.1 %) treatment blocks.

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Introduction

Many ericaceous understory plants of temperate forests such as *Kalmia angustifolia* var. *angustifolia* L. (Mallik 1994), *Gaultheria shallon* Pursh. (Bunnell 1990), and *Ledum groenlandicum* Oeder (Inderjit and Mallik 1996) exhibit vigorous growth and spread following disturbances such as forest fire and logging (Mallik 1995). The aggressive and opportunistic response of these species to forest disturbance has been explained in terms of rapid demographic (A.U. Mallik, unpublished data; Huffman et al. 1994), morphological (Messier and Kimmins 1991; Mallik 1992; Messier 1992) and physiological acclimation (Marshall and Waring 1984) to increased light availability following the removal of forest canopy. The most aggressive ericaceous species in temperate forests (e.g. *K. angustifolia*, *G. shallon*) respond to overstory removal with a survival strategy linked by life-history traits (Grime 1979) that promote rapid site colonization and resistance to invasion by other species (Messier and Kimmins 1991; Mallik 1995). These life history traits include: continuous recruitment of new shoots from stem bases (Mallik 1992); underground rhizomes (Bunnell 1990, Mallik 1992) and/or layered stems (Calmes and Zasada 1982; Moola and Mallik, unpublished data); high fruit and seed production (Bunnell 1990; Mallik 1994); rapid vegetative expansion (Bunnell 1990); and increased allocation of biomass to organs that maximize the capture of above- and below-ground resources (Messier and Kimmins 1991). The possession of these life-history traits by certain ericaceous plants delays and in many areas prevents conifer regeneration following canopy removal by clearcut logging (Weetman et al. 1990; Messier and Kimmins 1991; Mallik 1995).

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In contrast, some ericaceous species such as the lowbush (*Vaccinium angustifolium* Ait.), velvet leaf, (*V. myrtilloides* Michx.) and Alaskan blueberry (*V. alaskaense* How.), bilberry (*V. myrtillus* L.) and early huckleberry (*V. ovalifolium* Smith) respond less aggressively to the sudden increase in light availability associated with overstory removal, even when present in the understory prior to disturbance (Hall 1955; La Roi 1967; Stoyanov 1986; Alaback and Tappeiner 1991). After canopy removal due to clearcutting, minimal recovery by certain *Vaccinium* species has been attributed to poor seedling regeneration (Vander Kloet and Hill 1994); sensitivity to sudden microclimatic changes (Hoefs and Shay 1981; Atlegrim and Sjöberg 1996); mechanical damage to aerial stems (Zager 1980; Atlegrim and Sjöberg 1996); increased susceptibility to damaging frosts (Hoefs and Shay 1981) and intense competition from fast growing species (Stoyanov 1986; Atlegrim and Sjöberg 1996). Alternatively, the poor ability of certain *Vaccinium* spp. to form a dense understory following canopy removal may reflect a more conservative life history strategy than that of more aggressive ericaceous plants such *K. angustifolia, L. groenlandicum* and *G. shallon*. For example, the slow establishment of *V. ovalifolium* in canopy openings following windthrow has been attributed to trade-offs in biomass allocation that favour storage of photosynthate in rhizomes and roots at the expense of aboveground stems and foliage (Alaback and Tappeiner 1991). In other forest plants such as tanoak (*Lithocarpus densiflorus* [Hook and Arn] Rhed) the investment of starch and other nutrients in below-ground biomass may contribute to long-term survival despite costs to reproductive and vegetative performance (Tappeiner and MacDonald 1984). This survival strategy in many ways corresponds to Grime's (1977) conceptual

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model of stress-tolerance during succession and may explain *Vaccinium* species' long-term persistence in the understory of many second-growth forests under extremely low light conditions (Alaback and Tappeiner 1990; Atlegrim and Sjöberg 1996). With the closing of the overstory canopy during secondary succession, many species lacking the biomass allocation plasticity associated with a "stress-tolerant" life history (e.g. red raspberry, *Rubus idaeus* L.) are eliminated, despite their often significant abundance immediately after canopy removal (Ricard and Messier 1996).

Velvet leaf blueberry (*V. myrtilloides*) has been reported to be quite shade tolerant (Vander Kloet and Hill 1981) and is common in the understory of second-growth forests in northwestern Ontario (Usui et al. 1994; Moola et al. 1997, submitted). Unlike its congeners *V. vitis-idaea* and *V..angustifolium*, *V. myrtilloides* is able to persist in closed-canopy forests, although in a depauperate form. After overstory removal by logging and fire, *V. myrtilloides* bushes flower and produce abundant fruits (Vander Kloet and Hill 1981). Many wildlife species feed on the fruit and foliage (Martin 1951; Rogers 1976, 1987; Arimond 1979; Vander Kloet and Hill 1981) including black bear (*Ursus americanus* Pallas), American robin (*Turdus migratorius* L.), white-tailed deer (*Odocoileous virginianus*) and eastern cottontail (*Sylvilagus floridanus* Allen).

Because fire is actively prevented today, clearcutting is the main disturbance affecting *Vaccinium* spp. in boreal forests (Atlegrim and Sjöberg 1996). However, the negative perception of clearcutting among the public (Hannerz and Hånell 1997) as well as pressure to maintain the coniferous composition of mixedwood forests (Scarratt 1996) has focused attention on alternative harvesting techniques that more closely mimic natural

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disturbances (Johnston 1996). Several authors have reported that partial canopy removal by shelterwood logging is less damaging to understory vegetation, including *Vaccinium* spp., than clearcutting. Hence, it may be a better alternative than clearcutting for the conservation of understory species during timber harvesting (Reader and Bricker 1992; Atlegrim and Sjöberg 1996; Hannerz and Hånell 1997).

This study documents the relationships between understory light availability and *V. myrtilloides* growth and fruit production in a second growth boreal mixedwood forest following different intensities of canopy removal by clearcutting and shelterwood harvesting. The main objectives of the study were to: (a) determine if changes in light intensity following partial and full canopy removal affect abundance, growth, morphological plasticity, biomass allocation and fruit production of *V. myrtilloides.*; and (b) interpret such changes in terms of the concept of life history strategies (Grime 1979).

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Study Area

The study area was located in the Black Sturgeon Boreal Mixedwood Research Forest, approximately 120 km northeast of Thunder Bay, Ontario. Established in 1993, this experimental area consists of a second-growth boreal mixedwood forest about 55 years of age that was previously horse-logged between 1939 and 1942. The most recent forest inventory was conducted in 1975. At that time, the stand comprised primarily of balsam poplar (*Populus balsamifera* L.), trembling aspen (*P. tremuloides* Michx.) and balsam fir (*Abies balsamea* [L.] Mill.) and to a lesser extent black spruce (*Picea mariana* [Mill.] B.S.P.), white spruce (*Picea glauca* [Moench] Voss) with isolated pockets of white birch (*Betula papyrifera* Marsh) and/or jack pine (*Pinus banksiana* Lamb.). However, pre-harvest data collected in 1993 indicates that significant changes in the overstory composition of the area has occurred since the 1975 inventory; in part due to a ten-year spruce budworm (*Choristoneura fumiferana* Clem.) infestation that killed many balsam fir and white spruce trees (Scarratt 1996). Presently, much of the mature balsam fir and white spruce trees are either dead or moribund in the treatment area (Scarratt 1996).

The present experiment used a completely randomized design with three replicates in each of the following two harvesting treatments: i) uncut forest as a control and ii) clearcut by conventional feller-buncher and grapple skidder (full-tree extraction); and two replications of iii) high intensity shelterwood cut by conventional feller-buncher and grapple skidder (full-tree extraction, hereafter referred to as partial cut). All treatment blocks were 10 ha in size with 100 m-wide uncut buffer strips between them.

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Approximately two-thirds of the merchantable trees were removed from the partial cut blocks, leaving an overstory canopy that in 1996 (three growing seasons post-treatment) consisted primarily of trembling aspen with scattered white spruce (2 - 3 / ha) and black spruce trees (Scarratt 1996). The clearcut and partial cut blocks were not site prepared nor did they receive any form of conifer release treatment. The clearcut blocks were planted with overwintered containerized (Styroplug) black spruce seedlings in June 1996.

The soils of the treatment blocks were fresh, well-drained, and fertile and supported a diverse assemblage of herbs, graminoids and shrubs. When the study was initiated (August 1996) the clearcut blocks were dominated by young hardwoods such as trembling aspen and white birch that overtopped *V. myrtilloides* and other ground vegetation. Ground vegetation in the clearcut and partial cut blocks consisted mostly of large-leaved aster (*Aster macrophyllus* L.), raspberry (*Rubus* spp.), bush honeysuckle (*Diervilla lonicera* Mill.), velvet leaf blueberry (*V. myrtilloides* Michx.), violets (*Viola* spp.), mountain maple (*Acer spicatum* Lam.), twinflower (*Linnaea borealis* L.), and sedges (*Carex* spp.). The understory species composition of the uncut blocks did not differ significantly from the harvested blocks, with the exception of a greater abundance of mosses such as *Pleurozium schreberi* (Brid.) Mitt. and *Ptilium crista-castrensis* (Hedw.) De Not.

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Materials and Methods

Experimental design

Destructive and non-destructive sampling of *V. myrtilloides* as well as measurements of PPFD[1] were made from twelve 2 x 2 m systematically placed sample plots from within each 10 ha treatment block. With the treatment blocks replicated three times, this produced 36 sample plots in the uncut and clearcut blocks (3 x 12). In the shelterwood blocks, twenty-four sample plots were examined since this treatment was replicated two times (12 x 2). Ninety-six sample plots were examined in total.

Berry production and the number reproductive shoots

In August 1996 berries of *V. myrtilloides* were collected from each 2 x 2 m sample plot in each treatment block. The harvested berries were frozen after picking and brought to the laboratory. All berries were thawed, counted and weighed fresh and again after drying at 70° C for 36 hours.

The number of reproductive shoots of *V. myrtilloides* was counted in each 2 x 2 m sample plot. The identification of reproductive shoots was based on evidence of reproductive buds, faded flowers, or fruit.

Leaf area and specific leaf area

Ten mature leaves of *V. myrtilloides* were harvested at random in August 1996 from all the 2 x 2 m sampling plots. Harvested leaves were flattened and then immediately placed in plant presses in the field. The leaves were brought back to the laboratory and their area determined using a Delta-T, MK2 leaf area meter (Delta-T Devices, Ltd.

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[1] Photosynthetic photon flux density (PPFD: 400-700 nm).

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Burwell, Cambridge, England). Dry biomass of the harvested leaves was determined after oven drying at 70° C for 36 hours. Specific leaf area was calculated by dividing leaf area by oven dry weight.

Vegetative characteristics

The cover and average height of *V. myrtilloides* was measured in each of the sample plots at the end of August 1996. Above-ground stems and foliage were examined in greater detail from two randomly sampled bushes clipped at ground level from each 2 x 2 m sample plot. Bush size was standardized by including all above-ground stems that were connected below-ground within a 40 x 40 cm frame randomly located in each sample plot. The above-ground biomass of each harvested bush was divided into foliage and stem components and oven-dried at 70°C for 48 hours. The age of individual harvested bushes was estimated by counting the number of annual rings present on the base of the oldest cut stems using a dissecting mircroscope at 10 x magnification. In estimating the age of the harvested bushes it was assumed that the oldest stem on a shrub represented the maximum age of the entire ramet. This assumption may not be valid (Harper 1977), especially among species that can re-sprout from surviving rhizomes or stem bases following the destruction of aerial biomass after fire or some other disturbance (Luken 1988). Although there was no evidence of recent fire in any of the treatment blocks, extensive mortality of above-ground stems in the clearcut blocks was observed in this study and elsewhere (Zager 1980; Atlegrim and Sjöberg 1996). For this reason, the age estimates derived from harvested aerial stems may not reflect the actual age of blueberry

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ramets in the clearcut blocks. Rather, it represents the maximum age of emergent stems originating from older below-ground rhizomes or surviving stem bases.

Percent photosynthetic photon flux density (% PPFD) and cover of overtopping vegetation

An estimate of sunlight (% PPFD) available to blueberry bushes was measured above the 108 2 x 2 m plots using a Sunfleck PAR ceptometer (Decagon Devices, Inc. Pullman, Washington, USA) following the methodology of Messier and Puttonen (1995a). On a completely overcast day, the mean of five instantaneous light measurements was recorded above the blueberry canopy in each 2 x 2 m plot (*Iu*). In sample plots without *V. myrtilloides* present, light measurements were taken from a height of approximately 25 cm above the ground. This height corresponds to approximately the average height of blueberry observed in the study plots. Ambient overstory PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$) (*Io*) conditions were measured with a quantum sensor linked to a LI-1000 datalogger (LI-COR, Lincoln, NE, USA) placed in an open parking area adjacent to the treatment plots. The data logger was programmed to compute the mean PPFD every 5 sec. over a 1 min period. Dividing instantaneously taken readings of *Iu* by *Io* provided an estimation of the percent of above canopy PPFD (% PPFD) transmitted above the blueberry canopy in each 2 x 2 m sample plot.

The cover of vegetation that overtopped *V. myrtilloides* was measured in all the sample plots in late August. The abundance of vegetation taller than blueberry, such as trembling aspen, white birch, balsam fir and black spruce was estimated as the proportion

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of the blueberry canopy obscured by a perpendicular projection of the foliage of overtopping vegetation.

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Data Analysis

The data did not meet the assumptions required for the use of a one-way analysis of variance, since the samples were not taken from normally distributed populations of blueberry. Therefore, nonparametric analysis was employed to determine the differences among the reproductive and vegetative characteristics of *V.* myrtilloides. Moreover, the sample size for each case was small and some samples had outliers. Since the Mann-Whitney and Kruskal-Wallis tests involve rank comparisons, outliers were less influential on the test results (Norusis 1995). Following the detection of significant differences among means with the Kruskal-Wallis test, a series of Mann-Whitney tests were employed for the pair-wise comparison of treatment means. This was done in order to identify which treatments were significantly different from each other. The observed significance level for the Mann-Whitney test was adjusted with the Bonferroni procedure: for 3 comparisons, the observed significance level for each comparison had to be less than 0.05/3, or 0.02 for the difference to be significant at the 0.05 level.

Discriminant Analysis was initially performed on 12 vegetative and reproductive characteristics of *V. myrtilloides.* (height, % cover, number of reproductive shoots/m^2, dry weight of stems and leaves, age, leaf area, individual leaf dry weight and specific leaf area, and the number, dry weight and fresh weight of berries/m^2). The data were log transformed prior to analysis since it did not meet the criterion of homogeneity of variance. The number and fresh weight of berries variables were removed from the analysis after they were found to be highly correlated with the dry weight of berries. The data were then re-analyzed with the remaining 10 variables.

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Linear regression was employed to examine the relationships between % PPFD (the independent variable) and *V. myrtilloides* cover, growth, fruit production, leaf morphology and biomass allocation (the dependent variables). Percent PPFD; number, dry and fresh weight of berries and specific leaf area variables were log transformed prior to regression analysis.

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Results

Percent PPFD and cover of vegetation overtopping *V. myrtilloides*

Canopy removal significantly affected the amount of full sunlight (% PPFD) that reached the level of blueberry foliage in the treatment blocks (Table 1). *V. myrtilloides* plants in the uncut control blocks received only 3.9 % of full sunlight, whereas those growing in the partial cut and clearcut blocks received an average of 25.3 % and 32.5 % PPFD, respectively. Although the two harvesting treatments differed in the intensity of canopy removal, clearcutting did not increase the amount of sunlight reaching the field layer over that of partial cutting three-growing seasons after the treatments. This was due to the rapid re-establishment of an immature tree canopy in the clearcut blocks by regenerating hardwood species, such as aspen (*P. tremuloides*). Regenerating hardwood stems in the clearcuts shaded blueberry bushes to the same extent as the older conifer/hardwood overstory left standing in the partial cut blocks. Cover of vegetation over-topping blueberry plants was highest in the uncut forest (90.3 %), but was not significantly different between the partial cut (45.5 %) and clearcut (50.1 %) treatment blocks (Table 1).

Abundance of *V. myrtilloides*

Blueberry cover consisted entirely of discrete ramets. Bushes were for the most part relatively small in diameter and evidence of extensive underground networks of connected rhizomes was not found. Regeneration was entirely from either basal sprouting or buried rhizomes. No evidence of regeneration by seed was observed in any of the treatment blocks. At the end of the 1996 growing season (three growing seasons post-

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treatment) the cover of *V. myrtilloides* was highest in the partial cuts but not statistically different between the uncut and clearcut blocks (Table 2). Similarly, the density of bushes was greatest in the partial cuts intermediate on the clearcut blocks and lowest on the uncut blocks; although the differences were not statistically significant.

The density ($P > 0.05$, $R^2 = 0.0002$) and cover ($P > 0.05$, $R^2 = 0.02$) of *V. myrtilloides* was not related to understory light availability (% PPFD).

Fruit production and number of fruiting shoots of *V. myrtilloides*

When compared with the uncut blocks, the number, fresh weight and dry weight of berries significantly increased following partial cut and clearcut harvesting, three growing seasons after treatment (Table 3). The highest fruit yields per hectare was obtained in the partial cut blocks where the number, fresh weight and dry weight of berries were approximately 94 % greater than that of the clearcut blocks. Similarly, *V. myrtilloides* produced a far greater number of fruiting shoots per m^2 in the partial cuts compared to the clearcutand uncut treatment blocks (Table 3).

Fruit number ($P < 0.001$; $R^2 = 0.20$), fresh weight of berries ($P < 0.001$; $R^2 = 0.20$) and dry weight of berries ($P < 0.001$; $R^2 = 0.20$) increased slightly with greater light availability (Fig. 1). There was a moderate relationship ($P < 0.001$; $R^2 = 0.37$) between the number of fruiting shoots and % PPFD (Fig. 2). Although, above 30 % PPFD, the number and weight of fruits (Fig. 1) as well as the number of fruiting shoots (Fig. 2.) increased dramatically.

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Leaf morphology

V. myrtilloides responded to overstory removal with significant changes in leaf morphology. Leaves of *V. myrtilloides* bushes in the uncut blocks were significantly larger in size but smaller in dry weight than those from the partial cut and clearcut blocks (Table 4). Leaves produced by blueberry bushes in the uncut forests were 54 % and 59 % higher in specific leaf area than those produced in the partial cut and clearcut blocks, respectively. However, the differences in leaf parameters between the harvesting treatments were not statistically significant.

Differences in leaf morphology of *V. myrtilloides* between the cut and uncut treatments were partially related to the change in % PPFD following the canopy removal. There was a logarithmic relationship between specific leaf area ($P < 0.0001$, $R^2 = 0.50$) of *V. myrtilloides* foliage and increasing % PPFD. Leaves from bushes receiving more than 10 % PPFD were progressively smaller in specific leaf area (Fig. 3).

Height and biomass allocation

Canopy removal by partial cutting and clearcutting had no significant effect on the height of *V. myrtilloides*. However, the blueberry bushes responded to canopy removal with significant changes in the dry weight of above-ground biomass (Table 2). A significantly higher investment of biomass in stems and leaves was found in the partial cut and clearcut blocks, as compared to the uncut blocks, in which many blueberry bushes were depauperate and showed evidence of etioloation. The intensity of canopy removal (i.e. partial cutting vs. clearcutting) did not have any significant effect on dry weight of

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stems. Conversely, blueberry foliage dry weight in the clearcut blocks was 49 % greater than that in the partial cut blocks (Table 2).

The greater above-ground biomass of *V. myrtilloides* in the clearcut blocks compared to uncut blocks was related to the change in % PPFD resulting from canopy removal. Both the dry weight of stems ($P < 0.001$, $R^2 = 0.36$) and leaves ($P < 0.001$, $R^2 = 0.57$) were strongly limited below 10 % PPFD, but that increased linearly in response to greater light availability to the understory (Fig 4.)

The proportion of total above-ground biomass allocated between leaves ($P < 0.001$, $R^2 = 0.33$) and stems ($P < 0.001$, $R^2 = 0.33$) was related to light availability in the forest understory (Fig. 4). *V. myrtilloides* allocated proportionately more biomass to stems (82.5 %) compared to leaves (17.5 %) under deep shade associated with the uncut blocks where PPFD was below 20 %. However, in sample plots receiving more than 30 % PPFD (predominately in the clearcut and partial cut blocks), the relative investment of biomass in stems (58.2 %) and leaves (41.7 %) was more equitable.

Age of *V. myrtilloides* bushes

V. myrtilloides bushes in the clearcut blocks were much younger in age compared to those in the partial cut and uncut treatments (Fig. 5). Eighty percent of bushes sampled from clearcut treatment were three years old or younger, and no bushes older than four years were found. Conversely, in the uncut and partial cut blocks, the majority of bushes were between three and nine years with an average age of six years. This was significantly different from the clearcut blocks, where the mean age of harvested bushes was three years. Stem replacement by *V. myrtilloides* was slow in the uncut and partial cut blocks, as

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less than 5 % and 0 %, respectively, of stems were ≤ two years. Conversely, approximately 17 % of blueberry stems in the clearcut blocks were ≤ two years.

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Discriminant Analysis of *V. myrtilloides*

The results of significance tests for univariate equality of means indicated that of the 10 vegetative and reproductive parameters investigated in the Discriminant Analysis, nine were significantly different among the treatment groups. The treatment means for age, dry weight of berries, number of fruiting shoots, height, leaf area and weight, specific leaf area, and the dry weight of leaves and stems were significantly different amongst the three treatments (Tables 2, 3, 4). The cover of *V. myrtilloides* was not significantly affected by partial cutting or clearcutting. Discriminant Analysis confirmed the separation of the 96 sample plots into three groups (Fig. 6) with 95.8 % accuracy. The first discriminant function accounted for 94.8 % of the variance (Table 5). Function 1 was highly correlated with the biomass of leaves and stems, leaf area, specific leaf area and age, indicating that these morphological and demographic characteristics are likely the best predictor variables for the separation of the three treatment groups on the basis of differences in *V. myrtilloides* growth in logged and uncut forests. Function 2 accounted for slightly over 5 % of the variance and was strongly correlated with the dry weight of berries, height and the number of fruiting shoots (Table 6).

As displayed in the ordination diagram (Fig. 6), above-ground biomass, fruit production, leaf morphology and age of *V. myrtilloides* were significantly affected by both partial cutting and clearcutting. Plots from the uncut blocks formed one group in the ordination diagram quite separate from plots that were either partially cut or clearcut. Blueberry bushes growing under deep shade of the uncut blocks were distinct from those in the partial cut and clearcut blocks primarily by their older age, smaller above-ground biomass, large leaves and absence of fruiting.

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Discussion

Response to canopy disturbance

As with other ericaceous species, the performance of *V. myrtilloides* following canopy removal depends upon both the duration and intensity of increased light availability (Bunnell 1990; Smith 1990; Huffman et al. 1994; Luken et al. 1995). However, our results suggest that following logging of mixedwood boreal forests in northwestern Ontario, both of these factors are limited as a result of rapid canopy re-establishment from regenerating hardwoods, particularly trembling aspen. On our sites, the early dominance of hardwood stems in the partial cut and clearcut blocks may account for the minimal response of *V. myrtilloides* that we observed in both small (i.e. partial cut) and large (i.e. clearcut) canopy openings. Compared to the uncut blocks, the cover of *V. myrtilloides* did not increase following partial or full canopy removal, even though it was present in the understory prior to canopy disturbance. The suppression of understory species in clearcuts and partial cuts due to intense competition from hardwood species has been observed in other boreal mixedwood forests in Ontario (La Roi 1967; Hendrickson 1988; Groot et al. 1995). Hendrickson (1988) attributed the poor growth of non-woody species in regenerating mixedwood clearcuts in north-central Ontario to rapid occupancy by aspen suckers and red maple sprouts.

Although above-ground biomass of *V. myrtilloides* increased following partial cut and clearcut harvesting, this response was not associated with the greater availability of sunlight in canopy openings. We failed to find any significant relationship between understory light availability and *V. myrtilloides* cover. The understory PPFD explained

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only 19-22 % of the total variability in above-ground biomass. The remaining variability may be attributed to several other factors associated with logging (Ricard and Messier 1996) such as mechanical stimulation of sprouting (Bunnell 1990), higher soil temperatures (Groot et al. 1995) and improved nutrient conditions for growth due to increased mineralization (Vitousek et al. 1982). However, the latter factor may have been of lesser importance, as many *Vaccinium* spp. have been found to respond only slightly to increases in nutrient availability (Hester et al. 1991; Eaton 1994; Atlegrim and Sjöberg 1996).

The young age of blueberry stems (one to four years) in the clearcut blocks indicates that *V. myrtilloides* doesn't rely on the growth and spread of existing stems from uncut forests to quickly colonize the above-ground environment in second-growth forests. No blueberry stems ≥ four years were observed in the three year old clearcuts; older stems were presumably destroyed by logging. Conversely, the older age of bushes in the three year old partial cut blocks (three to fourteen years) indicates that a majority of bushes growing there (mean = six years) had been established before partial canopy removal. Extensive damage to above-ground biomass following clearcutting has been observed in *V. angustifolium* (Hoefs and Shay 1979; Moola and Mallik, submitted), *V. myrtillus* (Atlegrim and Sjöberg 1996) and *V. myrtilloides* (Moola and Mallik, submitted) and has been attributed to sudden microclimatic changes (Hoefs and Shay 1981; Atlegrim and Sjöberg 1996), mechanical damage to aerial stems from logging equipment (Zager 1980; Atlegrim and Sjöberg 1996) and increased susceptibility to drought and spring frosts (Hoefs and Shay 1981). In regenerating patch cuts approximately 100 km west of the

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study area, 31 % of tagged one-year old *V. myrtilloides* shoots died in the first growing season (Moola and Mallik, submitted). However, despite the heavy initial mortality of above-ground stems, *Vaccinium* spp. are generally tolerant of logging due to their ability to regenerate vegetatively from persistent underground bud-banks (Calmes and Zasada 1982; Matlack et al. 1993). In this study, re-sprouting of *V. myrtilloides* from the base of surviving stumps and/or from underground rhizomes was extensive in the clearcuts. This is a common observation in other ericaceous species (Mallik 1991, 1993). Nevertheless, the inability to immediately rely on advanced regeneration for photosynthesis and above-ground colonization, and the subsequent delay in establishing new photosynthetic biomass, was problematic in an environment marked by intense above-ground competition for light. Indeed, the suppression of *V. myrtilloides* by faster-growing tree species may be due to its inability to rapidly establish photosynthetic biomass in the above-ground environment or resist being overtopped by fast growing competing vegetation whose regeneration strategies facilitate the pre-emption of available resources. Tilman and Wedin (1991) have shown that in asymmetric competition for light among grasses, species which established photosynthetic biomass early in competition grew much faster and ultimately suppressed their shorter, slower-growing neighbours. In regenerating mixedwood clearcuts, competition for light between aggressive hardwood species such as aspen and slower-growing blueberry clones results in a similar outcome.

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Persistence in the uncut forest

A "stress-tolerator" strategy may be adaptive for *V. myrtilloides* in an environment marked by intense above-ground competition for light. Indeed, persistence in a depauperate vegetative form may enable *V. myrtilloides* to maintain a long-term presence in second-growth forests until self-thinning occurs and the canopy eventually opens up (Alaback and Tappeiner 1991; Messier and Mitchell 1994). Of particular importance to the "stress-tolerator" strategy of *V. myrtilloides* is its ability to modify its leaf morphology and biomass allocation in response to heavy shading. A high degree of phenotypic plasticity in response to differences in the growth habitats of forest environments likely accounts for *V. myrtilloides* ability to survive in all stages of secondary forest succession (Moola and Mallik, unpublished data). In this study, leaf morphology and the proportion of biomass allocated to stem and foliage varied significantly along the light gradient. This indicates that blueberry can express a high degree of morphological and allocation plasticity in response to changes in understory irradiance. Such plasticity has been suggested to enhance the ability of shade-tolerant species to survive for long periods under low light conditions (Chazdon 1985; Messier 1992; Messier and Puttonen 1995b). The plasticity of *V. myrtilloides* is reflected in the discriminant analysis. In shaded conditions of the uncut blocks, bushes of *V. myrtilloides* remained small, produced significantly less above-ground biomass, refrained from costly sexual reproduction, and developed leaves lower in weight but higher in individual leaf area and specific leaf area. Specific leaf area is an indication of photosynthetic efficiency of plants (Hunt 1982). By producing large, thin leaves, *V. myrtilloides* was able to improve the capture of

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photon energy. As indicated by regression analysis, the expression of these particular traits were significantly correlated with decreasing light availability.

Populations of *V. myrtilloides* in uncut forests were also older and had a higher proportion of biomass in non-photosynthetic tissue. The greater relative allocation of biomass in stems as opposed to leaves has not been observed in other ericaceous shrubs in forest habitats (Messier 1992; Alaback and Tappeiner 1991) and would appear counter-productive in light of the need to maximize the capture of light under conditions of heavy shading (Messier and Puttonen 1995). This may explain the minimal growth of *V. myrtilloides* at low light levels. Given blueberry's deciduous nature, investment of photosynthates in leaves is costly due to the loss of foliage after one growing season. Although it has been established in *V. angustifolium* that nutrients such as nitrogen are translocated from leaves to woody tissue prior to leaf drop in autumn (Eaton and Patriquin 1990), some resources are retained in the foliage and forfeited by the plant with leaf abscission (Karlsson 1985). The proportional decrease in leaf biomass of *V. myrtilloides* with increasing shade may be an adaptation to minimize this loss by allocating photosynthates preferentially in longer-living woody stems. Assimilates invested in woody tissue can be utilized in subsequent growing seasons for the development and maintenance of new foliage and shoots (Karlsson 1985).

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Management Implications: effect of canopy removal on fruit production

Dramatic increases in vegetative and reproductive performance of many understory shrubs have been observed in tree canopy openings (Minore 1984; Alaback and Herman 1988; Luken 1988; Alaback and Tappeiner 1991; Hughes and Fahey 1991; Matlack et al. 1993; Clinton and Boring 1994). Consequently, canopy gaps may be essential for the maintenance of forest biodiversity and wildlife habitat values in boreal mixedwood forests (Hanley and McKendrick 1985; Alaback and Tappeiner 1991). In mature temperate forests, mortality of individual trees from wind, disease and insects creates a heterogeneous mosaic of gaps (Frelich and Reich 1995; Johnston 1996) into which new stems of blueberry can emerge from underground rhizomes or buried seeds (Tappeiner and Alaback 1989; Eriksson and Fröberg 1996). However, in second-growth forest plantations similar small-scale disturbances, essential for the creation of canopy openings are usually infrequent (Alaback and Tappeiner 1991). The abundant overstory tree canopy and low availability of light in the understory (3 - 10 % PPFD) of the uncut blocks of this study are characteristic of many second-growth forests 20 - 55 years old (Alaback and Tappeiner 1991; Messier and Puttonen 1995; Lieffers et al. 1996). Measurements of light transmission to the understory of older boreal mixedwood stands indicates that irradiance needed for shrubs and herbs may remain low for many decades (Lieffers et al. 1996). Furthermore, as our results indicate, opportunities for the exploitation of available gaps by blueberry are short-lived due to intense competition from fast growing stems and suckers of hardwood species that rapidly form secondary canopy layers, consequently reducing understory light availability. Evidence of this has been

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reported for *V. ovalifolium* in the succession of second-growth western hemlock (*Tsugua heterphylla* (Raf.) Sarg.) forests following windthrow and thinning (Farr and Harris 1971; Alaback and Herman 1989; Alaback and Tappeiner 1991).

The suppression of fruiting shrubs, especially *Vaccinium* spp. in second growth forests is a management concern in some areas due to the decline in fruit availability for wildlife (e.g. bears) and berry pickers (Minore 1984; Hanley and McKendrick 1985; Alaback and Tappeiner 1991; Hamilton et al. 1991). A number of silvicultural techniques for the artificial creation of canopy gaps such as lower stocking standards, pre-commercial cutting, prescribed burning, pruning, biological control of canopy vegetation and herbicide application have been suggested for the promotion of understory shrub abundance (Minore 1984; Tappeiner and Alaback 1989; Alaback and Tappeiner 1991; Hamilton et al. 1991; Lautenschlager 1993). The results of this study indicate that berry production by *V. myrtilloides* does improve significantly following artificial canopy disturbance; especially with partial cutting of the forest. This positive effect may be in response to increased light availability in canopy openings as indicated by the relationship between berry production and the number of reproductive shoots and % PPFD. However, increased fruit yields will likely be temporary due to rapid canopy closure by regenerating hardwood species (e.g. aspen). Consequently, in order to maintain understory fruit production by blueberry ramets colonizing second-growth mixedwood forests, artificial canopy openings will likely require regular treatment to suppress secondary canopy development by regenerating hardwood species. The observation that reproductive vigour is encouraged through the suppression of successional changes such as canopy development has been reported for a number of

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species. A three-fold increase in fruit yield was reported by Smith (1972) in wild strawberries (*Fragaria viginiana* Duchesne) following experimental removal of competitors. Similarly, traditional methods of commercial blueberry management on abandoned agricultural land (Hall 1959), and clearcuts have depended upon the use of burning and mowing for the creation of early successional conditions that promote fruiting (Yarborough et al. 1986). Despite its apparent conservative response to canopy disturbance, the spread and dominance of *V. myrtilloides* has been reported in post-disturbance habitats with minimal or non-existent canopy development (Hall and Alders 1968; Vander Kloet and Hall 1981). These include managed blueberry barrens in Nova Scotia, New Brunswick, and Maine (Vander Kloet and Hall 1981; Yarborough et al. 1986), as well as nutrient poor ericaceous heathlands in Newfoundland that are inhosptiable for tree colonization and growth (A.U. Mallik, personal communication). Our results suggest that in the absence of silvicultural suppression of regenerating hardwood species, similar expansion and dominance of *V. myrtilloides* in the understory of second-growth boreal mixedwood forests is unlikely.

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Table 1. Means (and standard errors) of percent cover of vegetation overtopping *V. myrtilloides* and percent PPFD in treatment plots

Treatment	Percent cover of vegetation overtopping *V. myrtilloides*	Pecent PPFD transmitted above *V. myrtilloides*.
Uncut	90.3a (2.02)	3.9a (0.79)
Partial Cut	45.5b (5.27)	25.3b (2.57)
Clearcut	50.1b (3.98)	32.5b (2.64)

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Mann-Whitney nonparametric test. Observed significance level was adjusted with the Bonferroni procedure; ($P \leq 0.02$).

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Table 2. Means (and standard errors) of *V. myrtilloides* abundance, height, age and above-ground biomass following canopy removal

Treatment	Cover (%)	Height (cm)	Age (in years)	Dry weight of stems (g)	Dry weight of leaves (g)
Uncut	5.2a (0.78)	23.9a (1.89)	6.0a (0.3)	0.94a (0.19)	0.20a (0.03)
Partial Cut	6.8a (1.86)	28.8a (1.07)	6.0a (0.7)	2.87b (0.49)	1.24b (0.19)
Clearcut	5.1a (1.23)	26.5a (0.71)	3.0b (0.2)	3.44b (0.39)	2.47c (0.31)

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Mann-Whitney nonparametric test. Observed significance level was adjusted with the Bonferroni procedure; ($P \leq 0.02$).

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Table 3. Means (and standard errors) of fruit production in 1996 by *V. myrtilloides* following canopy removal

Treatment	Number of berries (/ha)	Fresh weight of berries (g/ha)	Dry weight of berries (g/ha)	Number of reproductive shoots (/m²)
Uncut	0a (0)	0a (0)	0a (0)	0a (0)
Partial Cut	122604b (74558)	21592b (12686)	3191b (1907)	7.6b (3.26)
Clearcut	7431c (4182)	1413c (945)	232c (150)	1.2c (0.64)

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Mann-Whitney nonparametric test. Observed significance level was adjusted with the Bonferroni procedure; ($P \leq 0.02$).

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Table 4. Means (and standard errors) of leaf characteristics measured from *V. myrtilloides* plants following canopy removal treatments

Treatment	leaf area (cm^2)	dry weight (g/leaf)	specific leaf area (cm^2/g)
Uncut	2.73a (0.18)	0.0076a (0.00076)	400a (21.16)
Partial Cut	1.88b (0.17)	0.0108b (0.00108)	185b (13.17)
Clearcut	1.65b (0.10)	0.0105b (0.00075)	166b (9.06)

Note: Unlike letters in a column indicate values significantly different at the 0.05 level determined by the Mann-Whitney nonparametric test. Observed significance level was adjusted with the Bonferroni procedure ($P \leq 0.02$).

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Table 5. Values of discriminant functions of ten characteristics of V. *myrtilloides*

Function	Eigenvalue	% Variance	Canonical Correlation	df	Significance
1	12.9873	94.80	0.9636	20	0.0000
2	0.7130	5.20	0.6452	9	0.0000

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Table 6. Pooled within-group correlations between discriminating variables and canonical discriminant functions of ten vegetative and reproductive characteristics of *V.myrtilloides*

Vegetative and reproductive parameters	Function 1	Function 2
Cover (%)	0.03463	0.15426
Height	0.10802	0.39025*
Age (in years)	0.25804*	0.69191
Dry weight of stems (g)	0.27653*	0.16822
Dry weight of leaves (g)	0.56670*	0.12746
Dry weight of berries (g)	0.07457	0.57354*
Number of reproductive shoots per m^2	0.07952	0.48844*
Leaf area (cm)	0.22090*	0.09120
Individual leaf dry weight (g)	0.14081	0.17370
Specific leaf area (g/cm^2)	0.42627*	0.34109

* denotes largest absolute correlation between each variable and any discriminant function.

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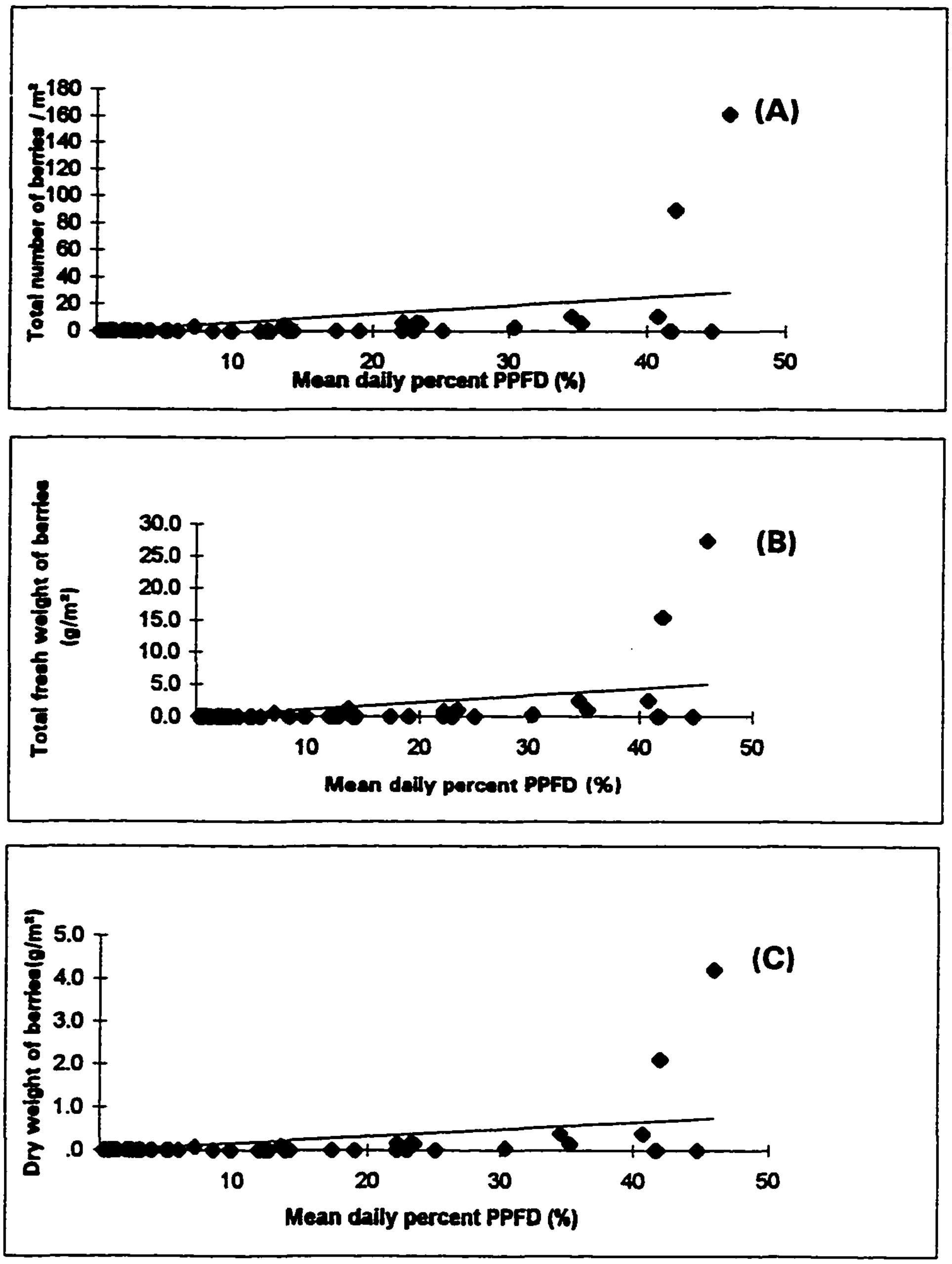

Fig. 1. Relationships between (A) number, (B) fresh weight and (C) dry weight of berries and the mean daily percent PPFD.

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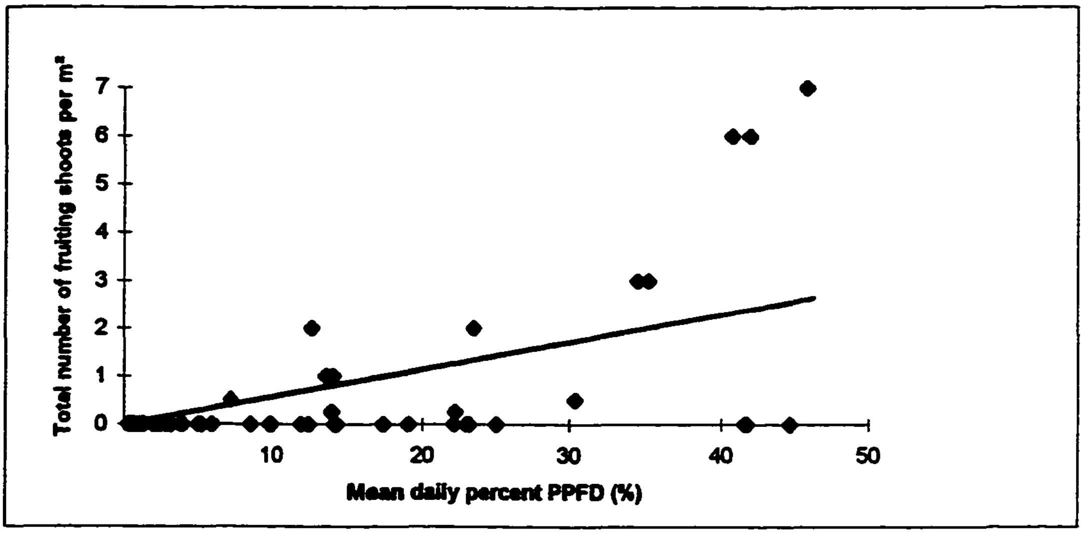

Fig. 2. Relationship between total number of reproductive shoots and the mean daily percent PPFD.

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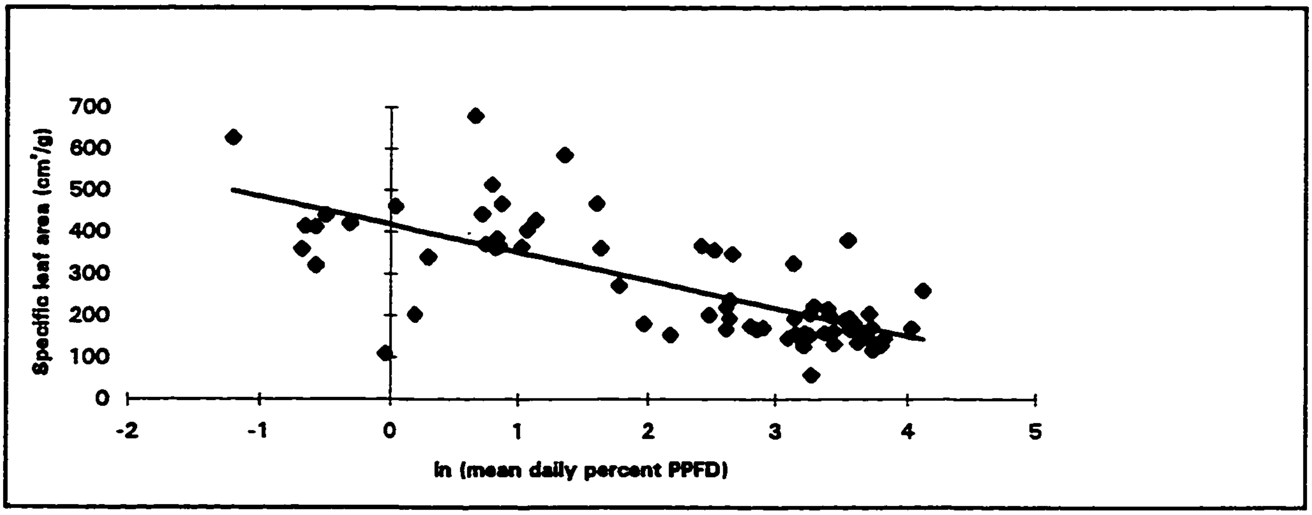

Fig. 3. Relationship between specific leaf area of *V. myrtilloides* foliage and the mean daily percent PPFD.

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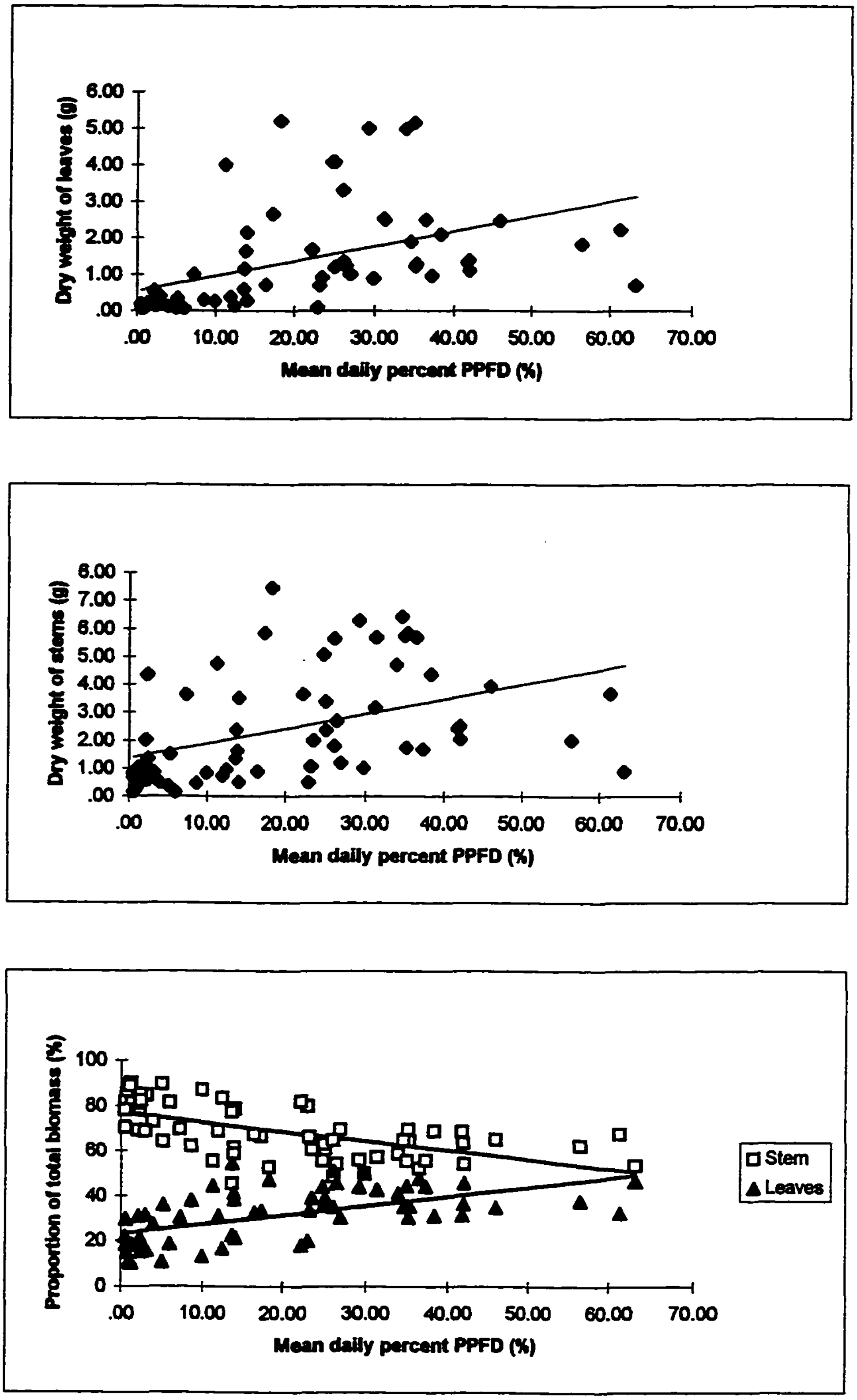

Fig. 4. Relationships between (A) dry weight of leaves and (B) stems, and (C) the relative allocation of biomass to stems and foliage and the mean daily percent PPFD.

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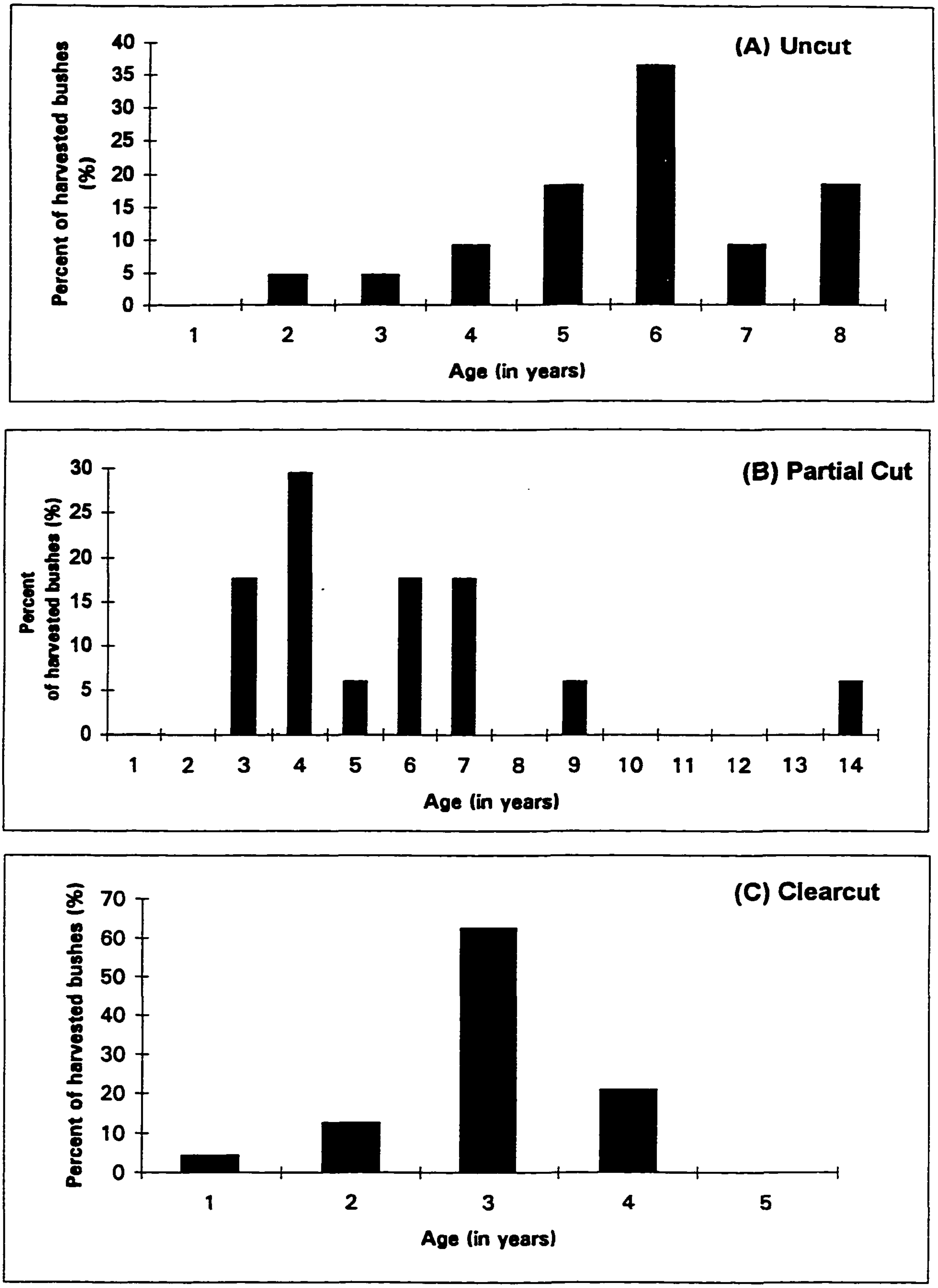

Fig. 5. Age-class distribution of harvested *V. myrtilloides* bushes from (A) Uncut; (B) Partial Cut; (C) Clearcut blocks.

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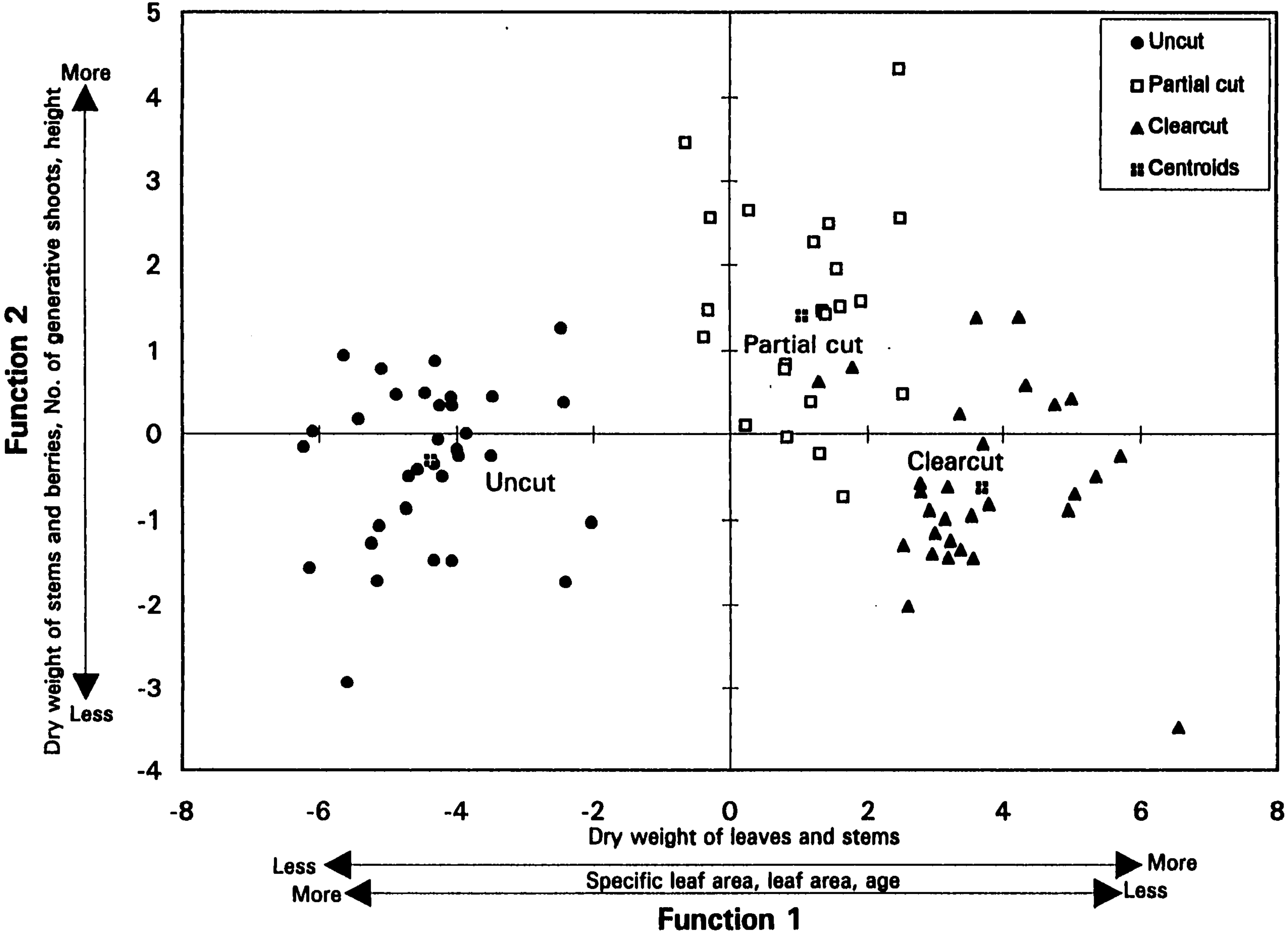

Fig. 6. Ordination diagram of Discriminant Analysis using 10 vegetative and reproductive parameters of *V. myrtilloides*

General Discussion

While little is presently known about the effects of management intervention on wild blueberry patches, the results of this thesis suggest that clearcut logging and silvicultural strategies of weed suppression such as herbicide application can adversely affect both the berry production and vegetative growth of *Vaccinium* spp. in northwestern Ontario. Conversely, partial cutting and conifer release with brushsaw cutting offer a silvicultural alternative that is less destructive to blueberry. This may be attributed to the “intermediate rate of disturbance” (Huston 1994) associated with partial cutting and brushsaw treatment which doesn’t significantly damage or kill aerial stems (Atlegrim and Sjöberg 1996) nor change microclimatic conditions to the same extent as clearcutting and/or herbicide application (Groot et al. 1995; Hannerz and Hånell 1997; Reynolds et al. 1997). From a conservation perspective, these practices are more consistent with the goal of protecting biodiversity and managing for the sustainability of less economically important ‘forest values’ (Reader and Bricker 1992) that are promoted in Ontario by the Crown Forest Sustainability Act 1994 (Baker et al. 1995). In fact, the significant increases in fruit production associated with both partial cutting and brushsaw treatment indicate that these silvicultural practices would be well suited for potential agroforestry initiatives in the management of boreal forests in northwestern Ontario. Unfortunately, there is little documentation on the economic significance of berry harvesting in boreal forest ecosystems. Minore (1972) estimated the economic and recreational value of huckleberries (*V. membranaceum* Dougl. ex. Hook.) in Oregon and Washington, U.S.A. Kardell (1979) reported that wild berries formed a significant portion of the export of agricultural produce from Poland and to a lesser extent

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Lithuania and Byelorussia. Although there are no reliable statistics on the economic contribution of wild berry harvesting to rural communities, berry picking provides supplementary income for people living in rural areas in many boreal forest regions of North America, Fennoscandia and Eastern Europe (Minore 1972; Saastamoinen 1977; Kardell 1979). The sale of wild blueberries from the road-side and in local grocery shops was observed by the author in several northwestern Ontario communities close to the study areas.

The response of *Vaccinium* spp. to operational herbicide (Vision®) application appears to be species specific. Unlike the lowbush blueberry (*V. angustifolium*), wild patches of velvet leaf blueberry (*V. myrtilloides*) do not appear to be as adversely affected by operational Vision® treatment. Nevertheless, the significant reduction in berry production by *V. angustifolium* can contribute to an overall drop in the availability of blueberries in sprayed clearcuts. The significant reductions in total blueberry yield following herbicide spraying could affect resident bear (*U. americanus*) populations and other wild animals that feed heavily on wild berries (Rogers 1976). Reduced use of Vision® treated clearcuts due to berry failure by shrubs such as *Vaccinium* spp. have been observed in radio-collared grizzly bears (*Ursus arctos* L.) in British Columbia (Hamilton et al. 1991). The direct effects of reduced blueberry availability on wildlife use of forest plantations in northwestern Ontario has yet to be examined.

Reproductive yields of both *V. angustifolium* and *V. myrtilloides* will progressively decline with forest succession after logging (Newton et al. 1989; Hamilton et al. 1991; Lautenschlager 1993). This may be especially true on mixedwood boreal sites as documented in Paper 3, given the speed at which plantations become dominated by regenerating

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hardwoods, particularly *P. tremuloides*, which can deprive blueberry of sunlight. These sites may even develop into non-productive blueberry habitats altogether given the apparent 'stress-tolerator' strategy (e.g. increased investment of assimilates in woody tissue at the expense of sexual effort) of *Vaccinium* spp. in response to heavy shading as well as the limited canopy gap openings in second-growth forests (Alaback and Tappeiner 1991). Evidence for a shift in reproductive strategies of understory species during succession has been reported in other ericaceous shrubs such as *Gaultheria Shallon* Pursh. (Bunnell 1990), *Kalmia angustifolia* var. *angustifolia* L. (Mallik 1994) and *V. ovalifolium* Smith (Alaback and Tappeiner 1991). Similarly, Newall and Tramer (1978) reported a decrease in reproductive effort with increasing successional maturity of old-field communities.

Berry yields would likely be maintained over a longer period of time in brushsaw treated plantations than on untreated or herbicided areas. Consistent with Lautenschlager's (1993) conceptual model of the effect of no treatment and conifer release on browse biomass, the non-toxic brushsaw treatment may maintain high berry productivity for several years after logging. Silvicultural suppression of regenerating hardwood species would delay overstory development and increase transmission of light to the understory. With increased availability of light, photosynthetic efficiency of *Vaccinium* spp. would be much greater. Hence, more photosynthate would be available for allocation to all plant functions, and internal competition amongst the various sinks (growth and maintenance, sexual and asexual proliferation) would be reduced (Weiner 1988). Evidence that reproductive vigour is encouraged through the suppression of successional changes such as canopy development have been reported for a number of species. A three-fold increase in sexual reproductive effort was reported by Smith

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(1972) in wild strawberries (*Fragaria virginaina* Duchesne) following the experimental removal of competitors. Similarly, commercial blueberry growers have long known that the cultural practice of pruning blueberry fields by fire, or by mowing, keeps patches in an early successional stage, and hence stimulates reproductive effort (Yarborough et al. 1986).

The need for silvicultural suppression of regenerating hardwoods in order to promote blueberry abundance and productivity may not be necessarry on sites where canopy closure is slower to occur as reported in Paper 1 and *Vaccinium* spp. have an opportunity to become established in the understory prior to significant overstory development. In the Maritime provinces, where it can take up to 30 years or longer for the forest canopy to re-establish after overstory removal, *Vaccinium* clones may grow up to 10 m in diameter before being overtopped by regenerating tree species (Vander Kloet and Hall 1981).

To better understand the response of *Vaccinium* spp. to successional changes in light availability initiated by overstory removal, the apparent trade-offs between reproductive effort and allocation of energy for growth and maintenance needs to be investigated. This can be studied at different successional stages for example one year, 10 years, and 20 years after clearcutting and in mature forest. Such an investigation may shed light on how carbon partitioning in blueberry plants can be manipulated through silvicultural treatments to obtain a more desirable investment of resources into sexual reproduction for the maintenance of abundant fruit production for wildlife. Scottish moors have been intensively managed since the thirteenth century for the maintenance of peak food production for domestic herbivores and game animals (Gimingham 1972). Traditional systems of Scottish heathland management since the 1850's have depended upon the use of burning and to a much lesser extent brushsawing for

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the creation of successional conditions that promote the development of ericaceous browse (e.g. green shoots, flowers and fruit) for red grouse, *Lagopus lagopus scoticus* L. In Canada, the burning of wild *Vaccinium* fields was under consideration in the 1950's for the promotion of Newfoundland's willow ptarmigan (*Lagopus lagopus alleni* L.) populations (Peters 1958). My results suggest that similar management of *Vaccinium* patches through partial cutting and brushsaw treatment may prove to be successful in facilitating greater food production for bears and other wildlife in boreal forests managed for timber production.

The results of this thesis indicate that regardless of treatment, berry productivity is often quite variable from year to year as reported by Eaton (1994). Research into commercial cultivation has revealed that in addition to management factors such as disease and insect control, fire pruning, open-field cultivation, irrigation and fertilization, climatic factors such as drought, early frost and severe winter temperatures can influence yields (Hoefs and Shay 1981; Eaton 1993). Poor berry yield in 1995 compared to 1994 and 1996 may be attributed to the adverse weather conditions that characterized that summer season. In particular, abnormally high afternoon temperatures and a severe deficit in precipitation might have induced drought stress in reproductive shoots. The detrimental effects of moisture shortage on growth and berry yield have been reported for wild blueberry patches in Manitoba and Alberta, which like northwestern Ontario, experience a sunny, dry, continental climate (Hoefs and Shay 1981). Unlike blueberry varieties of the Atlantic regions which experience frequent precipitation and lower exposure to sunlight due to fog, blueberries growing in open conditions in clearcuts of central Canada are often susceptible to drought stress given the high summer insolation, high ground temperatures

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and reduced soil moisture conditions that are created following the removal of the overstory canopy (Hannerz and Hånell 1997). The high fruit yields of blueberry observed in clearcuts treated with brushsawing and forests harvested with partial cutting may be due to the presence of more favourable near-ground microclimatic conditions; for example, cooler daytime temperatures, higher relative humdity and lower duff temperatures (Reynolds et al. 1997; Hannerz and Hånell 1997) for blueberry growth (Hoefs and Shay 1981). Nevertheless, the results of this thesis conifirm Vander Kloet and Hill's (1994) conclusion that *Vaccinium* spp. exhibit dramatic fluctuations in annual berry yield due to sensitivity to prevailing weather conditions.

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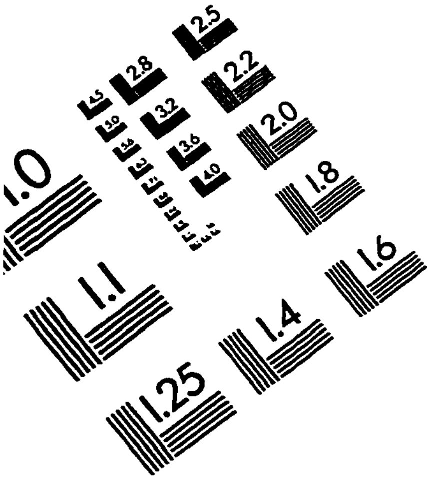

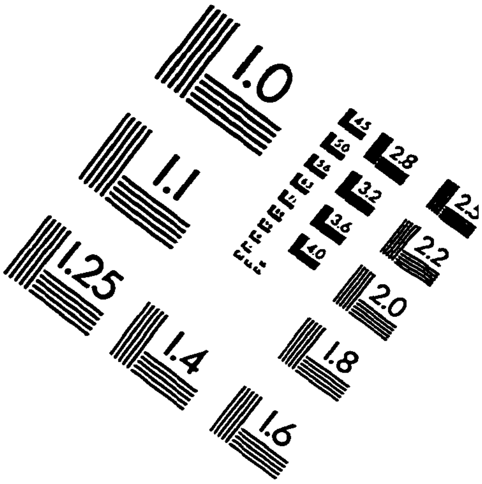

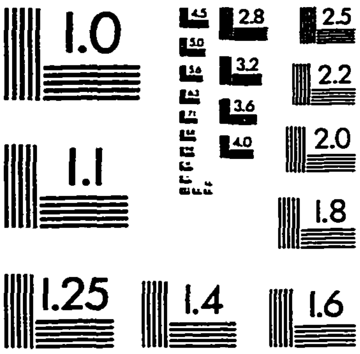

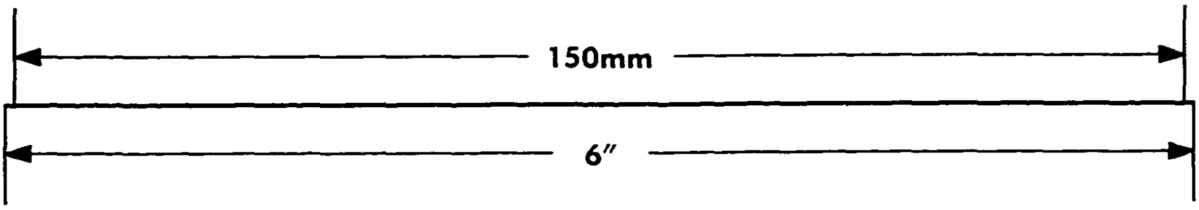

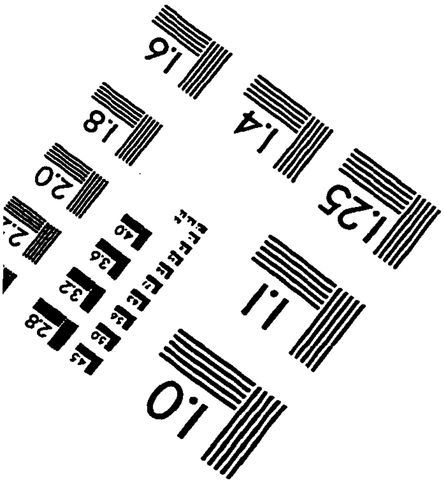

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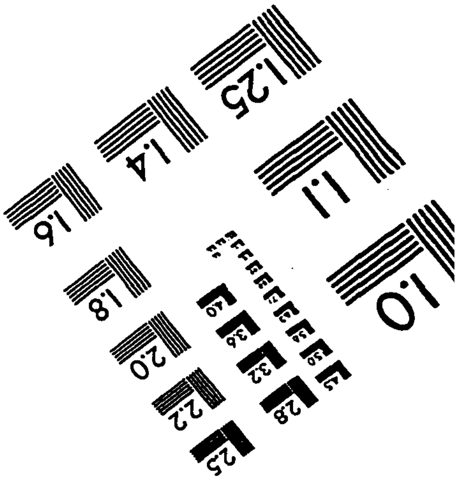

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